

NOTE / NOTE

Haldane's rule and American black duck × mallard hybridization

Ronald E. Kirby, Glen A. Sargeant, and Dave Shutler

Abstract: Species ratios and rangewide distributions of American black ducks (*Anas rubripes* Brewster, 1902) and mallards (*Anas platyrhynchos* L., 1758) have undergone recent changes. Mechanisms behind these changes are not known with certainty, but recent investigations have focused on the possibility of competitive exclusion and the consequences of hybridization. Consequences of hybridization have been difficult to assess because of the difficulty in identifying hybrids beyond the F₁ generation and lack of means to quantify introgression in wild populations. We documented a postmating isolating mechanism between the two species that follows Haldane's rule in controlled, interspecific matings in captive populations. Hybridization reduces the proportion of F₁ females available to return to the breeding grounds in the subsequent year. This effect, although likely small in overall population consequences in any year, may be of local significance and may contribute to recent reports of range shifts in both American black ducks and mallards.

Résumé : L'importance relative des canards noirs (*Anas rubripes* Brewster, 1902) et des canards colverts (*Anas platyrhynchos* L., 1758) et leur répartition à l'échelle de leur aire totale ont encouru des modifications récentes. Les mécanismes responsables de ces changements ne sont pas connus avec précision, mais des études récentes ont examiné l'exclusion par compétition et les conséquences de l'hybridation. Les conséquences de l'hybridation sont difficiles à évaluer car il n'est pas facile d'identifier les hybrides au-delà de la génération F₁ et il n'y a pas de moyen pour quantifier l'introgression chez les populations sauvages. Nous avons étudié un mécanisme d'isolement entre les deux espèces après l'accouplement lors d'accouplements interspécifiques contrôlés chez des populations en captivité. L'hybridation réduit le pourcentage de femelles de F₁ disponibles pour retourner sur les aires de reproduction l'année suivante. Cet effet, bien que limité en conséquences sur l'ensemble de la population pour une année donnée, peut être d'importance locale et peut contribuer aux changements dans les aires de répartition signalés tant chez les canards noirs que chez les canards colverts.

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Introduction

Several reviews have addressed the decline of the American black duck (*Anas rubripes* Brewster, 1902; hereafter, black duck), both absolutely and relative to the mallard (*Anas platyrhynchos* L., 1758) (Barske 1968; Rusch et al. 1989; Conroy and Kremenetz 1990; Nichols 1991; Nudds et al. 1996). Potential negative consequences of hybridization for the black duck have been a common theme. Discussion has led to extended debate (e.g., Ankney et al. 1987, 1989; Conroy et al. 1989); these authors viewed hybridization vari-

ously, from an extreme threat to the black duck to less important than competitive exclusion. Johnsgard (1963) considered the capacity of waterfowl to hybridize as evidence of an effective isolating mechanism that maintains the integrity of species, exactly the opposite conclusion from that drawn by many from observations of interactions between black ducks and mallards. Only Nudds et al. (1996) have distinguished between phenomena that might reduce black duck numbers and those that could cause the species to disappear. Experiments evaluating introgression have not been performed.

Primary sex ratios (at fertilization) of waterfowl are 1:1 (Johnson et al. 1992), which is also the case in other birds (Clutton-Brock 1986). Secondary sex ratios (at hatch) are likewise 1:1 (Blums and Mednis 1996). Hybrids between species, however, often show preferential sterility or inviability of the heterogametic (XY) sex, which in birds is the female. This phenomenon, called Haldane's rule, dates from 1922 when J.B.S. Haldane observed that

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R.E. Kirby^{1,2} and **G.A. Sargeant**, Northern Prairie Wildlife Research Center, US Geological Survey, Jamestown, ND 58401, USA.

D. Shutler, Department of Biology, Acadia University, Wolfville, NS B4P 2R6, Canada.

¹Corresponding author (e-mail: ronald_kirby@usgs.gov).

²Present address: US Geological Survey, Western Regional Office, 909 1st Avenue, 8th Floor, Seattle, WA 98104, USA.

When in the offspring of two different animal races one sex is absent, rare, or sterile, that sex is the heterozygous [heterogametic or XY] sex.

Recent surveys have suggested that this rule holds in all animals known to possess sex chromosomes (Orr 1997). Hybrid inviability in birds has long been known (e.g., Guyer 1909) and is widespread (Gray 1958), as is hybridization per se (Grant and Grant 1992). The cause of hybrid sterility and inviability is between-locus incompatibility, the mechanics of which are not of concern here (but for details see Orr 1997).

Given the ubiquity of Haldane's rule, and its known applicability to birds, the occurrence of this phenomenon in hybrids between black duck and mallard is predictable, but the question has not been investigated to date. In this paper, we report sex ratios of F_1 hybrids between black ducks and mallards, progeny of backcrosses to parental forms, and matings of F_1 inter se. We discuss the potential consequences of our findings to interpretations of species numbers and ratios of breeding waterfowl in the wild.

Methods

We analyzed results of mating trials between wild mallards and wild black ducks in propagation facilities. The original experiments were not designed to evaluate sex-ratio variation, thus obviating reporting bias of the sort identified by Palmer (2000) in other studies of sex ratios in birds. To the best of our knowledge, birds we included in this retrospective analysis constitute the only matings of these species wherein identities of parent birds were certain and initial sex ratios (the sex of all live-hatched young within clutches) were measured. Our analysis was of hybrid viability through measure of living (= viable) young at hatch. The data did not permit evaluation of other aspects of viability and fertility of hybrid offspring. Their subsequent survival was not consistently recorded in the original experiments or was truncated by experimental design. Infertility is a common F_1 postzygotic incompatibility in birds (Price and Bouvier 2002), but no useful quantitative data were recorded regarding subsequent fertility of the birds we assessed (i.e., numbers of eggs that failed to hatch or of causes of hatch failure). Birds reared in North Dakota were maintained under US Fish and Wildlife Service animal care protocols; birds reared in Canada were cared for under the principles and guidelines of the Canadian Council on Animal Care.

In the early 1970s, F.B. Lee reared a flock of captive P_1 mallards from California and P_1 black ducks from New Brunswick (some hand-reared in North Dakota) at Northern Prairie Wildlife Research Center near Jamestown, North Dakota. In 1974–1976, a captive breeding program was established to develop various hybrids from these parental forms. F.B. Lee recorded identities of adults used in each cross and the sex and number of offspring in each clutch. We sorted these records by type of cross (mallard male \times black duck female, black duck male \times mallard female, etc.) and by generation of hybridization (P_1 , F_1 , F_2 , F_1 backcross to mallard, F_1 backcross to black duck, etc.). Almost all of these birds were examined by R.E.K. as live specimens or frozen carcasses when this study began; representative specimens have been deposited in the National Museum of Natural History, Washington, D.C. (Kirby et al. 2000).

Shutler et al. (1996) reared F_1 black duck \times mallard hybrids from mallards and black ducks from Ontario and mal-

lards from Saskatchewan. Randomly chosen pairs of adults were isolated in outdoor pens and allowed to form pair bonds; duckling sexes were determined by cloacal palpation. We sorted the progeny (all F_1) by clutch.

Phillips (1914, 1915, 1921) reared hybrids between black ducks and mallards. Although we could not locate his original notes, his statements in the literature were unequivocal regarding sexes of offspring in some crosses. Those that included complete counts of young are included here. Some specimens from his work were available as study skins in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

Sex ratios can potentially vary among broods to a greater extent than predicted by the binomial distribution. To accommodate the possibility of such "extrabinomial" variation, we used a ratio estimator for cluster samples of variable size (Cochran 1977, p. 66) to estimate proportions of males in clutches recorded by F.B. Lee; D. Shutler, C.D. Ankney, and D.G. Dennis; and J.C. Phillips (Table 1). We included pooled broods when estimating means, but excluded pooled broods when estimating among-brood variances used to compute confidence limits. We did not know whether F_1 sex ratios would be influenced by the species of the female parent, so we compared sex ratios for F_1 progeny of female black ducks and female mallards before pooling data. Because Haldane's rule predicts a preponderance of males among F_1 progeny, we computed 95% lower bounds (equivalent to one-tailed tests) for F_1 hybrids. We computed 95% confidence limits for other groups because we had no reason to expect sex ratios to depart from unity.

Results

F_1 hybrid duckling progeny were preponderantly male and we found no evidence of differences in sex ratios associated with sexes of parents. Offspring of male black ducks and female mallards were 66% male (SE = 6.5%) and those of male mallards and female black ducks were 63% male (SE = 7.5%). Collectively, hybrid F_1 progeny were 65% male (SE = 4.9%, 95% lower bound = 0.56). Sex ratios did not vary significantly from unity for groups other than F_1 hybrids. Progeny of $F_1 \times F_1$ matings were 45% male (SE = 8.2%) and $F_1 \times P_1$ progeny were 50% male (SE = 6.5%). Collectively, non- F_1 offspring were 48% male (SE = 2.2%, 95% CI = 44%–53%).

Discussion

Our analysis was based on data collected for other reasons and thus lacked the experimental design and some of the controls one would wish. For example, selecting P_1 birds from allopatric populations to obviate the genetic consequences of previous contact between the species might have resulted in bias if mallard and black duck populations are genetically structured. *Anas* spp. have been variously considered panmictic (Parker et al. 1981; Ankney et al. 1986) or not (Rhodes et al. 1995), but there is reason to believe that male dispersal is not entirely random and that some genetic differences are likely (Anderson et al. 1992). Similarly, the circumstances of the captive rearing programs had some effects. The small size of some hybrid clutches in Jamestown

Table 1. Black duck (*Anas rubripes*) × mallard (*Anas platyrhynchos*) clutches for which sex was known for all hatched young.

Cross	Number of clutches of hatched young		Source
	Males	Females	
Male black duck × female mallard	3	4	Phillips 1915*
	10	2	This study
	11	6	This study
	2	2	This study
	5	2	Shutler et al. 1996
Male mallard × female black duck	3	0	This study
	8	6	This study
	2	2	This study
	5	4	This study
	5	0	Shutler et al. 1996
	0	1	Shutler et al. 1996
	1	0	Shutler et al. 1996
	1	0	Shutler et al. 1996
	3	5	Shutler et al. 1996
	3	0	Shutler et al. 1996
F ₁ backcrossed to P ₁	10	8	Phillips 1915 [†]
	9	5	Phillips 1915 [†]
	4	3	This study
	7	8	This study
	4	3	This study
	3	2	This study
	1	1	This study
	9	9	This study
	3	4	This study
	7	4	This study
F ₁ × F ₁	1	3	This study
	9	12	This study
	6	19	Phillips 1915 [‡]
	10	4	Phillips 1915 [§]
	7	4	Phillips 1921
	6	3	This study
	3	8	This study
	4	4	This study
8	11	This study	

Note: "This study" refers to data collected by F.B. Lee in Jamestown, North Dakota.

*May have been from mixed broods.

[†]Broods from two females that were combined.

[‡]Phillips confined three males and four females together in a single pen.

This value is the sum of the clutches.

[§]Same parents as depicted in the previous line but from another year.

may be explained by the fact that this effort was part of a much larger captive rearing program in which disturbance by animal caretakers and by predators trying to gain entrance to the pens was a constant concern. This may have resulted in partial destruction of some clutches that could not be unequivocally documented by review of decade-old records. In both the Jamestown and Canadian studies, egg inviability was reported in incubator records and was an ultimate factor that also reduced numbers of hatched birds. Contrarily, we also cannot explain a few of the large

clutches in both the Jamestown pens and in Phillips' (1915, 1921) studies (mean black duck clutch sizes vary from slightly more than 9 to 10 eggs, and decreases with season and whether the nest attempt is a re-nest or first attempt; Longcore et al. 2000). However, in Jamestown, eggs were sometimes removed to incubators if nests appeared abandoned and sometimes birds returned to laying thereafter. Continuous laying in these non-nutrient-limited birds was possible as has been observed in the wild (Arnold et al. 2002). We have no reason to believe that any of these circumstances would affect the sex ratio of eggs laid, but captive circumstances differ in many ways from circumstances in the wild. Similarly, we derived no insight in this study as to when differences in sex ratio occurred because reasons for inviability were not assessed. However, our postulate was that Haldane's rule, as a general explanation for the sex ratio observed, applied.

Notwithstanding the above caveats, F₁ young from black duck × mallard matings were preponderantly male as predicted by Haldane's rule; sex ratios of young in the other crosses were approximately 1:1. Considering the ubiquity of Haldane's rule, which applies even among domestic races of the mallard (Phillips 1914), this outcome was expected. Analyses have shown that this result is a nearly obligatory first step in the evolution of postzygotic isolation (Coyne and Orr 1989, 1997). Therefore, one would expect Haldane's rule to be expressed in matings between black ducks and mallards, which historically have been viewed as probably separated since the early Quaternary (Palmer 1976, p. 288; Avice et al. 1990; R.S. Palmer, personal communication). More recent analyses (McCracken et al. 2001) have suggested a much earlier origin of black ducks from a "monochromatic mallard-like ancestor that established itself in the New World well in advance of nominate mallards." This earlier origin (as opposed to peripatric speciation) lends greater weight to the expectation that Haldane's rule would apply in this circumstance. We cannot envision a simple means to expand this analysis to a reasonable field experiment because any such exercise would fail on the matter of determining the paternity of young.

The effects of hybridization on sex ratios of generations subsequent to the F₁ in waterfowl have not been investigated. We assumed that there were none for our analysis and found none in the few crosses for which we had data, but this was a very limited analysis from experiments not designed to address sex ratios per se. Price and Bouvier (2002) found that fertility of the homogametic sex in birds (male) was lost in the F₁ before viability of the heterogametic sex (female). This finding requires further study in black duck × mallard hybridization.

Given the imperfection of premating isolation in this species pair, there is a role for postmating isolation in maintaining species integrity even when F₁ fitness loss is modest (Price and Bouvier 2002). This phenomenon cannot be discerned within wild populations when species relations are assessed by relative counts of parental species and putative hybrids, and only F₁ hybrids can be consistently and accurately identified (Kirby et al. 2000). But there are population phenomena of interest that may be a consequence of this phenomenon. Reduction of proportions of females in clutches in the F₁, even while likely of little overall popula-

tion consequence in a given year, could be of significance locally through reduction of local population density on the breeding grounds. This then allows the possibility of population expansion by either black ducks or mallards through pioneering into unoccupied habitat. For example, over time, where wild mallards are in greater relative numbers, in areas where mallards have been propagated and released, or where large feral flocks of mallards occur, the consequence would be a diminution of the proportion of black ducks. This phenomenon adds additional difficulty in attempts to distinguish between the consequences of hybridization and other phenomena, such as competitive exclusion or simple loss of reproductive effort through formation of hybrid pairs.

Longcore et al. (2000) concluded that current rates of hybridization of black ducks with the mallard were not "critical," because assortive mating still occurs throughout black duck range even though island populations or others in circumscribed habitats were at risk. Ankney et al. (1989) drew essentially opposite conclusions from quite similar data sets. The data we present show that several phenomena may be of consequence locally and that distinguishing the factors contributing to range shifts between the species may be more difficult than suspected. Our analysis is the first to document a postmating mechanism that isolates black ducks and mallards.

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