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MORPHOMETRICS AND ECOLOGY OF THE NEW ZEALAND DOTTEREL (*Charadrius obscurus*), WITH A DESCRIPTION OF A NEW SUBSPECIES

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ABSTRACT

Morphometric data are presented for the northern and southern populations of the NZ Dotterel. There are significant differences between the two populations in all measurements of birds and eggs. The differences in midtoe and adult weight are pronounced; the former yields a Coefficient of Difference above the conventional level of subspecific difference. Plumage differs between birds of the two populations. Ecologically and behaviourally the two populations differ distinctly; southern birds breed inland and northern birds on the coast, the timing of flock break-up and movement to breeding sites is different and the ranges of the two groups are discrete. Based on these differences, the two populations are accorded subspecific status, and a new subspecies is described.

KEYWORDS: New Zealand Dotterel, plover, taxonomy, subspecies, morphometrics.

INTRODUCTION

The New Zealand Dotterel (*Charadrius obscurus*) is an endemic shorebird that was widespread in New Zealand until the late 19th century. Since then it has declined in range and numbers and is now found in two breeding populations separated by about 1100 km. The northern population numbers about 1400 and is found on the coast of the North Island, north of 39°S. The southern population currently numbers no more than 65 birds and is critically endangered. It now breeds only on Stewart Island but was formerly widespread in the South Island (Barlow 1993, Dowding & Murphy 1993).

The Banded Dotterel (*C. bicinctus*) is currently the only charadriid with recognised subspecies within the New Zealand region. The Auckland Island Banded Dotterel (*C. b. exilis*) is larger and darker than the nominate mainland subspecies and the breeding ranges of the two do not overlap (Falla 1978, Pierce 1980). The NZ Dotterel is currently considered a monotypic species (Turbott 1990) but very little work has been done on the Stewart Island birds until recently. Commenting on the different movement patterns of inland and coastal breeding NZ Dotterels, Falla (1940) noted that it "is not quite certain whether two races of birds are represented in this division of habits". He later observed them during the breeding season on the Stewart Island tops and at Mason Bay and stated that "the Southern N.Z. Dotterel... is well worth following up. It is so different in behaviour and habits from the northern race" (letter to M.L. Barlow, 3 December 1969).

In a recent study however, allozyme electrophoresis revealed no differences between birds from North Auckland, Coromandel and Stewart Island (Herbert *et al.* 1993). This is not surprising however, as the technique commonly shows very poor resolving power below species level in birds (Zink 1991). There are many examples of large changes in avian morphology not being reflected in genetic changes that can be measured by allozyme electrophoresis (see Herbert *et al.* 1993). In addition, intra-specific variation is often particularly low in shorebirds (Baker & Strauch 1988), even when measured by more sensitive techniques (Baker 1992), and measures of genetic divergence frequently overlap at the population, subspecies and species level.

There are few published values of standard measurements for the NZ Dotterel. Ranges were given by Oliver (1955) and Hayman *et al.* (1986), but in both cases the origin of the birds and the sample sizes were not stated. Measurements of 25 North Island adults were given in Marchant & Higgins (1993). During a study of movement patterns and site fidelity (Dowding & Chamberlin 1991), birds of the northern population caught for banding were weighed and measured. Birds of the southern population were measured during a study on the status of the species on Stewart Island (Dowding & Murphy 1993).

METHODS

Birds were weighed to the nearest gram with a 300 g Pesola spring balance. Weights were excluded from analysis if birds were obviously gravid or had incomplete clutches. Linear measurements were taken using the methods described by Marchant & Higgins (1990), except that wing chord was measured with the outer primaries flattened but not straightened. Wing and tail measurements were to the nearest millimetre; tarsus, total head length (THL), bill (exposed culmen) and midtoe and claw (MTC) were recorded to the nearest 0.1 mm using Vernier calipers. Wing and tail measurements were excluded from analysis if the outer primaries or central rectrices showed extreme wear or were in active moult. Eggs were weighed to the nearest 0.1 g with a 30 g Pesola spring balance and measured to the nearest 0.1 mm with Vernier calipers. All measurements were made by the author. Means of measurements (quoted \pm S.D.) were compared using two-tailed *t*-tests

and correlations were tested by computing the correlation coefficient r (Sokal & Rohlf 1981). Probability ≤ 0.05 was considered significant. The Coefficient of Difference between two populations is the difference in means of a measurement divided by the sum of the standard deviations of those means (Mayr 1969).

RESULTS & DISCUSSION

Morphometrics of adults

Weights and measurements of NZ Dotterels aged one year and older of the northern and southern populations are compared in Table 1. Differences in wing, tail, THL, bill and tarsus means are significant but small, with a large degree of overlap in ranges. There are highly significant differences in average MTC and weight.

TABLE 1 – Comparison of measurements (mm) and body mass (g) of adult New Zealand Dotterels of northern (N) and southern (S) populations

Measurement	Population	Mean \pm S.D.	Range	n	P
Wing	N	164.8 \pm 4.3	152 – 173	109	0.006
	S	167.0 \pm 4.5	160 – 174	39	
Tail	N	65.0 \pm 2.41	59 – 71	93	0.019
	S	63.9 \pm 2.85	57 – 69	48	
Total head length	N	63.7 \pm 1.58	60.2 – 67.3	109	0.0006
	S	64.6 \pm 1.38	61.7 – 67.3	49	
Bill	N	28.2 \pm 1.50	24.4 – 31.6	113	0.042
	S	28.7 \pm 1.13	26.5 – 31.5	48	
Tarsus	N	39.4 \pm 1.37	36.0 – 43.2	114	0.0003
	S	40.2 \pm 1.34	37.2 – 42.6	49	
Midtoe & claw	N	29.2 \pm 0.89	26.8 – 31.0	113	0.0001
	S	32.0 \pm 1.02	29.5 – 34.7	49	
Body mass	N	144.5 \pm 8.6	128 – 169	74	0.0001
	S	162.2 \pm 9.0	147 – 179	46	

On average, NZ Dotterels on Stewart Island are larger in all measurements except tail than those of the North Island population. The most significant difference is in the length of midtoe and claw; this has a Coefficient of Difference (CD) of 1.47, considerably above the value of 1.28 which is the generally-accepted level of subspecific difference (Mayr 1969). (A CD of 1.47 represents joint non-overlap of about 93%, i.e. 93% of the individuals of one population differ from 93% of individuals in the other.) Birds on Stewart Island average 12% heavier than those in the North Island but standard deviations are relatively large; the CD of 1.01 represents approximately 84% joint non-overlap between the populations.

Sexual dimorphism in measurements could bias these results if the sex ratios of northern and southern samples were not similar. The northern sample has approximately equal numbers of males and females but the southern sample is likely to have included more females than males (J.E. Dowding, unpubl. reports to Department of Conservation, Wellington, June 1993 and April 1994). In northern birds, there are sexual differences in only two standard measurements (THL and tarsus), with males larger on average in both cases (J.E. Dowding, unpubl. data). Assuming similar sexual size dimorphism in southern birds, the differences shown between northern and southern birds in THL and tarsus (Table 1) may therefore be slightly underestimated.

Figure 1 shows a plot of weight against MTC, the two largest differences. The populations can be separated almost completely into two clusters, with only two birds (one from each population arrowed) of a total sample of 120 falling into the wrong cluster. Although weights of individual birds will vary, weight is much the less-discriminating of the two variables, and fluctuations will affect the separation minimally. On the other hand, MTC (which provides much better separation) can be measured accurately and does not fluctuate.

The fact that differences in some measurements are large and others are small results in differences in proportion. For example, the ratio tarsus/MTC averages 1.35 in the northern population and 1.26 in the southern; this difference is highly significant ($t = 12.6$, d.f. = 161, $P = 0.0001$).

The increase in overall body size and the darker pigmentation (see Plumage below) seen in Stewart Island birds are consistent with Bergmann's Rule and Gloger's Rule respectively (Mayr 1963); on the other hand, lengths of bill, tarsus and MTC are not smaller (as predicted by Allen's Rule), suggesting that other selective forces may be operating on these features. For example, the longer MTC found in the southern population may provide better balance in the extremely windy conditions that prevail on Stewart Island, particularly in the mountain breeding areas. Auckland Island Banded Dotterels breed in similar exposed, windswept terrain and also have a proportionately longer midtoe than the mainland subspecies (Falla 1978); the tarsus/MTC ratios of *C. b. exilis* are 1.26 (male) and 1.24 (female), compared to 1.34 (male) and 1.36 (female) for North Island *C. b. bicinctus* (data from Falla 1978). These values are virtually identical to those given above for NZ Dotterels. Variable Oystercatchers on Stewart Island have on

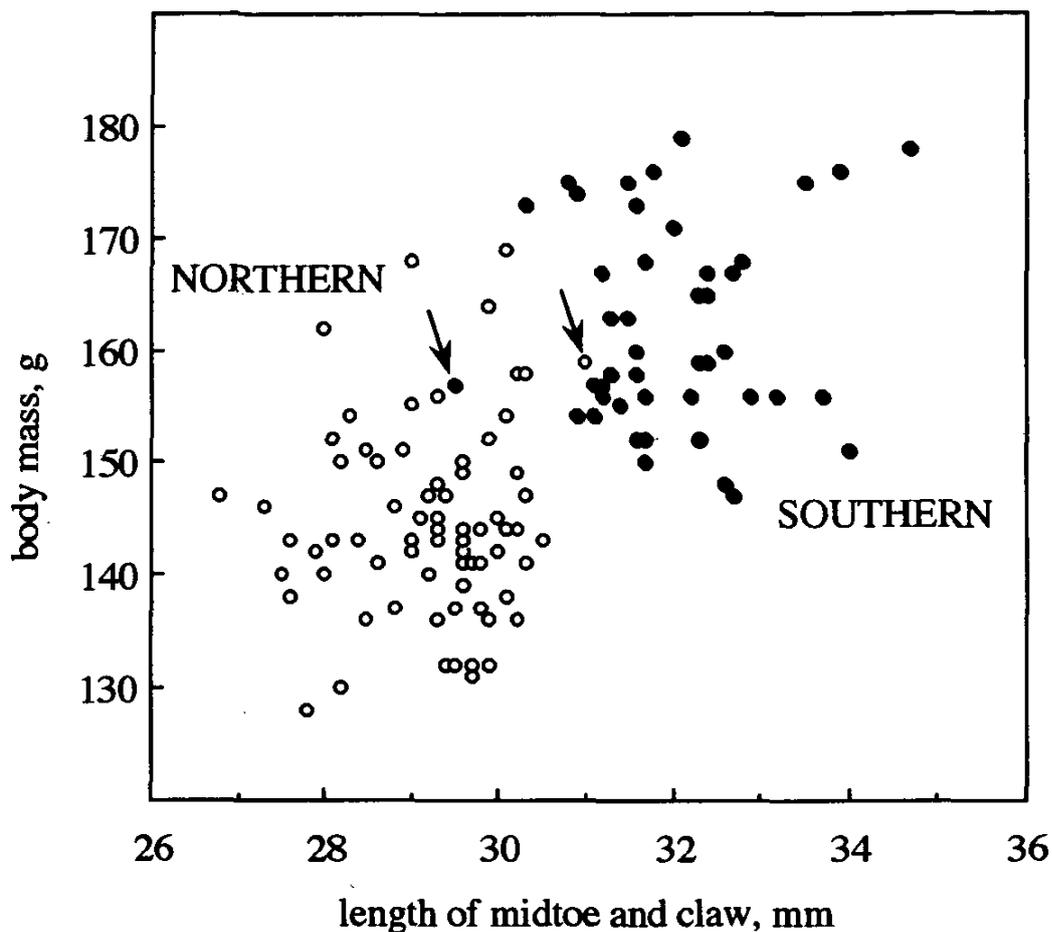


FIGURE 1 – Plot of body mass (g) against length of midtoe & claw (mm) for New Zealand Dotterels from the North Island (NORTHERN, open circles) and Stewart Island (SOUTHERN, closed circles). See text for discussion of arrowed points.

average the longest midtoe in the species' range and Baker (1991) has suggested that this is an adaptation to improve balance and agility on slippery rocky shores.

Eggs

Although there is overlap in all measurements, eggs of Stewart Island birds are significantly longer, wider and heavier on average than those from the North Island (Table 2). In both populations, there is a highly significant correlation between egg width and weight (northern $r=0.78$, d.f. = 53, $P=0.0001$; southern $r=0.78$, d.f. = 32, $P=0.0001$) but not between length and width or length and weight.

Plumage

Falla (1940) commented that "it is noteworthy that most southern birds are very much richer in colour than the northern examples". Although there is individual, sexual and seasonal variation in both populations, adult birds

TABLE 2 – Comparison of measurements (mm) and mass (g) of New Zealand Dotterel eggs from northern (N) and southern (S) populations

Measurement	Population	Mean \pm S.D.	Range	n	P
Length	N	44.3 \pm 1.33	41.3 – 46.5	64	0.0001
	S	46.1 \pm 1.49	42.7 – 49.7	39	
Width	N	31.4 \pm 0.68	29.2 – 32.7	64	0.0001
	S	32.7 \pm 0.77	31.4 – 34.2	39	
Mass	N	21.9 \pm 1.35	18.1 – 24.3	54	0.0001
	S	24.3 \pm 1.31	21.4 – 26.5	33	

on Stewart Island are normally a dark brown on the dorsal surfaces, compared to the mid-grey-brown of North Island birds. Breeding colour on the ventral surfaces also differs, with southern birds showing a darker brick-red than the orange-red of northern birds. These differences can be seen in McKenzie & Heather (1985); the photograph on p. 182 is of a Stewart Island bird, that on p. 183 of a North Island bird. Other photographs of Stewart Island birds are shown in Dowding (1992) and Gaze (1994). Downy chicks on Stewart Island are also noticeably darker on the dorsal surface (see photograph in Dowding 1993). The dark brown upper parts of the type specimen depicted by Forster (see Andrews 1986, p. 23) are typical of present-day Stewart Island birds (and noticeably darker than most North Island birds). Marchant & Higgins (1993) differentiated between light- and dark-plumaged birds among museum specimens and noted that all or most birds breeding in the North Island were light-plumaged, while all or most breeding on Stewart Island were dark-plumaged. For detailed descriptions of their two plumage forms (including references to a standard colour guide), see Marchant & Higgins (1993).

As noted above, the increased melanism seen in southern birds is consistent with Gloger's Rule, but it is also possible that selection is favouring paler plumage in the North Island (where birds normally nest on pale substrates such as sand and shells) than on Stewart Island (where they nest on darker cushion plants or among rocks).

Ecological and behavioural differences

Breeding habitat

Birds of the present North Island population breed on or very near the coast, often at the mouths of tidal estuaries or streams. Nests are most commonly on sandy beaches, sand banks, shell banks or in dunes, but also occasionally on stony beaches, short pasture or artificial sites (Marchant & Higgins 1993). On Stewart Island, remaining breeding sites are all inland above 300 m a.s.l. (Dowding & Murphy 1993). Barlow (1993) found no records of coastal

breeding in the South Island, and I can find none from there or from the southern part of the North Island (J.E. Dowding unpubl. data). Contemporary first-hand accounts agree that the species bred inland in the South Island and descended to the coast for the autumn and winter (e.g. Potts 1883, Pascoe 1957). Douglas (*in* Pascoe 1957) wrote that the NZ Dotterel "frequents the sea beaches and river flats during the winter, but in summer I have often found them in the mountains, almost to the snow line, where they lay their eggs and rear their young." Thomas Potts, who recorded much of what we know about the species in the South Island in the mid-late 19th century, recorded breeding in a variety of inland habitats, including on mountain tops, river terraces and grassy plains, and in riverbeds (Potts 1869, 1883). However, although Potts lived on the coast (at Governor's Bay, Lyttelton Harbour) for about 30 years (Star 1991) and recorded NZ Dotterels there in autumn and winter, he gives no records of coastal breeding.

One exception appears to be that a few pairs bred at Mason Bay, Stewart Island (Guthrie-Smith 1914) but this may have been an isolated and somewhat marginal case of coastal breeding. The little evidence available indicates that the birds at Mason Bay did not breed on the beach front but well back in the dunes. The only nest site that can be located accurately (Guthrie-Smith 1914) was on the rocky shoulder of Big Sandhill (grid reference NZMS260 D48 133516), more than 2 km inland and about 100 m a.s.l.; Guthrie-Smith's (1914) account suggests that there were also nests on the stony flats 1-1.5 km inland south of Duck Creek, close to the present daytime high-water roost site of the Paterson Inlet flock (Dowding & Murphy 1993). George Leask, who farmed at Mason Bay, found nests "between the big sandhill and the beach...George says nests more often *further back* than nearer beach. Nests also up Stony Ck - follow this rather dry ck. back to flats." (M.L. Barlow, pers. comm. from notebook of Olga Sansom, October 1968). In addition, I have found no breeding records from other apparently suitable sandy beaches on Stewart Island, e.g. Smoky Beach, Doughboy Bay or The Neck.

Although there could have been a few exceptions, it thus appears that a fundamental difference exists in breeding habitats of the two populations. Birds of the northern population breed on the coast, while all or most southern birds breed or bred inland in spite of the fact that there is clearly much suitable coastal habitat in the South Island and southern North Island similar to that now used in the northern North Island.

Nest lining

NZ Dotterels on Stewart Island nest either among cushion plants (see photographs in Dowding 1992) or in hollows among rocks (pers. obs.). In either situation, nests are deeply lined, usually with leaves of the snow tussock *Chionochloa pungens*. Soper (1984) described nests in southern Stewart Island as "well formed, using more material than one normally expects of dotterels". Nests in the South Island were also lined with grasses, although Potts (1869) described them as "merely a few stems...twisted into a slight hollow in the ground". Nests in the North Island are normally simple depressions in the substrate (usually sand); they are not lined with grasses but may be decorated with shells or small pieces of seaweed (pers. obs.).

Courtship behaviour

Males of a number of *Charadrius* plovers (including the Banded Dotterel) bow and give deep 'mooing' calls when courting females (Phillips 1980). During very limited observations of NZ Dotterel courtship on the Stewart Island breeding grounds, I have seen and heard this behaviour twice, once on Mt Anglem (31 October 1989) and once on Mt Rakeahua (24 November 1990). On both occasions two birds were present and the darker of the two (presumably the male) bowed, fanned its tail and gave the low-pitched mooing call repeatedly for 15-20 minutes. The incident on Mt Anglem appeared to be associated with nest-site selection and the mooing bird was picking up and tossing *Chionochloa* leaves. In spite of the fact that there has been a great deal more observation of NZ Dotterel behaviour in the North Island, mooing has not yet been recorded in the northern population. In an outline of the courtship behaviour of the NZ Dotterel, Phillips (1980) stated that he suspected the species did moo, but did not detect it. There may therefore be a difference in this aspect of courtship behaviour between the populations, although further observation may detect mooing among North Island birds.

Timing of flocking

Timing of movements to and from post-breeding flocks in the northern population was described by Sibson (1967), Reed (1981) and Dowding & Chamberlin (1991). Flocks begin to form in January or February and most breeding birds have returned to their territories by the end of May. Currently, about 15% of pairs on the North Auckland east coast remain on territory all year round and do not visit a flock (J.E. Dowding & S.P. Chamberlin unpubl. data). Birds breeding on Stewart Island begin to form flocks in January and these flocks stay together over winter, usually until August (Barlow 1993, Dowding & Murphy 1993). No birds are known to remain at breeding sites during the winter. This was formerly also the pattern in the South Island; birds began moving from inland breeding sites to the coast in the middle of January and appeared in the Canterbury back-country in August, on their way back to the mountains to breed (Potts 1883).

Range

There is general agreement that a subspecies should occupy a discrete geographic portion of the range of the species (see Criteria below). The two populations of NZ Dotterel clearly fit this criterion – their present breeding ranges are a minimum of 1100 km apart (Marchant & Higgins 1993) and there is little or no overlap in non-breeding ranges either (Dowding & Murphy 1993).

Criteria for recognition of subspecies

Mayr (1963) defined a subspecies as "an aggregate of local populations of a species, inhabiting a geographic sub-division of the range of the species, and differing taxonomically [i.e. by diagnostic morphological characters] from other populations of the species". The subspecies is probably a more heterogeneous taxonomic unit than any other; it is not necessarily an

evolutionary unit, although some subspecies are incipient species. In a forum on avian subspecies it was, however, widely agreed to be a useful taxonomic category, allowing definition of clearly distinct subsets of a species (Wiens 1982). There was also general agreement that (a) separation should not be based on a single character but on a suite of characters; (b) populations that vary only clinally should not be accorded subspecific status; (c) nearly all individuals of a subspecies should differ from nearly all individuals of other populations of the species; (d) geographic or ecological barriers should exist which allow very little gene flow between subspecies.

Populations of a species may show morphological variation in different parts of the species' range, but if that variation is smoothly clinal such populations are not now normally accorded subspecific status. For example, the Blue Penguin (*Eudyptula minor*) displays clinal variation in New Zealand and is now considered a single taxon (Turbott 1990) rather than five subspecies (Kinsky 1980). Current differences in size and plumage between NZ Dotterels from the North Island and Stewart Island could represent the surviving northern and southern extremes of clinal variation that might have existed when the species was widespread in New Zealand. The differences are now quite discrete however, and variation may never have been smoothly clinal. It should also be noted that the mensural differences between birds of the two populations are not due to a simple allometric effect; some differences (although statistically significant) are very small, while differences in weight and MTC are large, resulting in differences in proportion.

Previous distribution of the two populations

The exact breeding distributions of the two populations prior to the 20th century are difficult to determine but the dividing line appears not to have been Cook Strait, as it is for many New Zealand subspecies. Inland breeding birds were widespread in the South Island (Dowding & Murphy 1993, Dowding unpubl. data) and were present in the central North Island (e.g. Buller 1888, Falla 1940, Edgar 1969). The situation in the southern North Island is less clear; there are a few records of inland breeding (e.g. on the Rangitikei River near Bulls – Buller 1898) but I can find none from the coast. I am not aware of any extant museum specimens from inland North Island, and there is also little subfossil material which might help in determining ranges or whether size differences were clinal or abrupt. Falla (1940) noted that inland breeding birds of the South Island, Stewart Island and the central plateau of the North Island were migratory, arriving at their nesting grounds in spring, whereas coastal birds were more sedentary. He commented "It is not quite certain whether two races of birds are represented in this division of habits...." I suggest that the division in breeding range between the populations may therefore have been situated north of Cook Strait, somewhere in the central North Island.

The timing of reproductive separation of the two populations is not clear. There is little actual evidence available for or against the assumption (Hayman *et al.* 1986) that the species must be monotypic because the two populations are only recently separated. It is possible that inland-breeding birds on Stewart Island, in the South Island and in the central North Island have

been reproductively isolated from northern North Island coastal breeders for some time. Based on differences in morphology of museum specimens, Marchant & Higgins (1993) suggested that recent free interbreeding between the two groups was less likely than longer isolation.

Subspecies

The northern and southern populations of NZ Dotterel display distinct differences in a variety of characters. They can be almost completely separated on the basis of measurements, and there are differences in plumage. There are also a number of ecological and behavioural differences and the populations have widely-separated breeding ranges. On the basis of these differences, I recognise two subspecies.

The type locality of the species is Dusky Sound, Fiordland (Hoare 1982). As noted above, plumage colouration of the type specimen is typical of present-day Stewart Island birds. It was collected in early April, outside the breeding season at a time when South Island birds would have been on the coast and not inland. Given the location, time of year and the large population of NZ Dotterels in the South Island in the past, it must be assumed that this was a South Island or Stewart Island bird. The southern population therefore becomes the nominate subspecies.

Charadrius obscurus obscurus Gmelin 1789

Southern New Zealand Dotterel

Dorsal surfaces typically a darkish chocolate brown. Underparts in breeding (winter) plumage show a variable amount of deep brick-red. Significant differences from *aquilonius* in all measurements of adult birds (see Table 1); larger in all measurements except tail, especially weight (average 162 g) and mid-toe (average 32.0 mm). Eggs significantly larger than those of *aquilonius* (see Table 2). Now breeds only on exposed hill-tops on Stewart Island, but formerly in many inland areas of the South Island and the central and southern North Island. Some birds, probably mostly Stewart Island juveniles, currently wander the coast of the South Island. Nests deeply lined with vegetation, on Stewart Island usually *Chionochloa* leaves. After breeding, all birds descend to the coast and form winter flocks which stay together until August.

Charadrius obscurus aquilonius NEW SUBSPECIES

Northern New Zealand Dotterel

DIAGNOSIS: Dorsal surfaces typically mid-grey-brown and usually noticeably paler and greyer than the nominate subspecies. Underparts in breeding (winter) plumage show a variable amount of orange-red, also averaging paler than *obscurus*. Adult birds significantly smaller than the nominate race in all measurements except tail (see Table 1), especially weight (average 144.5 g) and mid-toe (29.2 mm). Eggs significantly smaller than those of the nominate subspecies (see Table 2). Breeds on or near the coast (most commonly on sandy beaches) in the North Island

north of 39°S; juveniles and unpaired adults occasionally wander the southern coastline of the North Island. Not normally seen far from the coast. Most nests unlined, but a few decorated with shells or seaweed. Some adult birds remain on breeding territories all year; most move a short distance to join post-breeding flocks for a variable period and return to breeding sites from April or May onwards.

HOLOTYPE: Selected as holotype is AIM (Auckland Institute & Museum) B 2709, adult male, Mangere International Airport, Auckland, early October 1967. Collector: Internal Affairs (Bird Patrol Scheme). Measurements in mm (study skin): exposed culmen 27.7, tarsus 40.1, MTC 28.6, wing 156, tail 66. Adult male in fading breeding plumage. Crown faded mid-grey-brown, some feathers suffused pale orange. Hindneck much paler, also suffused pale orange. Mantle, scapulars and back mid-grey-brown, feathers edged and suffused pale orange. Rump, upper tail and upper wings grey-brown, tips and outer vanes of outer primaries darker brown. Forehead, throat and undertail white. Breast diffused orange, belly with a central darker, more intense area of brownish orange.

PARATYPES: AIM B 2707, female, Parengarenga, Northland, 22 February 1934. Collector: R.A. Falla. AIM B 3664, sex unknown, Glendowie, Auckland, 22 September 1992. Collector: L.J. Wagener. NM (National Museum of New Zealand) 2366, female, Spirits Bay, Northland, 20 February 1929. Collector: C. Lindsay. NM 18370, male, Muriwai Stream, West Auckland, August 1937. Collector: W.P. Wardlow. NM 24163 (including NM 24163/1, spread wing), recently-fledged juvenile, Whale Island, Bay of Plenty, 15 December 1990. Collector: M. Harrison.

ETYMOLOGY: *aquilonius* (Latin, northern or northerly, from *aquilo*, the north wind) refers to the northern distribution of the subspecies in the species range.

In the foreseeable future, genetic distance between the two subspecies seems likely to increase, if the Stewart Island population survives. Selective forces in their respective ranges appear to be different and annual adult mortality is nearly three times higher on Stewart Island than in the North Island (Dowding & Murphy 1993). The sizes of the populations also differ greatly. The Stewart Island population is very small, numbering about 65 birds with few males remaining (J.E. Dowding, unpubl. report to Department of Conservation, Wellington, April 1994); the effective population size may be as low as 12 pairs and *C. o. obscurus* is therefore clearly going through a genetic bottleneck. However, the two subspecies are already distinct groups of birds. Clearly, every attempt should now be made to prevent the extinction of the Stewart Island population (and hence the nominate subspecies), in order to conserve the considerable morphological and behavioural diversity that exists within the species now.

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