

A Re-analysis of Hybridization between Mallards and Grey Ducks in New Zealand

MALCOLM HADDON¹

Department of Zoology, University of Otago, P. O. Box 56, Dunedin, New Zealand

In the literature there is some disagreement concerning the risk, in countries such as New Zealand, Australia, and South Africa, of losing pure stocks of indigenous duck species because of hybridization between those stocks and populations of introduced Mallards (*Anas platyrhynchos*). Dorst (1970: 252) claimed that "... in New Zealand, for example, pure stock of the wild duck (*Anas superciliosa superciliosa*) is disappearing because it has hybridized with the introduced mallard duck." (Weller 1969, 1980) also has expressed concern that pure stocks of both the New Zealand Grey Duck (*Anas superciliosa superciliosa*) and the Australian Black Duck (*Anas superciliosa rogersi*) could be eliminated at least partly as a result of hybridization with the Mallard. On the other hand, based on breeding and hybridization experiments with the New Zealand Grey Duck and the introduced Mallard, Williams and Roderick (1973) suggested that differences in fertility and hatching success resulting from hybridization would affect the Mallard stock to a greater degree than that of the Grey Duck. Williams (1981: 64) repeated this claim when he stated "At this time there is no evidence at all to support the rather wild notion that Mallards are interbreeding so freely with Grey Ducks that eventually no pure Grey Ducks will exist. What little evidence there is, suggests Grey Ducks are retaining their purity while Grey blood has more strongly infiltrated the Mallard."

Williams and Roderick's (1973) study has been cited by a number of workers who have been considering similar problems. Braithwaite and Miller (1975), for example, did not consider that the potential for hybridization between the Mallard and the native Black Duck of Australia was particularly great. When discussing the barriers to hybridization between the Black Duck and the Mallard they stated (p. 60) that "Apart from the restriction to gene flow enforced by species recognition and pairing behaviour, there is also evidence from studies of mallard-grey duck hybridization (Williams and Roderick 1973) of reduced hybrid fertility and, most important, of a high rate of infertility of eggs and a substantially increased rate of embryonic death from matings between the two species." Greig (1980), in a later paper, was trying to draw attention to the threat that he considered hybridization to pose to the genetic integrity of native dabbling ducks such as those found in New Zealand and in South Africa. He stated (p. 88) that "Williams and Roderick (1973) also studied the breeding success of the hybrids and found that, depending on the cross, there may be a proportion of infertile eggs

or embryo deaths." Greig accepted these conclusions but nevertheless pointed out that some introgressive hybridization could occur.

The work by Williams and Roderick (1973) thus has attracted some attention. Unfortunately, they did not analyze their data fully, and, when this is done, different conclusions can be reached. The purpose of this paper is to reanalyze their data and to discuss the significance of conclusions reached from this re-analysis.

The following notations will be used throughout this paper and were copied from Williams and Roderick. G/M means an F.1. hybrid derived from a Grey male \times Mallard female pairing. Similarly, M/G denotes an F.1. hybrid from a Mallard male \times Grey female pairing. The references made to $\frac{3}{4}$ hybrids concern the progeny obtained from pairing an F.1. hybrid with a pure Grey or pure Mallard. In reference to any pairing, such as G \times M or G/M \times M, etc., the species of the drake is mentioned first and that of the hen second.

Williams and Roderick (1973) concluded that pure populations of Grey Duck were not at risk from introgressive hybridization with the Mallard. This conclusion was reached and supported by pointing out the differences in fertility and the levels of embryo death that were observed in their experiments. They argued that (p. 69)

TABLE 1. Fertility and hatching success (from Williams and Roderick 1973).

Parents		Total number of eggs	Number of fertile eggs	Number of fertile eggs	Embryos living
G	\times G	10	10	10	10
M	\times G	74	74	74	70
G/M	\times G	33	33	33	31
M/G	\times G	43	33	33	29
$\frac{3}{4}$	\times G	9	9	9	9
G	\times M	84	47	104	85
M	\times M	22	22	22	21
G/M	\times M	130	98	95	85
M/G	\times M	50	47	47	44
$\frac{3}{4}$	\times M	29	18	18	18
G	\times G/M	89	70	71	48
M	\times G/M	64	64	64	54
G/M	\times G/M	9	9	9	0
G	\times M/G	43	43	41	37
M	\times M/G	68	63	63	59
G	\times $\frac{3}{4}$	47	36	36	34
M	\times $\frac{3}{4}$	26	26	26	25

¹ Present address: 13 Fairmile, Aylesbury, Buckinghamshire, HP21 7JT, England.

"Whichever pairing occurs, if breeding synchrony can be established, the eggs laid will usually be fertile. However, fertility can act as a barrier to further hybridization depending on the way the F.1. hybrids pair. The F.1. generation phenotypically resembles the paternal species and might be expected to pair with it. If this occurs as a Grey \times G/M pairing, some eggs in the clutch will be infertile [Table 1]. Less likely pairings, e.g. M/G \times Grey, may also produce infertile eggs.

Embryo deaths also lower the success of some of the pairings. In general the pairings which had a high percentage of infertile eggs also suffered most embryo deaths. Although a maternal effect cannot be excluded [bantam hens were used for incubation], the high percentage infertility and embryo deaths recorded for Grey \times G/M, and to a lesser extent for M/G \times Grey, is strongly suggestive of sex-linked genetic incompatibility. . . .

Thus, data from this captive study are corroborated by some from the wild and together they suggest that the mallard \times Grey pairing is more likely to occur and produce progeny than the Grey \times mallard combination and that the F.1. will breed back to the mallard more successfully (at the egg stage) than to the Grey."

These conclusions depend on the existence of significant differences between the breeding success of the various combinations of mated ducks. When these data are statistically analyzed, however, no significant differences are found. The columns in Table 1 (column 1 against 2 and column 3 against 4) were compared using 2×17 Chi-squared contingency tables. This enabled all combinations to be compared at once and would avoid artificially stressing any particular pairing.

The first comparison made was to answer the question of whether or not there was a significant difference in the proportion of fertile eggs produced between any of the 17 combinations considered by Williams and Roderick (1973). The contingency table showed there to be no significant differences ($\chi^2 = 12.24$, $df = 16$).

The second comparison made was to decide whether or not there was a significant difference in the proportion of embryos surviving (or conversely, proportion of embryo deaths) between the various combinations. Again, the respective contingency table showed no significant differences ($\chi^2 = 11.26$, $df = 16$).

Thus, in contradiction to the conclusions of Williams and Roderick (1973), the evidence from the breeding experiments implies that: (1) fertility differences do *not* act as a barrier to further hybridization deriving from the F.1. hybrids breeding back

either to pure Mallard or Grey Ducks or to other hybrids; (2) embryo deaths *cannot* be said to lower the reproductive success of any of the combinations of pairs significantly; (3) it may be that a Mallard \times Grey Duck pairing is more likely to occur than a Grey Duck \times Mallard combination (although complete overlap of the laying period between the Mallard and the hybrid forms was observed by Williams and Roderick), but it is not the case that one combination will be more successful than the other at producing progeny; and (4) there is no evidence of a sex-linked genetic incompatibility between the Mallard and the Grey Duck.

The analysis carried out in this paper implies that, if the pairing of disparate forms is successful in the wild, then reproductive success presents no significant barriers to successful introgressive hybridization between the Mallard and the Grey Duck. This means that Williams and Roderick's (1973) breeding experiments cannot be used, in a valid way, to support the idea that there is little risk of indigenous species of dabbling ducks losing their specific integrity through hybridization with introduced Mallards.

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