

S33-3 Indigenous gray ducks, *Anas superciliosa*, and introduced mallards, *A. platyrhynchos*, in New Zealand: processes and outcome of a deliberate encounter

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Abstract Three hypotheses — demographic and competitive ascendancy, genetic assimilation, and habitat destruction and disturbance — have been advanced to explain the demise of the gray duck and rise of the mallard in New Zealand subsequent to the introduction of the mallard a century ago. We modelled relative population change over the past 50–60 years, based on hunter kills, and evaluated the competing hypotheses. We conclude that capacity for survival, greater fecundity and productivity, physical domination of gray duck, and willingness to exploit novel feeding opportunities in man-disturbed environments, have contributed most to the present numerical dominance of the mallard. An apparently extensive hybrid swarm may be dominated by a mallard phenotype, but evaluation of genetic exchange based on phenotype alone remains problematic. Gray ducks and the gray duck phenotype may soon disappear from New Zealand.

Key words Hybridization, Ecological displacement, New Zealand, *Anas superciliosa*, *Anas platyrhynchos*

1 Introduction

The Anatidae feature commonly among animals now established in free-living populations beyond their native ranges. For example, 27 species were deliberately introduced to New Zealand with the intention of establishing populations for sport (Thomson, 1922; McDowall, 1994) and two, the mallard (*Anas platyrhynchos*) and Canada goose (*Branta canadensis*), are now among the most common birds in that country. Mallards have been introduced almost worldwide (Lever, 1987), including Australasia (Marchant and Higgins, 1990). The introductions there dropped the mallard directly into the core of the native range of the gray or Pacific black duck (*Anas superciliosa*), which extends from eastern Indonesia through Australia, New Zealand and New Guinea to Micronesia and Polynesia.

From 1867 to 1886, only occasional pairs or small numbers of mallards were imported into New Zealand, but from 1895 on, serious attempts were undertaken to propagate and release them (Thomson, 1922). Hunter organizations and acclimatization societies persisted with breeding and release of British game farm mallards for about 20 years, eventually establishing feral populations sufficient to permit hunting. The slow spread of these populations, and the ongoing decline of the gray duck in New Zealand, especially on the North Island, prompted importation of mallards from North America in 1937. The ensuing breeding program continued to 1963, releasing over 20 000 mallards nationwide (McDowall, 1994).

Subsequent expansion of the mallard in New Zealand coincided with (1) a nationwide decline of the gray duck, and (2) the appearance of birds of obvious hybrid ancestry (Williams, 1981; Gillespie, 1985). Three hypotheses have been advanced to explain these changes: (1) demographic and competitive ascendancy of the mallard which outbred and outlived the gray duck, and displaced and dominated it in competition for essential resources (Williams, 1981); (2) genetic assimilation, a consequence of widespread interbreeding between the two species that created an extensive hybrid swarm in which the mallard phenotype dominated (Gillespie, 1985); and (3) habitat depletion and disturbance that forced the gray duck, with its apparent preference for wild and remote wetlands and wooded environments, to retreat as forest was replaced by pasture and natural wetlands were drained. In contrast, the mallard readily exploited wetlands and other resources available within the pastoral landscape, and tolerated human-induced disturbance much better (Caithness, 1982).

In this paper we examine some predictions arising from each of these hypotheses.

2 Materials and methods

Patterns of historic mallard population growth were deduced from changes in the relative proportions of mallards and gray ducks in hunter kills. Records in available diaries from hunters mostly cover the period 1968–1990, although one extends back to 1933 (Caithness, 1980). Nationwide telephone surveys of hunters provided similar data

annually for 1992–2000 (NZ Fish and Game Council, unpubl. data). We also used regional banding studies (see Table 1) and field surveys (1963–1995; M. Williams, unpubl. data) to provide further measures of the mallard-to-gray duck ratio over time and species-specific survival and productivity estimates.

We used regional changes in mallard-to-gray duck ratios in hunters' kills to establish models of population trend for the two species, namely a continuous model:

$$dG/dt = b_G(t)G(t) - (1 - s_G(t))G(t);$$

$$dM/dt = b_M(t)M(t) - (1 - s_M(t))M(t);$$

and a discrete model:

$$G(t+1) = s_G(t)G(t) + b_G(t)G(t);$$

$$M(t+1) = s_M(t)M(t) + b_M(t)M(t),$$

where $s_{G/M}$ = species-specific annual adult survival, $b_{G/M}$ = species-specific recruitment rate (proportion of young per adult surviving one year), and G and M are the numbers of gray duck and mallard respectively. By substituting field-derived estimates of survival and/or productivity, we estimated likely changes in regional species populations over varying time periods.

3 Results and discussion

3.1 Demographic and competitive ascendancy hypothesis

This hypothesis predicts, first, differential survival, fecundity, productivity and recruitment rates for the two species, and, secondly, that mallards are physically dominant at shared feeding and breeding sites.

Survival Contemporaneous estimates of survival of mallard and gray ducks are shown in Table 1. Balham and Miers (1959) reported that survival rates for mallards averaged significantly (10%+) higher than for gray ducks in all sex and age categories examined. Reanalysis of their data sets using MARK (White and Burnham, 1999) confirmed their comparative findings but lowered their survival estimates. Caithness et al. (1991) reported no statistically significant differences in mallard and gray duck survival in the decades after the Balham and Miers (1959) analysis.

They reported, however, that low banded sample sizes yielded tests of low power, and only for males could they have detected large (40%+) differences in survival had they existed.

Both studies reported recovery rate estimates (15%–25%) for gray ducks that are among the highest yet recorded for wild ducks, indicating that they were 1.3–2.0 times more likely to be shot than sympatric mallards. Barker et al. (1991) concluded, from the same data, that such hunter-induced mortality was mostly additional to natural mortality rather than compensatory, thereby implicating hunting as an important determinant of gray duck survival. The lower survival and higher recovery rate estimates for 1949–1954 than those subsequent suggest significant over-exploitation and hunting as an understated contributor to gray duck decline.

Subsequent analyses of mallard survival (Nichols et al., 1990) have identified significant regional variation, especially for males. Within regions, the greater temporal variations in survival were in adult females. However, for neither sex were the differences indicated in Table 1 significant (Nichols et al., 1990; P. Taylor, pers. comm.).

Fecundity, productivity and recruitment The most frequently reported clutches for mallards and gray ducks are 10–12 and 8–10 respectively (Balham, 1952; Balham and Miers, 1959; Marchant and Higgins, 1990; M. Williams, unpubl. data). These records do not discriminate between initial clutches and re-nesting attempts. Broods of near-fledged mallard young are generally reported as larger than those of gray duck: 5.7 vs. 5.0 in a Manawatu wetland (Caithness, 1970), 5.8–6.9 vs. 3.9–4.8 in the Waikato wetlands in 1963–1970 (M. Williams, unpubl. data). None of these records indicate the percentage of ducks successfully raising young, and there are no data on the frequency with which each species re-nests. The mallard starts breeding earlier each season than the gray duck and ends later (Caithness and Pengelly, 1973), which implies more re-nesting by mallards.

Balham and Miers (1959) determined that the average productivity required of mallard and gray duck females to replace annual losses during the 1950s was 2.9 and 4.4

Table 1 Mean survival estimates (S) for adult mallard and gray duck, 1947–1990

Period	Male mallard S ± SE	Male gray duck S ± SE	Female mallard S ± SE	Female gray duck S ± SE	Region	Source
1949–1954	0.62 ± 0.05	0.39 ± 0.02	0.44 ± 0.03	0.32 ± 0.02	Waikato and Manawatu, female estimates adult + young combined	Balham and Miers (1959), reworked using MARK (White and Burnham, 1999)
1957–1965	0.69 ± 0.02	0.51 ± 0.02	0.59 ± 0.08	0.57 ± 0.05	Waikato	Caithness et al. (1991)
1966–1974	0.59 ± 0.03	0.58 ± 0.09	0.53 ± 0.07	0.52 ± 0.25	Waikato	Caithness et al. (1991)
1979–1983	0.66 ± 0.06 0.49 ± 0.03	* *	0.44 ± 0.05 0.41 ± 0.04	* *	Waikato Manawatu	Nichols et al. (1990)
1986–1990	0.48 ± 0.09	*	0.45 ± 0.09	*	Manawatu	P. Taylor (pers.comm.)

* Too few for reliable estimation.

fledglings, respectively. The many possible solutions in our models for relative population change in the Waikato region during 1960–1970 suggest that average mallard productivity then was not less than 3.1 fledglings per female, and for gray ducks not greater than 1.6. There are no direct field estimates of recruitment, that is, the number of progeny per duck surviving to breeding age. Applying known juvenal survival estimates (Caithness et al., 1991) to our models suggests that annual mallard recruitment was 0.58–0.71 per female and only 0.38–0.5 for gray duck in the Waikato region. These solutions indicate that annual mallard recruitment in the 1960s and 1970s averaged approx. 15% above replacement, and gray duck approx. 5% below.

Competitive displacement Mallards are 15%–20% heavier than gray ducks, and up to 10% larger in bill, wing and leg (Marchant and Higgins, 1990). They use their size advantage to physically displace and exclude gray ducks at feeding sites. In mixed species flocks at urban parks, for example, mallards dominate public feeding sites and physically prevent gray ducks from accessing the food: on one occasion, mallards initiated 413 interactions and won all but 3 (M. Williams, unpubl. data). Mallards also usurped gray duck breeding sites. Between 1963 and 1970, the numbers of gray duck pairs in the Waikato wetlands declined by 70% as numbers of mallard pairs rose by 145%; gray duck declined from 78% to 28% of the combined duck population then (M. Williams, unpubl. data). Specific sites previously used by gray ducks for loafing or waiting for mates became occupied by mallards. Pair and brood densities of gray ducks declined 22% and 17% respectively as mallard numbers increased, implying greater preoccupation of space by mallards.

3.2 Genetic assimilation hypothesis

Mixed species pairings and birds of apparent hybrid phenotype were observed soon after the initial mallard introductions (Thomson, 1922). Consistent with the reported dominance of the mallard, a mallard-like phenotype can be expected to prevail within the hybrid swarm. Progeny of mixed species pairings superficially resemble the paternal species (Williams, 1981). Although genuinely intermediate phenotypes may arise, more mallard-like than gray-like phenotypes result from mixed species, F1 hybrid-hybrid and backcross pairings. For mallard-like phenotypes to dominate in hybrid swarms, the initial mixed species pairing should involve primarily mallard drakes and gray ducks.

Despite experimental evidence that females of both species mate assortatively when given a choice (B. Bakker, pers. com), field observations indicate no courtship interaction among mixed species (Hitchmough et al., 1990). Yet breeding studies on the Waikato wetlands between 1963–1970 (M. Williams, unpubl. data) recorded 1%–4% of pairs as mixed species. Of 92 pairs observed in 1967, all but five were mallard drake × gray duck. Rhymer et al. (1994) confirmed, nevertheless, that mixed species matings of both types occur, and identified introgression of gray duck mtDNA into the mallard population as well as the reverse.

Phenotypic criteria discriminating between F1–F3 hybrids and parental species are not reliable (Green et al., 2000). Thus wing and face plumage characters and wing length could together only discriminate F1 hybrids from parental species with 85% confidence. Progeny of F1 hybrids backcrossed with gray ducks could be distinguished from gray ducks in 90% of specimens, but no comparable resolution of mallard-like hybrids and mallards was possible. The lack of plumage specificity in mallards may be a legacy of the inbred, game-farm stock from which the introductions were derived.

Using plumage characters, Green et al. (2000) estimated the gray-like hybrid component of the combined mallard-gray duck population. They identified varying levels of F1 and gray-like hybrids within regional duck populations, and recorded gray duck-like hybrids as more numerous than “pure” gray ducks in regions where the mallard phenotype comprised >80% of the total anatid population. This finding is consistent with rising hybridization as conspecific mates become difficult to find; but it does not preclude forced copulations as an important mechanism also.

3.3 Habitat depletion and disturbance hypothesis

The New Zealand landscape has been significantly modified during 150 years of European settlement. In little more than a century, indigenous forests on 26% of New Zealand’s land area were felled and replaced by grassland and pastoral farming (Wards, 1976). By 1970, almost 90% of the original wetlands had been reduced to inconsequential vestiges or converted to farmland (Cromarty and Scott, 1996). The ubiquitous gray duck found much of its native habitat obliterated, and as a direct consequence its populations declined (Balham, 1952).

Attributing the relative change in mallard and gray duck populations in the 20th century to the destruction of wild wetlands implies mallard and gray duck have different habitat preferences, the latter keeping more to remote or unmodified wetlands. This is not, however, the contemporary observation. Mallards have dispersed to and settled remote and uninhabited Auckland and Campbell Islands, 300–500 km south of New Zealand, from which gray ducks have subsequently disappeared. Mallards are presently expanding their presence in remote and forested Fiordland, the sole remaining region of New Zealand in which they have yet to achieve numerical dominance. It is now possible to find mallards at all sites where gray ducks presently survive: river headwaters, mountain tarns, high country lakes, and coastal stream mouths.

We are not aware that the hypothesis of differential tolerance of mallard and gray duck to human disturbance has been evaluated experimentally. However, we have observed that gray ducks feed and breed on created habitats on farmland with abundant marginal cover and/or riparian trees; that gray ducks were formerly conspicuous on lakes in urban parks as they are in Australia today; that areas where gray ducks formerly occurred in close proximity to

humans are now populated exclusively by mallards; and that mallards exploit agricultural habitats such as field drains and streams without riparian cover, and grain, grass and brassica crops, from which gray ducks are rarely reported.

4 Conclusion

There is clear evidence that the mallard has demographic ascendancy over the gray duck. The higher productivity and higher survival attributes of mallards fuelled their rapid expansion, especially following the persistent post-1937 releases. Being larger than gray ducks and thus able to physically dominate them, mallards were able to usurp the remaining lowland wetland habitat in which gray ducks persisted while concurrently exploiting new habitats and feeding opportunities within the expanding pastoral landscape. At the same time, gray ducks appear to have been hunted excessively (Balham and Miers, 1959). Such combined demographic and competitive ascendancy appears to be a particularly important contributor to mallard success.

Not so clear is the role of hybridization in the demise of gray duck. Until nuclear markers for discriminating gray duck and mallard from their hybrids have been identified, quantitative assessment of gray-mallard hybridization based on plumage characters alone must remain conjectural (cf., Gillespie, 1985; Green et al., 2000). Nevertheless, if mixed species pairings have occurred as frequently as described above, the introgression recorded by Rhymer et al. (1994) demonstrates that the genetic integrity of both species in New Zealand, particularly that of the gray duck, has already been compromised.

Loss of wild wetlands characteristic of pre-human New Zealand certainly impacted on the gray duck population. On its own, however, it does not explain its stunning displacement by the mallard. Gray ducks formerly occurred on lakes in urban parks, as they presently do in Australian cities and towns. Their present-day absence from pastoral and urban wetlands may be due to their physical or competitive displacement by mallards rather than to their inability to colonize or exploit these modified environments. Mallards have proved successful opportunists and ecological generalists worldwide. These traits have enabled them to occupy the full range of gray duck habitats in New Zealand. Given their demographic and competitive ascendancy over the past 60 years, mallards can be expected to continue to displace gray ducks everywhere; a further retreat of the gray duck phenotype appears inevitable. Whether a gray duck-like phenotype will persist alongside that of the mallard awaits further evaluation of the present hybrid swarm. Yamashina (1948) identified two hybrid phenotypes within the only other population reportedly derived from these two species, the so-called Mariana mallard (*Anas oustaleti*), but its extinction has precluded evaluating their stability.

What future for *Anas superciliosa* in its stronghold of Australia? Although mallards are mostly confined to urban parks there (P.J. Fullagar, pers. comm.), the post-1970s

expansion of mallards in rural South Australia (Marchant and Higgins, 1990) is reminiscent of past New Zealand events. Left unchecked, this expansion has the potential to repeat the New Zealand experience and to extend throughout southern Australia and Tasmania.

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