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MITOCHONDRIAL ANALYSIS OF GENE FLOW BETWEEN NEW ZEALAND MALLARDS (*ANAS PLATYRHYNCHOS*) AND GREY DUCKS (*A. SUPERCILIOSA*)

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ABSTRACT.—One of the more well-known examples of hybridization in birds is the frequently documented occurrence between sexually dimorphic Mallards (*Anas platyrhynchos*) and several closely related nondimorphic species in the mallard complex. In New Zealand, the Grey Duck (*Anas superciliosa superciliosa*) is the indigenous, nondimorphic Mallardlike species, and extensive hybridization with introduced Mallards has been implicated in the population decline of Grey Ducks. Individuals from throughout the country were classified phenotypically as parentals or hybrids based on variation in plumage, bill color, and leg color. We confirmed species-specific mitochondrial DNA haplotypes by comparing restriction-enzyme fragment patterns in Grey Ducks and New Zealand Mallards to those of Pacific Black Ducks (*A. superciliosa rogersi*) from Australia and Mallards from North America, respectively. Our data indicate that hybridization has led not only to introgression of Grey Duck mtDNA into Mallard populations (the predicted direction of gene flow), but also to significant introgression of Mallard mtDNA into Grey Duck populations. Thus, the contention that hybridization between Mallards and nondimorphic species involves primarily Mallard males with females of the other species is not upheld for this example from New Zealand. The speciation process appears to be undergoing reversal. *Received 1 April 1993, accepted 2 July 1993.*

THE INCIDENCE OF interspecific and intergeneric hybridization in the order Anseriformes is higher than in any other order of birds, reaching 30 to 40% by some estimates (Grant and Grant 1992). In addition, a substantial proportion of interspecific hybrids (20%) in this order have been reported to be fertile (Scherer and Hilsberg 1982), so there is potential for extensive gene flow and introgression between some species.

Among the more well-known examples is the frequently documented incidence of hybridization between sexually dimorphic Mallards (*Anas platyrhynchos*) and several closely related, nondimorphic species. For instance, in North America, hybridization with Mallards has been implicated as one factor in the population decline of American Black Ducks (*A. rubripes*; Johnsgard 1967, Heusmann 1974, Ankney et al. 1987), Hawaiian Ducks (*A. wyvilliana*; Griffin et al. 1989), and Mexican Ducks (*A. platyrhynchos diazi*; Hubbard 1977). Increasing numbers of Mallard/Mottled Duck (*A. fulvigula*) hybrids also are being reported in some areas of Florida (Mazourek and Gray 1994). In fact, the AOU (1983) declared the Mexican Duck to be conspecific with the Mallard because of extensive hybridization between them.

In New Zealand, the Grey Duck (*A. superciliosa superciliosa*) is the indigenous, nondimorphic, Mallardlike species. Grey Ducks are thought to have colonized from Australia, like much of New Zealand's avifauna (Baker 1991), and the Pacific Black Duck (*A. superciliosa rogersi*) in Australia is virtually identical phenotypically to the New Zealand Grey Duck (Frith 1982). Mallards were introduced by the Otago Acclimatization Society into the southern region of South Island, New Zealand in the mid-1800s from European game-farm stock and into North Island by the Auckland Acclimatization Society in the 1930s from North America (Williams 1981).

Over the last few decades, Mallard populations have increased dramatically, while Grey Duck populations have declined. Extensive hybridization with Mallards, facilitated by the loss of natural habitats to agriculture, has been im-

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plicated in the population decline of Grey Ducks in a situation analogous to those in North America (Williams 1981, Gillespie 1985). By the early 1980s, levels of hybridization estimated from plumage variation had increased to over 50% in populations on South Island near Dunedin, while the proportion of pure Grey Ducks had declined to less than 5% (Gillespie 1985). This has led to concern that the Grey Duck may eventually disappear as a separate species from New Zealand (Weller 1980, Gillespie 1985), as it has from the Marianas Islands. The so-called Mariana Mallard (*A. oustaleti* Salvadori) is generally considered to be a hybrid between stray Mallard Ducks and *A. superciliosa* (Delacour and Mayr 1945, Yamashina 1948; but see Reichel and Lemke 1994).

Although assortative mating appears to prevail between Mallards and American Black Ducks in North America (E. Morton unpubl. data), and between Mallards and *A. superciliosa* in Australia (Braithwaite and Miller 1975) and New Zealand (Hitchmough et al. 1990), there is some experimental evidence that more colorful Mallard males outcompete dull-colored males for mates (Brodsky et al. 1988). Ankney et al. (1987) also suggested that the majority of hybrid matings in North America may result from forced copulations between Mallard males and Black Duck females during renesting.

Several studies have tried to estimate the extent of hybridization and introgression between Mallards and one or another of the nondimorphic species by qualitative assessments of phenotypic variation (Braithwaite and Miller 1975, Gillespie 1985, Heusmann 1974; Kirby, U.S. Fish and Wildlife Service unpubl. report), but it is difficult to distinguish hybrids morphologically after more than one generation of backcrossing to a parental species (Williams and Roderick 1973, Rhymer unpubl. data). In addition to the use of phenotypic characters to estimate levels of gene flow, some biochemical techniques have been applied to the Mallard group. However, no species-specific markers have been found to distinguish Mallards from American Black Ducks using allozyme electrophoresis (Ankney et al. 1986) or restriction-enzyme analysis of mitochondrial DNA (mtDNA; Avise et al. 1990).

Allozyme studies also have been unsuccessful in separating Mallards from *A. superciliosa* both in Australia and New Zealand (Braithwaite and Miller 1975, Hitchmough et al. 1990). In this study, we sought species-specific markers for Mallards and Grey Ducks using restriction-enzyme analysis of mtDNA, a technique that is generally more sensitive than allozyme electrophoresis. Our study focused on the analysis of pure Grey Ducks and Mallards together with several individuals that had been classified as hybrids on the basis of their morphological characteristics.

We also used the results to infer the directionality of hybridization. If hybrid matings occur primarily between colorful Mallard males and Grey Duck females, then the majority of hybrid individuals should have a Grey Duck mitochondrial haplotype, since avian mtDNA is maternally inherited (Giles et al. 1980, Watanabe et al. 1985).

Methods

Sample collection.—We sampled Mallard, Grey Duck, and hybrid individuals from North and South Islands of New Zealand. We also analyzed Mallards from North America (as part of a larger study of the mallard complex of waterfowl) and Pacific Black Ducks from Australia to ensure that we could unequivocally identify the species-specific mtDNA haplotypes of the parental species.

Birds shot by hunters were collected in May 1991 from localities throughout the country, as part of a larger study by M.J.W. to assess the extent of hybridization in New Zealand. Samples from six areas on North Island (Lake Whangape, Cambridge, Ohakune, Wairoa, Wanganui, Lake Wairarapa) and one area on South Island (Lake Ellesmere) were selected for analysis in this initial study (Fig. 1). Samples were selected on the basis of phenotypic characters to include 12 Grey Ducks, 9 Mallards, 8 Grey Duck-like hybrids, and 14 Mallardlike hybrids. It has been observed that hybrids tend to be Grey Duck-like or Mallardlike in appearance (Yamashina 1948, Weller 1980).

Heart tissue from these birds was stored in 70% ethanol and shipped at room temperature. We also analyzed heart and liver tissue from additional birds that had been collected between 1986 and 1991 and stored at −80°C. These samples included seven Grey Ducks (Pohangina River; Apiti, Orua River), six Mallards (Apiti), and two Grey Duck-like hybrids (Rongotea; Apiti), all from North Island. We also analyzed tissue and blood samples of North American Mallards and blood samples of 10 Pacific Black Ducks. The Pacific Black Ducks were chosen from an area near Canberra in eastern Australia (where no Mallards are found) to compare with our pure Grey Duck samples.

Phenotypic scoring.—Variation in some phenotypic characters of each bird was quantified, using criteria similar to those outlined by Gillespie (1985) and

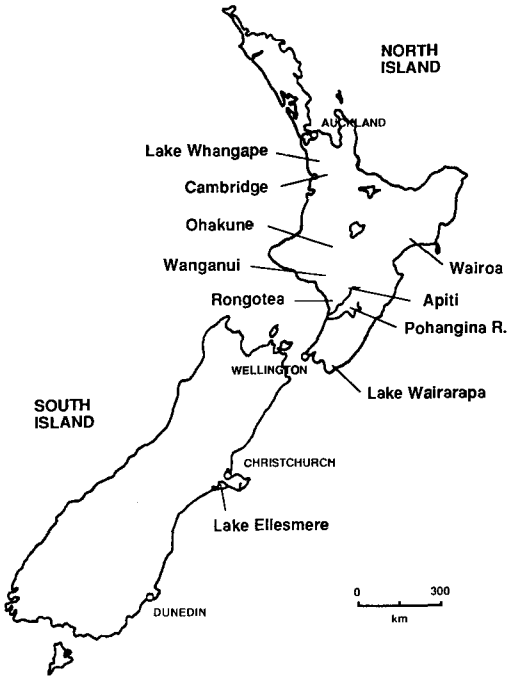

Fig. 1. Collection sites on North and South Islands, New Zealand.

Braithwaite and Miller (1975). These included plumage variation on the head and wing, and differences in leg and bill color (details in Table 1). Each character was assigned a score ranging from 0–1 up to 4–6, with Grey Duck characters scored at the low end of the scale (lowest overall cumulative score possible was 1) and Mallard characters at the upper end (highest possible cumulative score was 25 for a Mallard male). Cumulative scores were designed such that Mallard males tended to have the highest scores. Intermediate scores are indicative of hybrid characteristics.

Laboratory methods.—Total genomic DNA was isolated from each sample. Proteinase K (200 $\mu g/\mu l$) and SDS (0.5%) were added to 50 μl of blood in TNE extraction buffer (10 mM Tris, 100 mM NaCl, 100 mM EDTA pH 8.0) or 0.5 to 0.7 g of tissue homogenized in ice-cold TNE. Following an overnight incubation at 55°C, the NaCl concentration was raised to 200 mM and RNase was added to a concentration of 100 $\mu g/$ ml. Samples were incubated at 37°C for 1 h and extracted with equal volumes of phenol : chloroform : isoamyl alcohol (25:24:1) and chloroform : isoamyl alcohol (24:1) for 20 min each at 55°C. DNA in each sample was precipitated in ice-cold ethanol and resuspended in TLE (10 mM Tris, 0.1 mM EDTA pH 8.0) to a concentration of 0.5 to 1.0 $\mu g/\mu l$. The concentration and purity of each DNA sample were estimated spectrophotometrically.

DNA from each individual was digested with 16

TABLE 1. Phenotypic criteria used to score head, wing and leg characteristics of Grey Ducks and Mallards.

Face

(0) Two black stripes, the upper superciliary stripe of uniform width and extending well beyond eye; lower stripe tapering from gape to below eye and giving way to mottled cheek; clean cream stripe between eye and crown, throat and face cream.

(1) Two black stripes, upper stripe as described above, lower stripe merging with mottled face midway between bill and eye, clean cream stripe between eye and crown; face and cheek mottled cream but with obvious cream patch at base of bill between the two black stripes.

(2) Superciliary stripe obvious and extending from bill to well beyond eye, lower stripe absent but small patch of black feathers at bill base at gape; mottled cream stripe between eye and crown, face and cheek entirely mottled black on cream background, throat cream.

(3) Entire face mottled black on fawn background, superciliary stripe indistinct and narrow, small patch at gape more heavily mottled to appear darker than rest of face, small fawn patch at bill base between gape and bill top, throat clean to lightly mottled fawn.

(4) Dark mottled face and throat, black on fawn background in female, blackish-green on dark fawn in male; no obvious eye stripe, no fawn patch at bill base.

(5) Predominantly dark green head, face, and throat (males only).

Legs

(1) Dark olive greenish-brown; (2) khaki; (3) yellow-orange to dull orange; (4) bright orange; (5) red orange.

Bill

(0) Uniformly black; (1) black with very dark green particularly at base and along edge of upper mandible; (2) predominantly black/dark green, some yellow or brown at tip; (3) black and brown/yellow; (4) yellow-green; (5) green or a bluish shade (much more common in New Zealand than yellow or orange color found in North American Mallards).

Speculum and upper alar bar

(0) Green, no discernible bar; (1) green, obvious thin and narrow whitish/brown line; (2) green, bar distinct but narrow and mottled fawn color; (3) purple, bar distinct but narrow and mottled fawn color; (4) purple, bar distinct, wide, mottled fawn; (5) purple, bar narrow, pure white; (6) purple, bar wide, pure white.

Posterior border to speculum

(0) Black only; (1) black followed by thin (1 mm) white line; (2) black followed by narrow (1–2 mm) white line; (3) black followed by conspicuous (3–4 mm) white bar; (4) black followed by wide (>4 mm) white bar.

TABLE 2. Mitochondrial DNA haplotypes for Pacific Black Ducks, New Zealand Grey Ducks, and Mallards. Sequence of restriction enzymes is *Apa*I, *Ava*I, *Bam*HI, *Bcl*I, *Bgl*I, *Bst*EII, *Dra*I, *Hinc*II, *Hind*III, *Hinf*I, *Pst*I, *Pvu*II, *Rsa*I, *Sau*3AI, *Sty*I, and *Taq*I. Number of parentals and hybrids with each haplotype listed.

Haplotypes	Parentals	Hybrids	
		Gray Duck-like	Mallardlike
Pacific Black Duck			
1 A G E G L D A E C A E C B C D E	4		
2 - - - - - - - - G - - - - B - C	3		
3 B - - - - - - - - G - - - - B - C	3		
New Zealand Grey Duck			
1 B - - - - - - - - - - - - A A - B	2		
2 - D - - - - B - - B - - - - - C	8[a]	1	
3 B - - - - - - - - G - - - - B - C	8	4	1
Mallard			
1 - D - D F C - I - C F - C D C C	7	2	5
2 - D - D F C - - - C F - C D C C	6[b]	3	6
3 - D - D F C - K - C F - C D C C	1		2

[a] One was "pure" Mallard.
[b] One was "pure" Grey Duck.

different restriction endonucleases (2 μg per digest) under conditions recommended by the enzyme supplier. The enzymes included 4 enzymes that recognize four-base sequences, 2 that recognize five-base sequences, and 10 that recognize six-base sequences. Fragments in digested samples were separated on 0.7 to 1.2% agarose gels and transferred to nylon membranes (MSI Magnagraph) via Southern (1975) blotting. Purified mtDNA, isolated from fresh Mallard heart tissue in a cesium chloride gradient, was labelled with ^{32}P by random priming (Feinberg and Vogelstein 1983) and used to probe the total genomic DNA on each blot. A molecular size standard (φX174 *Hae* III plus lambda/*Hind*III) was used to determine fragment sizes on autoradiograms. The fragment profile for each endonuclease was assigned a letter using the letter designations of Kessler and Avise (1984), Avise et al. (1990) and Avise (pers. comm.) as a baseline for consistency among studies. Thus, each individual's mtDNA haplotype is coded as a series of 16 letters. Fragment sizes for each profile are available from the senior author upon request.

Statistical analysis.—Genetic distances were estimated for each haplotype pair according to the Nei and Li (1979) method for unmapped fragment data (see Nei 1987:106–107) using the analysis package RESTSITE (version 1.1; Nei and Miller 1990). The resulting distance matrix was then phenetically clustered by the unweighted pair-group method with arithmetic averages (UPGMA; Sneath and Sokal 1973), using mtDNA haplotypes as OTUs. Net divergence between subspecies and species was calculated, correcting for within-taxon haplotype variation (Nei and Miller 1990). We used PAUP 3.1.1 (Swofford 1991) to estimate a phylogeny for the haplotypes using different coding schemes for the restriction-digest data. First, we evaluated the presence or absence of each (unmapped) fragment observed for all 16 enzymes. This method has the advantage that it includes all of our data, but suffers from the fact that some characters (fragments) are not independent of one another. Second, we inferred the presence or absence of restriction sites for all enzymes where this was possible and deleted those enzymes where it was not (*Hinf*I, *Sty*I, *Rsa*I, *Sau*3AI, and *Taq*I).

RESULTS

We scored each individual for an average of 120 restriction fragments. In the circular mtDNA molecule, this corresponds to 120 restriction sites, representing about 600 base pairs of recognition sequence. To ensure that we had identified pure Grey Duck and Mallard haplotypes before attempting to characterize hybrid individuals, we compared New Zealand Grey Duck and New Zealand Mallard mtDNA haplotype profiles to those of Pacific Black Ducks and North American Mallards, respectively. Nine mtDNA haplotypes were observed altogether, three each in New Zealand Grey Ducks, Pacific Black Ducks, and New Zealand Mallards (Table 2). We found no fixed differences between Pacific Black Ducks and New Zealand Grey Ducks or between New Zealand Mallards and North American Mallards. Grey Duck haplotype 3 and Pacific Black Duck haplotype 3 were identical, and New Zealand Mallard haplotype 2 was identical to that of one North American Mallard haplotype (Rhymer unpubl. data, Kessler and Avise 1984).

TABLE 3. Nucleotide divergence among mtDNA haplotypes of Pacific Black Ducks from Australia (AU), New Zealand (NZ) Grey Ducks, and Mallards estimated from restriction-fragment data (method of Nei 1987).

Haplotype	1	2	3	4	5	6	7	8
1 AU Black Duck 1								
2 AU Black Duck 2	0.0026							
3 AU Black Duck 3	0.0040	0.0014						
4 NZ Grey Duck 1	0.0047	0.0047	0.0027					
5 NZ Grey Duck 2	0.0048	0.0066	0.0086	0.0090				
6 NZ Grey Duck 3	0.0040	0.0014	0.0000	0.0027	0.0086			
7 Mallard 1	0.0119	0.0161	0.0179	0.0180	0.0108	0.0179		
8 Mallard 2	0.0108	0.0160	0.0168	0.0170	0.0108	0.0168	0.0013	
9 Mallard 3	0.0120	0.0175	0.0180	0.0184	0.0131	0.0180	0.0013	0.0018

The mtDNA of Grey Ducks and Pacific Black Ducks are highly similar with an estimated nucleotide sequence divergence (after correction for within species variation) of only 0.09%, a reflection of their close historical affiliation. We found nine species-specific markers between *A. platyrhynchos* and *A. superciliosa*, however. Grey Ducks and Pacific Black Ducks have diverged from Mallards by 1.40 and 1.43%, respectively. All *A. superciliosa* haplotypes (New Zealand and Australia combined) were very similar (genetic divergence ranging from 0.00 to 0.90%), as were the three haplotypes within New Zealand Mallards (0.13 to 0.18%; Table 3).

Figure 2 shows the strict consensus of five equally-parsimonious trees derived from parsimony analysis of the unmapped fragment data. Key features of this tree include separation of *A. platyrhynchos* and *A. superciliosa* haplotypes into two distinct groups, clustering of Grey Duck and Pacific Black Duck haplotypes into a single group that does not subdivide along subspecies lines, and the basal branching of Grey Duck haplotype 2 from the Grey Duck/Black Duck group. All of these features also were apparent in the UPGMA analysis, in the parsimony analysis using only inferred restriction site changes, and in a high proportion of trees resulting from bootstrapping of either parsimony data set.

Phenotypic scores ranged from 1 to 4 for Grey Ducks and 18 to 24 for Mallards, with Grey Duck-like hybrids scoring between 5 and 10, and Mallardlike hybrids scoring between 12 and 16. The boundary between Grey Duck-like and Mallardlike hybrids is somewhat arbitrary. Hybrids were found at virtually all collection sites. One of the 19 individuals characterized phenotypically as a "pure" Grey Duck had the Mallard haplotype 2 and one of the 15 phenotypically "pure" Mallards had the Grey Duck haplotype 2. Thirteen of 14 Mallardlike hybrids had Mallard haplotypes (five had haplotype 1, six had 2, two had 3), and one had Grey Duck 3, while 5 of 10 Grey Duck-like hybrids had Grey Duck haplotypes (one had haplotype 2 and four had 3) (Table 2, Fig. 3). Of the five Grey Duck-like hybrids that had Mallard haplotypes, two had Mallard haplotype 1 and three had Mallard 2.

The proportion of hybrids with Mallard and Grey Duck haplotypes was compared to evaluate whether hybrid matings are primarily between Mallard males and Grey Duck females. This hypothesis predicts a predominance of Grey Duck haplotypes in hybrid individuals. There was, however, a significant tendency for hybrids to have Mallard ($n = 19$) rather than Grey Duck ($n = 7$) haplotypes ($X^2 = 6.54$, $P < 0.025$).

DISCUSSION

Species-specific mitochondrial DNA haplotypes were distinguished for Mallards and Grey Ducks in New Zealand. The genetic distance (corrected for within species variation) is 1.4%, considerably more than the 0.7% divergence between the two mtDNA lineages of North American Mallards (one of which contains American Black Ducks; Avise et al. 1990) and between Mallards and Mottled Ducks (Kessler and Avise 1984). It is also higher than that for the most divergent pair of *A. superciliosa* haplotypes (0.9%).

Hybridization and introgression appear to be extensive in New Zealand, despite the relatively large genetic distance between Grey Ducks and Mallards (for the Mallard complex of species; Rhymer unpubl. data). Individuals characterized by hybrid phenotypic traits are present throughout the country on both islands.

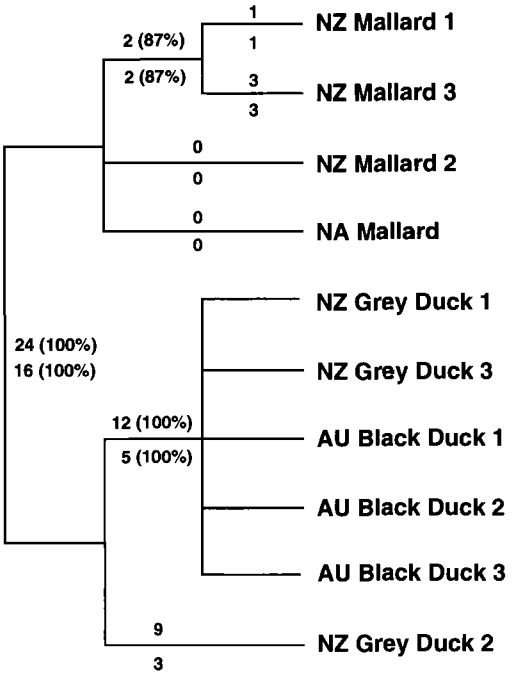

Fig. 2. Strict consensus of five most-parsimonious trees relating mtDNA haplotypes of Mallards, New Zealand (NZ) Grey Ducks and Pacific Black Ducks from Australia (AU) based on unmapped restriction-fragment data for 16 enzymes (one North American [NA] Mallard haplotype included for comparison). Each fully resolved tree was 69 steps long (consistency index excluding uninformative characters = 0.920, retention index = 0.971). Same topology obtained from analysis of reduced data set consisting of inferred restriction sites for 11 enzymes. In latter case, there were six most-parsimonious trees, each of length 34 (consistency index excluding uninformative characters = 0.912, retention index = 0.955). Branch-and-bound algorithm employed for all tree searches. Branch lengths that were invariant in all equally-parsimonious trees given both as number of inferred fragment changes (above) and as number of inferred site changes (below). Numbers in parentheses indicate percentage of times that node appeared in analyses of 1,000 bootstrapped pseudoreplicate data sets.

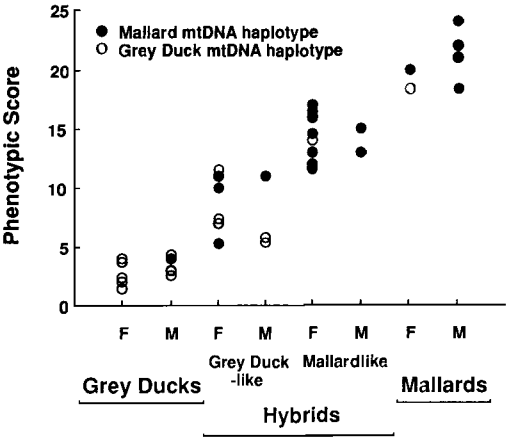

Fig. 3. Comparison of phenotypic scores and mtDNA haplotypes for birds categorized as pure Grey Ducks, Mallards, as Grey Duck-like hybrids, or Mallardlike hybrids.

Our genetic data for these individuals indicate that hybridization has led not only to introgression of Grey Duck mtDNA into Mallard populations (the predicted directionality of hybridization), but also to significant introgression of Mallard mtDNA into Grey Duck populations. This adds to the increasing number of examples of mitochondrial gene exchange between species in other taxa (e.g. mammals [Ferris et al. 1983, Carr et al. 1986, Tegelstrom 1987, Lehman et al. 1991], amphibians [Spolsky and Uzzell 1984, Lamb and Avise 1986], and fish [Avise and Saunders 1984]).

The contention that hybridization between Mallards and closely related nondimorphic species involves primarily Mallard males with females of the other species is not upheld in New Zealand. The higher proportion of hybrids having Mallard mtDNA as opposed to Grey Duck mtDNA indicates that crosses between Mallard females and Grey Duck males must occur frequently. Hybrid females apparently mate successfully with either Mallard or Grey Duck males. The fate of hybrid males is less predictable. If male plumage quality is an important factor in their selection as mates, the femalelike plumage of many hybrid males may reduce their chances of successfully attracting (and backcrossing with) females of either species. They could, presumably, be successful in obtaining forced copulations with any renesting females.

Our study provides only a conservative estimate of the degree of introgressive hybridization because it is based on phenotypic characters and uniparentally inherited genetic markers. Analysis of phenotypic traits of birds from controlled breeding crosses between Mallards and Grey Ducks has shown that phenotypic characters become less reliable indicators of hybridization, as the level of introgression increases (Williams and Roderick 1973). Although we were able to identify two "hidden"

hybrids, complete characterization of all hybrid individuals will require species-specific nuclear DNA markers, which are biparentally inherited.

The genetic similarity of Mallards in New Zealand to those in North America is not surprising given their intentional introduction from North America in this century. Despite the geographic isolation of Australia and New Zealand, however, there is no phylogenetic discontinuity of mtDNA haplotypes between *A. superciliosa rogersi* in Australia and *A. superciliosa superciliosa* in New Zealand. Baker (1991) suggested that post-Gondwanaland dispersal across the Tasman Sea via west wind drift was the principal route of colonization of avifauna from Australia to New Zealand. He discussed the idea that New Zealand subspecies of Australian species are about 20,000 years old. One might attempt to estimate the time of divergence using a molecular-clock approach. Based on our data, the sequence divergence between *A. superciliosa* subspecies (correcting for within subspecies variation) was 0.09%. Using a clock calibration of 2% mtDNA sequence evolution per million years (Shields and Wilson 1987), we estimate that the two subspecies diverged about 45,000 years ago. Given the expected error rate of such estimates (Sheldon and Bledsoe 1993), this date does not conflict with Baker's suggestion of 20,000 years ago.

However, this molecular-clock estimate is probably overly simplistic. Limited sample sizes and limited geographic sampling of Pacific Black Ducks make our sequence-divergence estimates somewhat uncertain. Also, the mtDNA haplotypes of the two subspecies do not resolve into separate clades. Some haplotype pairs (both among and within subspecies) are about 10 times as divergent as the weighted estimate (Table 3). Using the same clock calibration, we would be forced to conclude that these haplotypes diverged 330,000 to 450,000 years ago. Yet, one of the haplotypes was identical between subspecies, yielding an estimated time of divergence of zero. This shared haplotype might be due to more recent colonization or continuing gene exchange between subspecies. In fact, birds may be moving in both directions between populations; a Grey Duck banded in New Zealand in the 1950s was recovered in Australia (Williams 1981).

Given the extensive gene flow between Mallards and Grey Ducks in New Zealand, the integrity of *A. superciliosa superciliosa* as a separate species is doubtful (Williams 1981). There are few other examples of such geographically extensive introgression following the purposeful introduction of one species into the range of another (see also Echelle and Connor 1989).

Nondimorphic species in the Mallard complex often are presumed to have evolved from the Mallard (Johnsgard 1961), although it is possible that they evolved from a nondimorphic "proto-Mallard." Regardless of the evolutionary history of the group, it appears that the speciation process is undergoing reversal in New Zealand. *Anas platyrhynchos* and *A. superciliosa* could have diverged as long ago as 700,000 years (based on clock estimation), but it is clear that no pre- or postzygotic mechanisms have arisen to prevent extensive introgression. Evidence from captive studies indicates that hybrids survive and are as reproductively successful as the parental species (Haddon 1984). Our genetic data now lend support to the phenotypic evidence that points to the eventual loss of identity of the Grey Duck as a separate species in New Zealand, and the subsequent dominance of a hybrid swarm akin to the "Mariana Mallard." Thus, the loss of natural Grey Duck habitat to agriculture has been compounded by successful introductions of the highly adaptable Mallard and the subsequent effects of interspecific hybridization.

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