

Formidable carpal weaponry of *Anas chathamica*, Chatham Island's extinct flightless duck

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Abstract The Chatham Island duck (Anseriformes: Anatidae: *Anas chathamica*) had a pronounced and rugose enlargement to the tip of the *processus extensorius* at the proximal end of its carpometacarpus. This "carpal knob" was the equal in size of those found in some much larger waterfowl (e.g., steamer ducks, *Tachyeres* sp.), and was disproportionately larger than those of all other New Zealand waterfowl. The knobs on 20 carpometacarpi examined all showed evidence of continuous bone deposition at their tips and their use as weapons is implied. Comparisons with other duck species having similarly prominent and rugose carpal knobs suggests the Chatham Island duck maintained long-term pair bonds and occupied combined feeding and breeding territories year-round which both sexes defended belligerently.

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Keywords Chatham Island duck; *Anas chathamica*; intraspecific combat; carpal knobs

INTRODUCTION

A large and flightless duck, *Anas chathamica* (formerly placed in *Pachyanas*; Mitchell *et al.* 2014), was one of the early avian extinctions following Polynesian settlement of Chatham Island in the late 15th century (Millener 1999). The paucity of its bones so far retrieved, mostly from Chatham Island's sand dunes, suggests that this duck, the Chatham Island duck, was neither particularly common nor widely distributed. No bones have yet been retrieved from other islands of the Chatham archipelago. Nevertheless, it may have been a long-time resident of this isolated land, which lies 800 km east of New Zealand's main islands. Mitchell *et al.* (2014) extracted ancient DNA from fossil bone to show that Chatham Island duck was the basal

member of a sub-clade of 3 extant New Zealand teals (brown teal [*Anas chlorotis*], Auckland Island teal [*A. aucklandica*], Campbell Island teal [*A. nesiotis*]), and to suggest that its divergence time was in the order of 1.22 (95% confidence interval 0.69-1.80) mya.

Apart from its large body mass (c. 2 kg) and its shorter wing length and reduced sternum, indicative of its profound flightlessness (Williams 2015, and *contra* Mitchell *et al.* 2014), a particularly conspicuous feature of its osteology was the presence of an enlarged and heavily ossified *processus extensorius* (hereafter "carpal knob") projecting from the anterior face of the carpometacarpus on the proximal end. At the point of attachment of the wing's *musculus extensor metacarpi radialis* (McKittrick 1991) this process was enlarged to the extent that, in the live bird, it would have been visible as a very large, probably bare-skinned, calloused knob at the

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Table 1. Mean total lengths (mm) of carpometacarpi and carpal knobs of Chatham Island duck, and of selected New Zealand waterfowl species. See text for scientific names of species.

| Species | Sex | <i>n</i> | Carpometacarpus total length (mean ± SD) | Carpal knob length (mean ± SD) |
|----------------------|-----|----------|--|--------------------------------|
| Chatham Island duck | M+F | 20 | 51.4 ± 2.0 | 18.2 ± 2.6 |
| Brown teal | M+F | 13 | 41.4 ± 2.5 | 11.3 ± 0.9 |
| Auckland Island teal | M+F | 8 | 27.1 ± 2.0 | 7.8 ± 0.4 |
| Campbell Island teal | M+F | 6 | 25.2 ± 0.7 | 7.1 ± 0.3 |
| Grey teal | M+F | 11 | 42.7 ± 1.5 | 9.5 ± 0.4 |
| Mallard | M+F | 12 | 58.6 ± 2.2 | 13.1 ± 0.3 |
| Grey duck | M+F | 12 | 55.2 ± 2.3 | 12.5 ± 0.4 |
| Blue duck | M+F | 11 | 47.7 ± 2.9 | 13.2 ± 1.4 |
| Paradise shelduck | M+F | 11 | 71.3 ± 3.4 | 17.3 ± 1.7 |

wing's carpal flexure, as occurs in *Tachyeres* steamer ducks (Livezey & Humphrey 1985) and in some Columbiformes, spectacularly so in the extinct solitaire (*Pezophaps solitaria*) from the Mascarene island of Rodrigues (Hume & Steel 2013). Two other New Zealand waterfowl, brown teal and blue duck (*Hymenolaimus malacorhynchos*), also have prominent, bare carpal knobs.

In this paper I describe and illustrate the characteristics of the Chatham Island duck's carpal knobs and speculate on what they imply about the social behaviour and ecology of this remote island duck.

METHODS

I measured all known (20) Chatham Island duck carpometacarpi (sex unknown), held in Canterbury Museum, Christchurch, New Zealand (CMNZ) and Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ), the 2 main repositories of *Anas chathamica* subfossil bones. For indicative comparison, I measured the carpometacarpi of the 3 extant New Zealand teals and 5 other duck species resident in New Zealand (grey teal [*A. gracilis*], grey duck [*A. superciliosa*], mallard [*A. platyrhynchos*], blue duck, and paradise shelduck [*Tadorna variegata*], at NMNZ and was provided with comparable measurements from 2 species of steamer duck (flying steamer duck [*Tachyeres patachonicus*], white-headed steamer duck [*T. leucocephalus*]) from specimens held at the University of Kansas Natural History Museum, Lawrence, USA.

Measurements made, using digital vernier callipers accurate to 0.1 mm, were of carpometacarpus total length (*i.e.*, of *os metacarpale majus* from the

condyle of the *facies articularis digitalis major* to that of the *facies articularis ulnocarpalis*) and the extent of the carpal knob, from the tip of *processus extensorius* to the lateral extent of the condyle of *facies articularis ulnocarpalis*, at the proximal end of the bone. Anatomical names are as described by Baumel *et al.* (1993).

Statistical analyses used the statistical package R (R Foundation for Statistical Computing, Vienna, Austria). Means of measurements are presented ± SD.

RESULTS

Bone and carpal knob size

Chatham Island duck carpometacarpi total lengths ranged from 46.8 to 54.2 mm (mean 51.4 mm) and carpal knob lengths ranged from 13.7 to 22.1 mm (mean 18.2 mm; Table 1). Bone and carpal spur length distributions were examined for potential bimodality by fitting a normal distribution to each bone's length data and the AIC (Akaike Information Criterion) value obtained and compared to that for a mixture of 2 normal distributions of unequal variances. The distribution of total lengths (Fig. 1A) conformed best to a unimodal distribution (unimodal AIC = 89.12; bimodal AIC = 91.74) but if equal variances are assumed there was weak support for both models (unimodal AIC = 89.12; bimodal AIC = 90.30). The distribution of carpal spur lengths (Fig. 1B) conformed best, albeit weakly, to a bimodal distribution (unimodal AIC = 99.12, bimodal AIC = 97.99) with means of 15.3 ± 1.2 and 20.1 ± 1.2, respectively. This can be interpreted as reflecting an underlying sexual size dimorphism. None of the carpometacarpi showed evidence of healed fractures.

Fig. 1. Percentage size-frequency distributions of (A) total bone lengths and (B) carpal knob lengths of 20 Chatham Island duck carpometacarpi.

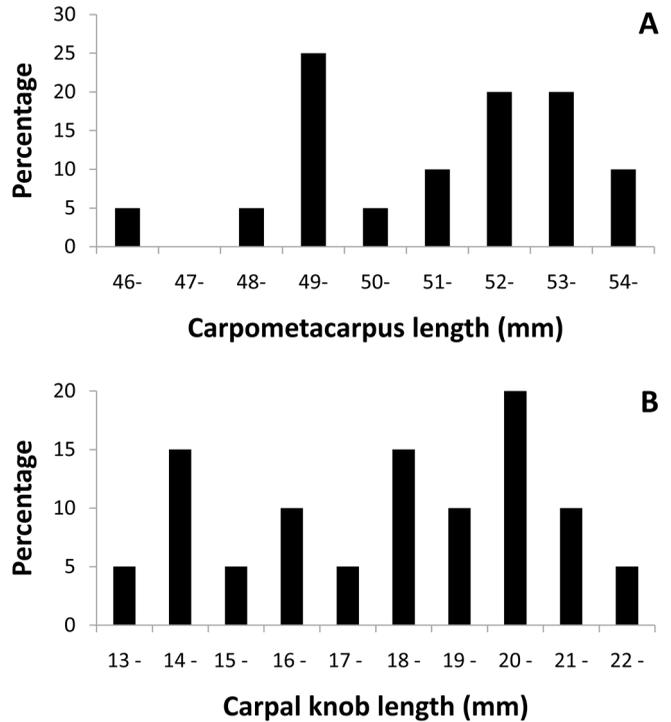
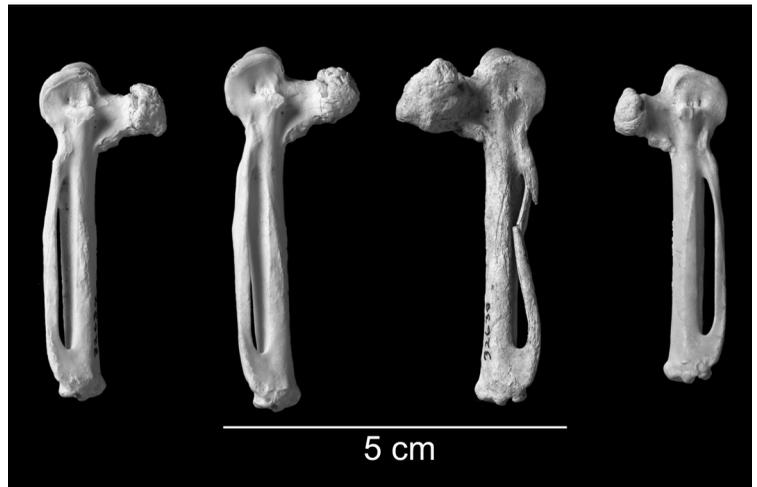


Fig. 2. Variability in rugosity and extent of bone deposition on the *processus extensorius* (carpal knob) in ventral aspect of Chatham Island duck.



The tip of the *processus extensorius* was expanded in all dimensions to create a large knob, the surface of which was highly rugose (Fig. 2), and indicative of continuous bone deposition that varied in shape and extent between bones. In all bones examined the *os metacarpale minus* was thin, was *c.* one-third of the diameter of the *os metacarpale majus*, and lay parallel to it (see Fig. 2). Carpal knobs on bones with lengths >52 mm formed 2 size clusters, as did those on bones 48 - 52 mm in length (Fig. 3). This

may indicate both sex and age differences. The conspicuously short carpal bone depicted in Fig. 3 is from specimen NMNZ S.29475 which also had the smallest of most other skeletal elements yet recovered (see Williams 2015).

Comparison with other New Zealand waterfowl
The mean carpal knob lengths of Chatham Island duck considerably exceeded those of all other New Zealand waterfowl with which it was

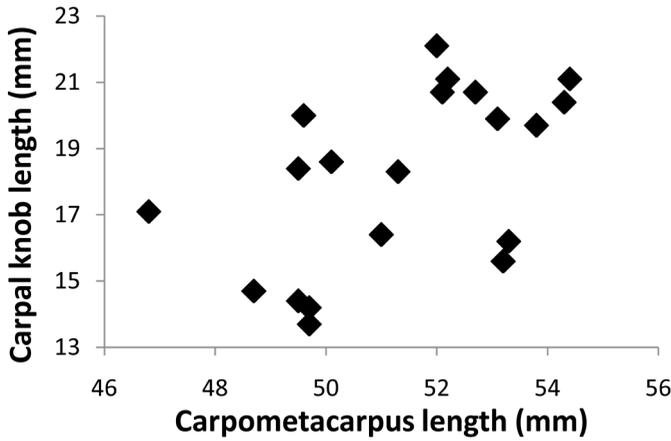


Fig. 3. Relationship between carpal knob length and carpometacarpus total length for Chatham Island duck.

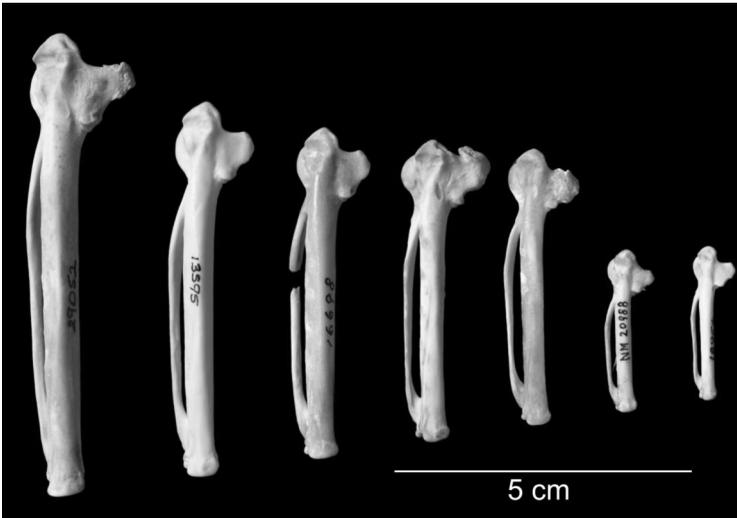


Fig. 4. Carpometacarpi in dorsal aspect of (from left) paradise shelduck, mallard, grey duck, blue duck, brown teal, Auckland Island teal, and Campbell Island teal illustrating the prominence and rugosity of the *processus extensorius* (carpal knob) in each species.

compared (Table 1, Fig. 4). Despite having a shorter carpometacarpus bone, but a body mass larger than grey duck or mallard (Williams 2015), the Chatham Island duck’s carpal knob was 40-50% longer, and its mean length also exceeded that of the 1.5-1.8 kg paradise shelduck.

None of 11 grey teal, 12 grey duck or 12 mallard carpometacarpi examined had an expanded or rugose tip to their carpal knobs and all lacked evidence of ongoing bone tissue deposition. This also included all 7 of the female paradise shelduck carpometacarpi examined, but the 4 males examined exhibited rounded and enlarged tips to their knobs, with one being particularly enlarged and conspicuously rugose.

The tips of the carpal knobs of all 11 blue duck carpometacarpi examined were expanded and rugose, more extensively in males. Of 13 brown teal, the carpal knobs from 3 females lacked terminal

expansion and had smooth surfaces, whereas the rest had expanded tips including 4 with rough or rugose surfaces; on the knob tip of one male the added bone formed a conspicuous cap similar to that on the smaller Chatham Island duck bones. Of 14 bones from Auckland and Campbell Island teals, only 2 (a male of each species) had obviously expanded tips to their carpal knobs and that of the Auckland Island teal individual was conspicuously rugose.

A scatterplot of carpal knob length relative to carpometacarpus total length of the 8 compared species (Fig. 5) highlights 2 distinct groupings: grey teal, grey duck, and mallard in one group, and the 3 New Zealand teals and blue duck in the other. Measurements from the paradise shelduck conform to those of the former grouping. Relative to these 8 species, the Chatham Island duck’s carpal knobs were particularly pronounced.

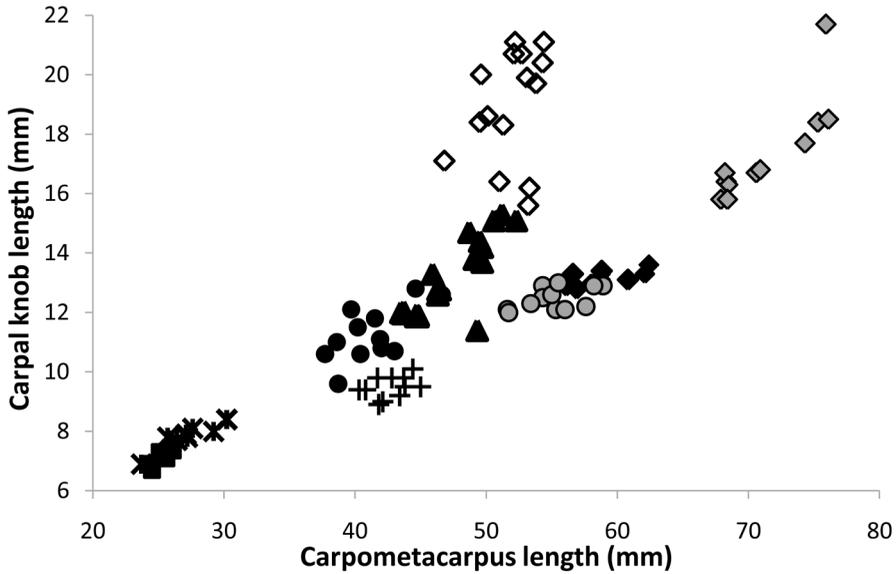
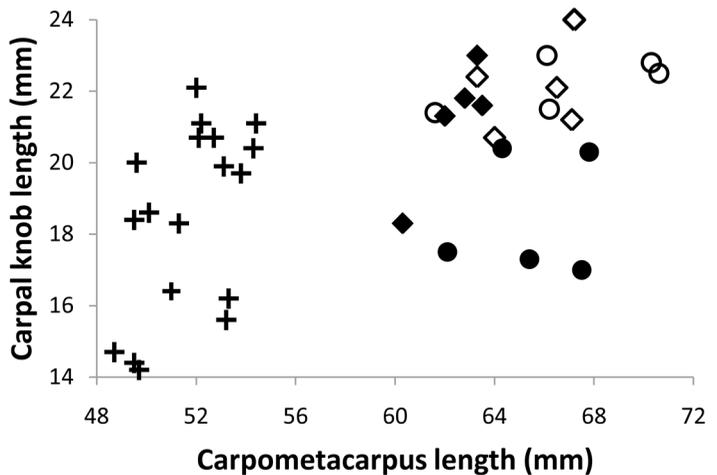


Fig. 5. Relationship between carpal knob length and carpometacarpus total length for Chatham Island duck, New Zealand *Anas* ducks, blue duck, and paradise shelduck. Symbols: open diamond - Chatham Island duck; grey diamond - paradise shelduck; black diamond - mallard; grey dot - grey duck; cross - grey teal; black triangle - blue duck; black dot - brown teal; star - Auckland Island teal; black square - Campbell Island teal.

Fig. 6. Relationship between carpal knob length and carpometacarpus total length for Chatham Island duck (+), flying steamer duck (circle), and white-headed steamer duck (diamond); open = male; filled = female. Mean carpometacarpus total lengths (mm) and carpal knob lengths (mm) were: flying steamer duck - male 67.0 ± 3.7 , 22.1 ± 0.7 ; female 65.4 ± 2.4 , 18.5 ± 0.7 ; white-headed steamer duck - male 65.8 ± 1.7 , 22.1 ± 1.1 ; female 62.4 ± 1.3 , 21.2 ± 1.7 .



Comparison with steamer ducks

Steamer ducks also have conspicuous and rugose carpal knobs. The flying steamer duck is the smallest of the 4 species (female 2.3 kg, males 2.9 kg) whereas the white-headed steamer duck is the smallest of the 3 flightless species (female 3.0 kg, male 3.8 kg; Livezey & Humphrey 1986); these 2 species are the closest in body mass to that estimated for Chatham Island duck. Five carpometacarpi and carpal knobs from each species and sex were measured, and their sizes relative to those from Chatham Island

ducks are depicted in Figure 6. In both species of steamer duck, total lengths of carpometacarpi and of carpal knobs were longer in males than females and although carpometacarpi were longer in the flying species, the carpal knobs were of similar size, or larger, in the larger flightless species.

Despite having been a smaller bird and having considerably shorter carpometacarpi, some Chatham Island ducks had carpal knobs equal to those of both flying and white-headed steamer ducks (Fig. 6), and of an even larger species of *Tachyeres* (Fig. 7).



Fig. 7. Comparative morphology of carpometacarpi in ventral aspect of Chatham Island duck (left, scale 10 mm) and Falklands steamer duck *Tachyeres brachypterus* (right, scale 10 mm; from Hume & Steel (2013): courtesy Julian Hume).

DISCUSSION

Augmentation of wing bones to serve as weapons has been recorded in a small number of avian families (Rand 1954; Hume & Steel 2013). Hume & Steel (2013) reviewed perhaps the most extreme example, the solitaire from Rodrigues Island in the Mascarenes, western Indian Ocean. A wing's carpal joint can deliver a forceful blow in defence or in aggression and its augmentation in members of the Anseriformes has included not only the enlargement of the *processus extensorius* as a club, as described here for Chatham Island duck, but also as a spike or spur covered with a horny sheath, as in the torrent duck (*Merganetta armata*). In larger waterfowl such as swans and geese, the general robustness of all the bones at the carpal flexure makes this part of the wing a useful club even without further augmentation. As both Rand (1954) and Hume & Steel (2013) illustrate, augmentation in some other bird families includes a modification of the radius and the development of a knob at both ends of the carpometacarpus.

The rugose tip to the Chatham Island duck's carpal knob clearly indicates impact callous growth, or at least suggests that the knob became expanded in direct response to its use. A possible interpretation of Figure 3 is that the knobs may have been less prominent in young birds or in those without territories, but otherwise they were proportionately of equal size in the larger of the presumed females as in the larger presumed males. Nevertheless, all 20 bones examined had rugose

tips, even on those of the shortest length and on the shortest carpometacarpus.

None of the carpometacarpi showed evidence of healed fractures, nor did any of 19 ulnae examined. Healed fractures were evident on both bones of some steamer ducks (Livezey & Humphrey 1985). In the solitaire there were healed fractures on other wing bones and ribs as well (Hume & Steel 2013), indicative of the severe damage inflicted by their profoundly enlarged carpal knobs. Although the number of Chatham Island duck wing bones found to date is probably too few to detect prevalent bone fractures, the extreme enlargement and rugosity of many of the carpal knobs relative to those of other waterfowl, and especially to some steamer ducks, suggests a powerful and well-positioned blow could have inflicted serious skeletal and soft tissue damage.

A well-chronicled example of the use of carpal knobs is that of the African black duck (*A. sparsa*), a river specialist and basal member of the mallard clade of dabbling ducks (Johnson & Sorenson 1999; Lavretsky *et al.* 2014). Its behavioural specialisations for river life include pair-bonds and territories being maintained year-round, and with pairs cooperating in aggressive, sometimes fatal, defence of the territory (McKinney *et al.* 1978). A feature of their territorial and mate defence behaviour is the use of carpal "spurs" (described by Frost *et al.* 1979 as "rounded cartilaginous outgrowths" but which have underlying expanded and rugose carpal knobs; E. Maas, *pers. comm.*) with which fighting birds flail at each other until damage or exhaustion results in victory. The vigour of these fights, which often draw blood on the wing edge and inflict an inability to fly, is such that fighting is a major cause of displacement or death of territorial birds (Ball *et al.* 1978). This behaviour is also seen in blue duck, another river specialist (Kear & Steel 1971). Similar vigorous territorial defence involving wing flailing and face-to-face fighting is characteristic of brown teal and Auckland Island teal defending contiguous territories along streams and beach shorelines, respectively (Williams, 1995, 2001, and *unpubl.*).

Interpreting Chatham Island duck behaviour

The development of a prominent carpal knob, or similar structure, in other waterfowl appears to be restricted to species with a year-round territorial habit. Amongst New Zealand's ducks (Fig. 6, but see also Worthy 2004: Fig. 7), those with a carpal knob (*e.g.*, the 3 New Zealand teals and blue duck), all hold feeding and breeding territories year-round, maintain pair bonds year-round, and both sexes are renowned for their aggressive disposition towards conspecifics (Marchant & Higgins 1990). Those ducks without carpal augmentation (*e.g.*,

mallard, grey duck and grey teal), are widely dispersing and flocking species in which defence of space is primarily mate-guarding behaviour and restricted to the immediate pre-breeding and breeding periods. Ducks elsewhere having conspicuous carpal knobs or spurs (e.g., African black duck, steamer ducks, torrent duck), are also renowned for their pugnacity and their exclusive year-round occupancy of combined feeding and breeding habitats.

These comparisons, and the occurrence of prominent carpal knobs on all of the carpometacarpal examined, suggest that the Chatham Island duck was a year-round territory-holder, that both sexes defended the territory, and that pairings were long-term. In these respects its social behaviour and mating system were probably more similar to brown teal (Williams 2001), Auckland Island teal (Williams 1995) and Campbell Island teal (Williams & Robertson 1995; McClelland 2002) than to any other of New Zealand's waterfowl.

However, the most significant factor about the Chatham Island duck's carpal knobs was their size. Relative to body mass, they are probably the largest "weapons" of any member of the Anseriformes. Their size and rugosity imply similar belligerence to that demonstrated by steamer ducks (Livezey & Humphrey 1985; Nuechterlein & Storer 1985). Nuechterlein & Storer (1985) highlighted that the skin surrounding the carpal knobs of steamer ducks was "cornified" and its orange colour made them visually conspicuous. They suggested carpal knob prominence and the belligerency males showed towards most animals transgressing their territories may have been under strong sexual selection. The Chatham Island duck's large carpal knobs would have been bared and the surrounding skin heavily calloused, and whether or not the skin was coloured, they would undoubtedly have been conspicuous.

If Chatham Island duck was the belligerent, year-round territory holder its formidable carpal weapons imply, what habitat did it occupy? Its flightlessness, and the extensive salt gland impressions on its skull, offer further insights to its ecology (see Williams 2015). The large salt gland impressions unequivocally indicate a marine or marine-influenced feeding environment whereas flightlessness suggests a sessile and predictable food supply was available year-round. Territoriality indicates feeding, breeding and brood-rearing occurred within a limited and, importantly, a defensible area. This is not unlike the habitat and behaviour of many Auckland Island teal and of most flightless steamer ducks occupying marine-edge territories in sheltered reaches or coves (Williams 1995; Livezey & Humphrey 1985; Livezey 2005).

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