# Size and flight capability of *Anas chathamica*, an extinct duck from Chatham Island, New Zealand

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## Abstract

Measurements of major bones from Chatham Island's extinct duck *Anas chathamica* (formerly placed in *Pachyanas*) were used to estimate the duck's likely mass and flight capability. Mass estimates derived from published regression equations relating least femur circumference to body mass for volant birds ranged between 1,500–2,300 g, and those based upon tibiotarsus least circumference ranged between 1,670–2,400 g, providing an overall average mass estimate of *c.* 1,900 g. The bimodal size-frequency distribution of femur lengths, used to establish putative sexes, indicated a *c.* 11% sexual body mass dimorphism. Distal wing bones were disproportionately short when compared with flighted *Anas* ducks, and were similar to those of the related, flightless Auckland Island Teal *A. aucklandica* and Campbell Island Teal *A. nesiotis*. A humerus length/femur length ratio of *c.* 1.40 is below the lowest ratio recorded for any flighted Anseriformes (*c.* 1.60), and also lower than those for flightless steamer ducks *Tachyeres* sp. (*c.* 1.50), but above that of three flightless *Anas* sp. (*c.* 1.30). Carina (keel) area relative to carina or sternum length was less than for any flighted New Zealand *Anas* sp. but greater than for the Auckland Island and Campbell Island Teals. In combination, these characteristics indicate that the Chatham Island Duck was flightless, and also the largest known of its genus.

**Key words:** *Anas chathamica*, *Pachyanas*, Chatham Island, Chatham Island Duck, flightlessness, island duck.

Among the eight species of waterfowl presently thought to have been resident on Chatham Island, 800 km east of New Zealand, prior to human arrival approximately 450–500 years ago, four (an undescribed shelduck *Tadorna* sp., a merganser *Mergus milleneri*, New Zealand Scaup *Aythya novaeseelandiae*, and a large duck) have been recorded only from fossil bones and are considered to have been exterminated by the island's initial Polynesian settlers (Holdaway 1989; Millener 1999; Worthy & Holdaway 2002).

Bones from the large duck, although gathered by early naturalists (*e.g.* by H.O. Forbes in 1892), were not highlighted until the bird was formally described from a cranium as a new species of a new genus by

Oliver (1955), who assessed it as lying within the Anatini and named it *Pachyanas chathamica.* The obvious size and robustness of the cranium, and of other bones later attributed to the species, subsequently elicited classification ponderings, notably Livezey's (1997) suggestion that it may be related to *Tadorna* (Anatidae, Tadornini), a perspective confused by Callaghan's (2005) reference to it as "Chatham Island Shelduck", but refuted by Worthy (2010) who retained it within the Anatini.

Mitchell *et al.* (2014) interpreted ancient DNA extracted from fossil bone as showing that Chatham Island Duck was the basal member of a sub-clade of three extant New Zealand teals (Brown Teal *Anas chlorotis,* Auckland Island Teal *A. aucklandica,* Campbell Island Teal *A. nesiotis*). These were considered a sister clade to similar-sized teals (the "grey teals") of Australia, Indonesia (probably also including Andaman Island) and Madagascar (see Fig. 2 in Mitchell *et al.* 2014). The phylogenetic nesting of *Pachyanas* well within the Anatini, in close company with all other modern *Anas* ducks, led Mitchell *et al.* (2014) to propose that *Pachyanas* (Oliver, 1955) become a synonym of *Anas*, and that Chatham Island's large extinct duck henceforth be referred to as *Anas chathamica.* The formal declaration of this change, which Mitchell *et al.* (2014) did not provide, is:

*Anas chathamica* (Oliver, 1955)

*Pachyanas chathamica* (Oliver, 1955): *New Zealand Birds*, 2nd edition: 599.

*Anas chathamica* (Oliver, 1955); Mitchell *et al.* 2014: 427. New combination.

Because *Pachyanas chathamica* (Oliver, 1955) is the type species of *Pachyanas* (Oliver, 1955), the genus *Pachyanas* becomes a junior synonym of *Anas* Linnaeus, 1758. This revised taxonomy is followed in this paper and the common name, Chatham Island Duck, applied.

Modern narratives describing extinct birds from the Chatham Islands archipelago comment on the relatively large size of Chatham Island Duck. For example, Millener (1999) described it as "robust, weighing as much as 2.5 kg", Worthy & Holdaway (2002) as "somewhat larger than a Mallard but substantially stouter", and Tennyson & Martinson (2006) as "1.5 kg…with a skeleton about the size of a Paradise Duck". These comments all imply a duck conspicuously larger than any extant *Anas,* the biggest of which may reach *c.* 1,500 g (Kear 2005), and possibly, in the light of Mitchell *et al*'s (2014) phylogenetic assessment, a unique example of an island *Anas* becoming larger than its nearest mainland relative (see Weller 1980; Livezey 1993; McNabb 1994a,b).

Individual bones, mostly the robust leg and wing bones, have been found in sand dunes around much of Chatham Island's northern coastline (see Fig. 1 in Mitchell *et al.* 2014) but not (yet) on other islands in the archipelago. Fragments of two bones were excavated from within Polynesian middens dated at AD 1500 ± 30 (Marshall *et al.* 1987). However, the stratigraphic assessments at this site have been challenged by Millener (1999) who identified that much of the so-called midden material at this site had been eroded from naturally accumulated deposits that considerably pre-date human occupation of Chatham Island. Two particularly important skeletal finds have been those of a partial skeleton from dunes near Waitangi (Canterbury Museum AV6748) and a complete skeleton (Museum of New Zealand S.29475) from an elevated, cliff-face cave, Te Ana a Moe (Millener 1999), the latter providing one of only two complete skulls and the only sternum and synsacrum yet collected.

From measurements of these bones I sought to determine the likely mass of the Chatham Island Duck, and whether it could fly. A complementary appraisal of its likely ecology and behaviour, based on the morphology of its carpometacarpus bone and carpal knob, is addressed elsewhere (Williams 2015).

## Methods

### Source

Chatham Island Duck bones were measured in the collections of Canterbury Museum, Christchurch (CMNZ) and Museum of New Zealand Te Papa Tongarewa (NMNZ). These two collections are thought to contain all bones of this species recovered to date.

To indicate the approximate size of Chatham Island Duck relative to some extant *Anas* species, measurements of bones from the three extant New Zealand teals and two other waterfowl resident in New Zealand: Grey Duck (Pacific Black Duck) *Anas superciliosa* and Mallard *A. platyrhynchos,* were sourced either from the literature, measured at NMNZ, or derived from the author's unpublished data (see Appendix 1). Campbell Island Teal measurements were from both wild (Dent Island; Williams & Robertson 1996) and captive-raised specimens (M. Williams, unpubl. data). For Mallard, wing and leg bone measurements were from USA specimens (Livezey 1993), skull, sternum and pelvis measurements were from a New Zealand-sourced specimen. Because Mallard is one of the largest extant *Anas* species (Kear 2005), only the larger male's measurements are presented to emphasise the Chatham Island Duck's relative size. Chatham Island Duck bones presumably include both sexes and for comparison measurements from other New Zealand species combine male and female data.

### Measurements

Digital vernier callipers were used to measure skull, wing and leg bones, sternum and pelvis. Measurements made (to 0.1 mm) were: skull length (maximum length from prominentia cerebellaris to tip of premaxilla), cranium (from prominentia cerebellaris to the lateral margin of the naso-frontal hinge), nares to tip (anterior edge of nares opening to tip of premaxilla), nail width (premaxilla width at commencement of terminal rounding), sternum length (maximum length taken along the midline, measured on the dorsal (visceral) surface), sternum anterior width (maximum width between the processus craniolaterali), sternum posterior width (maximum caudolateral width), carina sterni (keel) maximum length (maximum chord length from apex carinae to margo caudalis midline), carina sterni (keel) minimum length (chord length from apex carinae to sternum surface ahead of the margo caudalis (*i.e.* to planum postcarinale), carina sterni (keel) depth (vertical distance, carina sterni descends from the dorsal surface of the sternum, measured at sternum apex), carina sterni (keel) area (determined from 2–3 thin plasticine impressions of the carina sterni, each subsequently scanned against 1 mm grid graph paper to demarcate area, area measured to 1 mm$^2$, and the results averaged), coracoid(eum) length (maximum length from processus acrocoracoideus to angulus medialis), coracoid(eum) width (maximum width between processus lateralis and angulus medialis), humerus length (maximum length), ulna length (maximum length), carpometacarpus length (maximum length), pelvis length (length from anterior of ala preacetabularis ilii to rear of apex pubis), pelvis anterior width (maximum width between left and right ala preacetabularis ilii), pelvis posterior width (maximum width between left and right apex pubis), antitrochanter width (maximum width between left and right processus antitrochanter), femur length (maximum length parallel to shaft), femur circumference (at narrowest position on shaft), tibiotarsus length (maximum length from proximal articular surface, *i.e.*, excluding the crista cnemialis cranialis), tibiotarsus circumference (at narrowest position on shaft), and tarsometatarsus length (maximum length).

Measurements of minimum femur and tibiotarsus circumferences were made by wrapping fine cotton thread five times around the shaft at its narrowest point, the thread ends cut at the same relative position on the shaft, and the thread's length subsequently measured using vernier callipers, then divided by five. Anatomical names are as described by Baumel *et al.* (1993).

Mean values are given ± s.d. throughout.

## Data recording, analyses and presentation

All measurements were recorded in MS Excel spreadsheets and size-frequency distribution tables (in which most measurements are summarised in 1 mm (0.0–0.9) groupings) were obtained using the statistical analysis functions of MS Excel 2007. Using statistical package R (R Development Core Team 2012), potential bimodality of distributions was examined by fitting a normal distribution to each bone's length data and comparing the AIC (Akaike Information Criterion) value obtained with that for a mixture of two normal distributions of unequal variances. A difference of ≥ 2 in the AIC values was required to distinguish between the unimodal and bimodal models.

## Body mass estimation

Estimates of Chatham Island Duck body mass were derived from femur circumferences using the general structural relation (gsr) regression for Anseriformes in Campbell & Marcus (1992: Table 2) and the least squares regression equation for Anseriformes in Dickison (2007: Table 3.2, Fig. 3.3). Further estimates were derived from tibiotarsus circumferences based on the gsr equation for Anseriformes in Campbell & Marcus (1992: Table 2), the least-squares regression equation for Anseriformes in Iwaniuk *et al.* (2004: Table 1) and the least squares regression equation for Anseriformes in Dickison (2007: Table

3.2, Fig. 3.3). Two additional estimates of body mass were derived from least square regression equations calculated from Anseriformes (swans excluded) femur least circumference ($r^2 = 0.728$) and femur length measurements ($r^2 = 0.878$) in Table S1 of Field *et al.* (2013). This multiple approach was chosen because of the differences in species and sources of body mass data used to derive the published equations (see Discussion).

## Results

### Bone lengths

*Wing bones and coracoid*

A mean length was calculated for each of the three major wing bones and coracoid and compared with those of male Mallard, combined sexes of Grey Duck and each of the three New Zealand teals (Table 1).

Mean humerus length of the Chatham Island Duck was similar to that of male Mallard (Table 1) but its more distal wing bones were conspicuously shorter and the combined length of its three wing bones *c.* 4–8% shorter than for Mallard males and Grey Duck. As a consequence the humerus of Chatham Island Duck comprised a greater proportion of combined wing bone lengths (by *c.* 3.5%) than for these two species (Table 2). Proportional wing bone lengths of Chatham Island Duck were more similar to those of the flightless Auckland Island and Campbell Island Teals than of the flighted Brown Teal (Table 2).

Mean length of the Chatham Island Duck coracoid was similar to that of male Mallard and in both species was *c.* 55% the length of the humerus, proportionately a little longer than for Grey Duck and Brown Teal but shorter than for the flightless teals (Table 1). Its mean length was 24.5% of the combined mean wing bone lengths, greater than the *c.* 22% for Mallard males, Grey Duck and Brown Teal but less than the 26% for the flightless Auckland Island and Campbell Island Teals.

**Table 1.** Mean (± s.d., *n*) lengths (mm) of wing bones from Chatham Island Duck and other *Anas* ducks. Carpus = carpometacarpus. ($^1$from Livezey 1993; $^2$from Worthy 2004; $^3$from Livezey 1990).

| Species | Sex | Humerus | Ulna | Carpus | Coracoid |
|---|---|---|---|---|---|
| Chatham Is. Duck | M + F | 94.7 ± 2.9, 16 | 69.7 ± 2.7, 24 | 51.4 ± 2.0, 20 | 52.9 ± 2.1, 20 |
| Mallard$^1$ | M | 95.0 ± 2.1, 15 | 80.0 ± 2.0, 15 | 59.5 ± 1.4, 20 | 52.4 ± 1.5, 15 |
| Grey Duck$^2$ | M + F | 90.8 ± 2.9, 10 | 77.7 ± 3.1, 10 | 55.4 ± 2.6, 10 | 48.2 ± 1.7, 10 |
| Brown Teal$^2$ | M + F | 70.5 ± 3.1, 28 | 57.8 ± 2.7, 20 | 41.6 ± 2.3, 20 | 37.2 ± 1.7, 28 |
| Auckland Is. Teal$^3$ | M + F | 54.2 ± 2.2, 14 | 38.8 ± 1.8, 13 | 27.9 ± 1.1, 11 | 31.1 ± 1.5, 16 |
| Campbell Is. Teal | M + F | 48.2 ± 1.7, 12 | 36.5 ± 1.0, 7 | 24.9 ± 0.9, 6 | 28.2 ± 1.2, 9 |

**Table 2**. Lengths of wing bones from Chatham Island Duck and other *Anas* ducks as a percentage of total length of their three main wing bones (derived from means in Table 1), and similarly for the three main leg bones (derived from means in Table 3). Carpus = carpometacarpus, Tarsus = tarsometatarsus.

| Species | Sex | Humerus | Ulna | Carpus | Femur | Tibia | Tarsus |
|---|---|---|---|---|---|---|---|
| Chatham Is. Duck | M + F | 43.9 | 32.3 | 23.8 | 29.1 | 45.9 | 25.0 |
| Mallard | M | 40.5 | 34.1 | 25.4 | 27.7 | 47.3 | 24.9 |
| Grey Duck | M + F | 40.7 | 34.9 | 24.4 | 28.8 | 45.9 | 25.2 |
| Brown Teal | M + F | 41.5 | 34.0 | 24.5 | 28.0 | 45.8 | 26.3 |
| Auckland Is. Teal | M + F | 43.9 | 32.6 | 23.5 | 29.2 | 47.7 | 23.0 |
| Campbell Is. Teal | M + F | 44.0 | 33.3 | 22.7 | 29.4 | 46.7 | 23.9 |

**Table 3.** Mean (± s.d., *n*) lengths (mm) of leg bones from Chatham Island Duck and other *Anas* ducks. Tibia = tibiotarsus, Tarsus = tarsometatarsus. ([1]from Livezey 1993; [2]from Worthy 2004; [3]from Livezey 1990).

| Species | Sex | Femur | Tibia | Tarsus |
|---|---|---|---|---|
| Chatham Is. Duck | M + F | 66.8 ± 1.4, 18 | 105.4 ± 1.9, 15 | 57.5 ± 1.4, 22 |
| Mallard[1] | M | 51.5 ± 1.2, 15 | 87.9 ± 1.9, 15 | 46.3 ± 1.0, 15 |
| Grey Duck[2] | M + F | 50.1 ± 1.8, 10 | 79.9 ± 3.6, 10 | 43.9 ± 2.4, 8 |
| Brown Teal[2] | M + F | 43.4 ± 1.4, 27 | 71.1 ± 2.5, 20 | 40.8 ± 1.5, 21 |
| Auckland Is. Teal[3] | M + F | 42.6 ± 1.7, 14 | 69.6 ± 4.0, 12 | 33.6 ± 1.8, 16 |
| Campbell Is. Teal | M + F | 39.4 ± 1.3, 13 | 62.6 ± 1.8, 8 | 32.0 ± 1.0, 8 |

Size-frequency distributions for each bone are presented in Fig. 1. For all four distributions a unimodal(u) distribution was a better descriptor than a bimodal(b) distribution (humerus: $AIC_u = 83.34$, $AIC_b = 87.84$; ulna: $AIC_u = 119.74$, $AIC_b = 124.37$; carpometacarpus: $AIC_u = 89.12$, $AIC_b = 91.74$; coracoid: $AIC_u = 91.06$, $AIC_b = 95.30$).

*Leg bones*

For the size-frequency distributions of lengths of the three leg bones (Fig. 2), a unimodal(u) distribution was the better descriptor than a bimodal distribution(b) for both tibiotarsus and tarsometatarsus (tibiotarsus: $AIC_u = 65.96$, $AIC_b = 68.21$; tarsometatarsus: $AIC_u = 82.15$, $AIC_b =$

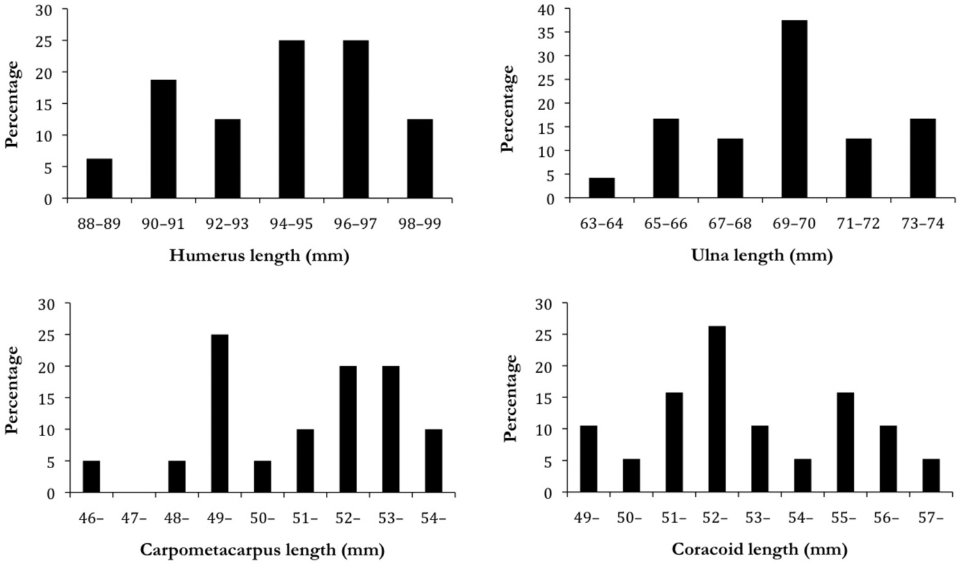

**Figure 1.** Percentage size-frequency distributions of Chatham Island Duck humerus, ulna, carpometacarpus and corocoid lengths.

84.54). However, for femur lengths there was weak evidence for the bimodal distribution being the better fit ($AIC_b$ = 64.95, $AIC_u$ = 65.94) and two modes (A: mean = 65.75 ± 0.13; B: mean = 67.23 ± 1.37) were identified. For the purpose of subsequent analyses and discussion, two femur length groupings, $< 67$ mm and $\geq 67$ mm, will be considered as putative females and putative males respectively.

All Chatham Island Duck leg bones were substantially longer (by 20–30%) than those of Mallard males and Grey Duck (Table 3), and 40–70% longer than those of the three New Zealand teals. A comparison with New Zealand's largest extant endemic waterfowl, the terrestrial grazing Paradise Shelduck *Tadorna variegata* (*e.g.* NMNZ 29052, male, femur 62.6 mm, tibiotarsus 110.6 mm, tarsometatarsus 69.3 mm; NMNZ 29042, female, femur 59.2 mm, tibiotarsus 103.0 mm, tarsometatarsus 62.2 mm) highlights the Chatham Island Duck's longer femur but slightly shorter tibiotarsus and tarsometatarsus.

As a proportion of the combined leg bone lengths, the Chatham Island Duck's femur length was more similar to those of the two small flightless teals than to the three flighted species (Table 2), whereas for tarsometatarsus length the reverse is true. Its tibiotarsus length was proportionately the smallest of the six species compared.

### *Skull, sternum and pelvis*

Specimen NMNZ S.29475 provided the only sternum and intact pelvis, and one of the only two intact skulls recovered to date.

Dimensions (mm) of crania in the NMNZ collection were: mean length = 65.0

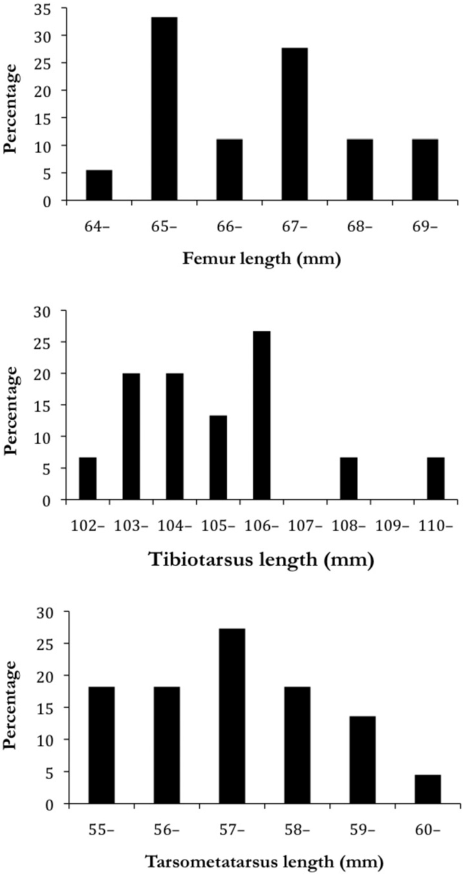

**Figure 2.** Percentage size-frequency distributions of Chatham Island duck leg bones.

± 3.0, range = 58.5–68.2, *n* = 8; mean inter-orbital width = 9.9 ± 0.72, range = 8.8–11.5, *n* = 11; mean postorbital width = 32.9 ± 1.51, range = 31.4–35.1, *n* = 8. Given that cranium length represents 57–60% of total skull length (Table 4), these crania represent skulls with approximate lengths of 105–120 mm.

Although the skull length of Chatham Island Duck, and males of Mallard and Grey Duck were similar, they differed most obviously in relative bill length and width (Table 4, Fig. 3). The crania of Chatham Island Duck, and of all three teal species, comprised > 56% of total skull length and the nares-to-tip measurement comprised 28–32% of skull length compared to *c*. 50% and 20% respectively, for males of Mallard and Grey Duck.

Skulls of Chatham Island Duck and the three New Zealand teals were similarly proportioned and contrasted with males of Mallard and Grey Duck, which in turn were similar to each other. The difference between these two groupings lies in the relatively longer and wider bills of the latter (Fig. 3).

A conspicuous feature of all Chatham Island Duck crania was the impression of the salt or nasal gland above the orbital cavity which extended to the cranial midline, indicative of the gland having been very large. No impression of the gland is discernible in the other species compared, except for Auckland Island Teal (see Fig. 3) but in which it is very small relative to that of the Chatham Island Duck.

The single Chatham Island Duck sternum was characterised by its diminished keel, both in depth and area (Table 5, Fig. 4) relative to length, contrasting with those of the three flighted ducks, but not so the two small and flightless teals. This implies the Chatham Island Duck sternum would have carried less total muscle mass than Mallard and Grey Duck, and relative to its length or that of its keel, less muscle mass than Mallard, Grey Duck and Brown Teal, but more so than the two small teals.

The Chatham Island Duck pelvis was conspicuously longer than that of male

**Figure 3.** Dorsal view of skulls of (from left) Mallard, Grey Duck, Chatham Island Duck, Brown Teal, Auckland Island Teal and Campbell Island Teal. (Photograph by Jean-Claude Stahl). The impressions of the salt gland surround the orbit on the Chatham Island Duck's skull.

Mallard or Grey Duck. Relative to its length however, it was narrower than all others with which it was compared (Table 6). The pelves of the two small teals, while proportionately identical to each other, were conspicuously wider posteriorly and narrower at the acetabulum than that of Brown Teal, suggesting a difference in ambulation.

### *Measurements from individual Chatham Island Ducks*

Only two specimens (CMNZ AV6748 and NMNZ S.29475) provided multiple bones (Table 7). As a consequence they assume a special importance when assessing size relative to other waterfowl species, and of relative bone proportions.

Whereas bone measurements of CMNZ AV6748 all lie at, or within ± 1 s.d. of the mean from all comparable Chatham Island Duck bones collected to date, those of NMNZ S.29475 indicate it to have been a particularly small bird. Its humerus and carpometacarpus lengths were the shortest measured, and its ulna the third shortest. The lengths of its leg bones were each the shortest measured, its tibiotarsus circumference the smallest measured, and its femur circumference the third smallest of 14 measured. Despite this specimen's size and unusual recovery location suggesting it could be a near-fledged duckling, unossified articular surfaces of its leg and wing bones are not apparent (A. Tennyson, pers. comm.).

Because NMNZ S.29475 is the only complete skeleton retrieved to date, the small size of its bones relative to all other Chatham Island Duck bones measured is

**Table 4.** Skull measurements (mm) of two Chatham Island Duck specimens and single specimens of other *Anas* ducks from New Zealand. (*sourced from Chatham Island).

| Species | Specimen | Sex | Skull length | Cranium length | Inter-orbital width | Post-orbital process width | Nares to tip | Nail width | Cranium as % of skull length | Nares-tip as % of skull length |
|---|---|---|---|---|---|---|---|---|---|---|
| Chatham Is. Duck | NMNZ S.29475 | ? | 113.9 | 65.2 | 9.7 | 32.2 | 32.0 | 18.6 | 57.2 | 28.1 |
| Chatham Is. Duck | NMNZ S.33302 | ? | 113.3 | 68.2 | 9.9 | 33.9 | 31.6 | 18.8 | 60.2 | 27.9 |
| Mallard | NMNZ 13595 | M | 114.5 | 59.3 | 10.2 | 30.2 | 37.5 | 23.2 | 51.8 | 20.3 |
| Grey Duck | NMNZ 16698* | M | 111.8 | 56.4 | 7.0 | 27.6 | 38.2 | 22.6 | 50.4 | 20.2 |
| Brown Teal | NMNZ 27221 | M | 93.3 | 52.8 | 9.1 | 25.8 | 29.8 | 16.9 | 56.6 | 31.9 |
| Auckland Is. Teal | NMNZ 21495 | M | 82.8 | 47.6 | 6.6 | 24.7 | 24.9 | 13.3 | 57.5 | 30.1 |
| Campbell Is. Teal | NMNZ 24051/1 | M | 75.2 | 42.0 | 6.4 | 23.0 | 21.5 | 13.2 | 55.9 | 28.6 |

**Table 5**. Sternum measurements (mm) of Chatham Island Duck (NMNZ S.29475) and single specimens of other *Anas* ducks from New Zealand. (*sourced from Chatham Island).

| Species | Specimen | Sex | Sternum length | Keel length | Keel depth | Keel area mm$^2$ | Keel area/ sternum length |
|---|---|---|---|---|---|---|---|
| Chatham Is. Duck | NMNZ S.29475 | ? | 91.7 | 95.1 | 22.9 | 1,009 | 11.0 |
| Mallard | NMNZ 13595 | M | 90.1 | 99.9 | 31.8 | 1,757 | 19.5 |
| Grey Duck | NMNZ 16698* | M | 90.2 | 100.0 | 28.5 | 1,562 | 17.3 |
| Brown Teal | NMNZ 27221 | M | 70.7 | 71.9 | 22.4 | 897 | 12.7 |
| Auckland Is. Teal | NMNZ 20988 | M | 46.8 | 45.5 | 12.6 | 291 | 6.2 |
| Campbell Is. Teal | NMNZ 24051/1 | M | 45.6 | 39.5 | 9.5 | 215 | 4.7 |

emphasised. It was a distinctly small member of its species.

## Estimation of body mass

Estimates of body mass were derived from measurements of femur and tibiotarsus least shaft circumferences inserted into the regression equations identified in Methods.

Mean femur least circumference was 21.4 ± 1.0 mm ($n$ = 14), range = 19.50–23.45 mm, and mean tibiotarsus least circumference was 18.0 ± 0.7 mm ($n$ = 15), range = 17.1–19.8 mm. The percentage size-frequency distributions are shown in Fig. 5 alongside the circumference – length relationships for each bone. The mean least circumference of eight femora of lengths < 67 mm (*i.e.* putative females; Fig. 2) was 20.9 ± 0.9 mm, and for six femora of greater lengths (putative males) was 22.1 ± 0.8 mm. Overall there is a statistically significant tendency for longer femora to have larger least circumferences ($r^2 = 0.29$, $P < 0.05$). This was not the case for 15 tibiotarsi ($r^2 = 0.03$, $0.2 < P < 0.5$, n.s.).

The range of mean body mass estimates, derived from seven different regression equations, was 1,780–2,200 g (Table 8), a maximum difference between mean estimates of 23%. Estimates derived from tibiotarsus least circumference-based equations were all larger than those derived from femur least circumference-based equations, while that based on femur length

**Figure 4.** Lateral views of sterna and size of carina of (top row, left to right) Mallard and Grey Duck, (middle row) Chatham Island Duck and Brown Teal, (lower row) Auckland Island Teal and Campbell Island Teal. (Photograph by Jean-Claude Stahl).

**Table 6.** Pelvis measurements (mm) of Chatham Island Duck (NMNZ S.29475) and single specimens of other *Anas* ducks from New Zealand. (*sourced from Chatham Island; posterior width estimated from doubling of undamaged half width).

| Species | Specimen | Sex | Anterior width | Posterior width | Width at Acetabulum | Length |
|---|---|---|---|---|---|---|
| Chatham Is. Duck | NMNZ S.29475 | ? | 22.0 | 55.6 | 41.8 | 102.6 |
| Mallard | NMNZ 13595 | M | 24.3 | 52.9 | 37.8 | 89.1 |
| Grey Duck | NMNZ 16698* | M | 20.0 | 61.5 | 37.1 | 91.6 |
| Brown Teal | NMNZ 27221 | M | 17.3 | 43.4 | 34.7 | 76.2 |
| Auckland Is. Teal | NMNZ 20988 | M | 14.8 | 38.7 | 28.5 | 65.0 |
| Campbell Is. Teal | NMNZ 24051/1 | M | 13.3 | 35.1 | 25.7 | 59.0 |

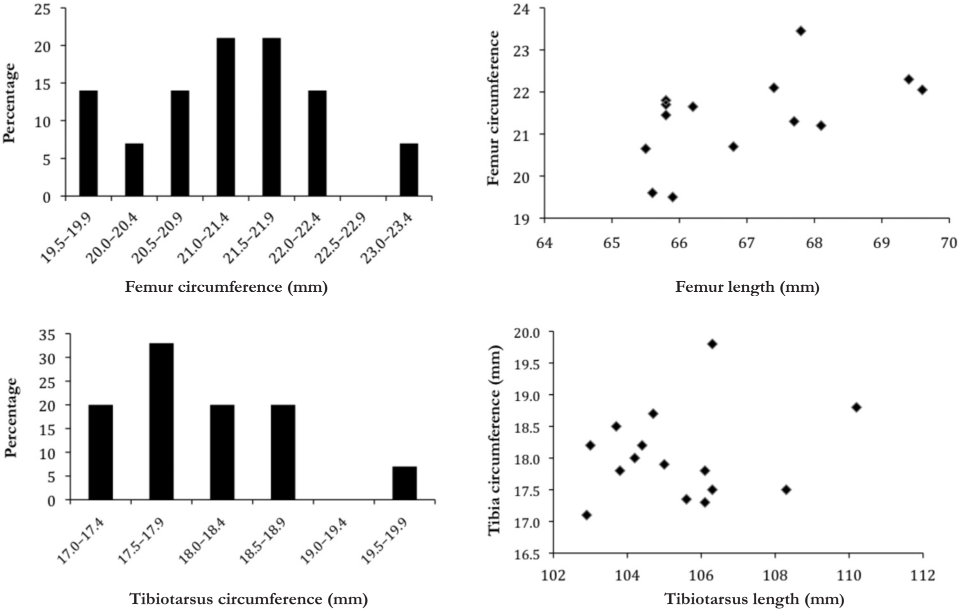

**Figure 5.** Percentage size-frequency distributions of Chatham Island Duck least femur and least tibiotarsus shaft circumferences, and their circumference-length relationships.

**Table 7.** Bone measurements (mm) from two Chatham Island Duck specimens.

| Specimen | Humerus length | Ulna length | Carpus length | Coracoid length, width | Femur length, circumference | Tibia length, circumference | Tarsus length |
|---|---|---|---|---|---|---|---|
| CMNZ AV6748 | 94.7 | 70.7 | 51.0 | 53.7, 23.9 | 66.2, 21.65 | 103.7, 18.5 | 58.7 |
| NMNZ S.29475 | 88.4 | 65.7 | 46.8 | 51.2, 22.5 | 65.5, 20.65 | 102.9, 17.1 | 55.2 |

produced the highest estimate. Individual tibiotarsus-based estimates ranged from 90–120% of the mean estimate, femur-based estimates were 80–123% of the mean estimate and the femur-length estimates were 95–110% of the mean estimate. No consideration is given here to the broad 95% confidence intervals associated with estimates from each of the algorithms, but is discussed later.

Estimated body masses of the two specimens from which both femur and tibiotarsus measurements were obtained (Table 9) provided divergent outcomes. For the smaller specimen (NZMS S.29474) the three tibiotarsus-based estimates differed by a maximum of 7% compared to 5% for the larger specimen (CMNZ AV6748). Using femur circumference measurements the three estimates differed by 4% for the smaller specimen and 7% for the larger. For both specimens the estimate derived from femur length was the largest obtained, 18–25% greater than the lowest estimates obtained from femur and tibiotarsus circumference-based algorithms.

Using the Anseriformes femur circumference-based algorithm of Campbell & Marcus (1992), the estimated mean body mass for putative females was 1,696 ± 141 g (range = 1,469–1,844 g) and for putative males 1,890 ± 130 g (range = 1,747–2,139 g). This represents a possible sexual body mass dimorphism of *c.* 11%.

Indicative mean body masses of the comparative species (from Kear 2005) are: Mallard (males = 1,209 g, females = 1,113 g), Grey Duck (males = 1,104 g, females = 1,007 g), Brown Teal (males = 586 g, females = 530 g), Auckland Island Teal (males = 551 g, females = 409 g) and Campbell Island Teal (males = 371 g, females = 310 g).

## Discussion

Chatham Island's large duck was larger than any extant *Anas,* the genus to which it has now been referred (Mitchell *et al.* 2014). Relative to a Mallard male it would have appeared larger, plumper and stood taller, but its head may have appeared smaller and its bill distinctly shorter and narrower. Relative to a Paradise Shelduck, New

**Table 8**. Estimated Chatham Island Duck body mass (g) based on published regression equations using femur and tibiotarsus least shaft circumferences ($n$ = 14 and $n$ = 15 respectively) and femur length ($n$ = 18). Regression coefficient is that from the source analysis. (*calculated from data in Field *et al.* 2013: Table S.1; see Methods).

| Method | Algorithm source | Regression coeff $r^2$ | Mean ± s.d. | Range |
|---|---|---|---|---|
| Tibia circumference | Iwaniuk *et al.* 2004 | 0.880 | 1,988 ± 153 | 1,786–2,396 |
| Tibia circumference | Campbell & Marcus 1992 | 0.909 | 1,850 ± 136 | 1,673–2,213 |
| Tibia circumference | Dickison 2007 | 0.863 | 1,905 ± 146 | 1,712–2,292 |
| Femur circumference | Campbell & Marcus 1992 | 0.908 | 1,779 ± 167 | 1,494–2,139 |
| Femur circumference | Dickison 2007 | 0.897 | 1,895 ± 200 | 1,532–2,325 |
| Femur circumference | Field *et al.* 2013 data* | 0.728 | 1,844 ± 184 | 1,521–2,223 |
| Femur length | Field *et al.* 2013 data* | 0.878 | 2,202 ± 107 | 2,100–2,419 |

**Table 9**. Estimates of body mass (g) of two individual Chatham Island Ducks based on published regression equations using femur and tibiotarsus least shaft circumferences and femur length (*calculated from data in Field *et al.* 2013: Table S.1; see Methods).

| Method | Algorithm source | NMNZ S.29474 | CMNZ AV6748 |
|---|---|---|---|
| Tibia circumference | Iwaniuk *et al.* 2004 | 1786 | 2091 |
| Tibia circumference | Campbell & Marcus 1992 | 1673 | 1994 |
| Tibia circumference | Dickison 2007 | 1712 | 2002 |
| Femur circumference | Campbell & Marcus 1992 | 1683 | 1818 |
| Femur circumference | Dickison 2007 | 1744 | 1941 |
| Femur circumference | Field *et al.* 2013 data* | 1677 | 1848 |
| Femur length | Field *et al.* 2013 data* | 2100 | 2152 |

Zealand's largest extant anatid, it would not have stood as tall, but its body may have appeared larger, and its head and bill longer. A big stocky duck in profile, its wings would have appeared short, and, by analogy with the two flightless teals, its primaries most likely extended only to the middle of its back, and may not have overlapped.

The bones measured in this study undoubtedly included birds of both sexes. Presumably, males were larger than females as is generally the case for all Anseriformes. Across 43 *Anas* sp., mean wing lengths of males average 6% longer than those of females, and mean male weights are, on average, 12% greater (Fig. 6; data from Kear 2005). The six (14%) *Anas* sp. with the greatest sexual weight dimorphism (*i.e.* ≥ 20%) includes both Auckland Island and Campbell Island Teals. In Brown Teal, males exceed females by *c.* 11% in mean weight, and by *c.* 8% in mean wing and mean tarsus lengths (Kear 2005) but wing and tarsus length measurements of the two sexes overlap by *c.* 76–80% (M. Williams, unpubl. data).

This study does not provide unequivocal support for sexual size dimorphism in Chatham Island Duck. The distributions of lengths for six of the seven bones measured (Figs. 1, 2) conformed best to a unimodal distribution, and even for the seventh (femur) support for bimodality was weak. However, small sample sizes and a likely overlapping of some male and female bone lengths have made the anticipated bimodality difficult to detect statistically.

Mean femur lengths for the putative sexes (*i.e.* those above and below a length of 67 mm) differed by 3.5%; similar groupings based on humerus lengths above and below 94 mm and coracoid lengths above and below 54mm (Fig. 1) provided mean length differences of 5.4% and 7.3% respectively. The calculated body mass dimorphism,

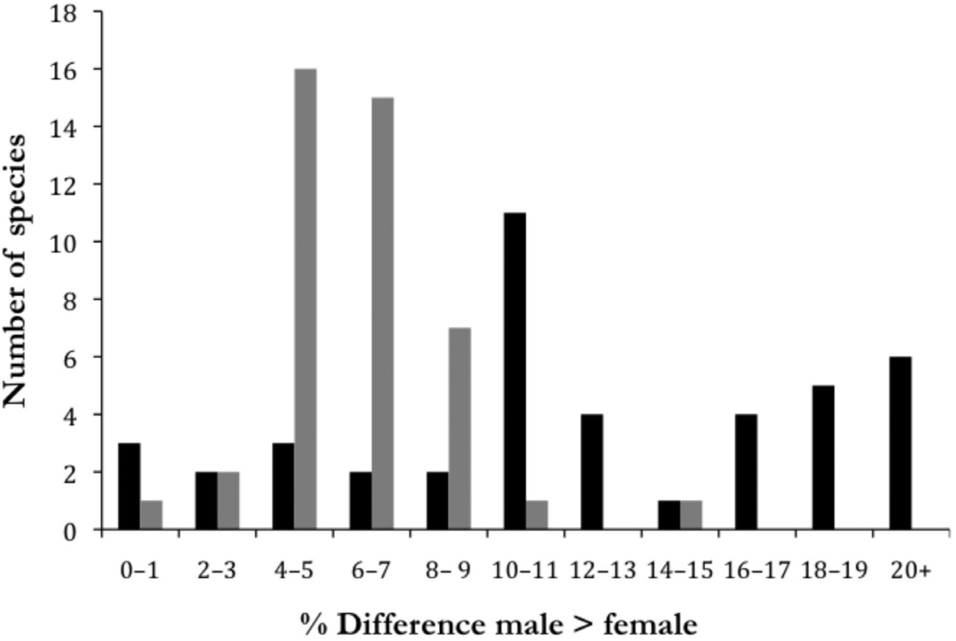

**Figure 6.** Frequency distribution of the magnitude of sexual size dimorphism in mean weight (black) and mean wing length (grey) in 43 *Anas* species. Data from Kear (2005).

based on least circumferences of femur bones above and below 67mm in length, was *c.* 11%, the average for the 43 *Anas* species examined (Fig. 6).

## Could the Chatham Island Duck fly?

Conflicting opinions have been expressed about the flight capability of the Chatham Island Duck; for instance, Millener (1999) suggested it was flightless whereas Worthy & Holdaway (2002) and Tennyson & Martinson (2006) considered it had poor flying ability. Evidence to support these opinions was not provided. Mitchell *et al.* (2014) concluded that the Chatham Island Duck "was certainly capable of flight", citing in support no apparent reduction in wing length relative to extant related taxa and no disproportional shortening of ulna and carpometacarpus bones. Wing bone measurements provided in their Table 3, however, contradict their interpretation of distal wing bone shortening; humerus length as a percentage of total wing bone lengths (whether including phalanx digit II or not) in Chatham Island Duck was almost identical to that of the two flightless teals and contrasted with that of the flighted Brown Teal. The contrast with other flighted *Anas* species is further highlighted in Table 2 above, and emphasises that there was considerable distal wing bone shortening in Chatham Island Duck.

Reliance on disproportional wing bone shortening as a sole indicator of flight capability is problematic given the expected variability in wing bone proportions within anseriform taxa with such diverse ecologies and weights. Furthermore there are few flightless waterfowl from which to derive a "cut-off" point to indicate flightlessness. In the steamer ducks *Tachyeres* sp., the only other anseriform taxon with flighted and flightless members, the "trend" in distal wing shortening with increasing body size is modest (< 1.5%; Table 2 in Livezey & Humphrey 1986), perhaps a consequence of the importance not of flight but of "steaming" across the water surface using the wings as paddles. Measurements of wing bones of the obviously flightless Amsterdam Island Duck *Anas marecula* (Table 1 in Olson & Jouventin 1996) indicate that the mean humerus length comprised 41.7% of the total length of the three main wing bones, almost identical to the flighted Brown Teal, although these data are derived from few bones and are of both sexes combined.

What seems crucial for flight is that the wing is large enough (*i.e.* wing bones are sufficiently long and thus the wing area large enough) to support the body weight, and to have the necessary pectoral muscle mass to power flight.

### *Evidence from sternum measurements*

Relative to its sternum length the area of the Chatham Island Duck's carina was substantially smaller than for Mallard, Grey Duck and Brown Teal but greater than for the two flightless teals (Table 5, Fig. 4). The depth of the carina was also considerably less than for Mallard and Grey Duck despite their sterna all being of similar lengths. Relative to sternum length the carina depth of Chatham Island Duck was more similar to the flightless teals than to the three flighted species and was also very similar to that of the Amsterdam Island Duck paratype (specimen USNM 486690; Olson & Jouventin 1996). In short, reduced area and prominence of the carina, when compared with other flighted and flightless *Anas* species, clearly indicates a comparative reduction of pectoral muscle mass.

### *Evidence from humerus length relative to femur length*

Wing area relative to body mass (*i.e.* wing loading) is a widely used metric to compare relative flight capability among taxa. A threshold value, above which a bird is flightless, was estimated by Meunier (1951) to be 2.5 $g.cm^{-2}$. However, Pennycuick (2008) demonstrated this is not necessarily so for flapping flight and Williamson *et al.* (2001) demonstrated how increased pectoral muscle power (in Mallard) can compensate for its comparatively smaller wing area. Anseriformes are one of few avian clades containing both flighted and flightless species and within which flighted members have shorter wings than expected relative to their body mass (McCall *et al.* 1998).

Wing area is not a measurable characteristic for an extinct species, and a rarely recorded one for many still extant. Because other wing and body size data needed to model flight characteristics (Pennycuick 2008) are not available for Chatham Island Duck, I have used a surrogate approach that relates humerus length (a surrogate for wing area) and femur length (a surrogate for body mass). Whether or not Chatham Island Duck was capable of flight may be assessed, albeit coarsely, by comparing its humerus length/femur length ratio with those of flighted and flightless waterfowl taxa (Table 10).

In none of 45 flighted species of Anatidae examined (Table 10) is their mean humerus length/femur length ratio < 1.60. In none of three flightless steamer duck

**Table 10.** Humerus length/femur length ratios for various Anseriformes tribes, genera and individual species (f = flightless). Body mass data from Kear (2005), bone measurements from Field *et al.* (2013: Table S1) except: 1 = this study; 2 = Livezey & Humphrey (1986); 3 = Livezey (1990); 4 = Olson & Jouventin (1996); 5 = Williams & Robertson (1996); 6 = Worthy (2004); 7 = Worthy (2005).

| Tribe | Genera, species | No. of species | Body mass (range, g) | Humerus length/ femur length ratio (range) | Source |
|---|---|---|---|---|---|
| Mergini | *Lophodytes/Mergus* | 3 | 554–1,709 | 1.70–1.95 | |
| | *Melanitta/Somateria* | 4 | 987–2,218 | 1.68–1.79 | |
| | *Clangula* | 1 | 813–932 | 1.71–1.78 | |
| | *Bucephala* | 2 | 470–1,120 | 1.61–1.65 | |
| Anserini | *Branta* | 4 | 1,230–3,815 | 2.01–2.44 | |
| Cygnini | *Coscoroba/Cygnus* | 3 | 4,854–9,670 | 2.59–3.00 | |
| Tadornini | *Tadorna* | 3 | 1,115–1,712 | 1.99–2.06 | |
| | *Tadorna variegata* | | 1,400–1,700 | 2.06–2.10 | 1 |
| | *Chloephaga* | 1 | 2,575 | 1.64–1.66 | |
| Aythyini | *Aythya* | 7 | 574–1,252 | 1.67–1.95 | |
| | *Aythya novaeseelandiae* | | 500–700 | 1.61–1.75 | 6,7 |
| Anatini | *Aix* | 2 | 512–635 | 1.66–1.75 | |
| | *Anas* | 10 | 400–1,400 | 1.77–2.03 | |
| | *Anas superciliosa* | | 900–1,100 | 1.75–1.86 | 1,6 |
| | *Anas chlorotis* | | 500–700 | 1.63–1.66 | 1,3 |
| | *Tachyeres* | 1 | 3,000 | 1.68–1.76 | 2 |
| | Flightless species | | | | |
| | *Tachyeres* sp. (f) | 3 | 2,300–5,400 | 1.47–1.52 | 2 |
| | *Anas aucklandica* (f) | | 400–600 | 1.22–1.28 | 1,3 |
| | *Anas nesiotis* (f) | | 300–500 | 1.23–1.27 | 1,5 |
| | *Anas marecula* (f) | | *c.* 300 | 1.27 | 4 |
| | *Anas chathamica* (f) | | 1,500–2,400 | 1.35–1.43 | 1 |

species is the ratio > 1.55. In neither of New Zealand's flightless teals, nor in the flightless Amsterdam Island Duck, is the ratio > 1.30. Whether considering the ratio derived from mean humerus and femur lengths (Tables 1, 3; ratio = 1.41) or from measurements of the two multi-bone specimens (Table 7; ratios = 1.35, 1.43), Chatham Island Duck compares most closely with flightless taxa, lending support to the hypothesis that it was incapable of flight.

## How large?

### *Estimating body mass*

Estimates of Chatham Island Duck body mass (Tables 8, 9) should be regarded as "approximate order of magnitude" only. The algorithms used to calculate these estimates are themselves highly problematic in their derivation: they arise from different regression approaches, are based on differing sample sizes, and the 95% confidence intervals surrounding the estimates (where given) are all extremely wide for the present purpose.

Whereas all seven algorithms used in this study were derived solely from Anseriformes species, all data (except where flightless steamer duck taxa were included) are from volant species. Most flightless birds are heavier, and their hind limbs more robust, than their closest volant relatives (Livezey 1995; Feduccia 1996).

Anseriformes exhibit a wide variety of foraging ecologies (from terrestrial grazing to underwater pursuit of active prey to benthic foraging) with consequent profound differences in skeletal proportions and in bone pneumaticity (underwater foragers have relatively denser bones and heavier skeletons: O'Connor 2004; Smith 2012). Terrestrial grazers (*e.g.* shelducks and sheldgeese (Tadornini), and geese (Anserini)) stand with a more erect body posture than do strictly aquatic species adapted for swimming or diving (*e.g.* pochards (Aythyini) and seaducks (Mergini)), and many other waterfowl (*e.g.* dabbling ducks (Anatini) and swans (Cygnini)) have a distinctly ungainly gait when on land, all a reflection of the differing angles at which the femur and tibiotarsus are held which, in all likelihood, impart differing transverse stresses on these bones whose dimensions undoubtedly do not reflect body mass the same way in all (see Cubo & Casinos 2000; Casinos & Cubo 2001). Thus, much of the variability in body mass : femur dimension or in body mass : tibiotarsus dimension relationships will be a consequence of using data from structurally and ecologically disparate taxa.

Another variable is the body weights used to derive the algorithms. Weights used by Campbell & Marcus (1992) and Iwaniuk *et al.* (2004) were those of the museum specimens at time of receipt; those used by Field *et al.* (2013) were mean species field weights from the literature; whilst Dickison (2007) used mean weights of museum specimens and mean bone measurements for each species used in his analyses. Thus, derivations of algorithms by Field *et al* (2013) and Dickison (2007) do not relate actual bone measurement to actual specimen weight. Weights of specimens used by Iwaniuk *et al.* (2004), and also by Iwaniuk *et al.* (2009: Table 3), are generally lower, some considerably so, than published field weights for most of the species used (see Kear 2005) resulting in algorithms that uniformly underestimate body mass. Whether the weights of the museum specimens used by Campbell & Marcus 1992 were also low relative to typical field weights cannot be established now that their entire dataset has been lost (K. Campbell, pers. comm.).

Body weight is not a fixed and unchanging entity. For example, body weights of northern hemisphere migratory species vary considerably during their annual cycle in a pattern under endogenous control and exacerbated by seasonal food constraints and energetic requirements (see references in Loesch *et al* 1992; Baldasarre & Bolen 2006). Weights of sedentary southern hemisphere species also vary throughout the year, *e.g.* pre-laying weights of female Brown Teal may exceed late summer weights by up to 30% (M. Williams, unpubl. data). Leg bone characteristics might be expected to relate more closely to maximum rather than minimum or average body mass.

With these variables at play perhaps it is unsurprising that estimates of body mass derived from the algorithms have wide confidence intervals. For example, the 95% confidence interval associated with the estimated body mass of Chatham Island Duck, based on its mean femur circumference of 21.4 mm and using the Anseriformes algorithm from Campbell & Marcus (1992), was 710–4835 g. For specimens CMNZ AV4748 and NMNZ S.29474 (Table 9) they were 725–4,970 g and 667–4,444 g respectively. Body mass estimates for these two specimens, based on least tibiotarsus circumferences (Table 9) and using the Anseriformes algorithm from Iwaniuk *et al.* (2004: Table 1) had 95% confidence intervals of similar magnitude. However, tighter confidence intervals might be achieved if the datasets from which the algorithms were derived were restricted to ecologically and structurally similar species (*e.g.* in the present case, restricted to *Anas* species), while a prior assessment of within-species variability might also aid interpretation.

### *The working body mass estimate*

Notwithstanding the necessity to consider confidence intervals about the body mass estimates (Field *et al.* 2013), the range of estimates provided in Table 8 (1,494–2,419 g) are credible, given (i) the relative sizes of Chatham Island Duck bones and those of the compared taxa, and (ii) the field weights of the compared taxa. Wing bones are at least the size recorded for Mallard males, even though the Chatham Island Duck was flightless. The sternum and pelvis from a particularly small specimen was longer than that of a Mallard male. Leg bones were distinctly larger than those of Mallard males, and also larger and more robust than those of a Paradise Shelduck. Field weights of male Mallard and Grey Duck may reach almost 1,500 g and 1,400 g respectively, and the mean field weight of male Paradise Shelduck is *c.* 1,700 g (Kear 2005).

Mallard and American Black Duck *A. rubripes* have similar skeletal dimensions (Livezey 1993) and similar mass (Kear 2005) and are the largest of all extant *Anas* ducks. The evidence assembled in this paper indicates that the Chatham Island Duck was larger than both.

Estimates of body mass for specimen NMNZ S.29475, provided in Table 9, contrast with that estimated by Mitchell *et al.* (2014: Table 3), as does the femur circumference measurement they reported and from which their body mass estimate was derived. Measurements of femoral circumferences for the three other ducks in their Table 3 were also larger than I obtained. These differences arise because (i) their circumference measurements were not actually measured but calculated from diameter measurements and the bone profile assumed to be circular, and (ii) the algorithm from Campbell & Marcus (1992) used to determine body mass was that calculated from 89 avian families combined, not solely from Anseriformes (R.P. Scofield, pers. comm.). Their estimate of 1,360 g for Chatham Island Duck implies that this bird was about the size of a Mallard male and slightly larger than Grey Duck, whereas measurements of major bones from these species, presented in this paper, clearly challenge that implication.

## Ecology of the Chatham Island Duck

The phylogenetic interpretation provided by Mitchell *et al.* (2014) places the Chatham Island Duck within a grouping of southern hemisphere teals all extant species of which are of 400–700 g body mass. Such a phylogenetic context, if corroborated, implies that at the time of its arrival on Chatham Island, the forebear of the Chatham Island Duck was of similar size, and became larger in isolation. No other island-dwelling *Anas* has shown a similar response (Weller 1980; Livezey 1993), although the ancient, large, herbivorous and profoundly flightless Moa-nalos *Thambetochen* sp. (and relatives) of Hawaii had dabbling duck (tribe Anatini) ancestry (Olson & James 1991; Sorensen *et al.* 1999). Conversely, both New Zealand and Hawaii provide examples of endemic geese that were larger than their mainland, or nearest, relatives (Olson & James 1991; Worthy & Holdaway 2002), a reinforcement of the influence of herbivory on body size and consequential flightlessness.

Mitchell *et al.* (2014) opined that the larger size of the Chatham Island Duck compared to its New Zealand teal relatives was a consequence of herbivory. If so, the conspicuous cranial salt gland impressions (Fig. 3) indicate that this duck was unlikely to have been a predominantly terrestrial herbivore. Rather they suggest the Chatham Island Duck fed in a marine or a marine-influenced environment, or on highly saline foods. Loss of flight capability suggests that these foods were available from a local, productive and seasonally dependable environment.

Williams (2015) has interpreted the Chatham Island Duck's enlarged and rugose processus extensorius at the proximal end of its carpometacarpus (carpal knob) as evidence of the duck's belligerency and year-round territorial habit, akin to the behaviour and social structure of the steamer ducks (Livezey & Humphrey 1985, 1986), Auckland Island Teal (Williams 1995) and some river-dwelling ducks (*e.g.* Blue Duck *Hymenolaimus malacorhynchos*; Kear & Steel 1971) which have similarly pronounced carpal knobs. This interpretation implies Chatham Island Duck fed, bred and reared its young within a limited and, importantly, a defendable area.

These observations and interpretations lend support to the hypothesis that the

Chatham Island Duck may have been a shore-line inhabitant, perhaps a convergent steamer duck, as first postulated by Holdaway (1989). Its larger size compared to its New Zealand relatives may have been a response to the predation risk, *e.g.* from Sub-Antarctic Skua *Catharacta antarctica*, associated with life on a broad and exposed shore-line that has undoubtedly been a feature of Chatham Island's geological history (Campbell 2008) and which dominates its Holocene (and contemporary) topography.

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**Appendix 1**. Specimen numbers of Chatham Island Duck and other waterfowl bones in the collections of Canterbury Museum, Christchurch, New Zealand (CMNZ) and the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ) measured for this study.

Chatham Island Duck *Anas chathamica*. CMNZ: AV6748, AV7881, AV11232, AV11236, AV11237, AV17744, AV17766, AV27398, AV27361, AV29575, AV30335. NMNZ: S.24167, S.24966, S.25090, S.25116, S.25247, S.25550, S.26386, S.26420, S.26460, S.26569, S.26946, S.27066, S.27108, S.27109, S.27233, S.27540, S.29475, S.30406, S.30713, S.30793, S.31110, S.31160, S.31191, S.31994, S.32620, S.32621, S.32622, S.32624, S.32626, S.32627, S.32628, S.32634, S.32635, S.32636, S.32637, S.32638, S.32639, S.32745, S.31994.

Mallard *Anas platyrhynchos*. NMNZ: 15929, 13595.

Grey Duck *Anas superciliosa*. NMNZ: 15030, 16698, 16476.

Brown Teal *Anas chlorotis*. NMNZ: 18898, 29097, 28030, 27249a, 29090, 27221.

Auckland Island Teal *Anas aucklandica*. NMNZ: 20988, 17614.

Campbell Island Teal *Anas nesiotis*. NMNZ: 27108a, 24051/1, 28974a, 29039, 28627, 28069, 28120a, 26742a, 28483, 18953, 18954, 18955, 18957, 19170.

**Photograph:** The enlarged and rugose carpel knobs of the Chatham Island Duck, in ventral aspect (from Williams 2015).