LOW GENIC VARIATION BETWEEN BLACK DUCKS AND MALLARDS

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ABSTRACT.—We used allozyme electrophoresis to estimate the degree of genetic differentiation among allopatric and sympatric populations of American Black Ducks (*Anas rubripes*) and Mallards (*A. platyrhynchos*). Mallards were collected in California, Saskatchewan, Manitoba, and Ontario, and Black Ducks were collected in Newfoundland, Nova Scotia, and Ontario. The mean genetic distances, $\bar{D}$, between Black Duck populations (0.0007), between Mallard populations (0.0010), and between Mallard and Black Duck populations (0.0006) were virtually identical; there was as much genetic differentiation within the two species as there was between them. Such small genetic distances are characteristic of local populations of avian species in other orders, and are consistent with what is known about the lack of reproductive isolation between Black Ducks and Mallards. Although the two taxa are still somewhat split on an east-west basis, our genetic data do not support even subspecific status for the Black Duck. *Received 12 August 1985, accepted 20 February 1986.*

MALLARDS (*Anas platyrhynchos*) and American Black Ducks (*A. rubripes*) hybridize wherever they come in contact (Goodwin 1956, Johnsgard 1967, Heusmann 1974). This contact, primarily in eastern North America, has occurred with increasing frequency since about 1900 (Johnsgard 1961, Johnsgard and Di Silvestro 1976). Concomitant with this increased interaction has been a very large increase in the number of Mallards in eastern North America and a decline in the number of Black Ducks (e.g. Bellrose 1976).

The frequent hybridization of these taxa has prompted speculation about whether the Black Duck is a valid biological species. Johnsgard (1961) concluded that "the most satisfactory status for *rubripes* is to consider it a subspecies of *Anas platyrhynchos* . . ." and "Neither a subspecific nor a specific relegation can be entirely satisfactory at present." The major problem with a subspecific designation, as pointed out by Delacour (1956), is the large area of sympatry of these two groups. Because subspecies are simply named geographic races (Mayr 1970), two populations that are largely sympatric cannot be subspecies. The area of sympatry between Mallards and Black Ducks has increased considerably since Delacour's comment was made. Therefore, the only taxonomic choices are to continue to consider them as separate species or to conclude that the Black Duck is a color morph of the Mallard.

We used allozyme electrophoresis to quantify the degree of genetic differentiation among allopatric and sympatric populations of Mallards and Black Ducks and related those data to information on genetic differences at various taxonomic levels in other birds.

METHODS AND MATERIALS

We examined 131 Black Ducks and 181 Mallards, all of which were either adult females or juveniles. They were collected in several localities during or immediately after the breeding season (Table 1); adult males were excluded because, unlike females, they commonly breed far from the area where they were raised.

Liver and breast muscle tissue were removed from each bird in the field, within 2 h of death, labeled and placed in plastic bags, and frozen on dry ice (Johnson et al. 1984). Tissues were stored at −70°C until they were processed.

Electrophoresis followed procedures outlined in May et al. (1979). Three buffer systems were used: (1) MF, a tris-boric acid-EDTA gel and tray buffer (pH 8.5) (Markert and Faulhaber 1965); (2) RW, a tris-citric acid gel buffer (pH 8.5), lithium hydroxide-boric acid tray buffer (pH 8.5) (Ridgway et al. 1970); and (3) AC, an amine citrate gel and tray buffer (pH 6.5) (Clayton and Tretiak 1972).

TABLE 1. Locations, sample sizes, and collection dates. Abbreviations in parentheses correspond to those used in other tables and in the figures to denote location.

Taxon	Sample size	Locality and date
Mallard (SASK)	49	Saskatchewan: 60 km NW of Saskatoon, September 1983
Mallard (ONT)	42	Ontario: E of a line joining Peterborough in S to Cochrane in N, May 1984
Mallard (MAN)	69	Manitoba: Delta Marsh at S end of Lake Manitoba, August–September 1984
Mallard (CAL)	21	California: Suisun Marsh 50 km NE of Oakland, April 1984
Black Duck (NFLD)	50	Newfoundland: 8 collected S and E of Goose Bay, Labrador, August 1983; 42 collected near Codroy, Newfoundland, September 1983
Black Duck (ONT)	41	Ontario: location as for Mallards; 4 collected May 1984, 37 collected August 1984
Black Duck (NSC)	40	Nova Scotia: Wallace Bay, September 1984

We used a system of nomenclature for loci and alleles first outlined by Allendorf and Utter (1979) and modified by Allendorf et al. (1983). For each electrophoretically detectable locus, the mobility (distance traveled) of the most common allelic product found in Mallards was used as a standard and designated 100. Other alleles were designated by the migration ratio of their protein products to that of allele 100. Multiple loci encoding the same enzymatic activity were numbered sequentially beginning with the form migrating closest to the origin.

Staining for enzyme activity followed methods outlined in Harris and Hopkinson (1976) and Allendorf et al. (1977). We examined 24 structural proteins and enzymes, encoded by 29 presumptive loci, in all individuals (EC stands for Enzyme Commission): Aco (aconitate hydratase, EC 4.2.1.3), Ada (adenosine deaminase, EC 3.5.4.4), Ak (adenylate kinase, EC 2.7.4.3), albumen, Aat (aspartate aminotransferase, 2.6.1.2), Ck (creatine kinase, EC 2.7.3.2), Est1,2 (esterase, EC 3.1.1.1, resolved using 4-methylumbelleferyl butyrate), Gda (guanine deaminase, EC 3.5.4.3), Gpi (glucose phosphate isomerase, EC 5.3.1.9), Gr (glutathione reductase, 1.6.4.2), G3pd (glycerol-3-phosphate dehydrogenase, EC 1.1.1.8), Idh1,2 (isocitrate dehydrogenase, EC 1.1.1.42), Ldh1,2 (lactate dehydrogenase, EC 1.1.1.27), Mdh1,2 (malate dehydrogenase, EC 1.1.1.37), Me1,2 (malic enzyme, EC 1.1.1.40), Mpi (mannose phosphate isomerase, EC 5.3.1.8), Np (nucleoside phosphorylase, EC 2.4.2.1), PepC2 (peptidase, EC 3.4.11, resolved using DL-leucyl-L-alanine), PepD (peptidase, EC 3.4.11, resolved using L-phenylalanyl-L-proline), Pgd (phosphogluconate dehydrogenase, EC 1.1.1.44), Pgm (phosphoglucomutase, EC 2.7.5.1), Pgk (phosphoglycerate kinase, EC 2.7.2.3), Sod (superoxide dismutase, EC 1.15.1.1), and Tpi (triosephosphate isomerase, EC 5.3.3.1).

Statistical analyses were performed using BIOSYS-1 (Swofford and Selander 1981). Heterozygosity (H), was defined as the number of heterozygous genotypes recorded in a sample divided by the product of the number of loci and the number of individuals assayed (after Gutiérrez et al. 1983). The percentage of polymorphism was calculated as the number of loci at which the frequency of the most common allele did not exceed 0.99 divided by the total number of loci examined.

We used Nei's (1978) unbiased D and Wright's (1978) modified Rogers' D to estimate genetic distances. Cluster analysis, summarizing the matrix of Nei's D-values, was performed with the unweighted pair-group method (UPGMA) using arithmetic means. A distance Wagner tree based on modified Rogers' D-values was constructed according to the methods of Farris (1972). The cophenetic correlation coefficients, r_{cc}, were used to evaluate how well the resultant branching diagrams represented the original distance matrices.

To evaluate our cluster analysis of the Mallard–Black Duck D-values, we did UPGMA analysis that included two confamilial taxa with data (Seeb and Wishard unpubl. ms.) from American Wigeon (*A. americana*) and Canada Geese (*Branta canadensis*). For that analysis, we excluded data for Est1, Pgd, and Aco, because they were not examined for wigeon and Canada Geese.

RESULTS

Allelic frequencies for 11 polymorphic loci are given in Table 2; all other loci were monomorphic.

The average percentage of polymorphic loci for the 7 populations was 24.1% and ranged from 17.2% to 31.0% (Table 3); the average percentage was 26.4% for Black Ducks and 22.4%

TABLE 2. Allelic frequencies for 11 presumptive loci in 3 populations of Black Ducks and 4 populations of Mallards. Abbreviations of locations are defined in Table 1.

	Black Ducks			Mallards			
Locus	NFLD	NSC	ONT	CAL	SASK	MAN	ONT
Ada							
100	0.870	0.850	0.854	0.881	0.776	0.754	0.786
107	0.100	0.150	0.098	0.095	0.163	0.203	0.036
95	0.010		0.012	0.024	0.041	0.014	0.036
110	0.010		0.037			0.007	0.131
113	0.010				0.010	0.007	
85						0.007	
103						0.007	
79					0.010		
120							0.012
Mpi							
100	0.704	0.737	0.829	0.738	0.837	0.855	0.821
120	0.235	0.063	0.049	0.024	0.010	0.022	0.167
133	0.061	0.175	0.110	0.190	0.143	0.101	0.012
55		0.012	0.012	0.024	0.010	0.007	
142		0.012		0.024		0.007	
85						0.007	
PepC2							
100	0.880	0.875	0.850	0.810	0.816	0.913	0.905
82	0.120	0.050	0.050		0.143	0.036	0.095
107		0.012	0.063	0.167	0.041	0.043	
95		0.063	0.037	0.024		0.007	
Np							
100	0.700	0.750	0.646	0.725	0.771	0.688	0.762
79	0.260	0.200	0.305	0.200	0.219	0.275	0.202
113	0.030	0.025	0.012			0.014	
73		0.025	0.037	0.075	0.010	0.022	
93	0.010						0.024
55							0.012
Est1							
100	0.920	0.912	0.915	0.857	0.908	0.870	0.905
125	0.080	0.087	0.085	0.143	0.092	0.130	0.095
Pgd							
−100	0.990	0.987	0.988	0.976	1.000	1.000	1.000
−50	0.010	0.012	0.012				
−200				0.024			
Idh1							
−100	1.000	1.000	1.000	1.000	1.000	0.993	1.000
−70						0.007	
Idh2							
−100	1.000	1.000	0.963	1.000	1.000	0.986	0.976
10			0.037			0.014	0.024
Aco							
−100	1.000	1.000	0.939	1.000	1.000	0.993	1.000
−70			0.061			0.007	
Sod							
−100	1.000	0.975	0.988	0.929	1.000	0.993	1.000
−33		0.025	0.012	0.071		0.007	
G3pd2							
−100	1.000	0.987	1.000	0.952	1.000	0.964	1.000
−50				0.048		0.029	
−120		0.013				0.007	

TABLE 3. Genetic variability at 29 loci in Black Ducks and Mallards. Abbreviations of locations are defined in Table 1.

Species (location)	$H_{obs} \pm SE$	Percentage of polymorphic loci[a]	Mean no. of alleles[b]
Black Duck (NFLD)	4.7 ± 2.1	20.7	3.0
Black Duck (NSC)	5.3 ± 2.2	27.6	2.9
Black Duck (ONT)	5.9 ± 2.3	31.0	2.9
Mallard (CAL)	7.6 ± 2.9	27.6	2.8
Mallard (SASK)	5.4 ± 2.4	17.2	2.8
Mallard (MAN)	5.9 ± 2.4	24.1	3.4
Mallard (ONT)	4.7 ± 2.0	20.7	3.0
Mean[c]	5.6	24.1	3.0

[a] Frequency of most common allele ≤0.99.
[b] Per polymorphic locus.
[c] Unweighted by sample sizes.

for Mallards. $\bar{H}$ for Mallards and Black Ducks combined was 5.6% and ranged from 4.7% to 7.6% (Table 3); $\bar{H}$ was 5.3% for Black Ducks and 5.9% for Mallards.

A matrix of genetic distances among the 7 populations is shown in Table 4. The mean genetic distances, $\bar{D}$, between Black Duck populations, between Mallard populations, and between Mallard and Black Duck populations were nearly identical (Table 5). There was as much genetic differentiation within the two species as there was between them. Furthermore, the $\bar{D}$ between Mallards and Black Ducks (0.0006) was only 1% of that between those groups and American Wigeon (0.075).

The UPGMA (Fig. 1) and distance Wagner (Fig. 2) procedures produced similar branching diagrams that had similar r_{cc}'s. The former diagram produced two distinct groups, both of which contained Mallard and Black Duck populations; the latter diagram also failed to separate populations of the two species into distinct groups. A further phenetic analysis (Fig. 3), which included data for American Wigeon and Canada Geese, emphasized the similarity of Mallards and Black Ducks relative to a congener and a noncongeneric member of their subfamily.

DISCUSSION

Protein variation.—The percentage (24.1%) of polymorphic loci that we found in Mallards and Black Ducks is higher than that reported for some other groups of birds (Avise et al. 1980, Zink 1982, Gutiérrez et al. 1983), but is similar to that (20%) reported for Mallards by Parker et al. (1981). Patton and Avise (1985) assayed 19 loci in tissues from 10 Mallards and 4 Black Ducks and found that 10.5% and 5.3%, respectively, were polymorphic. In 6 of the 11 polymorphic loci that we found, however, the frequency of the most common allele exceeded 0.90; samples of 10 or less, such as used by Pat-

TABLE 4. Matrix of genetic distances between 7 populations of Black Ducks and Mallards. Wright's (1978) modified Rogers' distance is above the diagonal and Nei's (1978) distance is below the diagonal. Abbreviations of locations are defined in Table 1.

	Population						
Population	1	2	3	4	5	6	7
1 Black (NFLD)	—	0.033	0.038	0.032	0.044	0.042	0.050
2 Black (NSC)	0.001	—	0.030	0.040	0.031	0.027	0.031
3 Black (ONT)	0.001	0.000	—	0.039	0.028	0.033	0.037
4 Mallard (ONT)	0.000	0.001	0.001	—	0.041	0.039	0.054
5 Mallard (MAN)	0.002	0.000	0.000	0.001	—	0.027	0.041
6 Mallard (SASK)	0.001	0.000	0.000	0.001	0.000	—	0.040
7 Mallard (CAL)	0.002	0.000	0.000	0.002	0.001	0.001	—

TABLE 5. Mean genetic distances (Nei 1978), within and among Mallard and Black Duck populations, and between Mallards and Black Ducks combined and American Wigeon and Canada Geese.

Comparison	No. of comparisons	$\bar{D}$
Black Duck populations	3	0.0007
Mallard populations	6	0.0010
Mallards vs. Black Ducks	12	0.0006
Mallards and Black Ducks vs. American Wigeon	7	0.075
Mallards and Black Ducks vs. Canada Geese	7	0.322

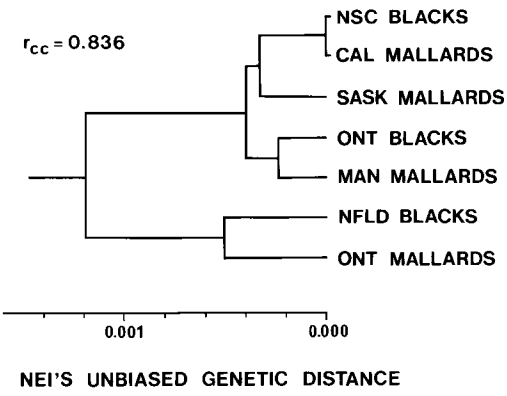

Fig. 1. Phenogram (UPGMA) of 7 populations of Mallards and Black Ducks using Nei's (1978) *D*-values from Table 4. Abbreviations are defined in Table 1.

ton and Avise, would be insufficient to detect many rare alleles. Clearly, the measure of polymorphic loci is dependent on both the sample size and the capability of the electrophoretic conditions used to detect allelic variation.

The $\bar{H}$s that we determined for Black Ducks (5.3%) and Mallards (5.9%) are within the range (2.0–14.6%) reported by Barrowclough et al. (1985) for 24 avian species, but higher than those reported by Patton and Avise (1985) for Mallards (3.7%) and Black Ducks (2.8%), and by Parker et al. (1981) for Mallards (2.7%).

Genetic distance.—The $\bar{D}$ (0.0006) that we found between Mallards and Black Ducks is the same as the $\bar{D}$ (0.001) that Patton and Avise (1985) found for a smaller sample of Mallards and Black Ducks. Such slight genetic distances are characteristic of local populations of avian species in other orders (Table 6). As pointed out by Patton and Avise (1985) in their study of 10 *Anas* species, the Anseriformes do not show unusually low levels of protein differentiation when compared with other birds (cf. Table 6). Note that the genetic distance between Mallards and Black Ducks is the lowest among members of the genus *Anas* (Table 6).

Cluster analyses (Figs. 1 and 2) produced groupings that neither separated Mallards from Black Ducks, nor showed any geographical pattern in the amount of genetic differentiation. The latter suggests considerable gene flow, particularly as our sampling areas spanned a distance of over 6,000 km. In eastern Ontario, where we obtained both Mallards and Black Ducks, hybrid Mallard × Black Ducks are common; Canadian Wildlife Service samples of wings from hunter-killed birds in that area contain 5–10% hybrids (Ankney and Dennis unpubl. data). Thus, a priori, we predicted that samples of Mallards and Black Ducks from eastern Ontario would show levels of genetic distance substantially lower than comparisons of samples from more geographically separate areas. This was not the case. We suggest that the amount of gene flow between groups is large enough to preclude differentiation.

For several reasons, the potential for gene flow among Mallard populations, and among Black Duck populations, is very great. First, pair formation in both species normally occurs during fall migration and on the wintering grounds (see Bellrose 1976: 236, 254–255), so that a female can easily become paired with a male raised in a different geographical area (see Bellrose 1976: 234 for a map of migration pathways and wintering areas). Second, the birds raised in a particular area do not all winter in the same area. Gollop (1965), for example, reported *direct* recoveries of three Mallard brood mates, banded in Saskatchewan, from Alberta, Oklahoma, and Oregon, and of two brood mates from another Saskatchewan brood that were recovered in Arkansas and California. Third, females normally return, with their mates, to nest in the area where they were raised (e.g. Gollop 1965). Fourth, because Mallards and Black Ducks are only seasonally monogamous, a male, during his life, may father broods in several geographic areas.

Mallard populations and Black Duck populations, throughout their North American ranges, are essentially panmictic. For example,

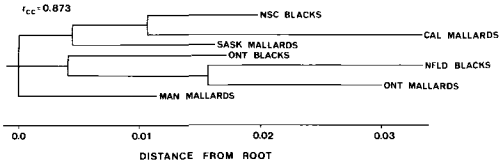

Fig. 2. Wagner Tree based on Wright's (1978) modified Rogers' *D*-values from Table 4. The tree is "rooted" at the midpoint of the longest path. Abbreviations are defined in Table 1.

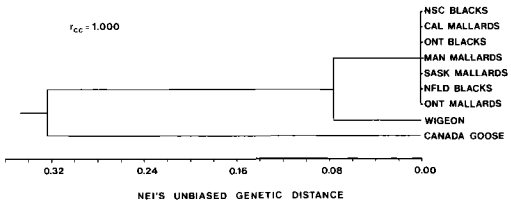

Fig. 3. Phenogram (UPGMA) derived from Nei's (1978) *D*-values in Tables 4 and 5. Abbreviations are defined in Table 1.

consider two female Mallards nesting on the Delta Marsh in Manitoba. Although both probably were raised there, one may have had a father raised in Ontario and the other a father from California. That presumably explains why we found no evidence of genetic differentiation on a geographical basis, even though we attempted to minimize the effects of gene flow by not sampling adult males.

For the foregoing reasons, and because Mallards and Black Ducks frequently hybridize (e.g. Heusmann 1974), gene flow between these taxa probably is very great. We show that a new allele, arising in a Newfoundland Black Duck, could appear in California Mallards within 5 years (Fig. 4).

Taxonomic implications.—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. Johnson and Zink (1983) argued against subspecific status for Red-naped and Red-breasted sapsuckers (*Sphyrapicus nuchalis* and *S. ruber*), despite their low genetic distance ($D = 0.004$), because "these forms have 'proved' their biological species status" by mating assortatively in sympatry. Similarly, Gutiérrez et al. (1983) argued against subspecific status for Gambel's and California quail (*Callipepla gambelii* and *C. californica*) because only F_1 hybrids, and not a hybrid swarm, have been found. Clearly, decisions about taxonomic status require information about mating preferences and behavior, hybrid fitness, and historical data about stability of hybrid zones. Fortunately, there are data about those aspects of Mallard and Black Duck biology, and we thus are able to make a conclusion about their taxonomic status.

Black Ducks apparently arose from an ancestral Mallard population during the Pleistocene

TABLE 6. Genetic distances vs. taxonomic levels in three avian groups.

	Comparison		
Taxonomic group	Local population	Subspecies	Congeneric species
Anas[a]			
n			45
$\bar{D}$			0.092
Range			0.001[d]–0.186
Galliformes[b]			
n	6		3
$\bar{D}$	0.0007		0.0067
Range	−0.0015 to 0.0033		0.0051–0.0078
Passeriformes[c]			
n	113	86	71
$\bar{D}$	0.0024	0.0048	0.0440
Range	−0.0014 to 0.0125	−0.0014 to 0.0214	0.0078–0.1267

[a] From Patton and Avise (1985).
[b] From Gutiérrez et al. (1983).
[c] From Barrowclough (1980).
[d] Mallards vs. Black Ducks.

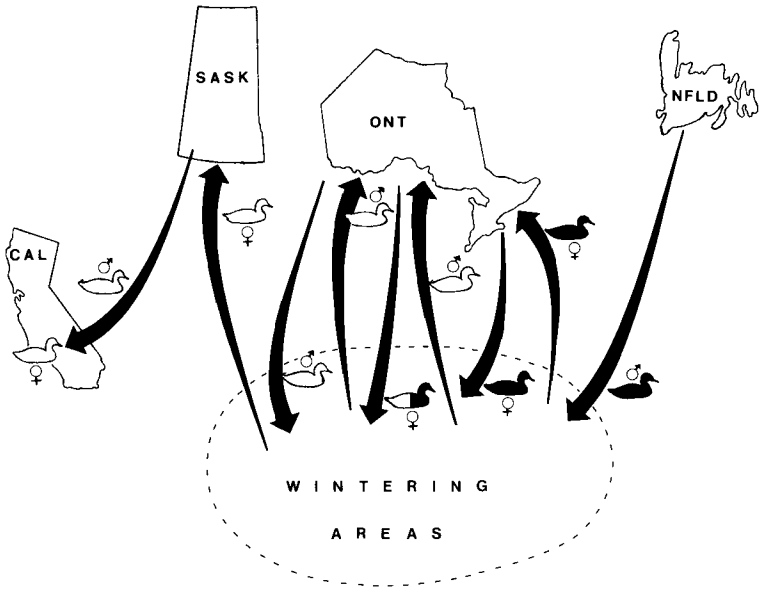

Fig. 4. Schematic demonstration of potential gene flow between Black Duck and Mallard populations. Closed symbols represent Black Ducks, open symbols represent Mallards, and the half-open, half-closed symbol represents an F_1 hybrid. A new allele, present in a male Black Duck in Newfoundland, is transferred to Ontario Black Ducks when the male pairs with an Ontario female; their daughter pairs with an Ontario Mallard . . . a male Mallard, raised in Saskatchewan, winters in California and pairs with a local female. Note: Many offspring of an F_1 × Mallard backcross are phenotypically Mallards (Phillips 1915).

(see Heusmann 1974) and were probably never very different genetically from Mallards, despite differences in plumage and habitat use. Before about 1900 there was relatively little contact between Mallards and Black Ducks (Heusmann 1974). Since then, however, due to the release of game farm Mallards in the eastern United States (Heusmann 1974) and a natural eastward range expansion of the Mallard (Johnsgard 1961), Mallards have become increasingly common in eastern North America. Coincidentally, Black Ducks have virtually disappeared from much of the western part of their range (e.g. southwestern Ontario; Dennis et al. 1985). During the past 50 years, hybrid Mallard × Black Ducks have been reported from virtually all parts of the Black Duck's range (Goodwin 1956, Johnsgard 1967, Heusmann 1974). Thus, it is inappropriate to try to delineate a hybrid zone, although some areas, e.g. eastern Ontario-western Quebec (Ankney and Dennis unpubl. data) and Massachusetts (Heusmann 1974), have a higher incidence of hybrids than do others. We predict that, based on what has happened in southern Ontario (Goodwin 1956, Dennis et al. 1985), this is not a stable situation. Rather, as the number of Mallards and hybrids increase, the number of Black Ducks will consequently decline, and eventually the number of hybrids will also decline as fewer and fewer Black Ducks will be available for mixed pairing.

The courtship displays of Mallards and Black Ducks are virtually identical (Johnsgard 1960). The factors that are important for mate selection in these groups have not been determined experimentally, but a recent field study (Brodsky and Weatherhead 1984) suggested that female Black Ducks, when courted by drakes of both groups, choose drake Mallards. That is not surprising because the bright plumages of male ducks in the genus *Anas* presumably have evolved through sexual selection (see Heusmann (1974) for an explanation of the dark, nonsexually dimorphic plumage of Black Ducks). We would be surprised if female Mallards chose drake Black Ducks over drake Mallards. Regardless, the high incidence of hybrids where both forms are common (Heusmann 1974, Ankney and Dennis unpubl.

data) suggests little if any behavioral, premating isolation. Estimates of the incidence of hybrids in an area are very conservative because many of the offspring of $F_1 \times F_1$ crosses and $F_1 \times$ Pure Type backcrosses look like one or the other parental type (Phillips 1915). This is particularly true for females. Therefore, it is highly unlikely that a classical hybrid swarm could be detected. The lack of philopatry by males (see above) reinforces the unlikelihood that a hybrid swarm could form. There is little evidence about selection for or against hybrids, but hybrid backcrosses are apparently as fertile as the parental types (Phillips 1915).

Thus, our data showing a very low level of genetic distance between Mallards and Black Ducks are consistent with the species' incomplete reproductive isolation. Until recently these taxa could have been best termed well-differentiated subspecies, analogous to, for example, Audubon's Warbler (*Dendroica coronata auduboni*) and the Myrtle Warbler (*D. c. coronata*). Although the two taxa are still somewhat split on an east-west basis—Black Ducks are virtually absent west of the Mississippi and Mallards are rare (although increasing) in northeastern Canada—our genetic data do not support even subspecific status for the Black Duck. We conclude that the Black Duck should be regarded as a melanistic morph of the Mallard. Furthermore, we suggest that continued interbreeding between the two forms will result in a continued decline of Black Ducks, a possibility that has been raised previously (e.g. Goodwin 1956; Johnsgard 1961, 1967; Heusmann 1974; Greig 1980; Dennis et al. 1985).

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