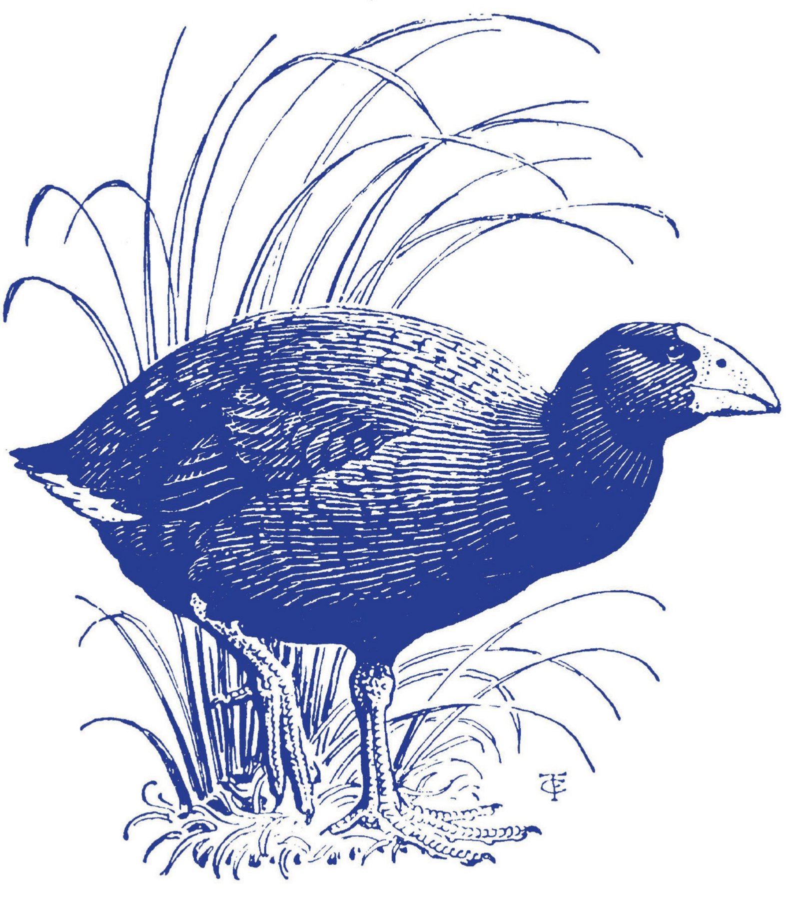
NOTORNIS

Ornithology of the Southern Pacific



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NOTORNIS

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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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Key words: mallard, *Anas platyrhynchos*, grey duck, *Anas superciliosa*, hybridisation, New Zealand

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.

Face type	Grey-like	Mallard-like	
		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

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, 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.

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.

Wing type	Grey-like	Mallard-like	
		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).

	Wing type			
Face 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

Face type	Wing 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).

Face type	Bill type			Leg 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.

Face type	Bill type				Leg 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.

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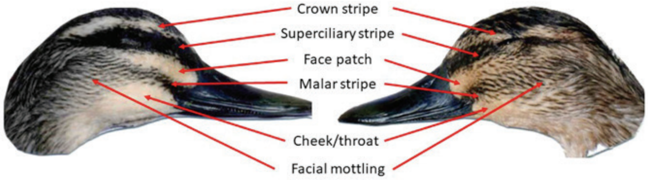
Appendix. Phenotype descriptors of face, wing, bill and leg used in this study (modified from Rhymer *et al.* 1994), with comments on their use as diagnostic field characters to discriminate grey ducks, grey-like ducks, and mallard-like ducks.



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.

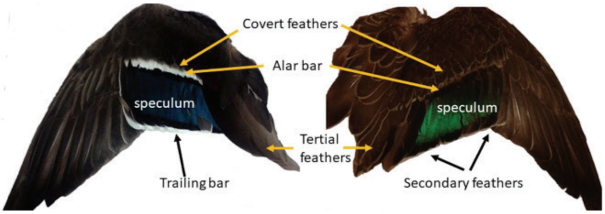
Type 4: Crown and nape mottled dark grey/black. A mottled black superciliary stripe extends from lateral crest of bill, through the eye to back of head, narrowing posteriorly. Short dark mottled malar stripe merges with extensive facial mottling well forward of eye. **Crown stripe is mottled fawn, face 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).

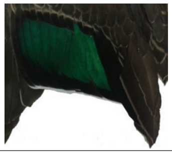
Type 6: Entire face and head has greenish lustre, either heavily mottled or entirely iridescent green. Shown by mallard drakes developing or having acquired nuptial colouration.

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).

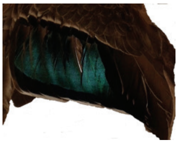
Wing descriptors



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.

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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.

Williams, M. 2019. Phenotypic variability within and between regional populations of *Anas superciliosa* (Anatidae). *Notornis 66(2)*: 64–73.

Key words: grey duck, Pacific black duck, lesser grey duck, *Anas superciliosa*, phenotype, taxonomy

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.

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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)

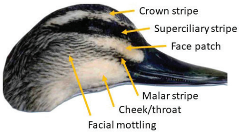
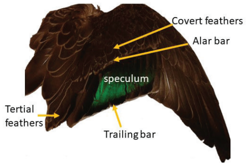
and confirmed to carry grey duck mtDNA, and, by their phenotype scoring system which assigned scores to head, wing and leg patterns, all to have a phenotype score of 5 (see below). The leg and bill characteristics reported here derive from all ducks in the 1991 collection with a Rhymer phenotype score 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 buff 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 overtone, 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 subdivisions 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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Breeding petrels of Chalky and Preservation Inlets, southern Fiordland – a test of the 'refugia from resident stoats' hypothesis

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Abstract: Forty breeding colonies of three petrel species were found on 35 of 71 islands surveyed in southern Fiordland, Fiordland National Park, New Zealand, in November and December 2017. Almost all islands in Chalky Inlet, Preservation Inlet, Cunaris Sound, Long Sound, and Isthmus Sound were surveyed. Sooty shearwater (*Ardenna grisea*) was the most widespread and abundant species, with an estimated 23,425 burrows on 25 islands. Broad-billed prions (*Pachyptila vittata*) were breeding on nine islands (9,940 burrows estimated), and mottled petrels (*Pterodroma inexpectata*) on five islands (1,240 burrows estimated). This is a 3-fold increase in the number of petrel colonies in Chalky and Preservation Inlets and associated waterways identified in published accounts, and the first estimate of the number of burrows on each island. Long-term survival of most of these colonies is dependent on ongoing control of stoats (*Mustela erminea*) on islands in these southern fjords. The persistence of remnant petrel colonies on small islands is probably due to stoats being infrequent invaders that are unable to persist when migratory petrels depart at the end of the breeding season.

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INTRODUCTION

The glaciated landscapes of Fiordland, in south-western New Zealand, contain many hundreds of islands that are within the broad breeding ranges of at least seven species of burrow-nesting petrels (Procellariiformes) – breeding ranges summarised in Marchant & Higgins (1990), and Taylor (2000a & b). While a few Fiordland breeding sites of mottled petrel (*Pterodroma inexpectata*) have been known for several decades (Warham *et al.* 1977; Taylor 2000b), information on burrowing seabird diversity, distribution, and colony sizes in the region remain poorly known, and many authors have recommended the need for further surveys (e.g. Taylor 2000b; Waugh *et al.* 2013; Jamieson *et al.* 2016; Wildland Consultants & Department

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of Conservation 2016). A first step to filling this information void occurred in November 2016, when a survey of 56 islands in Dusky Sound located 49 breeding colonies of three petrel species, with 27,640 burrows estimated (Miskelly, Tennyson *et al.* 2017). We here report the findings of a subsequent survey for petrels on islands in Chalky Inlet, Preservation Inlet and associated waterways in November and December 2017, and compare and contrast these results with those from the 2016 survey. Information on petrels breeding on the Green Islets, 16 km south-east of Preservation Inlet, is also presented based on surveys undertaken in December 2013 and 2018.

Chalky Inlet and Preservation Inlet and their connected inland waterways of Edwardson, Cunaris, Isthmus, and Long Sounds are the southernmost fjords in Fiordland. Each of the two major inlets is partially protected from the open sea by a single large island (Chalky Island and Coal Island respectively), and between them they contain more than 70 vegetated islands (Figs 1-3, and see Department of Conservation 2017). Conservation management on these islands has included some of the earliest stoat (*Mustela erminea*) eradications in New Zealand, on Chalky Island (514 ha) and the Passage Islands (177 ha) in 1999, followed by Coal Island (1,163 ha) in 2005 (Elliott *et al.* 2010; Department of Conservation 2017), and subsequent translocations of seven species of rare and threatened land birds to these islands (Miskelly & Powlesland 2013; Department of Conservation 2017; Miskelly *et al.* 2018).

Three species of petrels have been reported breeding in Chalky and Preservation Inlets. The earliest record was of mottled petrels breeding at an unspecified site on the South Island mainland in Preservation Inlet (Buller 1892), with more recent reports of this species from Single Tree Island in Preservation Inlet and on a nearby islet in Isthmus Sound (Morrison & Morrison 1982; McEwen 1987; McLean *et al.* 1993; Peat & Patrick 1996; Miskelly *et al.* 2019). Broad-billed prions (*Pachyptila vittata*) were found breeding on Zero Nugget and Finger Rock off the north coast of Chalky Island in 1986 (Kim Morrison in Cooper 1986; Miskelly, Tennyson *et al.* 2017), and sooty shearwaters (*Ardenna grisea*) were reported from Chalky Island, Great Island, Passage Islands, Garden Islands, and Small Craft Harbour Islands in Chalky Inlet (McLean *et al.* 1993; Miskelly, Tennyson *et al.* 2017) and Spit Island, Round Island, Single Tree Island, and outer Cording Island in Preservation Inlet (Miskelly, Tennyson *et al.* 2017 – based mainly on information provided by Pete Young).

Apart from the eradication of stoats on Chalky, Passage and Coal Islands, and the 2008 eradication of mice (*Mus musculus*) on Coal Island (Elliott *et al.* 2010; Department of Conservation 2017), little information has been published on the presence of introduced predators on islands in Chalky and Preservation Inlets. Stoats are presumed to have reached the area *c.* 1900, based on the documented date of their arrival in nearby Dusky Sound (Hill & Hill 1987). All the islands in Chalky and Preservation Inlets are within the swimming range of stoats (Elliott *et al.* 2010; Veale *et al.* 2012). Until their eradication, stoats were resident on the two most seaward islands (Chalky Island and Coal Island; Department on Conservation 2017), and they have been detected on at least 11 islands that are further inland (King & Murphy 2005; Veale *et al.* 2012, and data presented herein). Apart from sites exposed to extreme wave action, it is likely that stoats have periodically reached all the islands in these waterways.

Chalky and Coal Islands, and both of the Passage Islands, plus Steep-to Island (58 ha) in Preservation Inlet are now considered to be free of all introduced mammals (Department of Conservation 2017). Self-resetting traps with lures designed to attract both stoats and rats *Rattus* sp. are maintained on many of the smaller islands in the two inlets (Colin Bishop and Lindsay Wilson, Department of Conservation *unpubl. data*).

We report on a survey to identify the petrel species breeding, and estimate the number of burrows, on 71 islands in Chalky Inlet, Cunaris Sound, Preservation Inlet, Long Sound, and Isthmus Sound. We attempt to explain the distribution of petrel colonies on these islands based on stoat and petrel behaviour and ecology, and specifically in the context of the 'refugia from resident stoats' hypothesis proposed by Miskelly, Tennyson *et al.* (2017) to explain the paradox of numerous petrel colonies persisting on islands that are accessible to stoats. This hypothesis predicts that populations of migratory petrels will persist for many decades on islands that are within swimming range of stoats, provided that the islands are too small to provide sufficient permanent food resources to sustain a resident stoat population year-round. It is assumed that stoats are unable to extirpate a petrel population during a single invasion due to a proportion of the petrel population being absent from the colony (particularly pre-breeders), and (at larger colonies) due to the sheer number of potential prey present, with the stoats having to vacate the island once the migratory petrels depart at the end of the breeding season.

The minimum island size that can support a resident stoat population is unclear. King & Murphy (2005: 266) named Chalky Island (514 ha) as the smallest island in New Zealand known to have supported a permanent population of stoats (before they were eradicated in 1999), while Veale *et al.* (2012) suggested that stoats were resident on 57 ha Motuoruhi Island (near Coromandel) based on eight stoats being caught there during initial trapping, and considered islands under 50 ha to be too small for a resident stoat population to establish. On small islands it is assumed that stoat invasion events have been too brief and infrequent to kill all individuals of all age classes of the breeding petrels during the *c.* 120 years since stoats reached southern Fiordland. In contrast, petrels will be rapidly extirpated from islands that are large enough to sustain resident stoats.

METHODS

A boat-based survey of islands in Chalky Inlet, Cunaris Sound, Preservation Inlet, Long Sound, and Isthmus Sound, Fiordland National Park, south-west New Zealand, was undertaken 20–25 November 2017, with a primary focus of locating petrel breeding colonies. Outer headlands of Great Island, Chalky Inlet, were surveyed by Colin Bishop on 19 December 2017. Information on breeding petrels on the Green Islets (46.228°S, 166.800°E) is included following surveys undertaken there on 13 December 2013 and 15 December 2018 (Colin Bishop *unpubl. data*; Rebecca Jackson & Ben Barr *pers. comm.* to CMM Jan 2019; James Reardon *pers. comm.* to CMM 19 Feb 2019).

The November timing of the main survey was chosen to maximise the chance of simultaneously locating the three petrel species known to breed in Fiordland (broad-billed prion, mottled petrel and sooty shearwater), and in the knowledge that other possible breeding petrel species would also be present at colonies at this time of year. Landings were made from a small inflatable dinghy, with 1–7 team members landing on each island for between 5 min and 3 h 45 min (mean = 46 min, median = 30 min; Appendix 1). Most landings were during daylight, with two islands landed on at night. Spot-lighting was undertaken from the deck of the main vessel (the 22 m M.V. *Southern Winds*) while anchored or moored at night at five locations. Great Island was surveyed during a 9 h visit a month later.

Seventy-one islands were surveyed for the presence of burrow-nesting petrels by 1 or more team members. Few of the islands had individual names on available maps and charts (where most are named as clusters of islands), and so we created tag names mainly based on island size and location within each cluster. A central latitude and longitude reference point for each island is provided in Appendix 1.

Petrel burrow entrances were searched for and counted on each island during walk-through surveys. The proportion of each island surveyed was estimated, with the estimated number of burrows on each island based on the actual count extrapolated to allow for areas not surveyed. On large islands where burrows were apparently confined to a portion of the island, we estimated the proportion of the colony (rather than the entire island) that we surveyed. Landings were too brief to allow repeat surveys and estimation of error intervals. The accuracy of each estimate will vary in direct proportion to the proportion of each island surveyed (i.e. the ratio between counted and estimated burrows on each island, which varied between 0.4% and 100%).

The petrel species present were identified by any of: adults or chicks extracted from burrows or seen on the colony surface or in collapsed burrows; vocalisations from birds inside burrows; corpses, plucked feathers (by New Zealand falcons *Falco novaeseelandiae*) or failed eggs on the colony surface; burrow location and burrow entrance size. Any intact eggs were measured (length x maximum width) as a guide to species identification.

Basal areas of islands were obtained from ArcGIS. Distance from the sea for each island was estimated from Google Earth, as a straight-line distance from the midpoint of the nearest fjord entrance (north-west or south-east of Chalky or Coal Islands), based on straight lines between outer headlands of these two large islands and adjacent South Island headlands.

Distances from resident (or historically present) stoat populations are the shorter of the minimum straight line distance between the island and the nearest part of the South Island mainland (or other site with resident stoats), or the cumulative water gaps between 'stepping stone' islands (*sensu* Elliott *et al.* 2010) where present.

RESULTS

Evidence of breeding petrels was found on 35 islands in Chalky Inlet, Preservation Inlet, Cunaris Sound, Long Sound, and Isthmus Sound in November and December 2017, and on five of the Green Islets in December 2013 and 2018. Petrel breeding islands ranged in size from 0.02 to 727 ha, and were up to 29 km from the open sea (Tables 1–3). We found mottled petrel burrows, sometimes within a couple of metres of the shore, mainly on small low-lying islands, and usually among dense ground cover of moss and ferns. In contrast, sooty shearwater burrows (which had larger entrances) were mainly found in areas with less ground cover on the upper slopes and island summits of larger islands. Broad-billed prion burrows were smaller than for the two other species, and were mainly found on the tops of steep-sided stacks on exposed outer coasts.

Table 1. Evidence for mottled petrel presence on islands in southern Fiordland in November 2017, with the estimated number of burrows on each island (based on the proportion of each island surveyed). Islands are presented in a loop from Cunaris Sound to Chalky Inlet, then Preservation Inlet, and Isthmus Sound, finishing in Long Sound. See Appendix 1 for island locations and search effort.

Island name	Area (ha)	Distance from sea (km)	Evidence	Burrows counted	Estimated burrows on island
Small Craft Harbour Is 'north-east island'	2.2	14.9	small burrow	1	0
Small Craft Harbour Is 'small middle islet'	0.1	13.8	burrows, corpses, bird landed at night	28	35
South of Stripe head – north-east islet	0.1	7.9	small burrow	1	0
North Passage Island	8.7	4.7	small burrow	4	0
Passage I. south coast stack 6	0.1	3.5	empty burrows, feather	2	0
Passage I. south coast stack 5	0.02	3.6	burrows, adult	25	100
Chalky Island	453.0	0	burrows	55	155
Cording Island (main)	24.5	7.4	old inactive burrows	27	0
Cording Is, '35 spot height'	3.6	8.5	old inactive burrows	5	0
Single Tree Island	0.3	6.9	burrows, corpses,	326	450
Isthmus Sound Islet	1.8	9.8	burrows, skull, eggs, feathers	258	500
'Only islet'	0.2	29.0	old burrows, egg - not active	25	50
Total (5 active sites)	455.2	-		692	1,240

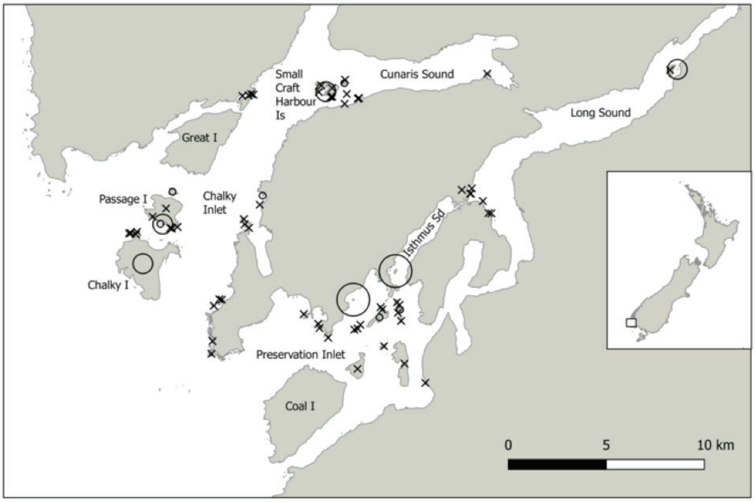

Figure 1. Distribution of mottled petrel colonies surveyed in Chalky Inlet, Preservation Inlet, Cunaris Sound, Long Sound, and Isthmus Sound in 2017. Circle sizes denote colony size, with large circles showing colonies with 400–500 burrows estimated, medium circles 30–160 burrows estimated, and small circles sites with fewer than 30 old or inactive burrows estimated. Crosses show islands visited without mottled petrels being recorded.

Mottled petrel (*Pterodroma inexpectata*)

Mottled petrels, or their burrows, were found on up to 12 islands, although on seven islands only old, inactive burrows were found, or evidence was based solely on burrow size (Table 1, Fig. 1). The five sites with substantial active colonies were Single Tree Island, the islet in Isthmus Sound, Chalky Island, a stack off the south coast of Passage Island, and a small islet within the harbour of Small Craft Harbour Islands.

Apart from Chalky Island (which is on the outer coast), these sites were 3.6–14 km from the open sea. An apparently vacated mottled petrel colony was found on the islet alongside Only Island in Long Sound, 29 km from the sea. With the exception of 453 ha Chalky Island, the four other active mottled petrel breeding sites were on very small low-lying forested islands of 0.08–1.8 ha.

The only live mottled petrel handled was on a stack off the south coast of Passage Island, but corpses or skulls were found on three islands, and failed eggs on two islands (Table 1). An intact egg from 'Only islet' measured 56.6 x 42.2 mm.

Single Tree Island and the islet in Isthmus Sound were the two largest colonies (450–500 burrows estimated on each), and were the only mottled petrel breeding sites previously known from the area (Miskelly *et al.* 2019). The highest actual burrow count was 326 burrows on Single Tree Island, and the total burrow estimate for the five islands with active burrows was 1,240 (Table 1).

The only mottled petrel island that we landed on at night was the small islet within the harbour of Small Craft Harbour Islands on the night of 24 November 2017. Many birds were calling in flight and one was heard to land among the vegetation, but no birds were seen on the ground. Mottled petrels were heard and seen in flight at three of the five spot-lighting locations (Table 2), all of which were alongside breeding islands.

Table 2. Petrels observed during spot-lighting sessions at five sites in southern Fiordland in November 2017. Minimum number of individuals (MNI) is the maximum number of birds seen at any one time; in most cases the actual number of individuals will have been higher than this, with an upper limit indicated by the number of sightings. Scientific names for all six species are given in the text.

Date	Location	Timed search	Petrels observed (MNI)
20 Nov	Off Only Island, Long Sound	2238 – 2338 h	Grey-backed storm petrel 1 (7 sightings)
21 Nov	Near Single Tree Island, Preservation Inlet	2300 – 2340 h	Mottled petrel 8 (continuously present) Sooty shearwater heard
22 Nov	Sealers Bay, Chalky Island	2255 – 0040 h	Mottled petrel 5 (continuously present) Broad-billed prion 1 caught Antarctic prion 1 caught Sooty shearwater 3 (continuously present; 1 caught) Common diving petrel 2 caught Grey-backed storm petrel 2 (4 sightings; 1 caught)
23 Nov	West of Little Island, Chalky Inlet	2255 – 2330 h	Nil
24 Nov	Small Craft Harbour, Chalky Inlet	2345 – 0015 h	Mottled petrel 2 (7 sightings) Sooty shearwater 1 (3 sightings; 1 caught) Grey-backed storm petrel 1

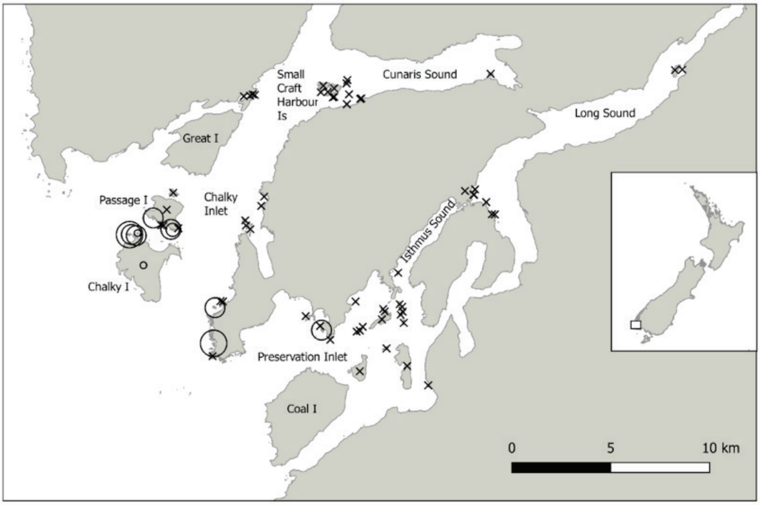

Figure 2. Distribution of broad-billed prion colonies surveyed in Chalky Inlet, Preservation Inlet, Cunaris Sound, Long Sound, and Isthmus Sound in 2017. Circle sizes denote colony size, with very large circles showing colonies with 1,000–7,500 burrows, large circles 100–900 burrows, and medium circles 10–25 burrows estimated. Small circles denote sites with fewer than 30 old or inactive burrows estimated. Crosses show islands visited without broad-billed prions being recorded.

Broad-billed prion (*Pachyptila vittata*)

Broad-billed prions were found breeding on nine small islets or stacks up to 0.2 ha, mainly in outer Chalky Inlet within 4 km of the open sea (Table 3, Fig. 2). All sites were close to adjacent shores (the South Island mainland, Chalky Island or south Passage Island), but were in high energy environments exposed to strong wave action.

The largest colony was of an estimated 7,500 burrows on an unnamed stack ('Riki Rock') west of Gulches Head (the headland separating Chalky and Preservation Inlets), with 1,000 burrows estimated on the main Zero Nugget (off the north-west coast of Chalky Island). The total population estimate on the nine sites was 9,940 burrows.

Prions were nesting under kokomuka (*Veronica elliptica*) and shore spleenwort (*Asplenium obtusatum*) at densities up to 3 burrows/m^{2}. Large downy chicks were found on one stack, eggs on three additional sites, and corpses or feathers on six further sites, although two prion kill sites (by New Zealand falcons) on Chalky Island may have

Table 3. Evidence for broad-billed prion presence on islands in southern Fiordland in November 2017, with the estimated number of burrows on each island (based on the proportion of each island surveyed). All sites are in Chalky Inlet apart from the last, which is in Preservation Inlet. See Appendix 1 for island locations and search effort.

Island name	Area (ha)	Distance from sea (km)	Evidence	Burrows counted	Estimated burrows on island
Passage I. south coast stack 7	0.2	3.4	burrows, 5 falcon kills	80	500
Passage I. south coast stack 4	0.1	3.7	burrows, feathers	50	100
Passage I. south coast stack 3	0.1	4.0	burrows, down	10	10
Zero Nugget (main)	0.1	1.9	burrows, 12 corpses, 3 eggs	367	1,000
Zero Nugget (eastern)	0.03	1.9	burrows, 2 corpses, old egg	20	100
Finger Rock (inner)	0.1	2.1	burrows	12	250
Finger Rock (tall stack)	0.04	2.2	old burrows, old egg	16	0
Chalky Island	453.0	0	possible burrow, 2 falcon kills	0?	0
'Hebe pyramid'	0.1	1.0	burrows, 5 chicks	58	240
'Riki Rock'	0.2	0	burrows, corpse	30	7,500
Southern stack west of Cavern	0.1	4.9	burrows, feathers	58	240
Total (9 active sites)	0.9	-		685	9,940

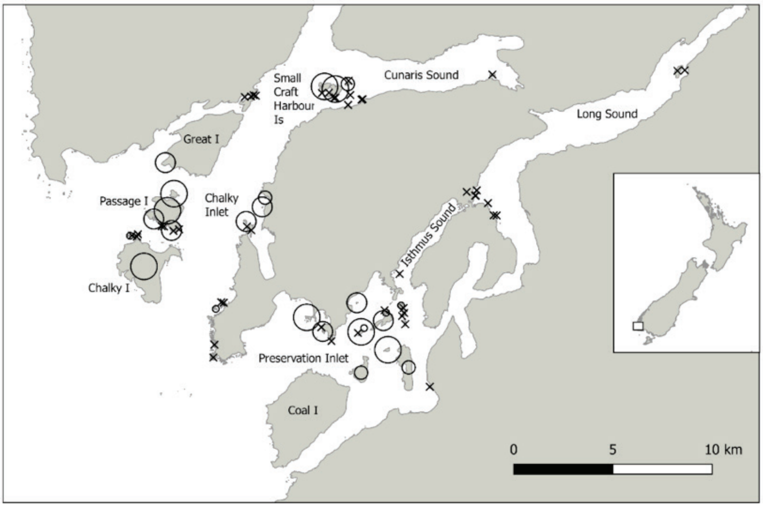

Figure 3. Distribution of sooty shearwater colonies surveyed in Chalky Inlet, Preservation Inlet, Cunaris Sound, Long Sound, and Isthmus Sound in 2017. Circle sizes denote colony size, with very large circles showing colonies with 1,400–5,000 burrows, large circles 100–780 burrows, and medium circles 20–75 burrows estimated. Small circles denote sites with fewer than 4 burrows found. Crosses show islands visited without sooty shearwaters being recorded.

been of birds captured on adjacent islets (Table 3). Three failed eggs measured 51.7 x 35.0 mm (eastern Zero Nugget), and 47.5 x 34.4 mm and 48.9 x 36.0 mm (main Zero Nugget).

An adult broad-billed prion landed on the deck of M.V *Southern Winds* during a spot-lighting session off Sealers Bay, Chalky Island, on 22 November 2017 (Table 2). No prions were seen at the four other more inland spot-lighting sites.

Sooty shearwater (*Ardenna grisea*)

The sooty shearwater was the most widespread and abundant petrel species found during the survey, with an estimated 23,425 burrows on 25 islands (Table 4, Fig. 3). Excluding islands where fewer than 5 burrows were seen or estimated, sooty shearwaters bred on 20 islands that were 0.05–727 ha in size (mean 80 ha), and 0–15 km (mean 6.8 km) from the open sea.

Our survey was about a week before peak egg-laying (Warham *et al.* 1982), and no fresh eggs were found. Old eggs were found on five islands in Chalky Inlet (Table 4), with two eggs sufficiently intact for full measurement: 75.5 x 46.1 mm (Chalky Island), and 79.0 x 48.4 mm (Small Craft Harbour Islands, western main island).

The largest colony was on north Passage Island (5,000 burrows estimated), with colonies of 1,400 to 3,500 burrows estimated on 7 other islands (Table

Table 4. Evidence for sooty shearwater presence on islands in southern Fiordland in November and December 2017, with the estimated number of burrows on each island (based on the proportion of each island surveyed). Islands are presented in a loop from Cunaris Sound to Chalky Inlet, then Preservation Inlet. See Appendix 1 for island locations and search effort.

Island name	Area (ha)	Distance from sea (km)	Evidence	Burrows counted	Estimated burrows on island
Small Craft Harbour Is ‘north-east island’	2.2	14.9	burrows	16	20
Small Craft Harbour Is ‘main east island’	24.2	14.1	burrows	141	1,400
Small Craft Harbour Is ‘main west island’	18.2	13.8	burrows, 5 corpses, 2 eggs, bird calling	507	2,150
South of Stripe Head – north-east islet	0.1	7.9	burrows	59	75
South of Stripe Head – south-west islet	0.1	7.5	burrows, 2 corpses	196	250
Garden Island (outer)	1.0	5.9	burrows, 5 corpses	564	780
Great Island[1]	726.9	5.2	burrows	50	200
North Passage Island	8.7	4.7	burrows	492	5,000
South Passage Island	167.9	4.0	burrows, egg	265	1,400
Passage I. south coast stack 7	0.2	3.4	burrows, corpse	92	200
Passage I. south coast stack 4	0.1	3.7	burrows, skull, egg	50	100
Zero Nugget (main)	0.1	1.9	burrows, old egg	2	2
Chalky Island	453.0	0	burrows, egg	918	3400
‘Hebe pyramid’	0.1	1.0	burrows	2	2
Spit Island	2.0	4.7	burrows	60	2,500
Stack west of Cavern Head	0.1	4.9	burrows	156	450
Steep-to Island	57.6	5.2	burrows	11	20
Weka or Long Island	109.7	8.6	burrows	28	40
Round Island	2.6	7.1	burrows	141	1,400
Cording Islands (outer)	3.7	6.1	burrows, 3	669	3,500
Cording Is, outer (NW islet)	0.4	6.4	burrow	1	1
Cording Islands (main)	24.5	7.4	burrows	47	200
Cording Is, NW islet (inner)	1.6	7.7	burrows	2	2
Cording Is, ’28 spot height’	4.3	8.5	burrows	3	3
Single Tree Island	0.3	6.9	burrows, feathers	230	330
Total	**1,609.5**	**-**		**4,700**	**23,425**

4, Fig. 3). Most burrows were under tall forest on island summits and spurs.

No live sooty shearwaters were seen in burrows or on the ground, but one was heard calling from a burrow at night on western main island of the Small Craft Harbour Islands on 24 November 2017, and several were calling from Single Tree Island on the night of 21 November (heard from offshore). Sooty shearwaters were common north-west of Chalky Inlet as we travelled from and to Dusky Sound on 20 & 25 November, but were not seen within the fjords during the daytime. At night while spotlighting, many sooty shearwaters were seen in flight off Chalky Island on 22 November and at least one bird in Small Craft Harbour on 24 November (Table 2).

Other petrel species

Three further petrel species were observed and captured during the spot-lighting session off Chalky Island on 22 November 2017 (Table 2). Two of these species, common diving petrel (*Pelecanoides urinatrix*) and grey-backed storm petrel (*Garrodia nereis*) are known or likely to breed nearby (Appendix 2; Miskelly, Stahl & Tennyson 2017). The nearest known breeding site for common diving petrel is on the Green Islets, 27 km south-east of Chalky Island (Appendix 2). The storm petrel and one of the two diving petrels had bare brood patches indicative of birds incubating or brooding. The Antarctic prion (*Pachyptila desolata*) and the second diving petrel had downy brood patches. Additional sightings of grey-backed storm petrels were made during spot-lighting sessions off Only Island in Long Sound and the Small Craft Harbour Islands at the entrance to Cunaris Sound (Table 2). Two diving petrels were seen off the entrance to Preservation Inlet during the day on 20 November 2017. Subantarctic skua (*Catharacta antarctica*) prey remains on the Green Islets on 15 December 2018 included a broad-billed prion (on the largest islet south of the headland to the west), a Cook's petrel (*Pterodroma cookii*), and three common diving petrels, but it is likely that some of these birds were caught at sea.

Spatial segregation of petrel breeding colonies in southern Fiordland

The 2016 and 2017 surveys between them located 95 breeding colonies of three petrel species on 83 islands in southern Fiordland (data herein and in Miskelly, Tennyson *et al.* 2017, plus unpublished data for four additional sites between Dusky Sound and Breaksea Sound surveyed in November 2017 held by the authors). Apart from two petrel species found breeding on each of 12 islands, the three species for the most part were found as single-species colonies on separate islands that can be categorised for each species based on island size and distance from the open sea (Fig. 4).

Sooty shearwaters bred mainly on medium to large islands (1–1,000 ha) within 15 km of the open sea. Mottled petrels were found mainly on very small islands (less than a hectare) up to 27 km from the sea, with nine colonies more than 20 km from the sea. Broad-billed prions were mainly found on very small steep-sided stacks (less than 0.3 ha) within 5 km of the open sea, with most sites on the exposed outer coast or receiving no shelter from other islands. Low numbers of sooty shearwaters were often found among larger colonies of the two other species, but mottled petrels and broad-billed prions were not found breeding on the same island.

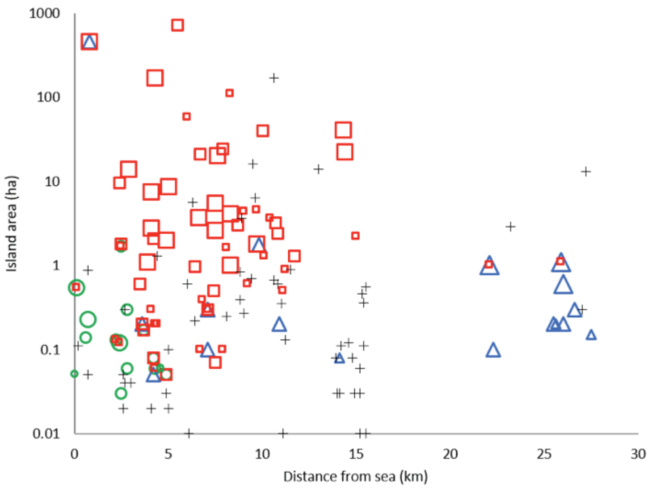

Figure 4. Segregation of breeding colonies of three species of petrels on 133 islands in southern Fiordland (from Breaksea Sound south to Preservation Inlet) based on island size (log scale ha) and distance from the open sea. Red squares = sooty shearwater; green circles = broad-billed prion; blue triangles = mottled petrel; black crosses = islands surveyed without breeding petrels being found. Symbol sizes are proportional to colony size: small symbols = 1 to 90 burrows; medium symbols = 100 to 900 burrows; large symbols = 1,000 to 9,000 burrows.

Testing the 'refugia from resident stoats' hypothesis

The 2016 Dusky Sound survey revealed that breeding populations of migratory petrels (mottled petrel and sooty shearwater) had persisted on more than 40 islands that were less than 100 ha in size despite all but one island ('Centre Island') considered likely to have been invaded by stoats on one or more occasion (Fig. 5A). No evidence was found of petrels persisting on larger islands in Dusky Sound that have (or had) resident stoat populations (Miskelly, Tennyson *et al.* 2017). A similar pattern was found in the 2017 survey of islands in Chalky and Preservation Inlets, with colonies of migratory petrels found on about 34 islands <170 ha and within swimming range of stoats (Fig. 5B). Stoats have been observed or trapped, or their scats and prey remains found, on at least 11 of these small to medium-sized petrel breeding islands, including Zero Nugget and Finger Rock off Chalky Island (Kim Morrison *pers. comm.* to CMM 15 November 2018), three of the Small Craft Harbour Islands, south Passage Island, three of the Cording Islands, Steep-to Island and Weka or Long Island (King & Murphy 2005; Veale *et al.* 2012; Lindsay Wilson *pers. comm.* to CMM 19 Mar 2019; authors *pers. obs.*). However, in contrast to Dusky Sound, migratory petrels were found breeding on two large islands (>400 ha) in Chalky Inlet that have (or had) resident stoats: Great Island and Chalky Island, with sooty shearwaters also breeding on 2 ha Spit Island, which is attached to the South Island mainland. These three islands lie along the Y-axis in Fig. 5B (and see Table 4 for island areas). We do not consider south Passage Island (168 ha) to have had a resident stoat population, as only a single animal was caught there during trapping concurrent with the 1999 Chalky Island eradication programme (Murray Willans *pers. comm.* to CMM, 4 February 2019).

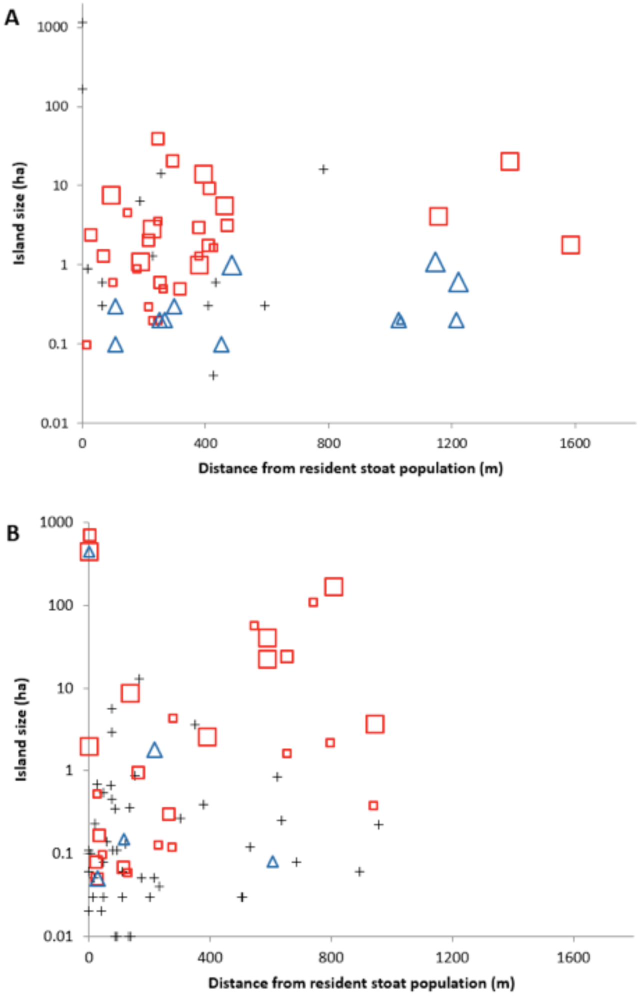

Figure 5. A. Sizes of sooty shearwater and mottled petrel colonies in Dusky Sound in relation to island size (log scale ha) and the minimum distance that stoats would have to swim from the nearest resident stoat population (including sites from which stoats have been eradicated). B. Comparative data for the same two species from islands in Chalky and Preservation Inlets. Red squares = sooty shearwater; blue triangles = mottled petrel; black crosses = islands surveyed without breeding petrels being found. Symbol sizes are proportional to colony size: small symbols = 1 to 90 burrows; medium symbols = 100 to 900 burrows; large symbols = 1,000 to 5,000 burrows.

DISCUSSION

Regional and national significance of Chalky and Preservation Inlet petrel colonies

The main finding of the 2017 survey was that Chalky and Preservation Inlets had many more, and far larger, petrel colonies than is evident in published accounts. Sooty shearwaters and broad-billed prions, in particular, are far more abundant there than indicated by recent reviews. Waugh *et al.* (2013) reported two known sooty shearwater colonies in Chalky Inlet, based on an old egg reported by McLean *et al.* (1993), and 500 burrows reported on Chalky Island (D. Scott in Newman *et al.* 2009). Jamieson *et al.* (2016) reported a single record of broad-billed prions breeding at an unspecified site in Chalky Inlet based on a 1986 report that this species was found "breeding in Breaksea Sd, Dusky Sd, and Chalky Inlet" (K. Morrison in Gaze 1988). Miskelly, Tennyson *et al.* (2017) reported 14 petrel colonies from Chalky and Preservation Inlets (10 sooty shearwater, 2 mottled petrel, 2 broad-billed prion), but did not provide colony sizes for any of them. The 40 breeding colonies found in 2017 therefore represent an almost threefold increase in the number of reported colonies, and a first estimate of colony size (based on burrow counts and estimates) for all but one of these sites.

The 23,425 sooty shearwater burrows estimated on 26 islands in Chalky and Preservation Inlets is similar in magnitude to the 21,400 burrows estimated on islands in Dusky Sound (Miskelly, Tennyson *et al.* 2017). When combined with the additional 16 breeding sites reported between Milford and Breaksea Sounds (Waugh *et al.* 2013; Miskelly, Tennyson *et al.* 2017), it is likely that up to 50,000 pairs of sooty shearwaters breed in Fiordland. Although much larger than other known populations north of Foveaux Strait, the combined Fiordland sooty shearwater population is far smaller than individual colonies on Whenua Hou/Codfish Island, Taukihepa/Big South Cape Island, Putauhinu Island, Poutama Island, and Snares Islands/Tini Heke to the south, all of which exceed 170,000 pairs or burrows (Lyver 2000; Newman *et al.* 2009; Waugh *et al.* 2013).

The 1,240 mottled petrel burrows estimated on five islands in Chalky and Preservation Inlets is considerably fewer than the 5,500 burrows estimated on 12 islands in Dusky Sound (Miskelly, Tennyson *et al.* 2017). Larger colonies of this New Zealand endemic species (of 10,000–160,000 pairs) have been reported from Whenua Hou/Codfish Island, Taukihepa/Big South Cape Island, and Snares Islands /Tini Heke (Warham *et al.* 1977; Scott *et al.* 2009; Miskelly *et al.* 2019).

In contrast to the two larger petrel species, the broad-billed prion colonies in Chalky Inlet are far larger than those reported elsewhere in Fiordland. We estimated 9,700 burrows at 8 sites in Chalky Inlet, compared to 240 burrows (1 site) in Preservation Inlet and 560 burrows (2 sites) in Dusky Sound (data presented herein and in Miskelly, Tennyson *et al.* 2017). Several broad-billed prion colonies have been reported from islets in Breaksea Sound and off the west coast of Resolution Island, but little information is available on the size of these colonies (Taylor 2000b; Jamieson *et al.* 2016; Miskelly, Tennyson *et al.* 2017). Sizes of New Zealand prion colonies are poorly known, however, Chalky Inlet holds the second largest reported broad-billed prion population, after the 340,000+ pairs reported from the Chatham Islands (West & Nilsson 1994; Jamieson *et al.* 2016).

Grey-backed storm petrels in Fiordland

The capture of a grey-backed storm petrel with a bare brood patch offshore from Chalky Island on 22 November, along with sightings of birds at two other widely-spread spotlighting locations, adds to the body of evidence that this species breeds in Fiordland (Miskelly, Stahl & Tennyson 2017). Although no breeding grounds have yet been found, records of grey-backed storm petrels continue to accumulate throughout Fiordland. In addition to the minimum of 16 records summarised by Miskelly, Stahl & Tennyson (2017) and the three records reported here, there were at least two further reports during 2017–18. A grey-backed storm petrel flew on to a vessel at the head of Broughton Arm, Breaksea Sound, on the night of 17–18 August 2017 (Fraser Goldsmith record and image on eBird https://ebird.org/newzealand/view/checklist/S38900677; viewed 24 January 2019), and one was found dead (stoat-killed) above Routeburn Falls hut, Routeburn Track on 22 December 2018 (CMM *pers obs.*).

Fiordland is more than 480 km from the nearest known breeding site for grey-backed storm petrel (Auckland Islands). When combined with the complete absence of records of any other storm petrel species from Fiordland, these numerous records indicate that grey-backed storm petrels are predictably present in the region, rather than being vagrants from a distant population.

The impact of stoats on Chalky and Preservation Inlet petrel colonies

Interpreting the current distribution and sizes of petrel colonies in southern Fiordland is challenging in the absence of historical data on their distribution, and the timing of predator colonisation events. In addition to stoats, other introduced predators are likely to have had a role in petrel colony declines and extinctions. Within Dusky Sound, extinction of the enormous broad-billed prion colony reported by Captain Cook on Anchor Island has been attributed to predation by Norway rats (*Rattus norvegicus*), as the prions disappeared before stoats reached western Fiordland (Medway 2011; Miskelly, Tennyson *et al.* 2017). However, stoats are far more capable swimmers than other predatory mammals present in Fiordland (Russell *et al.* 2008; Veale *et al.* 2012), and it is the only species present that is able to colonise the majority of islands without human assistance.

Several features of petrel behaviour and breeding ecology render them highly vulnerable to stoat predation, including burrow-nesting, low-breeding output (a maximum of one chick per pair per annum) and colonial nesting (Moors & Atkinson 1984; Warham 1996). The persistence of petrel colonies on islands that have been accessible to stoats for more than a century is counter-intuitive, unless stoats have been present too briefly and infrequently to kill all birds associated with a colony, or the petrel colonies are large enough for predation to have an insignificant impact on colony viability (Cuthbert 2002; Peck *et al.* 2008; Miskelly, Tennyson *et al.* 2017).

The 'refugia from resident stoats' hypothesis was proposed to explain the persistence of petrel colonies on islands in Dusky Sound that were within swimming range of stoats but which were too small to sustain resident stoat populations (Miskelly, Tennyson *et al.* 2017). A crucial parameter in the hypothesis is the minimum island size that can support a resident stoat population through provision of a year-round food supply. This island size remains unclear, and may require several years of monitoring or detailed genetic analysis of stoats to determine. Female stoats are pregnant almost continuously throughout their lives (including from the time juveniles leave the den), and produce an average of 8–10 kits (King & Murphy 2005). A single female stoat that reaches an island can therefore result in the impression that a substantial stoat population is present, if a survey or eradication attempt is undertaken soon after she has reached the island and given birth.

Six stoats were caught on 40 ha Parrot Island between 2001 and 2005 (Elliott *et al.* 2010), and Veale *et al.* (2012) reported eight stoats caught on 57 ha Motuoruhi Island in a short space of time, but were these animals resident? The near absence of stoats on 168 ha south Passage Island during the 1999 'eradication' (with only a single animal caught) points to stoats requiring the resources of islands in excess of 170 ha in order to persist in southern Fiordland. The Passage Islands are presumed to have been 'stepping stone' islands used by stoats to colonise Chalky Island, and a second stoat was trapped on south Passage Island in 2017 (C. Bishop *unpubl. data*).

The 'refugia from resident stoats' hypothesis is based on the assumption that petrels are unable to persist on (large) islands or South Island mainland sites with resident stoats, as the petrels will be exposed to stoat predation every breeding season until the colony is extirpated. This was suggested as the reason why petrels were apparently absent from the larger islands in Dusky Sound while persisting on nearby small islands (Miskelly, Tennyson *et al.* 2017). However, within Chalky and Preservation Inlets, petrel colonies were detected on at least three islands that have (or had) resident stoats: Great Island, Chalky Island, and Spit Island (this last 'island' is attached to the South Island mainland) – indicating that the hypothesis is invalid or requires further refinement based on the carrying capacity of each site for stoats when the seabirds are absent (Peck *et al.* 2008). The presence or absence of rat populations as an alternative prey will likely affect stoat persistence. However, apart from the presence of Norway rats on six of the Cording Islands (Lindsay Wilson *pers. comm.* to CMM 19 Mar 2019), we have found little information on rodent distribution on islands in Chalky and Preservation Inlets.

There are a few sites on the South Island mainland where petrel colonies have persisted in the presence of stoats, including sooty shearwaters in Otago and Hutton's shearwaters (*Puffinus huttoni*) in the Seaward Kaikoura mountains. Stoats were the main predators present at both sites. However, at the largest Hutton's shearwater colony, the more than 100,000 pairs present were able to produce sufficient young each year to more than offset losses due to predation by the small number of resident stoats, despite stoats killing *c.* 12% of chicks per annum plus 0.25% of adults (Cuthbert & Davis 2002). In contrast, small mainland colonies of both shearwater species suffered higher predation rates and lower breeding success than this one large colony, and were declining in the absence of effective stoat control (Lyver *et al.* 2000; Cuthbert 2002). The few sooty shearwater colonies that survived on the Otago coast are the dwindling remnants of formerly much larger colonies exposed to multiple threats, and protection of adults, eggs and young chicks from predators is crucial if these small mainland colonies are to persist (Hamilton 1998; Lyver *et al.* 2000; Cuthbert 2002).

Cuthbert (2002) reported inverse density-dependent stoat predation at South Island mainland shearwater colonies, meaning that large colonies suffered relatively less predation (in terms of the proportion of adults and chicks killed) than small colonies. He suggested a threshold of 600 pairs, above which colonies should not decline in the face of stoat predation alone. However, if other factors (e.g. habitat disturbance or predation by other species) impact on colony viability, stoat predation may contribute to and accelerate colony decline. We did not estimate burrow occupancy during our rapid survey, but it is likely that the eight largest sooty shearwater colonies found each held more than 600 pairs. These included Chalky Island and Spit Island where the birds were or are exposed to predation by resident stoats. The persistence of the small sooty shearwater colony on Great Island colony (estimated at 200 burrows only) in the presence of resident stoats is difficult to explain unless it is the remnant of a much larger colony, or the colony is sustained by immigration from nearby colonies, as proposed for Yelkouan shearwaters (*Puffinus yelkouan*) (see Bonnaud *et al.* 2009). This colony will have received some protection from stoat predation for the last 20 years or so as trap lines are maintained on Great Island to reduce the risk of stoats reaching the Passage Islands and Chalky Island.

Prions are more vulnerable to stoats than the two migratory petrel species, as they are not only smaller, but they visit colonies throughout the year and so transient stoats that reach prion breeding sites may persist longer than at sites where migratory petrels (e.g. sooty shearwater and mottled petrel) are absent for 3–4 months in winter (Miskelly, Tennyson *et al.* 2017). Broad-billed prion colonies in Fiordland have become confined to tiny stacks on the exposed outer coast, where extreme wave action is presumed to provide protection from stoat invasion. While the number of colonies and the number of birds surviving in Fiordland is substantially higher than reported by Jamieson *et al.* (2016), the colonies so far located in Fiordland are still far too small to have been the main source of the estimated 200,000 broad-billed prions killed in a storm in July 2011 (Tennyson & Miskelly 2011; Jamieson *et al.* 2016). The largest known broad-billed prion colony on Rangatira Island in the Chatham Islands was not impacted by this mortality event (authors *unpubl. data*), and the origin of these birds remains a mystery.

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Appendix 1. Island locations and search effort. Full names of water bodies = Cunaris Sound, Chalky Inlet, Preservation Inlet, Isthmus Sound, and Long Sound. 'Petrels' refers to whether evidence of petrels breeding was recorded in November or December 2017 (see Tables 1, 3 & 4). 'Trap' refers to whether at least one stoat trap was maintained on the island at the time of our visit. Note that many islands receive protection by being adjacent to islands that are trapped. 'Time' is the approximate length of time (in minutes or hours:minutes) that observers were ashore.

Island name	Water body	Latitude S	Longitude E	Petrels	Trap	Date	Observers	Day/Night	Time
Cliff Cove islet	Cunaris Sd	45.9620°	166.7508°	No	No	25-Nov	AT, CB, CM, GT, LM, RP & TG	Day	30
Cunaris sw islet (inner)	Cunaris Sd	45.9732°	166.6661°	No	No	25-Nov	CB	Day	15
Cunaris sw islet (middle)	Cunaris Sd	45.9734°	166.6653°	No	No	25-Nov	TG	Day	15
Cunaris sw islet (outer)	Cunaris Sd	45.9758°	166.6566°	No	No	25-Nov	CB & TG	Day	15
Small Craft Harbour Is main west	Chalky Inlet	45.9674°	166.6412°	Yes	Yes	24-Nov	AT, CM, GT, LM & RP	Day + night	3:15
Small Craft Harbour Is main east	Chalky Inlet	45.9686°	166.6483°	Yes	Yes	24-Nov	CB, LM, RP & TG	Day	1:15
Small Craft Hbr Is NE island	Chalky Inlet	45.9663°	166.6564°	Yes	Yes	24-Nov	GT, LM & RP	Day	55
Small Craft Hbr Is NE islet	Chalky Inlet	45.9648°	166.6569°	No	No	24-Nov	AT & CM	Day	20
Small Craft Hbr Is SW islet	Chalky Inlet	45.9704°	166.6395°	No	Yes	24-Nov	CB & LM	Day	25
Small Craft Hbr Is middle islet	Chalky Inlet	45.9702°	166.6441°	Yes	No	24-Nov	AT, CB, CM, GT & TG	Day + night	2:20
Small Craft Hbr Is SE islet 1	Chalky Inlet	45.9727°	166.6474°	No	No	25-Nov	AT	Day	15
Small Craft Hbr Is SE islet 2	Chalky Inlet	45.9725°	166.6484°	No	Yes	25-Nov	CM	Day	15
Small Craft Hbr Is east islet	Chalky Inlet	45.9713°	166.6580°	No	Yes	25-Nov	AT & CM	Day	15
Little Island (east islet)	Chalky Inlet	45.9716°	166.5963°	No	No	25-Nov	AT & GT	Day	30
Little Island (middle tiny islet)	Chalky Inlet	45.9714°	166.5949°	No	No	25-Nov	CM	Day	5
Little Island – northern peninsula	Chalky Inlet	45.9719°	166.5932°	No	No	25-Nov	CB & LM	Day	30
Little Island (west islet)	Chalky Inlet	45.9722°	166.5891°	No	No	25-Nov	CM, RP & TG	Day	25
Great Island	Chalky Inlet	45.9935°	166.5609°	Yes	Yes	19-Dec	CB	Day	9:00
Stripe Head – north-east islet	Chalky Inlet	46.0179°	166.6024°	Yes	No	24-Nov	CB, LM & TG	Day	10
Stripe Head – south-west islet	Chalky Inlet	46.0221°	166.6005°	Yes	No	24-Nov	AT, GT & RP	Day	30
Garden Island (outer or little)	Chalky Inlet	46.0287°	166.5900°	Yes	No	24-Nov	AT, CB, CM, GT, LM, RP & TG	Day	50
Garden Island (main)	Chalky Inlet	46.0327°	166.5934°	No	No	24-Nov	AT, CB, CM, GT, LM, RP & TG	Day	1:05
Garden Island (islet NW of main)	Chalky Inlet	46.0310°	166.5905°	No	No	24-Nov	CM & TG	Day	5
Passage Island (north)	Chalky Inlet	46.0161°	166.5429°	Yes	Yes	23-Nov	AT, CB, CM, GT, LM, RP & TG	Day	1:35
Passage Island (south or main)	Chalky Inlet	46.0238°	166.5386°	Yes	Yes	24-Nov	AT, CB, CM, GT, LM, RP & TG	Day	2:00

Appendix 1. cont.

Island name	Water body	Latitude S	Longitude E	Petrels	Trap	Date	Observers	Day/Night	Time
Passage Island sth coast stack 7	Chalky Inlet	46.0276°	166.5297°	Yes	No	23-Nov	AT, CM & LM	Day	1:05
Passage Island sth coast stack 6	Chalky Inlet	46.0309°	166.5349°	No	No	23-Nov	AT & LM	Day	15
Passage Island sth coast stack 5	Chalky Inlet	46.0310°	166.5364°	Yes	No	23-Nov	CM	Day	40
Passage Island sth coast stack 4	Chalky Inlet	46.0328°	166.5413°	Yes	No	23-Nov	AT & LM	Day	50
Passage Island sth coast stack 3	Chalky Inlet	46.0330°	166.5425°	Yes	No	23-Nov	CM	Day	15
Passage Island sth coast stack 1	Chalky Inlet	46.0323°	166.5462°	Yes	No	23-Nov	AT & LM	Day	10
Chalky Island	Chalky Inlet	46.0491°	166.5233°	Yes	Yes	23-Nov	AT, CB, CM, GT, LM, RP & TG	Day	3:45
Zero Nugget (main)	Chalky Inlet	46.0345°	166.5194°	Yes	No	23-Nov	AT, RP & TG	Day	1:25
Zero Nugget (eastern)	Chalky Inlet	46.0345°	166.5194°	Yes	No	23-Nov	CB & LM	Day	20
Finger Rock (inner)	Chalky Inlet	46.0345°	166.5194°	Yes	No	23-Nov	CB & LM	Day	10
Finger Rock (tall stack)	Chalky Inlet	46.0345°	166.5194°	Yes	No	23-Nov	CM	Day	45
‘Outer anisotome islet’	Chalky Inlet	46.0345°	166.5194°	No	No	22-Nov	RP & TG	Day	20
‘Inner anisotome islet’	Chalky Inlet	46.0345°	166.5194°	No	No	22-Nov	CB & LM	Day	15
‘Hebe pyramid’	Chalky Inlet	46.0345°	166.5194°	Yes	No	22-Nov	AT & CM	Day	1:10
‘Riki Rock’	Chalky Inlet	46.0345°	166.5194°	Yes	No	22-Nov	CB, LM & RP	Day	55
Gulches Head stack	Preservation	46.0904°	166.5686°	No	No	22-Nov	AT & CM	Day	30
Spit Islands	Preservation	46.0722°	166.6296°	Yes	No	22-Nov	CB, GT, LM, RP & TG	Day	1:05
Nthn stack west of Cavern Head	Preservation	46.0767°	166.6391°	No	No	22-Nov	AT	Day	55
Sthn stack west of Cavern Head	Preservation	46.0786°	166.6400°	Yes	No	22-Nov	CM	Day	55
Cavern Head headland	Preservation	46.0830°	166.6457°	No	No	22-Nov	AT & CM	Day	40
Steep-to Island	Preservation	46.0973°	166.6651°	Yes	Yes	22-Nov	AT, CB, CM, GT, LM, RP & TG	Day	2:00
Weka or Long Island	Preservation	46.0949°	166.6961°	Yes	Yes	22-Nov	AT, CB, CM, GT, LM, RP & TG	Day	2:05
Cemetery Island	Preservation	46.1037°	166.7099°	No	No	20-Nov	AT, CB, CM, GT, LM, RP & TG	Day	35
Round Island	Preservation	46.0869°	166.6826°	Yes	Yes	22-Nov	AT, CB, CM, CP, GT, LM, PK, RP & TG	Day	1:30
Cording Islands, main	Preservation	46.0737°	166.6796°	Yes	Yes	21-Nov	CB, GT, LM & RP	Day	2:05
Cording Is, outer	Preservation	46.0788°	166.6651°	Yes	Yes	21-Nov	AT, CM & TG	Day	1:15
Cording Is, outer (SW islet)	Preservation	46.0793°	166.6630°	No	No	21-Nov	AT, CM & TG	Day	20

Appendix 1. cont.

Island name	**Water body**	**Latitude S**	**Longitude E**	**Petrels**	**Trap**	**Date**	**Observers**	**Day/Night**	**Time**
Cording Is, outer (NW islet)	Preservation	46.0771°	166.6670°	Yes	No	21-Nov	AT, CM & TG	Day	30
Cording Is, NW islet (inner)	Preservation	46.0701°	166.6814°	Yes	No	21-Nov	CM & TG	Day	20
Cording Is, NW islet (outer)	Preservation	46.0690°	166.6804°	No	Yes	21-Nov	AT	Day	20
Cording Is, eastern islet	Preservation	46.0753°	166.6939°	No	No	21-Nov	AT, CB, CM, GT, LM, RP & TG	Day	30
Cording Is, ’35 spot height’	Preservation	46.0702°	166.6932°	Yes	Yes	21-Nov	AT, GT, LM & RP	Day	55
Cording Is, islet SW of ‘35’	Preservation	46.0716°	166.6918°	No	No	21-Nov	CM & TG	Day	10
Cording Is, ’28 spot height’	Preservation	46.0668°	166.6912°	Yes	No	21-Nov	CB, CM & TG	Day	40
Cording Is, islet SE of ‘28’	Preservation	46.0680°	166.6928°	No	No	21-Nov	CB, CM & TG	Day	15
Single Tree Island	Preservation	46.0656°	166.6623°	Yes	Yes	21-Nov	AT, CB, CM, GT, LM, RP & TG	Day	20
Isthmus Sound Islet	Isthmus Sd	46.0525°	166.6902°	Yes	No	21-Nov	AT, CB, CM, GT, LM, RP & TG	Day	1:10
Jane Coves – southern islet	Long Sound	46.0260°	166.7535°	No	No	20-Nov	CB, LM & TG	Day	20
Jane Coves – middle tiny islet	Long Sound	46.0259°	166.7517°	No	No	20-Nov	CB, LM & TG	Day	10
Jane Coves – main islet	Long Sound	46.0204°	166.7479°	No	No	20-Nov	AT, CM, GT & RP	Day	30
Lady Bay main islet	Long Sound	46.0153°	166.7340°	No	No	20-Nov	AT, GT, LM & RP	Day	30
Lady Bay SE inner tiny islet	Long Sound	46.0170°	166.7395°	No	No	20-Nov	CB, CM & TG	Day	10
Lady Bay SE outer tiny islet	Long Sound	46.0170°	166.7400°	No	No	20-Nov	CB, CM & TG	Day	10
Lady Bay northeast islet	Long Sound	46.0146°	166.7406°	No	No	20-Nov	CB, CM & TG	Day	15
Only Island	Long Sound	45.9603°	166.8716°	No	No	21-Nov	AT, CM, LM, RP & TG	Day	1:35
‘Only islet’	Long Sound	45.9600°	166.8764°	Yes	No	21-Nov	CB & GT	Day	50

Appendix 2. Seabird survey data from five vegetated islets within the Green Islets, off the southern Fiordland coast west of Big River. Surveys were undertaken by Colin Bishop, Lindsay Wilson, Brian Rance, and Rose Collen on 13 December 2013, and by Rebecca Jackson, Lynn Adams, Ben Barr, Andrew Legault, Jo Monks, James Reardon, and Dylan van Winkel on 15 December 2018.

Islet	Latitude S	Longitude E	Date	Seabird evidence	Burrow count or density
Attached to mainland	46.2275°	166.7879°	13 Dec 2013	Sooty shearwater burrows, fresh broken egg, corpse	*c.* 40 burrows, 3 in 9m^2
Inner islet	46.2262°	166.7915°	13 Dec 2013	Common diving petrel burrows, adults and downy chicks Sooty shearwater burrows, adults on eggs	11 burrows in 9m^2 Sparse on main ridge
Outer – north	46.2260°	166.7985°	13 Dec 2013	Common diving petrel burrows, adults and downy chicks Sooty shearwater burrows with adults Southern skua – 3 adults	28 burrows in 9m^2 Higher density than on the inner islet
Outer – central	46.2270°	166.7984°	15 Dec 2018	Common diving petrel burrows, skeletal remains Southern skua fledgling	
Outer – south-east	46.2292°	166.8035°	15 Dec 2018	Common diving petrel burrows, chick	

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SHORT NOTE

Update on North Island tomtit (*Petroica macrocephala toitoi*) at Atuanui, Mount Auckland

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Since an initial study of North Island tomtit (miromiro; *Petroica macrocephala toitoi*) at the 615 hectare Atuanui Scenic Reserve (36.447°S, 174.459°E) reported in Michaux (2009), a number of pest control programmes have been carried out. The Kaipara branch of Forest and Bird sponsored the Atuanui Restoration Project, and established 632 bait stations set out on two 100m X 100m grids (east and west of the ridge track), and baited with Ratabate™ (active ingredient diphacinone), for a three year period from 2007–2009 (Forest and Bird, 2009). Fifty-five DoC-250 stoat traps were also placed around the boundary and an unspecified number of Timms traps for common brushtail possum (*Trichosurus vulpecula*) control were set up in conjunction with the bait lines. Rat (*Rattus* spp.) numbers were monitored from 2007–2010 using 100 tracking tunnels arranged on ten randomly selected lines. The percentage of tunnels visited by rats and the number of possums caught in Timms traps were recorded. In April 2008 an Auckland Regional Council (ARC) possum control programme was carried out over an extended area which included the reserve. Atuanui was returned to Ngati Whatua o Kaipara as part of their Treaty of Waitangi Settlement in 2011. Nga Maunga Whakahii o Kaipara Development Trust was set up to manage the reserve, with the aim of restoring Atuanui's ecology and eventually releasing North Island brown kiwi (*Apteryx mantelli*). Pest control was re-established in 2014 and continues to the present (April, 2019). The bait station grid established by Forest and Bird was baited with Pindone™, and supplemented with 150 DoC-200 stoat traps and Sentinel possum traps arranged in four circuits.

Numbers of occupied miromiro territories were estimated using the method described by Michaux (2009) and compiled for the years 2012–2018. Counts of all birds seen or heard while walking the main track, a distance of approximately 3 km, were also recorded. All data were gathered by the same observer and every effort was made to minimise double counting of mobile species such as tūī (*Prosthemadera novaeseelandiae*) and New Zealand pigeon (kererū; *Hemiphaga novaeseelandiae*). The number of visits each calendar year varied between eight and thirteen, spread throughout the year. Because there are pronounced seasonal differences in species' abundance and conspicuousness, and visits were undertaken when possible rather than systematically, some of the variation in counts may be due to a seasonal effect. Data were entered into eBird (Scofield *et al.* 2012) and summary

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Table 1. Numbers of miromiro territories counted at Atuanui over 14 seasons between 2005 and 2019. Rat tracking indices are shown as % tunnels with rat prints present. Possum data show number of possums caught annually in Timms traps over 5 seasons. Miromiro figures in square brackets are based on fewer visits. nd = no data.

Season	Number of miromiro territories	Rat tunnel %	Number of possums trapped
2005/6	12	nd	nd
2006/7	16	15	23
2007/8	15	17	21
2008/9	17	23	0
2009/10	15	30	8
2010/11	14	73	25
2011/12	17	nd	nd
2012/13	16	nd	nd
2013/14	12	nd	nd
2014/15	16	nd	nd
2015/16	15	nd	nd
2016/17	[14]	nd	nd
2017/18	[13]	nd	nd
2018/19	22	nd	nd

statistics generated for the years 2012–2018.

Table 1 shows the estimated number of miromiro territories between 2005/6 and 2018/19. The estimations are based on calls and/or sightings recorded between July and July rather than over a calendar year, because the breeding season usually runs from August to December and better represents an annual cycle (i.e. breeding season to breeding season) for the birds. The percentage of tracking tunnels visited by rats and the number of possums trapped for 2007–2011 are also shown in Table 1. The success of possum control undertaken by the ARC during 2007 is clearly shown by the zero possum tally for 2008/9. Miromiro territory counts show only a weak negative correlation with possum numbers ($r^2 = 0.44$). Rat numbers were suppressed during 2007–2009 when Forest and Bird bait and trap lines were operational, but thereafter rat numbers increased rapidly. Again, there was only a weak negative correlation with miromiro territory numbers ($r^2 = 0.48$). A stronger negative correlation was seen when rat and possum numbers were combined ($r^2 = 0.66$). The most obvious feature of the data is the stability of the number of miromiro territories between 2005/6 and 2017/18 (range 12–17). The two territory count figures for 2016/17 and 2017/18 (shown in square brackets in Table 1), are based on fewer visits and may be underestimates. Natural variability in the number of breeding pairs in the reserve is possibly related to other factors such as weather and food supply, in addition to predation by introduced mammals.

The highest number of miromiro territories in the 15 years over which numbers have been recorded was in 2018/19 and may be the result

Table 2. Mean number of four common bird species (± standard error) recorded at Atuanui during 2012–2018. n = number of counts, P-values calculated from chi squared test.

Year (n)	kererū	tūī	riroriro	pīwakawaka
2012 (12)	3.6 ± 0.9	10.8 ± 2.4	10.8 ± 2.2	4.8 ± 1.0
2013 (13)	2.6 ± 0.7	7.8 ± 1.4	11.0 ± 1.6	6.4 ± 1.1
2014 (10)	5.7 ± 1.4	18.6 ± 2.1	19.4 ± 5.2	7.1 ± 1.2
2015 (12)	4.4 ± 1.1	17.1 ± 1.8	19.8 ± 3.0	14.9 ± 1.6
2016 (8)	4.3 ± 1.1	11.5 ± 2.4	16.0 ± 1.5	11.4 ± 3.0
2017 (9)	4.9 ± 0.9	16.0 ± 3.3	14.2 ± 2.2	11.6 ± 1.2
2018 (12)	4.5 ± 1.1	19.0 ± 1.6	23.3 ± 3.0	14.9 ± 1.6
P-value	0.97	0.25	0.23	0.13

of pest control carried out since 2014. Further indication of the control programme's efficacy is shown by the trend of increasing numbers of kererū, tūī, grey warbler (riroriro; *Gerygone igata*), and New Zealand fantail (pīwakawaka; *Rhipidura fuliginosa*). Table 2 shows the mean number of these four bird species encountered per visit (± standard error, n = number of visits), and probability values for each species. These data and their regression lines are also displayed in Figure 1. While the variability of the data resulted in low r^2 values for the regression lines and non-significant differences in average numbers observed, the four species do show a trend of increasing abundance.

Miskelly (2018) suggested that common and widespread native birds were only weakly limited by mammalian predation at Zealandia (Karori Sanctuary) in Wellington, while endemic birds outcompeted them when predatory mammals were removed. Baber *et al.* (2009) studied population sizes of common endemic species in the Hunua Ranges, South Auckland, following control undertaken to protect kōkako (*Callaeas wilsoni*). They showed that in areas with high intensity pest control there were significant

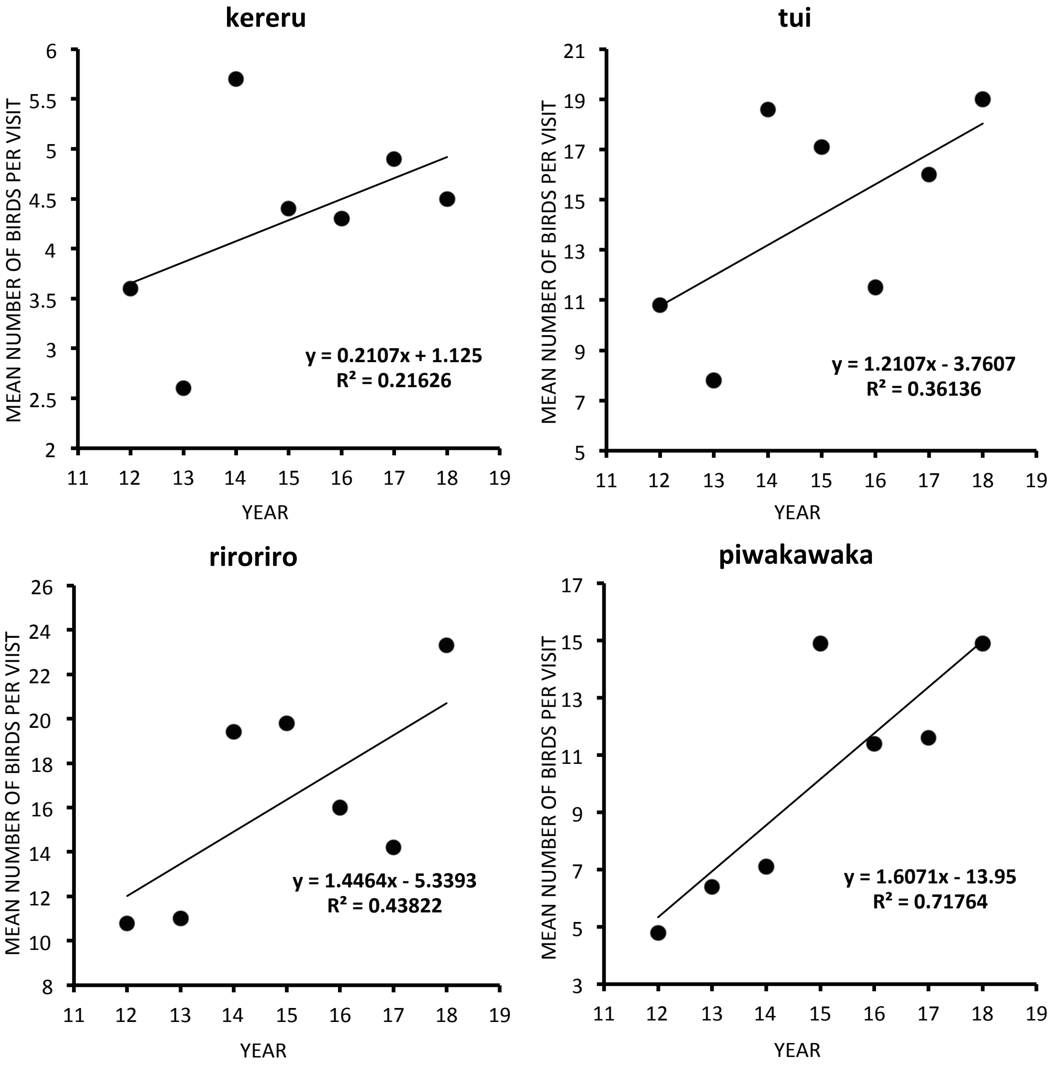

Figure 1. Mean number of four common bird species at Atuanui during 2012–2018, showing regression lines and equations.

increases in numbers of tūī, kererū, and miromiro. Tūī and kererū also appeared to benefit most at sites where pests had been eradicated in a regional-scale study reported by Ruffell & Didham (2017), and kererū nesting success increased at a Northland site when both ship rat *Rattus rattus* and possum levels fell below 4% (Innes *et al.* 2004). Robertson *et al.* (2019) showed that there was an increase in fantail nesting success following landscape-scale application of 1080 to protect North Island brown kiwi, although breeding success decreased in the years following 1080 application. The differing responses of various forest bird species to pest control is probably context-dependent (Ruffell & Didham 2017), that is they reflect the levels of pest removal or control that can be achieved, i.e. near-eradication of all pest mammals (Zealandia), compared with control of some of them (Tongariro, Atuanui).

Our study suggests a recovery of populations of widespread endemic forest birds, as forest ecology rebalances following control of some mammalian predators. How much these populations will continue to grow, and how the proportions of various species that comprise Atuanui's avifauna might change following ongoing intensive pest control and any future translocations, is unknown. Anecdotal observations certainly suggest that abundance and diversity of the undergrowth have increased with seedlings of palatable species such as hangehange (*Geniostoma ligustrifolium*), *Pseudopanax* spp, pigeonwood (*Hedycarya arborea*), and greenhood orchids (*Pterostylis* sp.) now noticeable, and skinks (unidentified species) commonly observed. As the ecosystem recovers and more resources become available for birds, carrying capacity would be expected to increase and the numbers of some species of birds could continue to rise, until they reach a new equilibrium.

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Keywords: miromiro, tomtit, mammal pest control, species recovery

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SHORT NOTE

The use of an Unmanned Aerial Vehicle to census large breeding colonies of black-billed gull (*Larus bulleri*) and white-fronted tern (*Sterna striata*) at the Ashburton River/Hakatere River mouth

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Aerial photography has been used to count a range of colonial nesting seabirds in New Zealand; including gulls (Frost & Taylor 2018; Mischler 2018), shags (Schuckard *et al.* 2015, 2018), gannets (Stephenson 2005), and albatross species (Frost *et al.* 2018). Recent innovations in Unmanned Aerial Vehicle (UAV) platforms with improvements and miniaturisation of navigation tools and cameras has revolutionised ecological studies (Anderson & Gaston 2013). However, the use of UAV's to census colonial breeding seabirds has not been reported from New Zealand. Here we test the use of a UAV to census two large colonies of a gull and tern species.

In mid-October 2017 a large colony of black-billed gull (*Larus bulleri*) established on the true left bank of the Ashburton River/Hakatere River mouth, directly below the bluffs adjacent to the Hakatere Huts, Canterbury, New Zealand (44.051986°S, 171.805860°E). Concurrently, a similarly large colony of white-fronted tern (*Sterna striata*) was established on the true right bank, at the base of the gravel spit that encloses the lagoon. To measure the size of these colonies two independent methods were employed: extrapolation from nest plots, and counts from aerial photos recorded from an Unmanned Aerial Vehicle.

The perimeter of each colony was measured using a handheld Garmin Map64St GPS by walking around the edge of the colony holding the GPS over the outermost nests on 12 November 2017. These data were uploaded to ArcView to create a polygon used to calculate colony size. To determine nest density, a series of non-overlapping 0.375 m radius circular plots (each 0.45 m²) were carried out along a transect running through the centre of the colony, and the number of nests counted in each. Mean nest density was calculated, and the number of breeding pairs in the two colonies estimated by extrapolating this density across the area of each colony.

For comparison, an aerial survey of each colony was carried out by a UAV (DJI Phantom 3), also on 12 November, and 2 hours after the completion of nest plot counts. The UAV flew 5–7 transects over each colony at a height of approximately 100m. Neither the black-billed gulls nor the white-fronted terns reacted to the UAV. The resulting images were digitally stitched together using Adobe Photoshop to provide a photomosaic of the entire colony. These aerial photographs were counted using ImageJ, an open source image processing program designed for scientific images. Each image was worked through systematically, during which all Apparently Occupied Nests (AON), and additional birds within and outside the nesting area, were counted.

The area of the black-billed gull colony was calculated to be 1,555 m². From 50 nest plots laid out through the colony, we calculated a mean nest density of 5.02 nests/m² (SD 1.668). Extrapolating from this the black-billed gull colony is estimated to be 7,807 nests (95% confidence interval 7,088–8,526).

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In comparison, a total of 7,485 Apparently Occupied Nests were counted on the aerial photograph of the black-billed gull colony. An additional 1,305 birds were counted within the nesting area, and a further 646 birds were recorded outside the nesting area. Assuming this count, like aerial counts of other species (Baker *et al.* 2014), is consistent with a Poisson model, a property of which is that the variance and mean are the same, the standard deviation of the count can be estimated as its square root. In the case of a single count, the standard deviation and standard error are the same, so the 95% confidence interval can therefore be estimated as 1.96*√[count]. For the black-billed gull colony, the 95% confidence interval is 7,315–7,655. Mischler (2018) estimated the National population of black-billed gull to be 60,000 breeding pairs, and highlighted that since the mid 1990's the Ashburton River has supported a significant breeding population. This colony appears to be the single largest black-billed gull colony recorded in New Zealand since the mid 1990's.

The size of the white-fronted tern colony was calculated to be 1,651 m². From 40 nest plots taken through the colony mean nest density of 3.72 nests/m² (SD 1.457) was recorded. Again, extrapolating from this the white-fronted tern colony was estimated to be 6,145 nests (95% confidence interval 5,400–6,891). By comparison, a total of 5,746 Apparently Occupied Nests were counted from the aerial photograph of the white-fronted tern colony. Another 334 birds were recorded within the nesting area, and none outside. The 95% confidence interval of this count is 5,597–5,895 using the methods described for black-billed gulls above. White-fronted tern is the commonest tern in New Zealand; colonies of several thousand birds have been recorded, but most colonies are 50–200 pairs (Heather & Robertson 2005). This colony of 6,000 breeding pairs is likely to be the largest colony of this species recorded.

The results of aerial photography and nest plots gave similar results and show that both methods are suitable for determining the colony size of these species (Table 1). Counts from aerial photos were 94–96% of colony size estimates from ground counts. Chabot *et al.* (2015) found that aerial photo counts from UAV yielded population estimates within 93–96% ground counts of common tern (*Sterna hirundo*) in New Burnswick. Similarly, our results highlight the potential value of UAV for surveying and counting large groups of colonial nesting seabirds.

The flight of a UAV over the breeding colony caused no disturbance to the breeding birds, whereas counting the nest-density plots created short-term disturbance because of the need to enter the colonies to measure nest densities. Borrelle & Fletcher (2017) highlight that UAV's can reduce disturbance impacts on surface nesting seabirds, and our study confirms the UAV's value for producing accurate counts while having little impact on densely nesting colonial seabirds.

Chabot & Francis (2016) point out that with the continued advances in camera and drone technology, in combination with increasingly sophisticated image analysis software, it is now possible for investigators involved in monitoring bird populations to save time and resources by increasing their use of computer-automated bird detection and counts from digital aerial images. These methods have not been tested in braided river systems, and would be a useful area of further research.

Table 1. Comparison of colony size estimates from ground counts (nest density plots) and counts from aerial photos of black-billed gull (*Larus bulleri*) and white-fronted tern (*Sterna striata*) breeding at the Ashburton River/Hakatere River mouth, November 2017.

Species	Ground count	Aerial count	Aerial/Ground ratio
Black-billed gull	7,807	7,485	95.9%
White-fronted tern	6,145	5,746	93.5%

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This research was conducted under contract to Environment Canterbury, using a commercial drone operator (NS) who held the relevant permissions from the local authority to fly drones on the land.

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SHORT NOTE

Sodium-rich clay soil geophagy by common redpoll (*Carduelis flammea*) in New Zealand

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Common Redpoll (*Carduelis flammea*) was introduced to New Zealand from Europe between 1862 and 1875 and is now naturalized and abundant throughout most of the country (Gill *et al.* 2010; Angus 2013). In North America, Europe and New Zealand, the redpoll feeds primarily on seeds of birch (*Betula* spp.), willow (*Salix* spp.), alder (*Alnus* spp.), grasses (Poaceae) and various conifers, with a larger proportion of arthropods during the breeding season (Knox & Lowther 2000). In New Zealand, redpolls appear to favour habitats with a mixture of young conifers and open habitat (Clout & Gaze 1984).

Geophagy is the deliberate consumption of clay or soil by an animal (Diamond *et al.* 1999). Hypotheses proposed to explain geophagy include: 1) neutralizing plant secondary compounds that may be toxic or impede digestion (Diamond *et al.* 1999; Gilardi *et al.* 1999), 2) acquisition of essential minerals rare in the typical diet (March & Sadleir 1975; Jones & Hanson 1985; Sanders & Jarvis 2000), and 3) acquiring grit to aid in physical breakdown of coarse food in the gizzard (Gilardi *et al.* 1999; Gionfriddo & Best 1999). A common element to these hypotheses is that geophagy is a behaviour that is adopted as an aid to digestion and nutrient acquisition and absorption. Although a review of published literature would suggest that geophagy is more common among certain bird orders (e.g. psittaciforms), it is not clear whether this is an artefact of parrots being generally large, social, and conspicuous compared to most birds. Moreover, many mammals including elephants, antelope, and bats (Voigt *et al.* 2008) also eat or lick soil mineral sources (Cowan & Brink 1949; Klaus & Schmid 1998). Thus, such behaviour appears to be important for many species and may be essential for some populations living in areas where their diet lacks sufficient minerals (Brightsmith & Aramburú 2004) or where geophagy serves some other important digestive function. The implications of geophagy for animal movement, distribution, and individual fitness are intriguing and, for most species, poorly understood, especially among birds (Wiener 1975).

To our knowledge, geophagy has never been reported in the common redpoll in Europe, North America (*Acanthis flammea*), or New Zealand, although other members of the subfamily Carduelinae such as crossbills (*Loxia* spp.) are known to engage in this behaviour (Tozer 1994; Latta 2012). Comprehensive accounts of the diet of Redpolls make no mention of soil consumption in North America (Knox & Lowther 2000). Geophagy has been widely reported among psittaciforms

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including communal consumption of clay in the Neotropics (Gilardi & Munn 1998; Brightsmith & Aramburú, 2004) and charcoal in New Zealand (Galbraith 2018).

On 20 January, 2019 at 1045 h, while walking along a track on the southeast slope of Sugar Loaf in the Port Hills off Summit Road above Christchurch, New Zealand, I observed a small group of 2–4 Redpolls perching on, and flying in the vicinity of, an outcrop of soil on a cliff face about 8 m above the track. The birds appeared to be pecking or actively feeding on the vertical soil surface or something on the soil surface (Fig. 1a); the soil, which adhered to the rock cliff, appeared to have been deposited in a rock fissure and then exposed when the outer rock fell away (Fig. 1b). Based on numerous recent geological studies in the area, it is highly likely that collapse of the outer rock face occurred at some point during the earthquake sequence that the wider Christchurch area experienced from September 2010 until February 2016.

The soil in this location was observed to be a pale yellowish tan colour with a few protruding roots (Fig. 1a). This is consistent with reports from soil surveys undertaken in the general area where the redpolls were observed; soils were characterized as having loess parent material overlaying basalt, forming a local "summit series" of yellow-brown and yellow-grey friable silt loams (Griffiths 1974). Soils from this region are typically fine and silty with up to 45% clay (loess) and were created in part during cold climate episodes during the last million years (Bell 1981; Yates *et al.* 2018). Parent material in the Port Hills is primarily heavily eroded volcanic material with soil geochemistry further influenced by glacial deposits, aeolian dust deposition, and biological processes (Lawrence *et al*. 2011).

Seen through Leica 10x50 binoculars, it appeared that the redpolls were using their bills to take bites of the soil itself (supplemental video).[1] Using a Canon 80D camera with a 100–400 mm lens, I videoed the birds at the highest magnification for approximately 1.5 minutes. During this time, at least one male foraged at the soil and at least one female/juvenile also perched on the soil cliff face or on protruding roots and repeatedly bit at the soil. On 29 January, at 0930 h, I again videoed a single male redpoll at the same site foraging on the soil surface while clinging to the soil and/or roots (see supplemental video).[1] The video was edited to reduce shaking and to slow down time periods when a bird was actively pecking and biting on the soil cliff face. The video clearly shows pieces of the friable soil falling away as the redpoll repeatedly pecks at the surface to take "bites" of the soil.

In total, I spent 2 h 57 min observing this soil cliff site and during that time saw visits by an estimated 4–5 redpolls. Only once were there two birds at the site simultaneously, so the exact number of individual birds cannot be determined from these observations. However, it does seem clear that redpolls return to this site with some regularity.

Because some birds appear to select soils with particular chemical characteristics (Powell *et al*. 2017), we decided to collect and analyze soil samples from the cliff site and from an accessible site with exposed soil of the same "summit series"

Figure 1. a) A common redpoll consuming soil on cliff face, Port Hills, Canterbury, New Zealand, b) Flaspohler using a bamboo pole to sample soil adhering to rock face (a sheet below was used to collect fallen soil) in Port Hills. The smooth, less weathered, and paler section of the cliff can be seen at top centre where the rock recently fell away to reveal the soil.

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[1] A composite edited (for stability and slow motion) supplemental video 3 min 47 sec. long can be viewed at: https://www.youtube.com/watch?v=1YogzjS6iP4

approximately 1 km away. On 1 February 2019, we used a long bamboo pole and a sheet to collect samples of the soil at the spot where the redpolls had perched and consumed soil (Fig. 1a). These two soil samples were sent to the Scion analytical laboratory in Rotorua to determine elemental concentrations (Mahaney & Krishnamani 2003).

A small subsample was used to test allophane content; this showed a moderate to strong reaction, agreeing well with the soil description in Griffiths (1974). Elemental analysis (LECO CNS-2000, Mehlich-3 extraction followed by ICP-OES analysis) determined that the "eaten" soil contained 2.32% carbon and 859 mg/kg sodium while the "not eaten" soil contained 0.98% carbon and 377 mg/kg sodium.

Many North American finch species regularly eat mixtures of salt and sand including gravel spread on winter roads for automobile traction (Flaspohler, *pers. obs.*). Finches also eat clay (Latta 2012) for reasons that remain poorly understood; the motivation for such geophagy may vary from species to species or even between populations. A closely related behaviour, lithophagy is defined as the ingestion of small stones and although we could find no mention of this behaviour among redpolls, it seems likely that, as with other finches, they engage in this behaviour to aid physical breakdown of food or as an antiparasite behaviour (Knezevich 1998; Robinson *et al*. 2008).

Because only two samples were collected, statistical analyses were not possible, but it is worth noting that the differences in sodium concentrations identified here agree very well with a more extensive study of soil properties that concluded that sodium content were an important factor in parrot geophagy (Powell *et al.* 2009); Powell *et al*. (2009) found that the mean sodium concentrations in a clay lick in Amazonian Peru was 1,137 mg/kg compared to 859 mg/kg for the soil eaten by redpolls in this study. The mechanism responsible for the greater sodium content in the "eaten" soil is not clear, but is likely related to the physical environment in which the soil formed prior to exposure following the rock slide. Sodium is highly soluble and is readily released from rock exposed to rain. The fissure may have allowed dissolved sodium to accumulate, gradually concentrating this element to levels exceeding that in nearby soils.

The difference in the carbon content between the soil samples is also likely an outcome of the physical environment of the soil prior to the earthquakes. The fissure in which the "eaten" soil formed would have trapped considerably more plant litter than the "not eaten" soil collected from a more exposed location; such inputs (and retention) of organic matter are often associated with increased soil carbon content (Smaill *et al.* 2008).

Many previous studies have suggested that sodium compounds are common in soils chosen by mammals for geophagy (Stockstand *et al*. 1953; Weeks & Kirkpatrick 1978), and this appears to be true for birds as well. In Peru, Brightsmith & Muñoz-Najar (2004) found that soil consumed by 15 species of birds (mostly parrots) had seven times more exchangeable sodium ions compared with unconsumed soil. Sodium supplementation is the most commonly reported reason for vertebrates to engage in geophagy (reviewed in Klaus & Schmid 1998). For birds, the preponderance of published studies suggests that the need for sodium is the primary driver of geophagy (Brightsmith *et al.* 2018).

The redpolls observed in the Port Hills may be deriving other benefits from soil consumption such as physical breakdown of coarse food in the gizzard or toxin absorption. However, the soils we collected were uniformly fine silt and clay with few particles larger than 0.1 mm, suggesting that their value as grit would be minimal. It seems likely that different bird species engage in geophagy for multiple and sometimes complimentary reasons (Symes *et al*. 2005). Birds may choose soils that have more than one appealing characteristic, and further experimental research is needed to clarify whether these soils provide other benefits beyond augmenting sodium in the diet.

More reporting of observations of geophagy among all birds would improve our understanding of this behaviour and how widespread it is among bird orders. We concur with Galbraith (2018) who recently wrote: "*I encourage other researchers to document and report any observations (historical as well as future) of charcoal consumption, or geophagy, among the wider New Zealand avifauna, so that we might better understand the prevalence of this behaviour and discuss what importance it may have in this region for avian herbivores in particular*."

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SHORT NOTE

Long-tailed cuckoo (*Eudynamys taitensis*) predation on rifleman (*Acanthisitta chloris*) nestlings

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The rifleman (tītipounamu*,* *Acanthisitta chloris*) is a small (5–7 g) New Zealand endemic bird that lives in forested areas throughout the country. It is socially monogamous, with occasional cooperative breeding behaviour. It builds dome-shaped nests with a single entrance (~2.5 cm) in a variety of locations, including tree cavities, the dead fronds of tree fern trunks, and on the ground underneath leaf residues or roots (Sherley 1990). It breeds from September to February and can successfully rear several broods a year (Gray 1969; Sherley 1985). Predators include native New Zealand species like the morepork (ruru, *Ninox novaeseelandiae*) (Denny 2009), as well as introduced mammalian predators such as rats (*Rattus* spp.) and stoats (*Mustela erminea*) (Robertson 1985; Gill 2019). However, predation by long-tailed cuckoos (koekoeā, *Eudynamys taitensis*) on rifleman has not previously been reported. Here we describe observations of long-tailed cuckoo predation on rifleman nestlings and the vocal response of rifleman towards long-tailed cuckoos. To our knowledge, these are the first documented cases of long-tailed cuckoo predation on rifleman.

The long-tailed cuckoo is a medium-sized (125 g) summer migrant to New Zealand. It is a brood parasite, targeting mainly whiteheads (pōpokotea, *Mohoua albicilla*), yellowheads (mohua, *Mohoua ochrocephala*), and brown creepers (pipipi, *Mohoua novaeseelandiae*) as its hosts (Gill 2013). It has a generalist diet that includes insects (Gill 1980; Reed 1980), lizards, and the eggs and nestlings of small birds such as tomtits (*Petroica macrocephala*) and silvereyes (*Zosterops lateralis*) (Stidolph 1949; Robertson 1985; Beaven 1997; Gill *et al.* 2018). It forages solitarily in habitats that include the forest canopy, second-growth bush, and cultivated lands. It breeds throughout New Zealand from October to March while it winters in the Pacific Islands from April to September (Robertson 1985).

As part of a larger project, we monitored rifleman nests in the Boundary Stream Mainland Island, New Zealand (39°06'15.8"S, 176°48'06.1"E), from September 2018 to February 2019. This area has been managed by the Department of Conservation since 1979, and due to intensive management and translocation efforts, it is host to many New Zealand native birds including long-tailed cuckoos. For each rifleman nest found on our study site, we set up a Bioacoustic Automated Recorder (BAR) by Frontier Labs (Nathan, QLD, Australia) and a trail camera by Bushnell (TrophyCam Model 119776; Kansas City, MO, USA) to record the vocalizations and the interactions between parents and nestlings. All BARs and trail cameras were placed within 1.5–2 m from the entrance to a nest. All observations are based on trail camera footage (the camera time and date were set to local time and date) and recordings from the BARs.

The first predation event occurred on the 22 November 2018 (Fig. 1a–c). The nest cavity was 4.1 m high in a mahoe tree (*Melicytus ramiflorus*), with a tree cavity entrance of about 15 cm x 15 cm.

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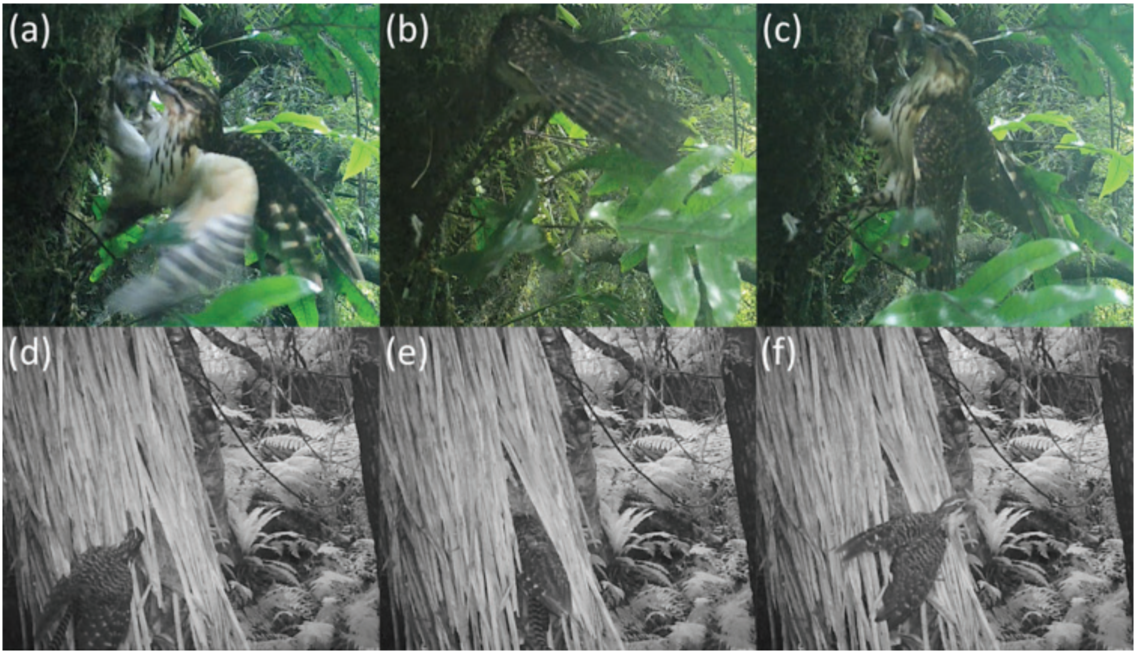

Figure 1. Screenshots of video footage of long-tailed cuckoo predation on rifleman nests at the Boundary Stream Mainland Island Reserve, New Zealand. Long-tailed cuckoos depredated rifleman nests on the 22 November 2018, at 1108 h (a–c), and another nest on the 30 November 2018 (d–f) at 1419 h. For both events, trail cameras detected the long-tailed cuckoos at the nest holes (a,d), reaching their heads inside the nests (b,e), grabbing a nestling in the beak (c), and swallowing a nestling (f). Low light levels at the second site (d–f) generated black and white footages. Video footages were taken from trail cameras Bushnell TrophyCam (Model: 119776; Kansas City, MO, USA).

Rifleman nestlings at this nest were 14 ± 2 days old (rifleman fledge at ~20 days). A long-tailed cuckoo arrived at this nest at 1103 h and stayed for five minutes. During this time, it removed nest material from the tree cavity, and made several attempts to grab nestlings. A rifleman adult – probably one of the parents – was audible in the background of the camera recording, and produced long and consistent series of agitated calls and a total of 9 trills with decrescendo notes (Fig. 2a, d). At 1108 h, the long-tailed cuckoo grabbed a single nestling in its beak and flew away. The nestling produced a high pitch, broad-band distress call when captured (Fig. 2b). Once the cuckoo left the area, the parent stopped producing agitated calls and trills. Thirty-four minutes after the cuckoo departed, the female rifleman entered the nest to feed the remaining nestlings. At 1640 h on the following day, a long-tailed cuckoo appeared again on the trail camera, and stayed 13 minutes at the nest. The long-tailed cuckoo removed more nesting material from the nest, including feathers and twigs, but it did not take any nestlings. During this time, a rifleman adult produced a series of agitated calls and a total of 13 trills (Fig. 2a, d). A day later, we found a live nestling outside its nest with its parents attending it at the base of the nest tree. We did not hear any begging sounds coming from the nest, suggesting that this nestling was the last of its brood. The nestling did not survive the night outside its natural nest. The trail camera did not pick up any subsequent predation events or visits by the long-tailed cuckoo. The long-tailed cuckoo was not banded, so we are unsure if the same individual visited the nest on those occasions.

The second long-tailed cuckoo predation event at a rifleman nest occurred on the 30 November 2018 and the 01 December 2018. This nest was built inside the dead fronds of a soft tree fern (kātote, *Cyathea smithii*), and was 2.9 m above the ground. The nestlings at this nest were 13 ± 2 days old. On the 30 November 2018, a long-tailed cuckoo visited this nest twice, roughly an hour apart, for two minutes in total, and consumed three nestlings (one nestling from 1308–1309 h and two nestlings from 1418–1419 h). At arrival, it pushed its head in the nest, retrieved a nestling, and immediately swallowed it before leaving. At 1309 h, a rifleman parent generated rapid high-frequency agitated calls and a rapid trill (i.e. similar to Fig. 2a, d). Seventy minutes later, the long-tailed cuckoo visited the nest a second time. It forced its head inside the nest again, and emerged

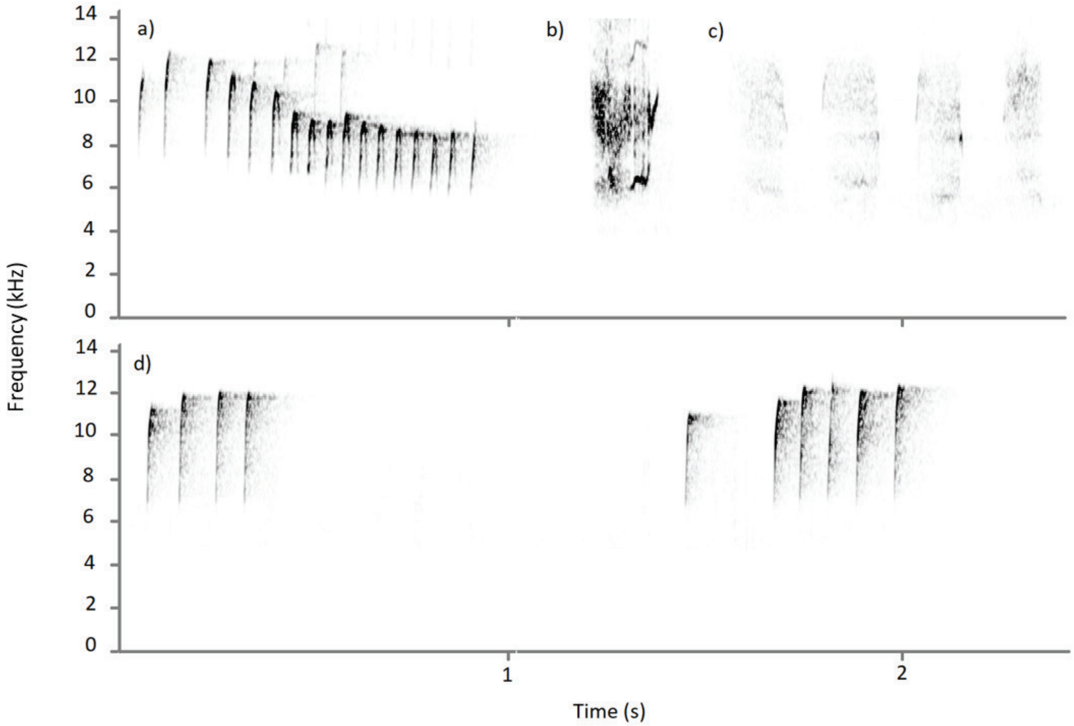

Figure 2. Selection of spectrograms of rifleman vocalizations during predation events by long-tailed cuckoos in Boundary Stream Mainland Island Reserve, New Zealand. Rifleman parents produced trills (a) and agitated calls (d) towards long-tailed cuckoos at their nests and rifleman nestlings produced distress calls (b–c) when picked up by long-tailed cuckoos. The adult trill (a) and the agitated calls (d) were recorded on the 22 November 2018. On the 22 November 2018, at 1108 h, a long-tailed cuckoo grabbed a nestling that produced a high pitch broad-band nestling call (b). On the 30 November 2018, at 1419 h, another nestling produced distress calls (c) before being swallowed by a long-tailed cuckoo. Spectrograms were created with Syrinx Version 2.6h (Transform size 512, FFT Window Type Blackman) (Burt 2006). All recordings can be found on xeno-canto (www.xeno-canto.org): catalogue numbers - Fig. 2a XC470957, Fig. 2b XC470956, Fig. 2c XC470958, Fig. 2d XC470955.

with a second nestling in its beak. It then reached inside the nest for a third nestling. Once in its beak, the third nestling produced a distress call (Fig. 2c, at 1419 h) before it was swallowed. The following day, at 0856 h, a long-tailed cuckoo visited the nest for the third time. However, it left the nest shortly after, without inserting its head in the nest and attempting to capture any nestlings. After this predation event, no rifleman adult was seen feeding at this nest, suggesting that the long-tailed cuckoo depredated the whole rifleman clutch. As with the first nest, the cuckoo was not banded, so we are unsure if the same individual visited the nest on each occasion.

We also recorded a third visit by a long-tailed cuckoo to a rifleman nest, but in this case, no predation occurred. This nest was also built in the dead fronds of a soft tree fern, along its trunk, and was 2.8 m high. On the 27 November 2018, a cuckoo visited a rifleman nest at three different times, a few minutes apart (0903 h, 0906 h, and 0908 h). The nest had fledged the same morning, and we were not aware of any predation on the nest in the days prior to fledging. This visit may suggest that this long-tailed cuckoo knew about the location of this nest but decided to delay its predation.

Throughout the breeding season, we documented the visit and predation events at three rifleman nests (Fig. 1). The long-tailed cuckoos visited two types of rifleman nests: a nest constructed in a tree-cavity (Fig. 1a–c) and two nests built in the dead fronds of tree fern trunks (Fig. 1d–f). This demonstrates the aptitude of long-tailed cuckoos to locate and access diverse types of nests. Rifleman also nest near or on the ground, but we have not yet observed predation by long-tailed cuckoos on these nests. This may be because cuckoos probably do not spend much time on the ground (I Moran *pers. obs.*). This may further explain why some rifleman nest near the ground:

to avoid cuckoo predation, a strategy that may have been adaptive before the introduction of terrestrial mammalian predators. It is also important to note that the long-tailed cuckoos visited nests built in large tree cavities with relatively large entrances which could have facilitated access to the nestlings. Furthermore, we found that all attempted predation events occurred late in the nestling period, within a week of the expected fledging date. This may indicate that long-tailed cuckoos prefer to prey on older nestlings. Alternatively, it may be that the loud begging noises of the nestlings, or the high rate of nest visitation by parents later in the nestling period, facilitate the ability of long-tailed cuckoos to locate nests. Finally, long-tailed cuckoos may delay their predation on known nests to prey on older nestlings, as suggested by the third visit to a nest. This last possibility would warrant future investigation as it would require planning on the part of the predator.

The vocal responses of riflemen towards long-tailed cuckoos were conspicuous and distinctive from the other vocalisations used by this species during nest feeding contexts (Fig. 2). The adult rifleman produced alarm responses including agitated calls (Fig. 2a), and trills (Fig. 2d) referred to by Higgins *et al.* (2001) as alarm calls with rapid high frequency decrescendo notes. Agitated calls consisted of a repetition of similar structured, short, sharp, elongated notes with a frequency range between around 6.5 kHz and 12 kHz, while the trills consisted of similarly structured notes that decreased in frequency from higher frequencies (~8–12 kHz notes) to lower frequencies (~6–8 kHz). We also documented the distress calls of rifleman nestlings in response to long-tailed cuckoo predation (Fig. 2b, c). The distress calls of the nestlings were broad-banded notes between around 6–11 kHz and were about ~0.2–0.3 s in duration.

Long-tailed cuckoo predation on rifleman opens up the possibility for cuckoo brood parasitism on rifleman nests. A study investigating cuckoo artificial egg rejection and desertion by New Zealand birds found that rifleman may recognize cuckoo eggs; two out of eleven rifleman pairs abandoned their nests with artificial shining cuckoos' eggs (Briskie 2003). Further studies on egg rejection and recognition in rifleman should be investigated. Alternatively, similarly to shining-cuckoos that seem to be general predators of avian eggs (Briskie 2007), long-tailed cuckoos appear to be general predators of nestlings, even for species they do not parasitize. In addition, unlike previous reports of cuckoo predation events, in which long-tailed cuckoos left no signs of nest destruction around the open cup nests of tomtits after predation (Beaven 1997), we show that long-tailed cuckoos substantially destroy the structure of rifleman nests. Future studies on rifleman nest destruction by long-tailed cuckoos may give additional insight on nest suitability for brood parasitism.

The three instances of long-tailed cuckoo predation and visit on rifleman nests reported here support the predatory status of long-tailed cuckoos on rifleman in New Zealand and suggest that long-tailed cuckoos may have important ecological impacts on the populations of rifleman in New Zealand. Further studies on how long-tailed cuckoos impact rifleman populations via predation and potential brood parasitism are needed and will improve our current understanding of the ecology and distribution of rifleman and long-tailed cuckoos in New Zealand.

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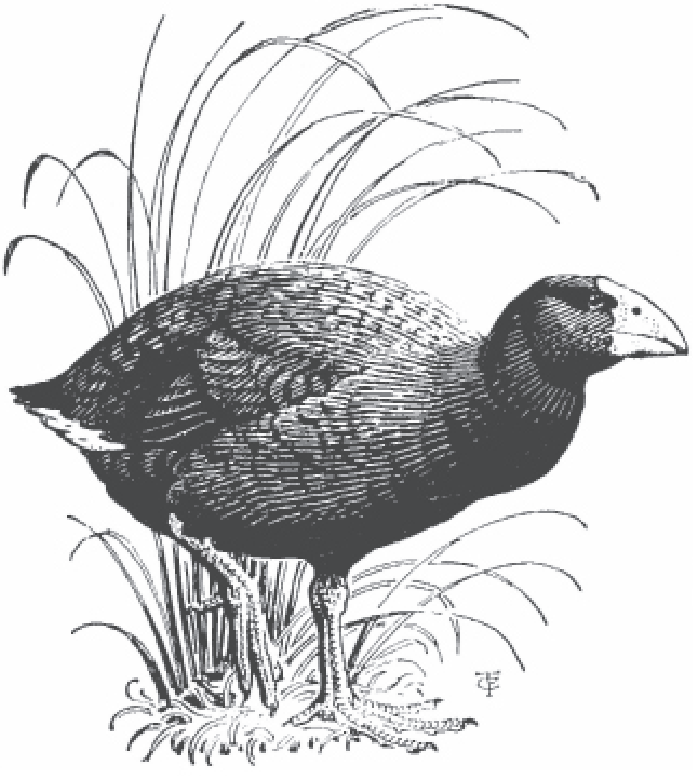

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