Phenotypic variability within and between regional populations of *Anas superciliosa* (Anatidae)

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Abstract: Variability of face and wing pattern and of leg and bill colour, and differences in bill and wing lengths, were assessed in *Anas superciliosa* (Anatidae) specimens from Pacific Islands, Australia, and New Zealand regional populations. The same 3 broad face patterns and 4 wing patterns were found in all populations. Frequency distributions of face patterns, but not wing patterns, differed significantly between populations. The most common face pattern in Australia was very rare in New Zealand and uncommon in Pacific Islands. A secondary face pattern in Pacific Islands and New Zealand was absent in Australia. Australian and New Zealand ducks did not share bill colour and pattern and no legs of New Zealand birds displayed yellow/orange hues common to 35% of Australian specimens. Bill and wing lengths of Pacific Islands specimens were significantly shorter than all others while wing lengths of male specimens from northern Australia were significantly shorter than those from southern Australia and New Zealand. These differences offer emphatic support for historic subspecific differentiation of Pacific Island specimens. Historic, but now discarded, taxonomic distinction between Australian and New Zealand populations based on phenotype could be reconsidered.

INTRODUCTION

The taxon *Anas superciliosa* Gmelin 1789 is distributed across 60 degrees of latitude on islands and landmasses of the south-western Pacific region (Marchant & Higgins 1990; Rhymer *et al.* 2004). Attempts to reflect perceived geographical distinctions within this range have featured in its taxonomic history; to the nominate *A. s. superciliosa*, sourced from New Zealand, was added *A. s. pelewensis* (Hartlaub & Finsch 1872) to represent distinctly smaller specimens obtained from Pelew Islands (Palau), and subsequently from many islands of Micronesia and Polynesia (Finsch 1875; Rothschild & Hartert 1905, 1914; Amadon 1943). Thereafter, another taxon, *A. s. rogersi*, was erected by Mathews (1912, 1914) to represent Australian birds he considered also to be smaller

than the nominate form. Riley (1919) established *A. s. percna* from Celebes specimens perceived as darker and smaller than Australian birds but larger than *A. s. pelewensis*; this was challenged by Amadon (1943) as having been based on specimens carrying ferruginous stains on neck and throat feathers, and he suggested *percna* be regarded as a synonym of *rogersi*. The distinction was, thereafter, disregarded. Nevertheless, Amadon (1943) raised the possibility of substantial size variation amongst birds grouped as *pelewensis* noting the smallness of Palau specimens relative to those from Solomon Islands and central Polynesia, and especially from southern Melanesia (Santa Cruz, Vanuatu). He also confirmed the size distinction between *rogersi* and *pelewensis* previously indicated by Rand (1942) who considered both taxa occurred in New Guinea, the larger taxon being more prevalent at higher altitude. Elsewhere, however, the ranges of large-bodied (*rogersi, superciliosa*) and small-bodied (*pelewensis*) taxa have not been reported as overlapping.

The *rogersi–superciliosa* distinction has subsequently been swept aside (Marchant & Higgins 1990), and the *pelewensis* distinction also; in current taxonomic lists of Australian and New Zealand birds (Worthy 2010; BLI 2019) *A. superciliosa* is regarded as monotypic and the former regional taxa devoid of mensural distinctions (Fullagar 2005; Worthy 2010).

The historic regional sub-divisions were primarily a response to perceived size differences. No plumage differences between regional populations of *A. superciliosa* have been documented except for Amadon's (1943) remark that "New Zealand specimens are paler than those from other localities". He identified this arising from "the feather margins (being) pale greyish or buffy white rather than buffy and brownish white (in *rogersi*); hence a paler bird with more conspicuous feather margins" and commented that "specimens in unworn plumage can probably be separated from *rogersi* with few exceptions.".

Establishing whether plumages of Australian and New Zealand ducks differ is of relevance to present-day field discrimination of *A. superciliosa* (grey duck) in New Zealand where it co-occurs with the now ubiquitous introduced mallard (*A. platyrhynchos*) and with hybrids between the two species (Robertson *et al.* 2007). Mallards were deliberately introduced to New Zealand for sporting purposes from about one century ago (Dyer & Williams 2010) and hybridisation between the species was observed soon thereafter. Concerted captive breeding and release programmes in the late 1940s and throughout the 1950s established mallard populations throughout the country and numbers burgeoned (Williams 2017b). In the wake of the mallard's numerical and distributional dominance uncertainty has arisen concerning the genetic integrity, and the plumage characteristics, of ducks now being identified in the field as "grey duck" (e.g. Gillespie 1985; Rhymer *et al.* 1994; Robertson *et al.* 2017; Williams 2017b). Any reconciliation of this uncertainty requires a reference group of *A. superciliosa* specimens that excludes potential cryptic grey duck x mallard hybrids (Rhymer *et al.* 1994).

Definitive studies relating grey duck genotype and phenotype have yet to be reported. Historic grey duck specimens in New Zealand museum collections that conclusively pre-date initial mallard releases are few, as are those that pre-date 1950 when mallard releases were approaching their zenith. Nevertheless, they provide the only available New Zealand-sourced reference group against which to compare contemporary specimens. However, if these historic specimens are indistinguishable phenotypically (other than perhaps being perceived as paler) from Australian *A. superciliosa* (Pacific black duck) specimens, then Australian specimens may also serve as a reliable reference group for appraising plumages of present-day putative grey ducks in New Zealand.

In this study I compare some plumage and soft-part characteristics of historic grey duck specimens with those of Pacific black ducks from Australia and specimens of the former *A. s. pelewensis* (lesser grey duck) from Pacific islands. I also assemble measurements of bill and wing lengths of *A. superciliosa* from throughout its range to test the hypothesis that there are no regionally-based mensural distinctions within this species.

METHODS
Source of specimens
Specimen skins of lesser grey duck came from 9 Pacific locations (Fiji, Tonga, Samoa, Moorea, Palau, Bougainville, Solomon Islands, Vanuatu, eastern and southern New Guinea lowlands). Specimen skins and contemporary photographs of Pacific black duck came from most Australian states, Macquarie Island, and New Guinea highlands. Grey duck specimen skins were from throughout New Zealand and its outlying islands (Kermadec, Chatham, Campbell). These groupings are treated in the text as separate "populations" – Pacific, Australia, New Zealand.

Specimen skins of Australian and Pacific ducks were viewed in collections of Victoria Museum and Art Gallery, Launceston, Tasmania, Victoria Museum, Melbourne, and the National Wildlife Collection, CSIRO, Canberra, ACT, Australia (ANWC). New Zealand and more Pacific specimen skins were viewed in collections of Auckland War Memorial & Museum, Auckland, and Museum of New Zealand Te Papa Tongarewa (MoNZ), Wellington. New Zealand specimens were restricted to those collected prior to 1970. Further Pacific specimens held at Museum of Vertebrate Zoology, University of California Berkeley, USA, (9), National Museum of Natural History, Smithsonian Institution, Washington, USA (7) and American Museum of Natural History, New York, USA (17), were appraised from photographs supplied by these museums. The MoNZ collection also included 145 grey duck wings collected in the 1950–60s and the author had historic records from 28 wings collected in Taranaki, New Zealand, in May 1966. Contemporary photos of Australian specimens were viewed from online sources (principally *birdlifephotography.org.au*) or were contributed by individuals at my request. I viewed Pacific black ducks on wetlands of the Australian Capital Territory and within or adjacent to Melbourne.

Bill and leg characteristics of grey ducks are reported from ducks collected throughout New Zealand in May 1991. Some putative grey ducks in this collection were sampled by Rhymer *et al.* (1994)

and confirmed to carry grey duck mtDNA, and, by their phenotype scoring system which assigned scores to head, wing and leg patterns, all to have a phenotype score of 5 (see below). The leg and bill characteristics reported here derive from all ducks in the 1991 collection with a Rhymer phenotype score of ≤5 (n = 50).

Study approach

Each specimen had its face pattern and upper wing characteristics, bill pattern and colour, and leg colour, assessed using phenotypic descriptors from Rhymer *et al.* (1994: Table 1) ("Rhymer descriptors"). Minor refinement of Rhymer face descriptors was necessary to embrace the full range of variability observed beyond New Zealand and to ensure that the defining characters (Table 1) were readily discernible and distinguishable in the field. Descriptors of wing amalgamated anterior and posterior characteristics of the speculum which Rhymer *et al.* (1994) assessed separately. Their bill and leg descriptors were used unaltered. Whereas Rhymer *et al.* (1994) assigned values to their descriptors which were then all summed to produce a cumulative score, in this study the descriptors for each character are simply numbered sequentially (1, 2 *etc.*) and referred to as "types" (Table 1).

Bill and wing lengths were measured on sexed specimens in each museum collection visited. Bill length is the length of the exposed culmen, from bill tip to commencement of feathers in the midline, and wing length is the length of the folded wing from the foremost extremity of the carpal joint to tip of longest primary feather.

Table 1. Descriptors of phenotypic characters (modified from Rhymer *et al.* 1994). Depictions of face and wing types are presented in Williams (2019).

FACE	WING
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.	**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: 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 2: Speculum green, thin but discernible** <u>buff</u> **alar bar** of similar width to buff edging of tertials (Note: presence of bar can be confused by the buff edges of upper wing coverts). Narrow white trailing bar up to 2x width to buff edging of tertial feathers.
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 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 2–3 x the width of buff edging to tertial feathers. Trailing bar up to 2 x width of buff margins on tertial feathers.
	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**.
BILL	**LEG**
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 orange
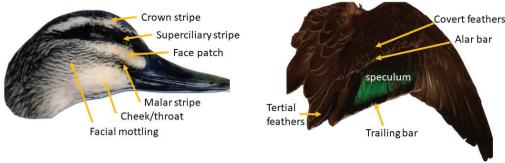
Presentation of results

Many *A. superciliosa* specimen skins examined had labels bereft of sex information. While measurements of bill and wing length, especially in combination, can be indicative of sex, there is too much overlap of ranges for each sex to allow a confident allocation of sex to any particular specimen (Marchant & Higgins 1990; Williams 2017a). In addition, longitudinal streaks on the vanes of tertial feathers, referenced by Hartlaub & Finsch (1872) and identified by Amadon (1943) as indicative of a female, were not consistently present on all specimens labelled as females. Nor could sex be readily established from photographs. Thus, tabulated results for plumage characters are for both sexes combined. Measurement data, however, were derived from the sexed specimens and summarised results presented separately for each sex.

To identify potential latitudinal or distributional differences in body size, the Pacific population was subdivided to separate widely scattered and small Pacific islands (Oceania) from the larger islands of archipelagos east and south-east of New Guinea and including eastern and southern New Guinea lowlands (Melanesia). The Australian population was subdivided latitudinally above and below latitude 26°S, the northern grouping also including Celebes (Sulawesi) and highlands of New Guinea, the southern grouping extending to Tasmania and Macquarie Island. New Zealand and its outlying islands were treated as a single geographic unit. Historic measurements from Rand (1942) and Amadon (1943) are included where appropriate. Welsh's t-test was used to compare sample means, chi-square tests were used to compare plumage frequency distributions between populations, and a permutational multivariate analysis of variance (PERMOVA; performed in Program PAST 3.24; Hammer *et al.* 2001) used to evaluate differences in face type/wing type combinations between the 3 populations.

RESULTS

Plumage characters

Face types

The frequency distributions of face types from the 3 populations (Table 2) indicate differences, most markedly in the relative frequency of face type 1 in Australia, the preponderance of face type 2 in Pacific birds, and the higher frequency of face type 3 in New Zealand (NZ). The frequency distributions between the populations are all significantly different (Australia–Pacific: $\chi^2 = 39.5$, $P < 0.0001$; Australia–NZ: $\chi^2 = 91.7$, $P < 0.0001$; Pacific–NZ: $\chi^2 = 8.0$, $P = 0.018$).

Although Australia was treated as a single unit, face type frequencies differed regionally within Australia. For example, eastern states, whether aggregated or sub-divided as northern (Queensland, Northern Territory, New Guinea) and southern (New South Wales, Victoria, Tasmania) blocs, had higher relative frequencies of face type 1 (all >55%, n = 156) than Western Australia (24%, n = 54). There may also be local clusters of facial similarity, e.g. Canberra, where face type 1 comprised 94% of 147 wild ducks viewed by the author (data not included in national analysis).

Amongst Pacific samples from 9 island groups, face type 1 occurred in 3 (Fiji, Tonga, eastern New Guinea), face type 3 in most (not Palau, Samoa, Tonga) but face type 2 was predominant in all. Hartlaub & Finsch's (1872) comment that, in Palau specimens "the dark stripe from the angle of the mouth also varies in intensity and is nearly altogether wanting in some specimens" is indicative of face type 1.

The New Zealand sample was initially examined as 2 groups, pre-1950 and 1950–70, to reflect periods before and during which mallards were released extensively (Dyer & Williams 2010). One specimen within the pre-1950 sample (from Campbell Island, 1943) had face type 1, otherwise the samples had almost identical frequencies of face types 2 and 3.

Table 2. Percentage frequency distribution of face types in *A. superciliosa* from Australia (n = 237), Pacific (n = 50) and New Zealand (NZ, n = 52) regional populations, both sexes combined. Australian data from specimen skins (120) and contemporary photos (117), New Zealand specimens (skins only) pre-date 1970.

Face type	Australia	Pacific	NZ
1	54.9	18.0	1.9
2	43.4	64.0	61.5
3	1.7	18.0	36.5

Wing types

The frequency distributions of wing types for the 3 regional populations of *A. superciliosa* (Table 3) indicate that a discernible alar bar, either as a thin buff line (type 2) or as a wider buff-white line (type 3) positioned sub-terminally on the secondary covert feathers and viewed anterior to the green speculum, was present in at least half of the ducks in all 3 populations. The 3 distributions do not differ significantly from each other (Australia–NZ: $\chi^2 = 2.54$, $P = 0.47$; Australia–Pacific $\chi^2 = 3.29$, $P = 0.19$; Pacific–NZ: $\chi^2 = 1.12$, $P = 0.57$).

Face and wing types in combination

In the Australian sample, almost 90% comprised one of 4 face type/wing type combinations, each occurring with similar frequency and involving the 2 most common face types and the 2 most common wing types (Table 4). In contrast, the New Zealand

sample displayed one dominant combination with an additional 5 less-frequent combinations being required to embrace 90% of the sample. The Pacific population also had a dominant face/wing combination, the same as that in New Zealand. By this measure, the New Zealand population is, phenotypically, the most variable of the 3 regional *A. superciliosa* populations. A permutational multivariate analysis of variance (PERMOVA) of the face type/wing type combinations (permutations n = 9999) highlighted statistically significant differences between the Australian population and both others (Australia–Pacific: F = 6.82, P = 0.0003; Australia–NZ: F = 17.17, P = 0.0001) while the difference between the Pacific and New Zealand populations was nearly so (Pacific–NZ: F = 2.34, P = 0.051).

Table 3. Percentage frequency distribution of wing types in *A. superciliosa* from Australia (n = 208), Pacific (n = 50) and New Zealand (NZ, n = 225) regional populations, both sexes combined. Australian data from specimen skins (120) and contemporary photos (88), New Zealand specimens from skins (52) and wings (173) collected before 1970.

Wing type	Australia	Pacific	NZ
1	48.6	36.0	44.0
2	39.9	54.0	47.1
3	11.0	10.0	8.4
4	0.5	-	0.4

Table 4. Percentage frequency distribution of face/wing type combinations in *A. superciliosa* from Australia (n = 208), Pacific (n = 50) and New Zealand (n = 52) regional populations, both sexes combined. Australian data from specimen skins (120) and contemporary photos (88), New Zealand specimens (skins only) pre-date 1970; "-" indicates no occurrence.

Face type	Wing type			
	1	2	3	4
Australia				
1	27.9	19.2	2.4	-
2	20.2	20.7	8.2	-
3	0.5	-	0.5	0.5
Pacific				
1	6.0	12.0	-	-
2	26.0	32.0	6.0	-
3	4.0	10.0	4.0	-
New Zealand				
1	1.9	-	-	-
2	9.6	36.5	13.5	-
3	11.5	13.5	11.5	1.9

Table 5. Percentage frequency distribution of face type/bill colour (n = 165) and face type/leg colour (n = 65) combinations in *A. superciliosa* from Australia, both sexes combined, data from contemporary photographs. "-" indicates no occurrence.

Face type	Bill colour				Leg colour			
	Slate blue	Black + slate blue	Dark green	Black + dark green	Olive-brown (type 1)	Khaki (type 2)	Khaki-yellow	Khaki-orange
1	4.3	-	53.3	2.4	9.2	21.5	10.8	12.3
2	4.3	1.2	32.1	1.2	3.1	29.2	10.8	3.1
3	-	-	1.2	-	-	-	-	-

Bill and leg colour associations with face type
Contemporary photographs of Pacific black ducks in Australia depicted bill colours and patterns not embraced by the Rhymer descriptors. Most (86.6%) Pacific black ducks had a uniformly dark green bill with a terminal black nail while in a further 8.5% the uniform colour was a dark slate-blue, also with a terminal black nail (Table 5). The dark green colour was generally lighter than the dark green recorded on type 2 grey duck bills. A small number (4.9%) had a conspicuous black base to their upper mandible with the dark green or slate-blue colour

extending forwards from about the nares. None had uniformly black or dark slate type 1 bills.

Four leg colours were discriminated (Table 5): leg types 1 (12.3%) and 2 (50.8%) and two colours distinctly intermediate between the khaki (leg type 2) and yellow-orange (leg type 3) Rhymer descriptors. These were perceived as a light khaki but with either a discernible yellow or orange over-tone, being displayed by 37% of the sample, and by ducks from most Australian states.

Bills of 50 New Zealand specimens (Table 6) were uniformly dark slate/black (44%) or had basal

dark green on an otherwise dark slate/black upper mandible (52%) while leg colour was restricted to shades of olive green or khaki. No hints of yellow or orange hues to the legs were recorded.

No photographs of live Pacific specimens were viewed. Rothschild & Hartert (1905, 1914) refer to bills being "slate and black" and legs being "dull pale clay-yellow" and "dull tan colour". ANWC collection records for 12 specimens from eastern New Guinea and Bougainville record bill colour as "grey-black" (5) and "grey-green" (7), and leg colour as "yellow-brown" (4), "grey-fawn" (3), and green-yellow-brown" (5).

Table 6. 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 (see Methods).

Face type	Bill type			Leg type	
	0	1	2	1	2
2	32	28	4	40	24
3	12	24	-	20	16

Body measurements
Bill length
There were no statistical differences in bill lengths for either sex between the Australian and New Zealand samples (Table 7). However, bill lengths of both sexes of the Pacific Melanesian cohort were significantly shorter than those of both Australian and the New Zealand samples (males: northern Australia t_{15} = 6.79, southern Australia t_{16} = 6.27, NZ t_{16} = 5.76, all P <0.0001; females: northern Australia t_{20} = 9.58, southern Australia t_{32} = 11.59, NZ t_{22} = 7.54, all P <0.0001).

Few bill lengths of Pacific Oceanic cohort birds were obtained, however, Amadon (1943) recorded a mean of 45.6 mm (range 42–50 mm) for 16 males from eastern and central Polynesia along with 48.4 (range 46–51 mm) for 5 males and 45.4 (range 42.5–48 mm) for 19 males from within the Melanesian region.

Wing length
Wing length, historically used as an indicator of relative body size, demarcates the Pacific population from the others (Table 7). Within the Pacific population, wing lengths of neither males nor females of the Oceania and Melanesian cohorts differed (males t_{34} = 1.42, P = 0.17; females t_{28} = 1.63, P = 0.11). Wing lengths of females in the northern and southern Australian cohorts did not differ ($t_{=40}$ = 1.67, P = 0.11) but males did so (t_{45} = 3.05, P = 0.004). Wing lengths of New Zealand and southern

Australian specimens were similar (males t_{35} = 0.43, P = 0.67; females t_{21} = 0.37, P = 0.72) and whereas northern Australian and New Zealand females had similar wing lengths (t_{27} = 1.68, P = 0.10), male wing lengths differed significantly (t_{36} = 2.65, P = 0.02). The main distinction therefore was between the combined Pacific cohorts (male: = 238 mm, *sd* = 6.9, n = 53; female: = 225 mm, *sd* = 7.6, n = 57) and all others and exemplified by the significance of the differences between them and the northern Australian cohort for both males (t_{59} = 7.58; P < 0.0001) and females (t_{38} = 7.49; P = 0.0001).

Historic wing measurements of Pacific region specimens are included in Table 7. These include wing lengths for 7 unsexed lesser grey ducks sourced from coastal wetlands near present-day Jayapura (West Irian) (211, 214, 221, 221, 224, 226, 230 mm) and data from Amadon's (1943) review.

Weights
Body weights were recorded in ANWC specimen records, but not in other collections. Male Pacific region specimens from Bougainville and eastern lowland New Guinea averaged 655 g (*sd* = 34, n = 6) and females 643 g (*sd* = 73, n = 6). Male northern Australian specimens averaged 1,088g (*sd* = 104, n = 14) and females 926 g (*sd* = 90, n = 4) while males and females from southern Australia weighed 1,077g (*sd* = 36, n = 16) and 962 g (*sd* = 103, n = 16) respectively. Comparative body weights of southern Australian and New Zealand ducks were reported by Williams (2017a) and indicated Australian birds of both sexes to be significantly heavier than New Zealand birds.

DISCUSSION
Face and wing patterns
All three *A. superciliosa* populations displayed variability in face and wing plumage patterns (types) but the same plumage patterns were identified in all. The principal difference between populations was the frequency of patterns within each; the differences in regional frequency distributions of face types being statistically significant, and while those of wing types were not, the combination of face type and wing type confirmed significant regional differences.

The most conspicuous difference in plumage was the near complete absence of face type 1 in New Zealand, a distinct contrast to its prominence in Australian specimens. It occurred in just 1 of the 52 New Zealand specimens examined, on a duck collected on Campbell Island, 1943 (MoNZ OR13047). It was not depicted in surviving photographs of 74 grey duck and grey duck-like specimens collected in 1991. By its apparent rarity in New Zealand, this character may serve to identify a

Table 7. Regional bill and wing lengths (mm), presented as mean $\bar{x}$ (standard deviation *sd*, sample n) of male and female *A. superciliosa*. Data from measurements of specimen skins made during this study, and from [a] Rand (1942), and [b] Amadon (1943).

Region	Male		Female	
	Bill length $\bar{x}$ (sd, n)	Wing length $\bar{x}$ (sd, n)	Bill length $\bar{x}$ (sd, n)	Wing length $\bar{x}$ (sd, n)
Oceania: Fiji, Tonga, Cook Is., Samoa, Tahiti, Micronesia	45.6 (-, 16[b])	239 (5.5, 30[a,b])	41.8 (2.0, 6)	227 (4.1, 32[a,b])
Melanesia: Solomon Is., Vanuatu, New Caledonia, Bougainville, eastern New Guinea lowlands	46.2 (3.1, 12)	236 (8.9, 23[b])	41.5 (1.9, 12)	223 (11.7, 25[b])
Northern Australia (north of latitude 26°S), New Guinea highlands, Indonesian Islands	52.9 (2.0, 23)	251 (8.4, 34[a,b])	49.1 (1.9, 11)	241 (9.4, 25[a,b])
Southern Australia, Tasmania, Macquarie Is.	52.4 (2.1, 25)	258 (7.5, 24)	49.4 (1.9, 22)	245 (6.3, 18)
New Zealand: North & South Is., Kermadec Is., Campbell Is., Chatham Is.	52.0 (1.9, 17)	257 (7.2, 17)	48.0 (2.4, 13)	246 (8.3, 13)

recent traverse of the Tasman Sea to New Zealand.

An equally conspicuous feature of face type distribution amongst the 3 populations was the near complete absence of face type 3 in Australia and its common (36.5%) occurrence in New Zealand. This pattern was at low frequency (18%) amongst Pacific specimens, but no more so than face type 1. The relatively high frequency of face type 3 in New Zealand suggests it is either a regional characteristic or an outcome of past hybridisation with early introduced mallard. That it occurred in association with all wing types with equal frequency implies the former.

The similar wing type frequency distributions for all populations clarifies that an observable thin whitish alar bar (wing type 3) is characteristic of the species and not necessarily indicative of hybridisation with mallard (contra Gillespie 1985; *https://ebird.org/newzealand/news/grey_ducks* - viewed 1 Nov. 2018). However, it is not a common character; both wing types 1 and 2 with no or a faintly discernible alar bar were considerably more abundant everywhere.

Bill and leg colours

Contemporary photographs of Pacific black duck revealed bill patterns and colours not shown by any of the grey ducks examined. While the dark green and slate-blue colours common to all Pacific black ducks occurred at the base of some grey duck bills (bill type 2), no bill was uniformly of either colour. Pacific black duck bills are distinctly different from those of grey ducks, and, like the type 1 face, its occurrence in a "grey duck" may indicate an Australian *A. superciliosa* having reached New Zealand.

Bills and legs of Pacific specimens have not been appraised sufficiently to establish the extent to which they share similarities with the other 2 regional populations.

Bill and wing measurements

The smallness of Pacific specimens relative to those from Australia and New Zealand has been confirmed. Previous examinations by Hartlaub & Finsch (1872), and Rothschild & Hartert (1905, 1914), who recorded wing lengths of 207–230 mm, and by Amadon (1943), all emphasised the relative smallness of the *pelewensis* taxon. The few weights presented above similarly contrast with those of Australian specimens. Pacific specimens are not slightly smaller than those elsewhere (Fullagar 2005), they are demonstrably and significantly smaller.

The Australian regional population may not be mensurably uniform. Wing lengths of male specimens from north of latitude 26°S were significantly shorter than those elsewhere in Australia and in New Zealand (Table 7). Although small sample sizes were involved it may suggest a latitudinal gradation in size of *A. superciliosa* from tropical to temperate regions of Australia.

The lack of mensurable distinction between southern Australian and New Zealand specimens is uninformative because of the small sample sizes involved. Variability in the extent of wing shrinkage as specimens dry (Williams 2017c) could overwhelm any distinction when samples are so few and potential differences small. Based on measurements from live birds, Williams (2017a) concluded southern Australian *A. superciliosa* to be heavier and to have longer wings than those in New Zealand.

For a species extending over 60 degrees of latitude and occupying such diverse land- and waterscapes as sparsely-distributed oceanic islands, tropical and temperate continental islands, and the coastal and interior wetlands of continental Australia it would be remarkable if local adaptations did not arise. Physiological responses to latitude and altitude include those embraced by Bergman's rule (larger bodies at higher latitudes: Olsen *et al.* 2009) while adaptive responses to life on resource-constrained islands are embraced by the "island rule" (changes in body and bill sizes: Clegg & Owen 2002).

Taxonomic considerations
The historic taxonomic subdivision of *A. superciliosa* into 3 geographically-constrained subspecies was very much in the spirit of the times, i.e. by assertion e.g. *rogersi* by Mathews (1912, 1914), or by observation of size differences displayed by few specimens e.g. *pelewensis* by Hartlaub & Finsch (1872), Finsch (1875), and Rothschild & Hartert (1905) and *percna* by Riley (1919). It was left to Amadon (1943) to assemble greater numbers of specimens, especially of *pelewensis* obtained during the American Museum of Natural History's Whitney South Sea Expeditions of the 1920s and 1930s, and to conclude: (i) specimens from the type locality of *pelewensis* (Palau in the Caroline Islands archipelago) and from elsewhere in the Polynesian and part of the Melanesian Pacific were distinctly smaller than specimens of *A. superciliosa* from Australia, New Guinea, and western islands of present-day Indonesia which, by then, were attributed to the taxon *rogersi*; (ii) there was uniformity of wing lengths (considered indicative of body size) in specimens from throughout eastern and central Polynesia but an apparent north–south gradation in wing lengths in birds from western to southern Melanesia; and (iii) there were altitude-related size differences in specimens from New Guinea (e.g. Saruwaged and Oranje mountains) that intergrade between otherwise large (*rogersi*) and small (*pelewensis*) taxa. He appraised only 5 specimens from New Zealand but nevertheless opined "size the same as in *rogersi*".

The modern rejection of these historic sub-divisions appears also to be by assertion (e.g. Marchant & Higgins 1990; Fullagar 2005); no evaluations of size differences between New Zealand and Australian specimens have been presented in support, nor any appraisal of *pelewensis* size variation subsequent to Amadon's. Meanwhile, Williams (2017a) demonstrated small but statistically significant differences in body weight, wing length, and bill length between live New Zealand and Australian *A. superciliosa.* However,

his analysis was hindered by a paucity of published measurements for Australian specimens and the absence of variance statistics accompanying Frith's (1967) compilation (from which all other published listings, e.g. Braithwaite & Miller (1975), Marchant & Higgins (1990) appear to be derived). Similarly, the absence of age distinctions in Frith's and Braithwaite & Miller's (*loc. cit.*) listings precluded more detailed appraisal; body weights and feather measurements of grey ducks in their first year of life were significantly smaller than for older ducks (Williams 2017a).

The short-lived declaration of *A. s. percna* (Riley 1919) is the only taxonomic delineation to have included a plumage distinction. Otherwise, Amadon's (1943) comment, "New Zealand specimens are paler than those from other localities; this is the only geographical colour variation that was found", has been the only comment on plumage variation within the species. As an aside, I concur with Amadon, perceiving live Australian specimens to appear brighter and evince greater contrast between the cream colour of face and throat, buff body feather margins, and the dominant brown body colour than is apparent in wild New Zealand specimens.

As this study demonstrates, there is regional plumage variation within *A. superciliosa*. However, it is one of relative frequency of plumage trait rather than of presence/absence of a trait. The greatest variation was in the relative frequency of face type 1, dominant within the Australian region, rare in the Pacific and seemingly absent in New Zealand. Similarly, face type 3 was common in New Zealand, less common in the Pacific and rare within the Australian population. Bill and leg characteristics also provide a regional contrast. Most Australian bill colours and patterns were not displayed by New Zealand specimens, nor the yellow or orange hues visible on legs of one-third of Australian specimens. By these phenotypic characters, most Australian *A. superciliosa* can be readily distinguished from those in New Zealand.

Historically, sub-specific levels of taxonomy were used to reflect population differentiation based on discernible phenotypic characters (e.g. body size, plumage) which, in turn, were presumed to reflect local adaptation and/or genetic isolation. Modern phylogeographic studies have introduced interpretations of population history that sometimes challenge phenotype-based taxonomic distinctions (Ball & Avise 1992), including for *A. superciliosa*. Rhymer *et al*. (2004) interpreted historic connectivity between the Australian and New Zealand populations as comprising (at least) 2 colonisation events, one historic (Pleistocene) and one more recent (Holocene) from Australia to New Zealand. This explanation of relationships

of mtDNA haplotypes, identified from 34 New Zealand and 21 eastern Australian specimens, highlighted 2 well-separated haplotype lineages divergent to a similar extent to that separating some *A. superciliosa* from mallard and from spotbill ducks (*A. poecilorhyncha*), and exceeding that separating mallard and spotbill ducks. Within one lineage, the single Palau-sourced specimen examined, from the northern extremity of the species' range, was as divergent from contemporary Australian specimens as was one from New Zealand. That 33 separate haplotypes were found in 57 specimens, 27 of which were obtained from just one specimen, implies a substantially more extensive haplotype network within the species than was sampled by Rhymer *et al*. (2004), and potentially, a matrilineal genealogy that may reflect a more complex phylogenetic history.

Rhymer *et al.'s* (2004) appraisal confirmed the presence of 2 well-differentiated matrilineal groupings, one exclusive to New Zealand, the other shared, and reported as displaying no phenotypic difference. However, this study has identified regional phenotypic differences that, by seemingly transcending underlying genetic history, imply local adaptive responses. If sub-specific differentiation is reflective of local adaptation, and since that adaptation can be discriminated by differences in body size (e.g. between Pacific and Australian/New Zealand specimens), and in plumage patterns (e.g. face type 1 and bill and leg colours between Australian and New Zealand specimens), perhaps a re-acceptance of the 3 historic geographically-constrained subspecific taxonomy could be contemplated.

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