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Can grey duck (*Anas superciliosa*) x mallard (*A. platyrhynchos*) hybrids be recognised in the field?

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Abstract: Face, wing, bill, and leg characteristics of grey ducks (*Anas. s. superciliosa*), of captive-raised F1 and backcrossed grey duck x mallard (*A. platyrhynchos*) hybrids, and of wild "grey-like" and "mallard-like" ducks in New Zealand were evaluated to assist recognition of grey duck x mallard hybrids in the field. Face pattern was the single character best able to discriminate grey ducks from all others, most grey-like hybrids from all mallard-like hybrids, but not most F1 and backcrossed mallard hybrids from mallards. Upper wing pattern, and bill and leg colours assisted discrimination alongside face pattern but not so on their own. The extensive phenotypic variability now apparent within the combined grey duck – mallard population in New Zealand restricts consistent discrimination to 3 "taxa": grey ducks, grey-like ducks ("grallard/greylard"), and mallard-like ducks ("New Zealand mallard").

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INTRODUCTION

A consequence of historic Acclimatisation Society breeding and releases of mallard (*Anas platyrhynchos*) in New Zealand (Dyer & Williams 2010) has been hybridisation with the native ecological equivalent, grey duck (*A. s. superciliosa*). More than a century after the initial reporting of hybrids (e.g. White 1885; Kingsley 1892; *Ashburton Guardian* 10 July 1914: 2), the combined grey duck and mallard population displays phenotypic and genetic evidence of that hybridisation, and of introgression (Rhymer *et al.* 1994), encouraging speculation that the population may now comprise an extensive genetic admixture (Williams & Basse 2006; Heather & Robertson 2015; Williams 2017).

Ducks displaying plumages that conform to historic descriptions of grey ducks (e.g. Falla *et al.* 1966) are still reported, but so too "grey-like" ducks often designated as hybrids (e.g. *http://e-bird.org/newzealand*). Field identification of hybrids, as distinct from mallards, remains problematic however, because of seasonal and age-related changes in mallard plumage (Cramp & Simmons 1977; Marchant & Higgins 1990) and mallard plumage variability arising from the prolonged captive history of the antecedents of mallards released in New Zealand (Dyer & Williams 2010). For example, and in contrast to northern hemisphere populations, many mallard males fail to develop the characteristic fully green head or conspicuous white neck ring; some females have faces that are entirely and darkly mottled; the white bars bordering the wing speculum are highly variable in width and whiteness, and both leucistic and melanistic forms are widely encountered (*pers. obs.*). Species confusion is greatest in discriminating between grey ducks and mallard females (Williams 2017).

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The genomic composition of the present wild population of grey ducks and mallards in New Zealand has yet to be appraised. An electrophoretic assessment (Hitchmough *et al.* 1990) found very low heterozygosity and an absence of differences between the taxa and was unable to elucidate the nature and extent of grey duck x mallard hybridisation. A mitochondrial DNA (mtDNA) analysis of selected wild ducks (Rhymer *et al.* 1994) confirmed the presence of cryptic hybrids in both species, i.e. ducks phenotypically resembling one species but having mtDNA genetic inclusion from the other. A nation-wide appraisal employing modern genomic techniques will be needed to clarify the genetic outcome of this century-long species interaction. Meanwhile, recorded field observations in which ducks are designated grey duck, mallard, and hybrid (e.g. Robertson *et al.* 2007; *http://e-bird.org/newzealand; www.birdingnz.net; www.inaturalist.org/places/new-zealand*) continue to accrue. Their validity and their subsequent interpretation as a record of changing life in New Zealand wetlands have become demonstrably problematic (Williams 2017).

Three schemata to assist field identification of grey duck x mallard hybrids have been published. An initial diagnostic approach was based on 6 phenotypic characters of Pacific black duck (*A. s. rogersi*) and feral urban mallards in Australia (Braithwaite & Miller 1975). That approach was expanded upon by Gillespie (1985) to discriminate wild hybrids in New Zealand, and his schema subsequently reproduced in Marchant & Higgins (1990). Unfortunately, Gillespie's expanded schema was not based on any supporting genetic evidence and was significantly confused by mallard female plumage variability and by seasonal and age-related plumage changes in males (Williams 2017). Rhymer *et al*. (1994), informed by unpublished plumage descriptors of captive-bred hybrids, also amended Braithwaite & Miller's (1975) criteria. All schemata assigned scores to each of several phenotypic characters (e.g. head, bill, wing, leg) and the aggregate score was used to provide a taxon diagnosis. None provided diagnostic keys however, and the efficacy of the character score summation approach, which accords a diagnostic equivalence to each character scrutinised, has yet to be demonstrated (e.g. see Rhymer *et al.* 1994: Fig. 3). These approaches all arose from close-order scrutiny of ducks in the hand whereas similar character evaluations have proved more difficult to apply in the field, particularly at distance and when all contributing characters are not visible.

When viewed in the field, whether on water or land, nearby or at distance, a duck's body and head are its most prominent features. In mallards, lateral body plumage colours and patterns, of breast, flank, and rump, undergo significant seasonal change in both sexes (Cramp & Simmons 1977; Drilling *et al.* 2002) and are difficult to describe succinctly and without reference to colours which not all observers are likely to interpret in the same way. Conversely, face markings are bold, readily discernible under most light conditions, including when the duck is back-lit, and although seasonally and sexually variable, appear to conform to one of few basic patterns (Rhymer *et al.* 1994). Face patterns of grey duck contrast with those of mallard and appear distinctive (Marchant & Higgins 1990; Rhymer *et al.* 1994). Thus, face pattern appears, *a priori*, a potential character for field discrimination of the two taxa, and possibly of their hybrids.

Other characters used in previous schema, are not quite so readily viewed. For example, the folded wing of a resting duck is often hidden by flank feathers, but if the duck is active, part of the wing's upper surface, the coloured speculum on the secondary feathers and the secondary covert feathers above them, may be glimpsed, e.g. when preening or flapping wings. Contrasting upper wing patterns are sometimes discernible when a duck is flying.

Leg colour, and bill colour and pattern were included in their respective schema by Braithwaite & Miller (1975) and Rhymer *et al.* (1994) and have assisted diagnosis of other hybridised waterfowl e.g. mottled duck *A. fulvigula* (Bielefeld *et al.* 2016). Legs of swimming ducks are seldom visible, and not always so when the duck is loafing. However, given the contrast in reported leg colours of grey ducks and of mallards (e.g. Marchant & Higgins 1990), leg colour may be a helpful confirming character. Rhymer *et al.* (1994) classified bill colour and pattern in grey duck and mallard into 6 types while Braithwaite & Miller (1975) suggested bills of hybrids had distinctive colouration. Bill colour can be difficult to discriminate in bright light or when viewed directly into the light but otherwise, like the head, is generally a visible field character.

In this study, I attempt to discriminate between grey ducks, mallards, and their hybrids using one, or a combination, of face, wing, leg, and bill characteristics visible in the field. Three questions defined the study approach: (1) how variable are face, wing, bill and leg characters of grey ducks?; (2) what are the face and wing characteristics of known F1 grey duck x mallard hybrids, and of hybrids backcrossed to parental species?; and (3) what range of face, wing, bill, and leg characters occur in the combined grey duck – mallard population in the wild?

METHODS

Study approach

This study builds upon the phenotypic criteria used by Rhymer *et al.* (1994) to assess face patterns, upper

wing patterns, bill, and leg colours of the combined grey duck – mallard population in New Zealand.

Two historic data sets were available: from the controlled breeding of F1 and backcrossed grey duck x mallard hybrids undertaken by the New Zealand Wildlife Service (NZWS) 1968–1972, and from a nationwide sampling of wild ducks shot by hunters in May 1998. The controlled breeding data did not include details of bill or leg colour.

Variability of face and upper wing plumage within *A. superciliosa* was assessed across the entire range of the taxon (Polynesia-Melanesia, Australia, New Zealand) and has been reported separately (Williams 2019). The New Zealand (grey duck) sample comprised historic museum specimen skins collected prior to 1970. Leg and bill characteristics of grey ducks were those recorded from specimens collected in 1991 for Rhymer *et al's* (1994) study ("the Rhymer collection") and were restricted to specimens phenotypically identical to those in that collection confirmed as carrying grey duck mtDNA.

No direct assessment of New Zealand's mallards was possible. Historic and contemporary descriptions and illustrations of mallards (e.g. Falla *et al.* 1966; Marchant & Higgins 1990; Heather & Robertson 2015) are all largely based on northern hemisphere descriptors (e.g. Witherby *et al.* 1939; Palmer 1976; Cramp & Simmons 1977) and do not adequately indicate the extensive plumage variability apparent in mallard-like ducks in New Zealand. A point of considerable significance is the origin of mallards released in New Zealand; they were derived from captive-confined stock, mostly from long-established English game farms, and those eventually released in New Zealand were, in turn, progeny of birds bred for multiple generations in captivity in New Zealand (see Dyer & Williams 2010). There are too few historic museum specimens of New Zealand-sourced mallards to be regarded as representative of those initially introduced.

Categorisation method

The descriptors established by Rhymer *et al.* (1994: Table 1) ("Rhymer descriptors") were the bases of "type" categories established for this study (Appendix). Rhymer *et al.* (1994) assigned a numerical value to each descriptor for eventual summation across all features to produce a cumulative score; in this study the descriptors for each character are simply numbered sequentially (1, 2, *etc.*) and patterns of character associations subsequently examined. No numerical values are applied.

Some refinement of Rhymer descriptors was necessary to embrace the full range of variability observed in wild specimens and, where necessary, made more fulsome to ensure that the defining characters were readily discernible and distinguishable in the field. For the taxon-wide *A. superciliosa* study (Williams 2019) an additional face descriptor was added to include a face pattern common in Australia but very rare in New Zealand (face type 1). That addition post-dated the phenotypic assessments reported here so records for face type 2 may have included some that conform to face type 1.

Initially, the white bar along the posterior edge of the speculum (i.e. on the tips of the secondary feathers, and referred to subsequently as "trailing bar") was measured and categorised as a possible independent character but its width was found to relate almost directly to the colour of the speculum – narrow (1–2 mm) in ducks with a green speculum, >3 mm in those with a purple/blue speculum. It proved more helpful as a comparative feature for discriminating the width and whiteness of the white bar – the alar bar – anterior to the speculum (see Appendix). Relative width of the alar bar and trailing bar was assessed against another conspicuous feature on the upper wing of grey ducks and grey-like hybrids, the width of the pale margins of tertial feathers lying immediately proximal to the secondaries. The edging of the tertials is usually the widest of the pale feather margins clearly discernible in the field.

Where possible, categorisation was restricted to pattern rather than colour, bearing in mind that colours are subjective descriptors not interpreted in a similar way by all and their perception influenced by viewing conditions. A difference between cream and fawn (or buff or beige) became necessary when discussing light-coloured patches on the faces of the two species, between white and a fawn when distinguishing the alar bar, and between green and purple-blue colour of the speculum on the secondary feathers.

I tested the face and wing descriptors when handling ducks at Eastern and Wellington Fish & Game Council duck trapping stations in January 2017 and 2018 and by extensive field observations in Manawatu, Taupo, and Wairarapa regions in April 2015 and during summer 2016–2017 and 2017–2018.

Source of specimens

Face and upper wing plumage characteristics of grey duck x mallard hybrids were assessed on ducks of known sex, age, and hybrid composition bred by the former NZWS at its Mount Bruce Native Bird Reserve 1968–1972. Specimen skins (432) from this breeding programme were stored by the NZWS, and later by the Department of Conservation; a representative sample (62) was eventually transferred to Museum of New Zealand Te Papa Tongarewa (MoNZ). Face and wing characters of hybrid specimens ≥5 months old and killed after April (to be contemporaneous with the

annual duck-hunting season) were categorised in 1998 and included in the analysis.

In 1998, heads, wings, and feet of 1,992 wild ducks were supplied by duck hunters from throughout New Zealand, scored using the Rhymer schema, and designated as "grey-like" (scores ≤10) or "mallard-like" (scores ≥11). All mallard-like ducks were sexed on wing characters (Carney 1992). Data for all 4 characters (face, wing, bill, leg) were available from 1,903 of the 1,992 specimens.

Presentation of results

Many *A. superciliosa* specimen skins contributing to Williams' (2019) study lacked sex information. Thus, his summations of *A. superciliosa* phenotypic variability were of both sexes combined. This is also the case for all grey-like ducks in the 1998 wild sample. Analyses of the hybrid sample, and of all mallard-like ducks in the 1998 wild sample, are reported separately for each sex.

Face and wing characters are reported separately and in combination for grey duck (directly from Williams (2019), and without ongoing attribution), hybrids, and wild New Zealand ducks. Leg and bill colours and patterns were not obtainable from hybrids and these characters are recorded in combination with face characters only from the wild New Zealand duck sample, and grey ducks from Williams (2019). Patterns of character associations are tabulated expansively to depict the extent and magnitude of phenotypic variability.

RESULTS

Face types

Grey duck

The percentage frequency distribution of grey duck face types (n = 52) was type 1 (1.9%), type 2 (61.5%) and type 3 (36.5%).

Hybrids

Females

The most common face type of F1 hybrid females (Table 1) reflected that of their maternal parent; 86% of hybrids from a grey duck female showed face type 3 typical of grey ducks but none had the most common grey duck face type 2. Similarly, 84% of F1 hybrids from a mallard female displayed face type 4 which was also common amongst wild female mallard-like ducks (Table 2).

When F1 hybrid females were backcrossed to grey duck (producing 3/4-grey hybrids) and these backcrossed again (producing 7/8-grey hybrids), the female progeny displayed a more equitable and broader distribution of face types than did F1 hybrids. A similar proportion of both 3/4-grey and 7/8-grey female hybrids displayed face types 2, 3, and 4. Backcrossed mallards, whether of 3/4- or 7/8-genealogy, displayed face types 4 and 5 common amongst wild mallard-like females (Table 2).

Males

Face patterns of male F1 hybrids also reflected that of the maternal parent but some older hybrids (>1 yr), derived from both parental combinations, displayed dark mottled black-green heads and faces common to mallard drakes. Of the backcrosses, 3/4-grey hybrids had face patterns of most types, one-third of which displayed the extensively mottled face types 4 and 5 while 7/8-grey hybrids displayed more typical grey duck face types. All backcrosses to mallards produced progeny with faces indistinguishable from those of wild mallard-like ducks (Table 2).

A note of caution is appropriate. Results presented in Table 1 are undoubtedly influenced by specimen age. The post-juvenile moult may not have been completed by some late-bred young killed in April or May. Face patterns of backcrosses may also have been influenced by their antecedent parentage, but the small sample sizes available did not allow for their partition to appraise this.

Wild New Zealand ducks

Despite having been assigned to a species grouping based on several characters, the overlap in face types between the 2 groupings was minimal: only 1.4% of 1,551 mallard-like ducks shared face type 3 with grey-like ducks, and 5.1% of 352 grey-like ducks had face types 4 or 5 common to mallard-like ducks (Table 2). Eight (38%) of the 21 mallard-like ducks with face type 3 had a green wing speculum and 39 (16.5%) of 237 mallard-like ducks with face type 4 likewise. All 18 grey-like ducks displaying face type 4 or 5 had a green wing speculum.

When this sample was evaluated in 1998, face type 1 was not discriminated as a separate category because its potential significance was then unrecognised. In photos of 74 grey-like specimens from the 1991 Rhymer collection none displayed face type 1.

Excluding the 18 grey-like ducks with face types 4 and 5, the percentage frequency distribution for grey-like birds is almost the same as for grey ducks.

Wing types

Grey duck

The percentage frequency distributions of wing types for grey ducks was type 1 (44.0%), type 2 (47.1%), type 3 (8.4%) and type 4 (0.4%).

Table 1. Percentage frequency distribution of female and male face types of F1 hybrids between grey duck (grey, G) and mallard (mall, M), and 3/4- and 7/8- backcrosses respectively). Parentage of F1 hybrids denoted by m (male) and f (female). Percentages expressed to nearest whole number, "-" denotes no occurrence (and similarly in all other tables).

Face type	7/8-Grey	3/4-Grey	Mm x Gf	Gm x Mf	3/4-Mall	7/8-Mall
Female hybrids						
2	33	17	-	-	-	-
3	33	44	86	16	4	-
4	33	39	5	84	57	43
5	-	-	9	-	40	57
n	15	18	22	19	47	21
Male hybrids						
2	57	8	-	-	-	-
3	21	58	52	24	-	-
4	21	13	35	59	10	-
5	-	21	4	6	12	6
6	-	-	9	12	79	94
n	14	24	23	17	52	16

Table 2. Percentage frequency distribution of face types of grey-like ducks (both sexes combined) and sexed mallard-like ducks in a New Zealand-wide sample of hunters' kills, May 1998.

	Grey-like	Mallard-like	
Face type		female	male
1&2	60.2	0.5	-
3	34.7	2.7	0.3
4	4.8	34.0	1.5
5	0.3	62.8	26.8
6	-	-	71.4
n	352	659	892

except that 19% of 3/4-grey hybrids displayed a purple/blue colour.

Females

The percentage distribution of wing types amongst females in the various hybrid categories is summarised in Table 4.

Wing type 4, with its obvious but narrow mottled white/buff alar bar, occurred in all hybrid categories except 7/8-grey hybrid. For F1 hybrids, there was a tendency for the wing pattern to reflect that of the maternal parent: 59% of Mm x Gf hybrids had wing types 2 and 3 typical of many grey ducks while 68% of Gm x Mf hybrids displayed wing types 4 and 5. A conspicuous whitish or pure white alar bar was shown by all backcrosses to mallard.

Table 3. Percentage frequency occurrence of green or purple speculum colour shown by grey duck x mallard F1 and backcross hybrids (sexes combined). Abbreviations as for Table 1.

Hybrid/ Speculum colour	7/8-Grey	3/4-Grey	Mm x Gf	Gm x Mf	3/4-Mall	7/8-Mall
Green	100	81	65	53	2	-
Purple	-	19	35	47	98	100
n	29	42	45	36	99	37

Hybrids

Green was the predominant, but not exclusive, speculum colour in F1 hybrids of both parental combinations (Table 3); 35% derived from a grey duck female displayed a purple/blue speculum as did 47% derived from a mallard female. Amongst backcrossed hybrids, the speculum colour of the predominant species was shown almost exclusively,

Males

The tendency for wing characteristics of F1 hybrids to reflect that of their maternal parent was apparent in Mm x Gf hybrids, where 70% had wing types 2 and 3, but not so in Gm x Mf hybrids where 77% evinced the same 2 wing patterns (Table 4). Wing patterns of backcrossed hybrids reflected those of the predominant species but in backcrosses to

Table 4. Percentage frequency distribution of female and male wing types of F1 hybrids between grey duck (grey, G) and mallard (mall, M), and 3/4- and 7/8-backcrosses respectively. Parentage of F1 hybrids denoted by m (male) and f (female). Percentages expressed to nearest whole number.

Wing type	7/8-Grey	3/4-Grey	Mm x Gf	Gm x Mf	3/4-Mall	7/8-Mall
Female						
1	27	6	-	-	-	-
2	53	44	9	-	-	-
3	20	29	50	32	-	-
4	-	22	23	63	40	16
5	-	-	18	5	30	68
6	-	-	-	-	30	11
7	-	-	-	-	-	5
n	15	18	22	19	47	21
Male						
1	36	38	-	-	-	-
2	57	42	9	12	-	-
3	7	4	61	65	4	-
4	-	17	22	18	25	-
5	-	-	5	6	13	44
6	-	-	5	-	29	38
7	-	-	-	-	29	19
n	14	24	23	17	52	16

mallard, most alar bars, whether mottled white/buff or white, were narrow.

Overall, there was a clear difference between hybrid groupings with grey duck backcrosses mostly showing wing types 1 and 2, F1 hybrids wing types 3 and 4, and mallard backcrosses wing types 5-7.

Wild New Zealand ducks

The percentage frequency distribution of wing types for wild grey-like ducks (Table 5) was significantly different from that for grey ducks ($\chi^2 = 30.6$, $P < 0.0001$) with proportionately more of the 1998 wild sample displaying evidence of a thin white/buff alar bar (wing type 3). Variability amongst wings of mallard-like ducks was highlighted in females by those with broad alar bars (wing types 5, 7) being twice as numerous as those with narrow alar bars (wing types 4, 6). Included amongst the type 4 wings were 20 (14%) where the secondary coverts had terminal white, not black, and 9 (6%) whose alar bar was irregularly interrupted by black, the sub-terminal white being absent from some, but not all, secondary coverts.

Wings of male mallard-like ducks were less variable than of females (Table 5) and almost 75% displayed conspicuously white alar bars (wing types 6, 7). The frequency distribution of male wing types was significantly different from that of females in this sample ($\chi^2 = 165.72$, $P < 0.0001$) a consequence of the differing proportions displaying type 5 and 6 wing patterns wherein many female alar bars were judged not vivid white but lightly mottled with fawn.

Table 5. Percentage frequency distribution of wing types of grey-like ducks (both sexes combined) and sexed mallard-like ducks from a New Zealand-wide sample of hunters' kills, May 1998.

	Grey-like	Mallard-like	
Wing type		Female	Male
1	32.1	-	-
2	39.9	-	-
3	26.2	1.7	1.2
4	1.5	22.1	13.4
5	0.3	29.5	10.7
6	-	13.3	32.4
7	-	33.4	42.2
n	352	659	892

Face and wing types in combination

Grey duck

The face type 2/wing type 2 combination was displayed by 37% of 52 grey ducks examined with an additional 5 less-frequent combinations being required to embrace 90% of the sample (Table 6).

Table 6. Percentage frequency distribution of face type/wing type combinations in *A. superciliosa* from New Zealand, n = 52 (from William 2019).

Face type	Wing type			
	1	2	3	4
1	1.9	-	-	-
2	9.6	36.5	13.5	-
3	11.5	13.4	11.5	1.9

Table 7. Percentage frequency distribution of face type/wing type combinations in F1 hybrids between grey duck (G) and mallard (M). Parentage of F1 hybrids denoted by m (male) and f (female). Percentages expressed to nearest whole number, sample sizes indicated alongside sex.

Gm x Mf

Female (19)	Wing type				Male (17)	Wing type				
Face type	**2**	**3**	**4**	**5**		**2**	**3**	**4**	**5**	**6**
3	-	5	5	5		6	12	6	-	-
4	-	26	59	-		6	47	-	6	-
5	-	-	-	-		-	6	-	-	-
6	-	-	-	-		-	-	12	-	-

Mm x Gf

Female (22)	Wing type				Male (23)	Wing type				
Face type	**2**	**3**	**4**	**5**		**2**	**3**	**4**	**5**	**6**
3	9	41	18	18		5	43	5	-	-
4	-	5	0	-		5	17	13	-	-
5	-	5	5	-		-	-	5	-	-
6	-	-	-	-		-	-	-	5	5

Hybrids

F1 hybrids displayed dominant face type/wing type combinations which, for each parental combination, paired its most common face type with its most common wing type (Table 7). These differed between parental combinations, and between sexes within the Gm x Mf combination.

Although amongst both sexes of backcrossed grey duck hybrids (Table 8), the dominant face type and wing type were most often paired, a minimum of 4 combinations embraced 75% of the sample. The previously-noted difference in wing type frequencies between sexes of 3/4-grey hybrids remained apparent.

In the larger sample of 3/4-mallard hybrids, there was a widespread distribution of face type/wing type combinations, especially for males. Face type 4 of 3/4-mallard males indicate birds that had not replaced their initial juvenile head plumage, and the apparent wider distribution of face type/wing type combinations likely reflects the young ages of many ducks in this sample.

Wild New Zealand ducks

All but 6% of grey-like specimens (Table 9) combined face types and wing types that characterised grey ducks (face types 2, 3; wing types 1, 2, 3). Within the mallard-like sample (Table 9) females with face types 4 and 5 combined with wing types 4-7 in all but 5% of the specimens while in males, just 3.1% displayed other than the dominant face type/wing type combinations.

These data indicate that, based on the defined face and wing types, there was strong phenotype structuring within the wild population rather than broad intergradation. Backcrossed grey duck hybrids had the same face type/wing type combinations that were the dominant combinations of the wild grey-like ducks (face types 2, 3/wing types 1, 2, 3). Mm x Gf F1 hybrids mostly corresponded to the less-common combinations of face type 3/wing types 3, 4 that comprised approximately 13% of the wild sample. Gm x Mf F1 hybrids corresponded to the rarer face type 4/wing types 3, 4 combinations that comprised 2.9% of the wild grey-like sample.

Table 8. Percentage frequency distribution of face/wing type combinations in female and male 3/4- and 7/8-backcross hybrids between grey duck and mallard. Percentages expressed to nearest whole number, sample sizes indicated alongside sex.

3/4-grey duck

Female (18)	Wing type				Male (24)	Wing type			
Face type	**1**	**2**	**3**	**4**		**1**	**2**	**3**	**4**
2	6	6	-	6		8	-	-	-
3	-	33	11	-		21	33	-	4
4	-	6	17	17		-	-	4	8
5	-	-	-	-		8	8	-	4

7/8-grey duck

Female (15)	Wing type				Male (14)	Wing type			
Face type	**1**	**2**	**3**	**4**		**1**	**2**	**3**	**4**
2	7	20	7	-		29	29	-	-
3	7	20	7	-		7	14	-	-
4	13	13	7	-		0	14	7	-
5	-	-	-	-		8	8	-	4

3/4-mallard

Female (47)	Wing type				Male (52)	Wing type				
Face type	**4**	**5**	**6**	**7**		**3**	**4**	**5**	**6**	**7**
3	-	4	-	-		-	-	-	-	-
4	28	17	11	-		2	4	-	4	-
5	13	9	19	-		-	2	2	6	2
6	-	-	-	-		2	19	12	19	27

7/8-mallard

Female (21)	Wing type				Male (16)	Wing type				
Face type	**4**	**5**	**6**	**7**		**3**	**4**	**5**	**6**	**7**
3	5	10	-	-		-	-	-	-	-
4	10	20	-	-		-	-	-	-	-
5	-	40	10	5		-	-	-	6	-
6	-	-	-	-		-	-	44	31	19

Amongst the female mallard-like face type/wing type distributions, most F1 hybrids (Table 7) would be subsumed within the approx. 10% of wild specimens with face types 3, 4/wing types 3, 4 combinations, but 3/4- and 7/8- backcrossed hybrids (Table 8) would be encompassed within the most common face/wing combinations of the wild sample. Within the male mallard-like distribution, the main face type/wing type characteristics of F1 hybrids (Table 7) would be included within approx. 0.5% of the wild sample but face type/wing type characteristics of mallard backcrossed hybrids (Table 8) would lie subsumed within the bulk of the wild sample's distribution.

Overall, these data from the wild sample suggest that while the face type/wing type combination may help distinguish F1 hybrids from grey ducks, and from male mallards when in nuptial plumage (i.e. after April in any year), their discrimination of mallard-like females is much more problematic; they offer no assistance in discriminating backcrossed hybrids.

Bill and leg colour associations with face type

Grey ducks

There was little variation in bill or leg characteristics of grey ducks (Table 10). Bills were either uniformly dark slate/black (type 1, 44%) or had basal dark green on an otherwise dark slate/black upper mandible (type 2, 52%). Leg colours were restricted to shades of olive green-brown (type 1, 60%) or khaki (type 2, 40%). No hints of yellow or orange hues to the legs were recorded.

Table 9. Percentage frequency distribution of face/wing type combinations in grey-like ducks (n = 352, both sexes combined), and sexed mallard-like ducks (female n = 659, male n = 892) from a New Zealand-wide sample of hunters' kills, May 1998.

Grey-like ducks

	Wing type				
Face type	**1**	**2**	**3**	**4**	**5**
1 & 2	23.6	24.4	11.7	0.3	0.3
3	7.6	14.3	12.2	0.6	-
4	0.6	1.2	2.3	0.6	-
5	0.3	-	-	-	-

Mallard-like ducks

Female	**Wing type**					**Male**	**Wing type**				
Face type	**3**	**4**	**5**	**6**	**7**		**3**	**4**	**5**	**6**	**7**
2	-	0.3	-	-	0.2		-	-	-	-	-
3	-	0.8	0.8	0.3	0.9		0.1	0.1	0.1	-	-
4	0.8	8.8	10.6	3.0	10.8		0.3	0.1	0.2	0.3	0.4
5	0.9	11.8	18.4	9.9	21.9		0.6	3.7	4.1	7.8	10.5
6	-	-	-	-	-		0.3	9.2	6.7	23.9	31.3

Table 10. Percentage frequency distribution of face type/bill type and face type/leg type combinations in grey ducks (n = 50), both sexes combined, from a New Zealand-wide sample, May 1991 (from Williams 2019).

	Bill type			Leg type	
Face type	**1**	**2**	**3**	**1**	**2**
2	32	28	4	40	24
3	12	24	-	20	16

Table 11. Percentage frequency distribution of face type/bill type and face type/leg type combinations in grey-like ducks (n = 352, both sexes combined), from a New Zealand-wide sample of hunters' kills, May 1998.

	Bill type				Leg type			
Face type	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
1 & 2	19.0	38.8	2.0	0.3	32.1	24.4	3.7	-
3	8.8	21.2	4.2	0.3	17.6	13.6	3.4	-
4	0.3	3.4	1.4	-	0.6	3.7	0.3	0.3
5	-	0.3	-	-	-	0.3	-	-

Table 12. Percentage frequency distribution of face type/bill type and face type/leg type combinations in mallard-like ducks (female n = 659, male n = 892) from a New Zealand-wide sample of hunters' kills, May 1998.

	Bill type						Leg type				
Face type	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**
Female											
2	0.2	0.3	-	-	-	-	-	0.2	0.3	-	-
3	0	0.8	1.7	0.3	-	-	-	0.9	1.5	0.2	0.2
4	0.5	4.4	11.7	15.8	0.9	-	0.6	4.9	18.4	8.1	1.4
5	1.4	6.7	17.3	30.8	5.9	-	1.4	9.0	34.1	15.8	3.2
Male											
3	-	-	0.2	-	-	0.1	-	-	0.3	-	-
4	-	0.2	1.0	0.2	-	-	-	0.4	1.0	-	-
5	0.1	0.3	2.0	1.3	15.1	7.9	0.3	2.1	9.3	9.5	5.5
6	-	0.1	-	0.2	50.1	20.9	-	1.5	18.9	33.2	17.8

Wild New Zealand ducks

Grey-like ducks

Bills of grey-like ducks (Table 11) were mostly uniformly dark slate (bill type 1; 28.1%) or that colour combined with a very dark green or dark slate-blue base to the upper mandible (bill type 2, 63.7%). Specimens showing yellow or brown on the bill (bill types 3, 4) comprised 8.2% (29) of the sample. Dominant leg colours were apparent (Table 11); dark olive green-brown (leg type 1, 50.6%) or lighter khaki (leg type 2, 42.0%). Hints of a dull yellow or yellow-orange occurred on legs of 26 (7.4%) specimens, only 1 of which did not have the characteristic face type 2 or 3 shown by 94.9% of the grey-like ducks.

Of the 29 ducks having bill types 3 or 4 (i.e. showing patches of brown or yellow), 4 had leg type 3 and 1 leg type 4 (i.e. yellow-orange): thus, just 5 (17%) of these 29 had other than the main leg colours of grey-like ducks. The leg type 4 was associated with face type 4.

The very strong bill type and leg type associations with the characteristic face types of grey ducks emphasise they are diagnostic of *A. superciliosa* in New Zealand.

Female mallard-like ducks

Almost two-thirds of the mallard-like female sample (Table 12) had a bill that was variously patterned with black and brown, or black and yellow (bill type 4) while another 30% had a more extensively black/dark green bill with yellow or brown near the tip (bill type 3). These occurred with similar frequency in combination with face types 4 and 5. That 5.9% of ducks with face type 5 were recorded with a yellow-green bill (bill type 5) characteristic of most mallard-like males (Table 12) suggests they may have been wrongly sexed. Dark bills (bill types 1, 2) characteristic of most grey-like ducks were displayed by 14.3% of the mallard-like females and occurred in association with all face types (Table 12).

The frequency distributions of leg types for females with face type 4 and face type 5 were not different ($\chi^2 = 0.45$, $P = 0.98$), and collectively yellow-orange or orange legs (leg types 3, 4) occurred in 78.3% of the sample, with a further 4.7% having brighter red-orange (leg type 5) legs. However, amongst all females (Table 12), 17% had leg colours that gave no hint of orange at all, these occurring in equal frequency (16.3%) amongst females with face types 4 and 5 and in 6 of the 18 females with face type 3.

Male mallard-like ducks

Bill colours of mallard-like males (Table 12) were almost exclusively of 2 types: yellow-green (bill type 5, 65%) sometimes with variable black marking around the nares, and a distinctly bluish or entirely greenish shade (bill type 6, 28%). Only 1 of 840 males with these bill colours did not have a face type 5 or 6. Of the other 7%, 41 of these 52 males had dark bills displaying patches of brown or yellow (bill types 3, 4) characteristic of most mallard-like females.

Almost all (95.8%) mallard-like males had legs of orange hue (Table 12). Those interpreted as yellow-orange (leg type 3) were significantly more frequent amongst males with an incomplete green face and head (face type 5, 34.7%) than amongst those more intensively coloured (face type 6, 26.2%; $\chi^2 = 11.3$, $P < 0.001$). Brighter orange legs (leg types 4, 5) were displayed by similar proportions of drakes with face types 5 and 6. Four of 16 males with face types 3 or 4 had khaki or yellow-orange legs (leg types 2, 3) while just 35 (4%) of males with face types 5 and 6 had khaki-coloured legs.

DISCUSSION

This study used broad categories of face and wing plumage patterns, supplemented by bill and leg colours, to describe the phenotypic variability amongst grey and mallard ducks and their hybrids in New Zealand. Using these characters, grey ducks were clearly distinguishable from all seasonally- and sexually-variable mallard-like ducks. Distinguishing F1 and backcrossed hybrids from parental species however, proved more equivocal.

No single face or wing character clearly differentiated hybrids from parentals. In combination, the main face and wing characteristics of F1 hybrids, irrespective of parental combination, were recorded within the historic grey duck museum sample used by Williams (2019). Backcrosses to grey duck had the same patterning dominant within that historic sample and in the contemporary wild grey-like sample. Any distinction was based on relative frequency of face and wing pattern occurrence, not on pattern itself.

Differentiation of hybrids from mallards was problematic because there was no "pure" mallard reference sample available (other than descriptors from North American or European populations) and because of novel wild phenotypes, interpreted as reflecting the exclusively captive-origin of New Zealand's mallards. Characteristics of F1 hybrids and of backcrosses to mallard were also identified within the contemporary wild mallard-like sample so that their distinction was more of relative frequency of face and wing pattern occurrence, rather than of pattern itself.

Can hybrids be recognised?

The schema used in this paper cannot discriminate,

with certainty, grey duck x mallard hybrids in the field. For example:

- Face characteristics, alone, could categorise ducks as "grey" (face types 1, 2), "grey-like" (face type 3), or "mallard-like" (face types 4, 5, 6). However, by using face type 3 alone the "grey-like" category would include 36% of grey ducks (Williams 2019: Table 2), encompass most F1 hybrids (86% of females, 52% of males) of mallard male x grey duck female parentage, and some F1 hybrids (16% of females, 24% of males) derived from the alternate parentage (Table 1). It would also include 52% of 3/4-grey and 28% of 7/8-grey backcross hybrids and 1% of 3/4-mallard female backcross hybrids. In the wild population, face type 3 was displayed by 34.7% of grey-like ducks and by 2.7% of females and 0.3% of males of mallard-like ducks (Table 2).
- Wing characteristics, alone, could categorise ducks as "grey" (wing types 1, 2), "grey-like" (wing type 3), or "mallard-like" (wing types 4–7). However, by using wing type 3 alone the "grey-like" category would include 8% of grey ducks (Williams 2019: Table 3), encompass a majority of F1 hybrids (50% of females, 61% of males) of mallard male x grey duck female parentage, fewer F1 hybrids (32% of females, 65% of males) derived from the alternate parentage, 14% of 3/4- and 7/8-grey backcross hybrids, but no mallard backcross hybrids (Table 4). In the wild population, wing type 3 was displayed by 26.2% of grey-like ducks, and by 1.7% of females and 1.2% of males of wild mallard-like ducks (Table 5).
- Used in combination to define "grey-like", face type 3/wing type 3 would encompass 11.5% of grey ducks (Table 6), 42% of F1 hybrids of mallard male x grey duck female parentage, 8% of F1 hybrids of the alternate parentage (Table 7), and 4% of grey backcross hybrids but no mallard backcross hybrids (Table 8). In the wild population the face type 3/wing type 3 combination was displayed by 12.2% of grey-like ducks and by just 8 (0.05%) of 1,552 of mallard-like ducks (Table 9).

Within the wild grey-like duck sample (Table 11), 94.9% had face types 2 or 3, and of these 92.8% had an entirely dark bill (bill types 1, 2) and 93.1% had olive brown-khaki legs (leg types 1, 2). These are the characteristic bill and leg colours of grey ducks (Williams 2019: Table 6). Any duck categorised as "grey" or "grey-like" based on face type and/or wing type but displaying different bill and/or leg characteristics may be regarded as having recent hybrid ancestry.

Without a reference sample of mallard indicative of those bred and released in New Zealand, mallard-like ducks of putative hybrid ancestry are particularly difficult to discriminate. For example:

- Face type 4 was the dominant but not exclusive facial pattern of F1 hybrids of grey duck male x mallard female parentage. Amongst female mallard backcross hybrids face types 4 and 5 were equally common, and almost all male mallard backcross hybrids had face types 5 and 6 (Table 1). Using face type 4, alone, to discriminate hybrids would encompass most F1 hybrids (84% of female, 59% of male) with mallard female parentage, few F1 hybrids (5% female, 35% male) with grey duck female parentage, about half of female mallard backcross hybrids but almost no male mallard backcross hybrids, and 36% of female and 16% of male grey backcross hybrids (Table 1). In the wild population, face type 4 was displayed by 34.0% of females and 1.5% of males of mallard-like ducks and 4.8% of grey-like ducks (Table 2). Face type 4 was readily apparent in images of wild mallard females in North America (Macaulaylibrary 2019).
- Wing types 3 and 4 were displayed by most F1 hybrids (95% of female, 83% of male) of grey duck male x mallard female parentage. Of mallard backcross hybrids, most (78% of females, 43% of males) displayed wing types 4 and 5 (Table 4). Thus, the bulk of mallard-like hybrids displayed a distinctly mottled white/buff alar bar, mostly narrow (wing types 3, 4) but some wide (wing type 5). Whether this characteristic, alone, discriminates a recent hybrid is problematic however when, in the wild population, wing types 4 and 5 were displayed by 51.6% of females and 24.1% of males of mallard-like ducks and 1.8% of grey-like (Table 5). Distinctly mottled white/buff alar bars, narrow or wide were not apparent in >400 images of North American wild mallards examined (Macaulaylibrary 2019) but, potentially, may have been a common characteristic of the captive-raised mallards established in New Zealand.
- Face and wing characters in combination can provide no better discrimination than either alone (Tables 7, 8). Face type 4 combined with wing types 3 or 4 encompass 85% of female and 47% of male F1 hybrids from a mallard female (Table 7). However, multiple face type/wing type combinations were displayed amongst mallard backcross hybrids (Table 8). In the wild population of mallard-like ducks, face type 4/wing types 4 and 5 combinations were displayed by 19.4% of females and just 0.3% of males (Table 9).

Within the wild mallard-like population, 77.5% of females had bill types 3 or 4, i.e. patterns which combined black with extensive areas of brown or yellow, and 78.1% had yellow-orange legs (leg types 3,4) (Table 12). By inference, these may be regarded as characteristic of New Zealand mallard females, as they are of mallards elsewhere (Cramp & Simmons 1977). For male mallards in the wild duck sample, 94.1% had yellow-green or green-blue bills and all but 4.1% had legs of orange hue.

Although direct corroboration is lacking, a mallard-like hybrid will display yellow-orange legs and, depending upon sex and age, will have a dark bill with areas of brown or yellow (female, juvenile males) or uniformly yellow-green, green or bluish bill (male).

What can be viewed in the field: the necessity for broad categorisation and the inability to see all characters simultaneously

The face, wing, bill and leg categories used in this study were established following close-order inspection of specimens. For subtlety of pattern and colour to be avoided categorisation of obvious phenotypic differences was necessarily broad. For their discrimination at distance in the field, these distinctions had to be obvious.

Potentially, some of the subtlety that might have distinguished hybrids may have been masked by these requirements. For example, Williams (2019) recognised three *A. superciliosa* face patterns with type 1 being very rare in New Zealand (it was not encountered in this study). Thus, grey ducks were considered to show just 2 face patterns (face types 2, 3). Distinction between face type 3, common to approximately one-third of grey ducks, and face type 4, common to approximately one-third of mallard-like females is based on the malar and superciliary stripes delimiting a conspicuousness cream patch extending from bill base to below or slightly forward of the eye. By using this broad categorisation, variability in the extent of the cream face patch, especially of its contraction forward of the eye, and of associated facial mottling, went unrecorded. However, face type 3 was recorded in 86% of female and 52% of male F1 hybrids derived from a mallard male x grey duck female mating and of approximately half of 3/4-grey backcross hybrids. In contrast, there was no apparent variability within face type 4 where a small, semi-circular, pale fawn patch occurs at the base of the bill. This category is displayed by one-third of mallard-like females, 84% of female F1 hybrids of grey male x mallard female parentage, and almost 60% of female 3/4-mallard backcross hybrids.

Wing patterns also proved challenging to define as a useful field character. In the hand, colour and width of the alar bar could be readily discriminated, but not so in the field. There, the upper wing surface was often difficult to view clearly or expansively and discrimination of alar bar colour (pure white or obviously whitish-buff) and width (narrow or broad) were dependent on being able to view comparative features simultaneously; for colour the trailing bar, and for width the trailing bar or the light-coloured margins of the tertial feathers. The distinction between wing types 3 and 4, both having a narrow whitish-buff alar bar, depends upon speculum colour, green or purple/blue, which can sometimes be confused depending upon light intensity and viewing angle. Nevertheless, it is an important distinction to discern.

Determining bill and leg colours in the field can also prove challenging. The bill surface is highly reflective and when the bill is viewed against the light, green or bluish colours shown by some mallard-like ducks are easily confused. So too is any subtlety of pattern involving the bill base being somewhat darker than the rest of the upper mandible. Thus, distinctions of bill colour and pattern, as determined in the hand, can be difficult to discern in the field, especially between bill types 1 and 2 and which are probably best amalgamated for field purposes. As the preceding analyses have demonstrated, little discriminatory ability would be lost if bill categories were amalgamated, e.g. types 1 + 2 (predominantly dark bills), types 3 + 4 (i.e. bills displaying yellow or brown) and types 5 + 6 (restricted to mallards-like ducks, mostly males).

Whilst leg colours present less confusion in the field, legs may be the least frequently viewed character. A quick glimpse may, however, suffice to make the key distinction between the olive-brown or khaki shades characteristic of grey and grey-like ducks and the yellow-orange characteristic of almost all mallard-like ducks.

Notwithstanding that some of the categories of face, wing, bill, and leg used in this study may prove difficult to discriminate in the field, perhaps of greater importance is the general inability to discern all characters at a single viewing. The prominence accorded to face pattern in this study reflects this reality.

Study purpose and genetic realism

This study sought to address a field conundrum: discriminating between grey ducks, mallards, and their hybrids.

After a century of interaction between the species in New Zealand wetlands, and with evidence of genetic introgression "impacting" both species (Rhymer *et al.* 1994), the understandable desire to discriminate and categorise may already have been overtaken by ongoing processes: the

mallard's demographic ascendancy and the grey duck's genetic subsummation within an evolving mallard-dominated hybrid taxon (Williams & Basse 2006; Williams 2017). No evidence has yet accumulated to indicate that F1 hybrids are selectively disadvantaged, nor that backcrosses may be so, although such evidence has not been specifically sought. Historic survival studies (e.g. Caithness *et al.* 1991; Barker 1991) indicate similar survival rates for the two species and the grey duck's greater vulnerability to hunting. Contemporary studies wherein grey ducks and grey-like ducks were not separately discriminated, indicate the same (McDougall *et al.* 2016; M. McDougall *pers. comm*.). In the absence of selection against hybrids, there is an inevitability about the admixture of each species' genes into the genome of the other.

It was pointed out in review that levels of introgression detected by Rhymer *et al.* (1994) suggest nearly all ducks in the current grey duck – mallard population will have some hybrid ancestry. Their study detected one mallard-type mitochondrial sequence among 19 ducks which morphologically appeared "pure grey", i.e. 5.3%. However, hybrids arising from mating of a male mallard or hybrid with a female grey duck would not be detected by this method. Therefore, true hybrid levels would have been at least double that, i.e. >10%, even when those ducks were collected in 1991. Since then (and unless there is extremely strong population structuring and/or assortative mating between cryptic hybrids and non-hybridised individuals, which seems extremely unlikely) each additional generation will have resulted in nearly a doubling of the spread of cryptic hybrids into the grey duck population, at least until unhybridized grey ducks became significantly rarer than cryptic hybrids (R.A. Hitchmough *pers. comm*). The same perspective can be applied to mallard where Rhymer *et al.* (1994) identified one grey duck mitochondrial sequence among 15 morphologically "pure" mallards, i.e. 6.7%.

Phenotype is undoubtedly the expression of multiple genes (e.g. Ng & Li 2018) and what is viewed in the field reflects a complex and unpredictable genetic amalgam. Unless there is strong selection favouring a specific hybrid phenotype, the likelihood is one of extensive phenotypic variability of hybrids, including entirely cryptic hybrids where the phenotype is indistinguishable from that of a parental form.

Perhaps the best that can now be hoped for may be to agree on the phenotypes we call grey duck and mallard, and then refer to things which are neither by other designations. "Grey-like" and "mallard-like" are terms used in this narrative. "Grey-like" has a point of reference, being the plumage patterns demonstrably associated with *A. superciliosa* throughout its Australasian and Pacific range, notwithstanding the regional variability of that standard phenotype (Williams 2019). If a duck looks mostly like *A. superciliosa*, but has observable characters (e.g. bill pattern, leg colour, wing marking) that do not conform to the "standard" *superciliosa* phenotype, then differentiating it as "grey-like" or referring to it by some other agreed common name (e.g. greylard, grallard) would seem both appropriate and pragmatic.

It is more problematic for mallard-like ducks in New Zealand, however. The captive-origins of mallards released in New Zealand, derived mostly from United Kingdom game farms but also including a small infusion from North America (Dyer & Williams 2010; Guay *et al.* 2015), have compromised the "standard" mallard phenotype as described for wild northern hemisphere populations (e.g. Palmer 1976; Cramp & Simmons 1977; Kirby *et al.* 2000; Drilling *et al*. 2002). Even without hybridisation with grey duck, mallards in New Zealand can confuse those not appreciative of sexual and seasonal plumage change or of the plumage variability derived from multi-generational captive confinement. Add hybridisation to the mix and the phenotypic variability is that recorded within the "mallard-like" wild ducks evaluated in this study. Perhaps the simplest, and most pragmatic approach is this: if it resembles a mallard, call it a mallard, and if wider differentiation is needed, a "New Zealand mallard". What is there to be gained by trying the virtually impossible – discriminating a mallard-like hybrid from a duck we choose to call mallard. A duck with a purple/blue speculum, a conspicuous whitish alar bar anterior to the speculum and an equally conspicuous white trailing bar, with yellow-orange or orange legs could be designated as a "mallard", irrespective of its bill colour and pattern, and attempts to differentiate a mallard-like hybrid resisted. Adding that category is a license for further descriptive confusion and, as this study has demonstrated, would be a category of little rigour.

A generalised distribution of phenotypic characters across three putative categories of ducks – "grey duck", "grey-like" and "mallard-like" – is illustrated in Table 13.

Need for fulsome genomic appraisal

This study is a poor substitute for a fulsome genomic appraisal of grey and mallard ducks in New Zealand. All studies or reports based upon phenotypic discrimination, whether using plumage and soft part features with or without supporting measurement data (e.g. Green *et al.* 2000), or from hunters reporting what ducks they think they shot (Caithness 1968 *et seq*.; Williams 2017) suggest considerable regional differences in the

Table 13. Generalised distribution of phenotypic characters across 3 groupings of ducks in New Zealand - grey duck (grey), grey-like, and mallard-like.

Character	Group	Type 1	Type 2	Type 3	Type 4	Type 5	Type 6	Type 7
Face	Grey							
	Grey-like							
	Mallard-like							
Wing	Grey							
	Grey-like							
	Mallard-like							
Bill	Grey							
	Grey-like							
	Mallard-like							
Leg	Grey							
	Grey-like							
	Mallard-like							

relative abundance of the two "species" and of the proportion of the population regarded as "hybrid".

Field pragmatism aside, a compelling, and instructive, natural experiment is unfolding in New Zealand wetlands. How, and to what likely outcome, has been speculated upon (e.g. Rhymer & Simberloff 1996; Rhymer 2006; Williams & Basse 2006; Guay *et al*. 2015) but diagnostic evidence beyond that provided by an initial mtDNA analysis (Rhymer *et al.* 1994) is lacking. Guay *et al.* (2015) summarised the value, and the limitations, of mtDNA based analyses, highlighting their utility to identify directionality of hybridisation, e.g. bi-directional between grey duck and mallard (Rhymer *et al*. 1994), asymmetric between hybridising mottled duck and mallard in Florida, USA (Williams *et al*. 2005), and between koloa (*A. wyvilliana*) and mallard in Hawai'i (Fowler *et al.* 2009). However, it is use of nuclear markers that is required to disentangle current process and indicate likely outcome of the grey duck x mallard hybridisation process (e.g. Lavretsky *et al*. 2015, 2019), that is best able to relate genotype to phenotype (e.g. Bielefeld *et al*. 2016), and, potentially, provide field observers with a suitably rigorous diagnostic schema. The latter may prove challenging if the multi-trait (7 for females, 9 for males) schema provided for the recognition of mottled duck x mallard hybrids (Bielefeld *et al*. 2016) is to be avoided. It is one thing to provide a diagnostic schema that necessitates close multi-character examination of the duck in the hand thereby conferring the comfort of apparent precision, but field observers, the providers of most ecological, distributional and status data, require something simpler and readily able to be discriminated at a distance. An uncomfortable forgoing of precision in favour of pragmatic categorisation may be necessary. But whatever standard is aspired to, a more fulsome relating of genotype with phenotype is clearly needed, and enquiry of the unfolding evolutionary process encouraged.

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Appendix. Phenotype descriptors of face, wing, bill and leg used in this study (modified from Rhymer *et al.* 1994), with comments on their use as diagnostic field characters to discriminate grey ducks, grey-like ducks, and mallard-like ducks.

Type 1: Crown and nape dark grey/black. Strong black superciliary stripe extends from lateral crest of bill, through the eye (generally broadening around eye) to back of head. A uniformly narrow mottled black malar stripe extends from gape, across face, to back of head. A conspicuous cream (crown) stripe lies between superciliary stripe and crown, **cream face patch separates superciliary and malar stripes extending to rear of head,** and a broad cream patch occupies lower area of cheek and throat. Rarely seen in New Zealand.

Type 2: Crown and nape dark grey/black. Strong black superciliary stripe extends from lateral crest of bill, through the eye (generally broadening around eye) to back of head. The mottled black malar stripe extends from gape across face broadening forward of the eye and **links with superciliary stripe rear of the eye.** Extensive facial mottling extends from rear of eye to rear of head. Cream crown stripe is conspicuous, cream face patch **between superciliary and malar stripes extends to rear of eye,** and a broad cream patch occupies lower area of cheek and throat.

Type 3: Crown and nape dark grey/black. Mottled black superciliary stripe extends from lateral crest of bill, through the eye (sometimes broadening around eye) to back of head. Broad mottled black stripe (malar) extending from gape across the face **to merge with the superciliary stripe below or forward of the eye.** Facial mottling is extensive, extending from rear of head to below or forward of eye and down across cheek. **Crown stripe mottled black and cream, cream face patch diminished,** and the cream area on cheek/throat mostly restricted to throat.

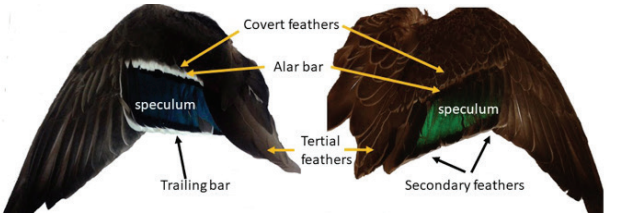
Type 4: Crown and nape mottled dark grey/black. A mottled black superciliary stripe extends from lateral crest of bill, through the eye to back of head, narrowing posteriorly. Short dark mottled malar stripe merges with extensive facial mottling well forward of eye. **Crown stripe is mottled fawn, face patch reduced to a small fawn patch at bill base.** Face predominantly mottled black on fawn, throat fawn. (Mallard drakes in non-breeding (eclipse) plumage, mallard fledglings of both sexes, and mallard females fall within this category).

Type 5: Face entirely mottled black on fawn but with a discernible dark superciliary stripe of varying conspicuousness extending from lateral crest of bill, through the eye to back of head, narrowing posteriorly. Fawn throat area may or may not be present. No green lustre to head and face plumage. (Mostly mallard females).

Type 6: Entire face and head has greenish lustre, either heavily mottled or entirely iridescent green. Shown by mallard drakes developing or having acquired nuptial colouration.

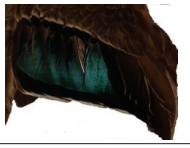
Field evaluation of face: Although face type 3 is shown by approx. one-third of grey ducks, it is diagnostic of almost all F1 hybrids and most initial backcross hybrids of grey duck maternity (see Table 1). Discrimination between a grey duck and a grey-like hybrid requires evaluation of alar bar on wing and leg colour. Almost all F1 hybrids of mallard maternity show face type 4 and immature initial backcross hybrids also (see Table 1).

Wing descriptors



Type 1: Speculum green, no discernible alar bar, narrow trailing bar no wider than buff edging to any wing covert or tertial feather.

Type 2: Speculum green, thin but discernible buff alar bar of similar width to buff edging of tertial feathers (Note: presence of bar can be confused by the buff edges of upper wing coverts). Narrow white trailing bar up to 2x width of buff edging of tertial feathers.



Type 3: Speculum green, conspicuous whitish-buff alar bar which is distinctly not as white as the trailing bar and may even appear finely mottled fawn. Width of alar bar variable up to 2-3 x the width of buff edging to tertial feathers. Trailing bar up to 2 x width of buff margins on tertial feathers. Resembles Type 4 but with green speculum.

Type 4: Speculum purple/blue but, in some lights, may appear green. **Alar bar conspicuous (2–4 mm width) whitish-buff** contrasts with the whiteness of trailing bar and is of similar width or narrower than trailing bar. **Both bars >2 x width of buff margins on tertial feathers.**

Type 5: Speculum purple/blue. Conspicuously whitish-buff broad (>4 mm) alar bar contrasts with the whiteness of the trailing bar and is of similar width. The distinction between a mottled fawn and a white alar bar in mallard-like ducks can best be perceived by contrasting the alar bar with the white of the trailing bar and the light-coloured covert feathers on the wing. A white alar bar contrasts with the pearl/brown of the covert feathers under almost all viewing conditions whereas the mottled fawn is perceived as dull and lacking contrast.

Type 6. Speculum purple/blue, conspicuously white alar-bar (<4mm) and generally of lesser width than the black bar below it (i.e. on tips of the secondary covert feathers) and of lesser width than the trailing bar. (Considerable variability in width of alar bar in this category but the alar bar is unmistakeably white.

Type 7. Speculum purple/blue, white alar-bar prominent and broad (generally >4mm) widening distally (i.e. closer to primary feathers) and broader than the black bar below it (i.e. on tips of the secondary covert feathers). Trailing bar conspicuously broad (>4mm)

Field evaluation of wing: Determining speculum colour is essential. The second key feature is the alar bar – narrow but obvious and whitish-buff above a green speculum (type 3) mostly denotes a F1 or initial backcross hybrid of grey duck maternity when associated with face type 3; narrow, obvious and whitish-buff above a purple/blue speculum (type 4) mostly denotes a F1 or initial backcross hybrid of mallard maternity. A wider whitish-buff alar bar (type 5) or an obviously white alar bar (types 6, 7) is characteristic of most mallard-like ducks.

Bill descriptors	Leg descriptors
Type 1: Uniformly black or dark slate.	**Type 1:** Dark olive greenish-brown.
Type 2: black/dark slate with very dark green or a dark slate blue base and edge to upper mandible.	**Type 2:** Khaki.
Type 3: predominantly black/dark green, some yellow or brown at tip.	**Type 3:** yellow-orange to very dull.
Type 4: blackish and brown/yellow.	**Type 4:** orange.
Type 5: entirely yellow-green.	**Type 5:** red-orange.
Type 6: entirely greenish or a bluish shade.	

Field evaluation of bill: When viewed at distance, especially in poor light, it is difficult determining whether the bill is uniformly dark (type 1) or has a basal region that is darkish green (type 2). This distinction appears unnecessary (see Tables 10-12). Likewise, bills with brown or yellow anywhere (types 3, 4), being mostly restricted to mallard-like females, may be needlessly subdivided (see Table 12). The yellow-green and green bills (types 5, 6), common to most mallard-like males, may be indicative of age and state of nuptial cycle.