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Pairing in mallards and American black ducks: a new view on population decline in American black ducks

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Abstract

Data on mating systems suggest that mate choice and dominance advantages by mallard (*Anas platyrhynchos*) males are not sufficient to explain declines in American black ducks (*Anas rubripes*). Courtship and pairing of mallards and American black ducks overwintering at a site on the Chesapeake Bay were studied from 1976–1993, during October–March. Mallards declined relative to American black ducks during this period at the study site. Courtship groups and pairs (one exception) consisted of conspecific individuals. Mallards and American black ducks segregated when courting but not when resting. Hybrid males joined courting groups of either species but did not pair successfully with either parental species. Handraised American black ducks hatched from eggs, imprinted on humans, and fledged at the study site, paired with American black ducks even though they were initially the rarer species. Handraised American black ducks avoided pairing with siblings. American black ducks and mallards pair assortatively and hybrids are selected against on the Chesapeake Bay. American black ducks may be declining due to human disturbance rather than due to direct interactions with mallards. Mallards may be increasing because they tolerate human disturbance and through direct release by humans into the American black duck's breeding range.

INTRODUCTION

American black ducks (*Anas rubripes*) are declining, and mallard (*A. platyrhynchos*) numbers rising, in eastern North American (Johnsgard 1961, 1967; Johnsgard & DiSilvestro, 1976; Dennis, Fisher & McCullough, 1984; Ankney, Dennis & Bailey, 1987). The mallard increase is often cited as the cause of the decline of the American black duck. Mallards are viewed as more aggressive or more competitive than American black ducks. Here I develop the hypothesis that the two species respond differently to human disturbance and that this behavioral difference in neophobia is causing the American black duck's decline, not competition from the mallard. Neophobia as a factor in species decline has been rarely addressed by conservation biologists.

Here, I review the interactions of American black ducks and mallards, provide new data on mate choice, and suggest ways that behavioral ecology may shed light on the interactions between these species. These data show that the two species are reproductively isolated and that hybrids are probably selected against. They support the notion of Seymour (1990) that most hybrids probably result from forced extra-pair copulations by mallard males on renesting female American black ducks.

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METHODS

I studied courting groups and pair formation in a wild population of mallards and American black ducks on the Chesapeake Bay. In addition, clutches of wild American black ducks were hatched in captivity, handraised, released at my study site, and their subsequent pairing behavior assessed.

The study site was Sullivan's Cove on the Severn River, Anne Arundel County, Maryland, a tributary of the Chesapeake Bay. The Severn River is 2.2 km wide at this point, and is brackish with salinities ranging from 6–13 parts per thousand (ppt). The only tidal marshes on the river occur at Sullivan's Cove, and include a 5 ha brackish-water marsh dominated by cordgrass (*Spartina* sp.) and a small fresh-water swamp of Atlantic Cedar (*Chamaecyparis thyoides*). Other than these marshes and natural woodlands on the shoreline, the surrounding area is a highly developed suburb (the town of Severna Park) of Baltimore and Annapolis. The habitat changed little during the study period, with a small amount of forest loss on one lot due to clearing to afford a view of the river.

From 1976–1993, almost daily observation of mallards and American black ducks overwintering on the Severn River were made from my residence, located 10 m from the river and immediately adjacent to Sullivan's Cove, and by walking along a path adjacent to the marshes. Only a few game-farm mallards were seen in 1976, and could be distinguished from wild mallards by plumage aberrations and bill and body shape (Byers & Cary, 1991; and many years of pers. obs. of domestic forms of mallard). Game-farm mallards generally carry their tail in a slightly upright position when on the water whereas the tails of wild mallards are carried horizontally. When standing, game-farm mallards are more upright than the wild mallard, whose body plane is nearly horizontal to the ground. The bodies of wild mallards are teardrop-shaped and their bills are long, whereas game-farm birds are less streamlined and their bills are stubbier. Mallards were attracted to whole corn, approximately 5 kg/day, intended for overwintering canvasbacks (*Aythya valisineria*) and redheads (*Aythya americana*). The small amount of corn was not sufficient to constitute the complete daily food intake of the waterfowl, which often left the cove flying towards the open waters of the Chesapeake Bay following feeding and resting. From 1983–1993, I made >50 observations each year of courtship parties of both species from November until March, when the birds dispersed for breeding sites. Each observation included a count of the number and sex of birds of each species, including male hybrids (female hybrids were difficult to discern, although a few were identified). Hybrids between mallards and American black ducks were identified by plumage and were probably all F1s (Morgan *et al*., 1976). Since many of the same individuals were involved in multiple observations within a given winter, mean values per year are used for comparisons.

Pairs were counted each year in late February and early March to compare numbers of heterospecific and homospecific pairings. Pairs were determined by behavior, especially their close proximity when resting and swimming. In flight, paired males typically follow their mates (Derrickson, 1986), and when groups take flight, pairs maintain close proximity within the flock (Stotts, 1958). Paired birds often took part in 'courtship parties', separating out with the male following the female when the female swam away and with females 'inciting' their mates to displace other birds (pers. obs.).

In addition, in 1979–1982, wild American black duck eggs (n = 5 clutches, 45 ducklings) were obtained from Poplar Island on the Chesapeake Bay, and were banded and released at 5–6 weeks of age on Sullivan's Cove. Broods were tame and imprinted on me. Broods were kept separated during handrearing as would occur in wild broods. Ten of these birds (4 males, 6 females) were shot by hunters at scattered locations throughout the Chesapeake Bay. Five were shot on the Severn River, 4 at sites on the Eastern Shore of the Chesapeake Bay, and 1 on the Patuxant River. In 1985 and 1986, a total of 79 full-winged, 1–3 year old American black ducks, handraised at the National Zoological Park's Conservation and Research Center were banded (United States Fish and Wildlife Service aluminum bands) and then released at Sullivan's Cove, and then observed for mate choice. These were second generation from the wild. Four pairs of these birds bred successfully at Sullivan's Cove for 3 years during the study period, and nesting attempts have been made each year following the release of the first captive-raised brood. Although American black ducks did not breed near or on the study site prior to these releases, game-farm mallards nested throughout the area both before and during the study period. American black ducks and mallards often rested on a 30 m pier. I observed these for bands and was able to determine band numbers using a 40× telescope.

Aggressive interactions between mallards and American black ducks were tallied to see if one species was dominant over the other. I compared only interspecific male–male interactions immediately following corn feeding, when individuals of both species were active and in close proximity. These observations were made from inside my house when most of the corn had been eaten and birds were active in searching for the widely scattered kernels that remained.

RESULTS

Courting parties and pairing

Mallard and American black duck numbers varied considerably between years, with the population changing from only game-farm mallards to primarily American black ducks (Table 1). Although most of the initial population of American black ducks were handraised, by 1989, these comprised <15% of the study population, as judged by the percentage of banded birds present. Wild mallards also increased in numbers over game-farm mallards. There was complete separation of courting parties by species. Courting party size ranged from 3–22 males (mean = 6.4) in American black ducks and from 5–14 males (mean = 7.2) in mallards. These groups remained separated in space, but not in time. Courting parties of one species did not appear to stimulate courting parties of the other to begin or terminate. Rather, warmer than normal temperatures during winter appeared to stimulate courtship party formation in both species. Courtship activities were not restricted to specific locations in either species, and typically occurred in shallow water within 30 m of the river's shoreline or in the salt marsh. When both species were courting, I never observed courtship parties closer than 10 m and they were usually farther apart. Female mallards and American black ducks were only observed to interact with courtship parties of conspecific males. Hybrid females, which had some orange at the base of their bill, rather than a uniform dull greenish coloration, were most often observed in American black duck courting parties. Although, mallards and American black ducks were in close proximity while resting or feeding, they separated when courting, and nearly all paired ducks (99.8%) were composed of conspecifics (560 out of 561 pairings observed; Table 2).

Table 1. Summary of mallards and American black ducks at Sullivan's Cove, Severn River, Anne Arundel County, Maryland

High count date	Mallards	Black ducks	Hybrids
January 2, 1977	110 (95)[a]	2	0
March 13, 1978	125 (102)	2	1
February 23, 1979	78 (58)	2	1
January 12, 1980	93 (46)	11	0
January 16, 1982	52 (14)	13	3
January 4, 1983	56 (14)	10	2
January 10, 1984	60 (12)	38	2
December 19, 1986	54 (18)	63	3
January 22, 1988	113 (36)	100	5
January 11, 1989	46 (10)	98	2
December 18, 1991	16 (2)	53	3
January 18, 1992	19 (4)	57	3
December 15, 1993	30 (0)	46	3
Total	852	495	28
Mean/year	65.5	38.1	2.2

[a]Numbers in parentheses are number of game-farm mallards.

Table 2. Number of conspecific and heterospecific pairs of mallards and American black ducks at Sullivan's Cove, Severn River, Anne Arundel County, Maryland

Year	Mallard × mallard	Black duck × black duck	Mixed
1977	40	1	0
1978	60	1	0
1979	29	1	0
1980	35	5	1[a]
1982	19	6	0
1983	25	5	0
1984	26	17	0
1986	21	25	0
1988	50	46	0
1989	20	45	0
1991	5	23	0
1992	5	24	0
1993	8	20	0

[a]Handraised female American black duck paired with wild male mallard.

Hybrid males joined courting parties of both species, but never successfully paired with females of either species. Two pairs composed of a hybrid male and hybrid female were observed, but most hybrid males clearly did not obtain mates by April, when nesting was underway locally.

Behavior of captive-raised American black ducks

Seventeen pairs consisting of one or two captive-raised American black ducks were identified when birds rested together on the pier. The only instance of mixed pairing, involving a handraised female American black duck in her hatching year and a wild mallard, occurred in 1980. All other pairings were strictly within species. All pairs were composed of non-siblings, as determined by either one bird being unbanded, indicating the mate was not from any of the released American black ducks (all of which were banded), or between banded birds from different broods. Five American black duck pairs from previous years, identifiable by bands, reformed for from 1–4 years, and were noted as early as late September to be associating as mates.

Dominance interactions

There was no consistent dominance of wild mallards over American black ducks or vice versa. American black ducks displaced mallards more (873 out of 1536 observations, 56.8%, $\chi^2 = 14.4$, $P < 0.001$) than mallards displaced American black ducks. Males of breeding pairs of American black ducks in Sullivan's Cove excluded game-farm mallards from their territories; wild mallards did not remain to breed at the site. None of the four broods of American black ducks hatched and reared at Sullivan's Cove contained hybrids.

DISCUSSION

Species status and hybridization

Abundant data support the idea that American black ducks are declining because of introgressive hybridization with mallards. Hybridization between the two species is suggested to be deleterious to American black duck populations because its gene pool is smaller than that of the widespread mallard (Johnsgard, 1967). Some authors suggest that hybridization is common because American black duck females may prefer mallard males as mates (Johnsgard, 1961, 1967; Ankney, Dennis, Wishard *et al.*, 1986; Brodsky & Weatherhead, 1984). Ankney, Dennis, Wishard *et al.* (1986), citing lack of genetic differentiation, shared courtship displays (Johnsgard, 1960), and a reported absence of reproductive isolation, concluded that the American black duck is a melanistic morph of the mallard. Avise, Ankney & Nelson (1990) discovered two clonal arrays in mitochondrial DNA, differing by about 0.8% in nucleotide sequence, in mallards and American black ducks. One was found only in mallards and the other in both mallards and American black ducks, again supporting a close paraphyletic relationship between mallards and American black ducks. While mallards and American black ducks are closely related, Avise *et al.* (1990) advised that the mtDNA data cannot be used to decide on their species status.

If American black duck females preferred to pair with mallard males, both the hybridization hypothesis for American black duck declines and lack of species distinctiveness would be strongly supported. Studies of the process of pair formation in American black ducks and mallards wintering in sympatry have produced mixed results. Brodsky & Weatherhead (1984) observed American black ducks, mallards, domestic mallards and hybrid mallard–American black ducks wintering farther north than is usual and where the birds were dependent upon artificially provided food. Initially, American black ducks and mallards paired and courted intraspecifically, but when excess mallard males joined American black duck courting parties, female American black ducks seemed to prefer mallard males as mates. They called for more studies of courtship and pair formation in these species.

At the Chesapeake Bay site, neither the hybridization hypothesis nor the competition hypothesis was supported. Mallards and American black ducks paired assortatively, and obvious hybrids did not form pair

bonds with either parental species. I found no support for the suggestion that the two species are merely color morphs or that female American black ducks prefer to pair with male mallards. Brodsky & Weatherhead's (1984) data also showed that the two species separated when courting and that mixed pairing did not occur, in accord with my observations. They found, however, that mallard drakes associated with American black duck females 'only after all possible intraspecific pairs had formed'. They suggested that mallards form pair bonds earlier than American black ducks, freeing mallard males to court American black duck females, but I found no evidence for earlier pairing in mallards (see also Hepp & Hair, 1983). Furthermore, the close presence of domestic mallards and hybrids might have complicated their data (see below). My observations lasted until nesting began locally, whereas Brodsky & Weatherhead's study lasted until 18 March. My data showed that American black ducks and mallards were never together in mixed courting parties at any time in the overwintering period. Perhaps our data differ because the potential to find mates at Brodsky & Weatherhead's Ottawa site may have been limited by an abnormally small and artificial overwintering population. this was not the case within the Chesapeake Bay region with its large and far-ranging population of American black ducks. Band returns, and observations of the birds flying into the Chesapeake Bay, prove that the Sullivan's Cove birds are not an isolated population restricted to the Severn River.

The hybridization hypothesis is not supported by a study of the development of species recognition (Brodsky, Ankney & Dennis, 1989). They showed that American black ducks and mallards, in laboratory choice tests, preferred the species they were raised with since hatching, whether they were the same species or not. Because interspecific egg parasitism has not been reported between mallards and American black ducks, both species in the wild will normally acquire the 'correct' social experience that will assure assortative pairing. That my captive-raised black ducks paired with black ducks, even when outnumbered by mallards, supports the social experience factor identified in the Brodsky *et al*. study. Species recognition will be possible as long as hybridization through forced copulations does not reach the level where it eliminates the distinctive American black duck plumage, assuming that the overall dark coloration of American black ducks underlies their species recognition. My naive handraised American black ducks not only paired with American black ducks but did not pair with siblings, suggesting that sibling recognition in addition to species recognition also occurs during early social experience. The single pairing by a handraised female American black duck to a wild mallard male took place in the first year of the American black duck releases, when no other non-sibling American black ducks were present. The remaining handraised females paired with wild American black ducks.

Social experience within broods may also explain the lack of pairing in hybrid males that I observed. Hybrid males are clearly at a disadvantage and I observed no hybrid to successfully pair with either species.

Given the social basis of the development of species recognition, hybridization should not continue to produce American black duck population declines in the long run. Assortative mating will result in the continued separation of mallards and American black ducks as distinct species, based upon the obvious plumage differences between them. Experimental backcrosses showed that the black duck plumage or the mallard plumage predominates in the F2 generations, depending upon which species was forced to mate with the hybrid (Phillips, 1915; Morgan *et al*., 1976). Because of this, it is likely the two species will maintain present species-typical plumage differences, even in the face of hybridization.

If mixed pairing is rare, as I found on the Chesapeake Bay, then hybrids may arise largely from forced extrapair copulations (Ankney, Dennis & Bailey, 1987; Seymour, 1990; pers. obs.; but see D'eon, Seymour & Boer, 1994). Forced copulations are prevalent in wild mallards and much less so in American black ducks (McKinney, Derrickson & Mineau, 1983; Seymour & Titman, 1979; Seymour, 1990).

Hybridization loses ground as a *natural* cause of American black duck declines when the game-farm mallard release programs are considered. Game-farm mallards increased due to releases beginning in the early 1900s, and Heusmann (1974, 1991) has discussed the long-standing nature of such releases in the American black duck's breeding range. While speculative, it appears likely that captivity selects for persistent forced copulation behavior and no pair bonding, because this behavior results in more fertilizations. When coupled with incubator-hatching, the standard practise amongst game farms, this assures that forced copulations result in more offspring in the next generation from males that force copulate rather than 'pair' (McKinney, Cheng & Bruggers, 1984). Millions of game-farm mallards have been released into the breeding range of the American black duck. As much as 50% of Maryland duck stamp revenues went to purchase game-farm mallards in the last two decades (Dolesh, 1993). In Maryland alone, the State released more than 150 000 game-farm mallards per year – more than five times the number of black ducks wintering and nesting on the Chesapeake Bay (Krementz, Stotts, Stotts *et al*., 1991). Private landowners in Maryland annually release another 100 000 5–10 week old game-farm mallards (Soutiere, 1989).

Hybridization is seen as a new threat to the American black duck because of recent invasions of the mallard. But the increase of the mallard into the American black duck's range may not be new. Heusmann's (1991) analysis of historical mallard distribution suggests that mallards were common on the east coast of North America at the time of European colonization and became rare there due to market gunning and spring shooting.

Habitat loss for American black ducks

If Heusmann is correct, mallards and American black ducks may have been largely syntopic over the wintering period during evolutionary time rather than coming

together recently as a result of habitat changes wrought by humans. Forest cover and beaver (*Castor canadensis*) populations that produce the forested ponds preferred by black ducks in inland areas, have not declined in recent decades. Habitat loss for American black ducks was discounted by Ankney, Dennis & Bailey (1987) for Ontario. It is unlikely that the habitat structure for breeding American black ducks has been reduced sufficiently to cause the observed decline.

Competitive exclusion of American black ducks

Competitive exclusion of American black ducks by mallards is often espoused as the cause of American black duck declines but few data to support this exist (e.g. Merendino & Ankney, 1994). In most reports a causal relationship between increases in mallards and decreases in American black ducks is not documented. Controlled laboratory trials are mixed on this point. Brodsky, Ankney & Dennis (1988) found that mallard males were almost always dominant to American black duck males. Hoysak & Ankney (1996), however, were unable to show any difference in dominance. I found no dominance balance in favor of mallards to displace American black ducks from a feeding location at my study site. Furthermore, four broods were raised by American black ducks at my study site in the presence of game-farm mallards. The male American black ducks were frequently observed defeating and chasing male mallards intruding upon their territories. None of the young in the four broods observed to fledging were hybrids. All of these broods were from first nesting attempts, as judged by hatching date.

Human disturbance, neophobia, and American black duck declines

I suggest that mallards are not the primary cause of American black duck declines but that mallards increase due to their greater tolerance of human disturbance. American black ducks have survived human settlement for hundreds of years, but human disturbance has increased. There has been an increase in numbers of humans, their recreational use of waterfowl breeding habitat and the building of cottages along shorelines of formerly remote lakes. These sorts of human activities have increased tremendously during the last 30 years, especially in American black duck breeding areas where mallards have replaced them (pers. obs.).

A major behavioral difference between mallard and American black duck is their tolerance of human-induced disturbance. American black ducks are often described as more wary than mallards (Kortright, 1942; Wright, 1954), and Ankney, Dennis & Bailey (1987) suggest that this wariness should lower hunting pressure for American black ducks relative to mallards. This argument could be turned on its head if hunting pressure, and other human disturbances, reduce the actual amount of usable habitat for American black ducks relative to mallards.

American black duck 'wariness' has not been assessed developmentally but it can be studied in the field. Throughout the 16 years of my study, when I walked out on a pier throwing corn to feed ducks, canvasbacks moved towards me, within range of the falling corn, American black ducks flew 100–200 m towards the middle of the cove and mallards swam a short distance farther offshore. American black ducks approached to feed only after I had returned inside the house, whereas mallards approached the corn in the water as soon as I turned to leave the pier. Even my handraised ducks flew off with the wild American black ducks that moved into the cove during the winter, remaining with them until I disappeared from view.

The hypothesis that the greater 'wariness' of black ducks could impact habitats available to them for feeding and breeding, effectively decreasing American black duck habitat while increasing mallard habitat is supported by several studies. Morton, Kirkpatrick & Vaughan (1989) suggested that human disturbance of wintering American black ducks impaired their physiological condition, reducing winter survival and perhaps nutrient reserves carried to the breeding grounds. They also documented nocturnal foraging flights to off-refuge feeding areas that the American black ducks could not afford to use, energetically, during daylight due to human disturbance. It is known that low body mass reduces survival of female American black ducks and increases susceptibility to hunting mortality (Conroy, Costanzo & Stotts, 1989). Krementz *et al*. (1989), however, found no relation between late-winter body mass and annual survival along mid-coastal Maine. Hanson, Ankney & Dennis (1990) found lower body weights in adult male and juvenile female American blacks ducks compared to their mallard counterparts. Diefenbach & Owen (1989) predict that human disturbance is affecting American black ducks in Maine. In Maryland, Krementz, Stotts, Pendleton *et al*. (1992) found equal productivity in American black ducks and mallards, except on Bodkin Island, where American black duck productivity declined. American black duck females were more likely to abandon nests than mallards as a result of human disturbance, and more human disturbance occurred on Bodkin Island.

The evidence indicates that the influence of human disturbance may limit American black duck use of otherwise productive habitat but not affect mallards. American black ducks may be declining because they have a lower ability to survive in the face of human disturbance, in both breeding and wintering periods. If true, the mallard increase is an epiphenomenon and not a cause of the decline of American black ducks.

American black ducks may have a generalized fear response to novelty higher than that found in mallards, that underlies their different responses to human disturbance. Fear of novelty (neophobia) is likely to have a simple genetic mechanism yet it can have profound effects on adult behavior (Greenberg, 1983).

The development of neophobia has been studied experimentally in birds by Greenberg (1983). The

experimental protocol is straightforward: expose young birds to stimuli during their exploratory period of development then, later, when adulthood is attained, test for less fear of approach to these same stimuli compared with novel ones. His methods could be modified to test the genetic basis of behavioral differences in 'wariness' in mallards and American black ducks, and the results may have direct conservation implications. American black ducks are suggested to have greater neophobia than mallards, and this potential causal mechanism underlying American black duck declines can be addressed. In general, more consideration of behavior that arose before humans modified environments, such as American black duck 'wariness', may provide insight into subtle causes for declines when these environments are changed.

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