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Feeding ecology analysis supports a marine diet in the extinct Chatham Island Duck (*Anas chathamica*)

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ABSTRACT

The Chatham Island Duck, *Anas chathamica*, is one of many New Zealand bird species that became extinct after Polynesian arrival. The Chatham Island Duck was a large flightless bird, with salt glands on its skull, which led to the hypothesis that it lived in a marine habitat. We tested this hypothesis using a combination of stable isotope analysis (carbon and nitrogen) and analysis of morphoanatomical features. We also conducted a comparative analysis with other anatids from the Chatham Islands and New Zealand. Furthermore, we trialled the non-destructive technique of portable X-ray fluorescence (elemental composition of bones) to assess whether it can be helpful for reconstructing the ecology and habitat of extinct species. We obtained data from museum specimens: 12 samples of *A. chathamica* and 55 of other anatids for isotope analysis; and 23 samples of *A. chathamica* and 63 of other anatids for X-ray fluorescence. Results from isotope analysis, supported by anatomical features, show that *A. chathamica* had a more fully marine diet than previously hypothesised, mainly composed of invertebrates. The large body size of *A. chathamica* is possibly related to territoriality and combat, which is also supported by the presence of carpal weaponry. Our data demonstrate the importance that the marine environment likely played in the life of this extinct species, while highlighting the key role natural history collections can have in ecological studies.

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Anas chathamica; Anatidae; New Zealand; stable isotopes; X-ray fluorescence

Introduction

Recent technological and methodological advances allow us to explore a vast and still largely untapped wellspring of ecological information in natural history collections (Webster 2017; Meineke *et al.* 2018; Salvador and Cunha 2020). Besides the more usual studies focusing on current anthropogenic effects of environment and global change (Meineke *et al.* 2018; Schmitt *et al.* 2018), another important aspect of using museum specimens is the reconstruction of the ecology of species that became extinct in historical times due to anthropogenic activity. Given that typically very few specimens remain of such species, it is important that they are analysed in as much detail as possible, balancing destructive and non-destructive techniques (Webster 2017). Among the new methodologies now available to us are isotope analysis (destructive) and portable X-ray fluorescence (non-destructive).

Stable isotope analysis is an established methodology for acquiring environmental and ecological information. The ratio between the stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are particularly useful to reconstruct habits of extinct species by defining their feeding ecology (Peterson and Fry 1987; Kelly 2000; Inger and Bearhop 2008). The $\delta^{13}C$ and $\delta^{15}N$ values of organisms reflect those of their environment and, thus, can be used to infer diet and trophic relationships (Mizutani *et al.* 1992; Post 2002; Fox and Bearhop 2008; Bond and Jones 2009). Nitrogen isotopes are indicative of trophic level (e.g. DeNiro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002), while carbon isotopes are related to sources of carbon from the animals' feeding environment (e.g. marine versus freshwater; Kelly 2000; Fry 2006; Fox and Bearhop 2008; Inger and Bearhop 2008).

Portable X-ray fluorescence (pXRF) provides the elemental composition of a sample, determining the abundance of major and trace elements assimilated from the bird's habitat and diet (Plummer *et al.* 1994; Rogers 2019). This method is widely used in archaeology to determine the provenance of human bones and artefacts (e.g. LaBrecque *et al.* 1998; Adan-Bayewitz *et al.* 2007; Byrnes and Bush 2016), but can also be used to investigate bones of other species, including fossils (e.g. Plummer *et al.* 1994; Rogers 2019). However, besides its use for detection of pollutants (e.g. Radu and Diamond 2009;

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This article has been corrected with minor changes. These changes do not impact the academic content of the article.

Peinado *et al.* 2010), the use of pXRF in zoo-ecological analyses has not been thoroughly explored yet.

New Zealand's avifauna, although not particularly rich, is among the most recognisable in the world due to its numerous flightless 'oddities'. Unfortunately, the country also ranks high in the number of extinct species during the Holocene as more than a third of its breeding bird diversity has been extirpated, including several waterfowl species (Holdaway 1989; Young *et al.* 1996; Tennyson and Martinson 2007). The Chatham Islands (located ca. 800 km east of mainland New Zealand), despite its limited size, had a reasonably diverse waterfowl fauna comprising nine species, four of which became entirely extinct via anthropic action, with another four species locally extinct in the Chathams but surviving elsewhere in New Zealand (Holdaway 1989; Millener 1999; Tennyson and Martinson 2007; Miskelly 2008). One such casualty was the endemic Chatham Island Duck, *Anas chathamica* (Oliver 1955), extinguished through hunting by early Polynesian settlers (Williams 1964; Tennyson and Martinson 2007).

Anas chathamica had some unique and unusual features, including its size (largest in genus), flightlessness, carpal weaponry (proportionally the largest in Anseriformes) and the presence of large salt glands on the skull (Figure 1; Williams 2015a, 2015b; Watanabe 2017). Very few bones of this duck have been collected so far, either from natural settings or middens (Marshall *et al.* 1987; Williams 2015b), and this lack of physical material makes it difficult to study the species in more detail. Previous authors proposed that *A. chathamica* had a marine-based diet due to the physiological presence of salt glands (Williams 2015a), but that hypothesis has not been tested so far.

Figure 1. Skull of *A. chathamica* (NMNZ S.029475), from Maunganui Beach, Chatham Island, showing the impression of the salt glands above each orbital cavity (arrow). Photograph by Jean-Claude Stahl, Te Papa. Credit: NMNZ, CC BY-NC-ND 4.0.

Herein we use a combination of independent lines of evidence to assess whether *A. chathamica* lived primarily in a marine environment. Namely, we analyse morpho-anatomical features that are potentially related to marine habits and use stable isotope data to gain information about diet, and thus habitat. To provide better support to our analyses of *A. chathamica*, we also supply comparative data on other anatid species that inhabit the Chatham Islands, as well as other oceanic islands around New Zealand. Finally, we test whether pXRF can offer useful information for ecological studies of extinct species through the retention and accumulation of dietary or environmentally specific elements in bones. Being a portable and non-destructive procedure, it is worthwhile exploring its potential uses for cases where only few precious museum specimens are available.

Material and methods

Our comparative analyses included specimens of *A. chathamica*, as well as other *Anas* spp. present in New Zealand: Brown Teal, *A. chlorotis* G.R. Gray, 1845; Grey Duck, *A. superciliosa* Gmelin, 1789; Auckland Island Teal, *A. aucklandica* (G.R. Gray, 1849); Campbell Island Teal, *A. nesiotis* (J.H. Fleming, 1935). The former two were present both on the Chatham Islands and on New Zealand's mainland (we analysed specimens from both settings), and the latter two inhabit other archipelagos south of the New Zealand mainland and are flightless like *A. chathamica*. We also included the extinct endemic Chatham Island Merganser, *Mergus milleneri* Williams & Tennyson, 2014, for comparison, which likely had a marine-based diet.

The isotope dataset stems from a joint project of Murray J. Williams and Richard N. Holdaway that took place in 2000–2005, to which we have been granted access. Part of the dataset has already been published by Holdaway *et al.* (2013: *A. chlorotis*) and Williams *et al.* (2012: *M. milleneri*), but the remaining values are reported here for the first time.

Samples for stable isotope analysis were largely obtained from bone specimens housed at the Museum of New Zealand Te Papa Tongarewa (NMNZ, Wellington) and Canterbury Museum (CM, Christchurch) (Supplementary Material: Table S1). Furthermore, stable isotope values reported here include samples taken from bones during fieldwork by Murray J. Williams (MJW), of which no voucher specimens remain (Table S1). The bones were prepared and analysed at the Stable Isotope Laboratory of GNS Science (Lower Hutt, New Zealand). Bone collagen extraction followed the protocol of Holdaway and Beavan (1999). Stable isotope values acquired from bone collagen represent an averaged diet history throughout the life of the bird (Hobson and Clark 1992).

Carbon and nitrogen content and stable isotopic composition were analysed using an Isoprime isotope ratio mass spectrometer (VG Micromass, UK) interfaced to a EuroEA elemental analyser (UK) in continuous-flow mode (EA-IRMS). Bone collagen was weighed in duplicate into 4 × 6 mm tin capsules for $\delta^{13}C$ and $\delta^{15}N$. The EA oxidation and reduction furnace temperatures were set at 920°C and 600°C, respectively, with high-purity (>99.99%) CO_2 and N_2 as reference gases. Helium was used as the carrier gas and with a flow rate of 60 mL/min. Stable isotope ratios were calculated referring to the equation $\delta(‰) = R_{sam}/R_{ref} - 1$ (Coplen 2011), where δ represents either $\delta^{13}C$ or $\delta^{15}N$, R_{sam} denotes the abundance ratio of heavy isotope against light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$), R_{ref} is the isotope ratio of reference standard versus primary standards, i.e. Vienna Pee Dee Belemnite (VPDB) for carbon, Air gas (AIR) for nitrogen. Working reference standards (leucine, EDTA, caffeine, and sucrose) were calibrated against international reference materials (IAEAN1, IAEA-N2, IAEA-CH6 and IAEA-CH7) and blanks were included during each run for calibration. Analytical precision of the measurements is ±0.1 ‰, and reproducibility of the results is within ±0.1 ‰ for carbon and ±0.2 ‰ for nitrogen (1σn).

There is a global change in the ratio of atmospheric carbon isotopes, which is caused by the large amount of ^{13}C-depleted CO_2 released by the burning of fossil fuels (Keeling 1979). This phenomenon is known as the Suess effect and requires the correction of carbon isotope measurements from samples subsequent to the Industrial Revolution (Verburg 2007). Thus, we used equation #4 of Verburg (2007) to correct our bulk carbon measurements of freshly collected specimens, according to the year they were collected (Table S1). Subfossil specimens predate the Industrial Revolution and did not require correction (Table S1).

The specimens analysed using non-destructive pXRF were likewise obtained from the NMNZ collection (Table S1). A portable handheld X-Ray Fluorescence analyser gun (Olympus Innov-X 50 KV) was used in ‘Geochemistry mode’. Samples were placed over the detector window of the pXRF mounted in a test stand provided by the manufacturer, which enclosed the X-rays within a metal case. Objects were scanned for 90 s with beam settings at 50 kV for 60 s and 15 kV for 30 s. Calibration checks (using a Stainless-Steel Calibration Check Reference Coin provided by Olympus) and reference materials (NIST2710a, NIST2711a) were taken every 20 samples. Contents of major and trace elements were recorded by Innov-X Delta Advanced PC software. Elemental abundance was measured in ppm (1 ppm = 1 mg/kg) or percentage (where 1% = 10,000 ppm). Limits of detection (LoDs) for elements analysed by pXRF are in the ppm range. Elemental abundance was not linearity corrected and was used for comparative purposes only.

We tested if species and specimen location (islands versus mainland) explained differences in bulk isotopic values of carbon and nitrogen using multiple regression analysis in R 4.0.2 (R Core Team 2020). To define the minimal model, we used backward model selection, dropping non-significant terms in each step. We then did a post hoc pairwise *t*-test comparison between each pair of species, accounting for multiple testing via Bonferroni adjustment.

To evaluate chemical elements in relation to habitat and species differences determined by pXRF, we used an orthogonal partial least squares discriminant analysis (OPLS-DA) with the pXRF results using SIMCA-p software (v.13.0, Umetrics, Germany). OPLS-DA is widely used as a supervised recognition tool, which decomposes the raw sample-variable matrix by partial least squares (PLS) and extracts characteristic information from all variables and fits them into the first few latent variables (LVs) to realise dimensionality reduction of data. Score matrices of samples projected on the first few latent variables generate a new variable matrix summarising raw data (e.g. t1 and t2) and present the classification of observations (samples) and outliers. The first component (t1) explains the largest variation of the X space, followed by t2. In addition, key characteristic variables used to discriminate the origin of samples can be identified according to variable loadings plot and importance for the projection values (VIPs >1 indicates importance).

Results

The carbon and nitrogen isotope values, as well as the major and trace elemental abundance obtained by pXRF are listed in Table S1.

$\delta^{15}N$ values were significantly different between species ($F = 22.51$; $p < 0.01$), but there was no difference between island and mainland specimens of each species ($F = 1.17$; $p = 0.28$) (Figure 2(a,c)). The post hoc comparison revealed significantly higher $\delta^{15}N$ values for *A. chathamica* (mean ±se: +14.4 ± 0.8 ‰) than *A. chlorotis* (+8.1 ± 0.3 ‰) and *A. superciliosa* (+9.6 ± 1.4 ‰), but no significant difference between *A. chathamica* and *A. aucklandica* (+15.2 ± 1.2 ‰), *A. nesiotis* (+17.6 ± 2.7 ‰) or *M. milleneri* (+19.3 ± 1.1 ‰). For a full comparison, see Supplementary Material (Tables S2, S3).

$\delta^{13}C$ values were also significantly different between species ($F = 38.80$; $p < 0.01$) and were generally more

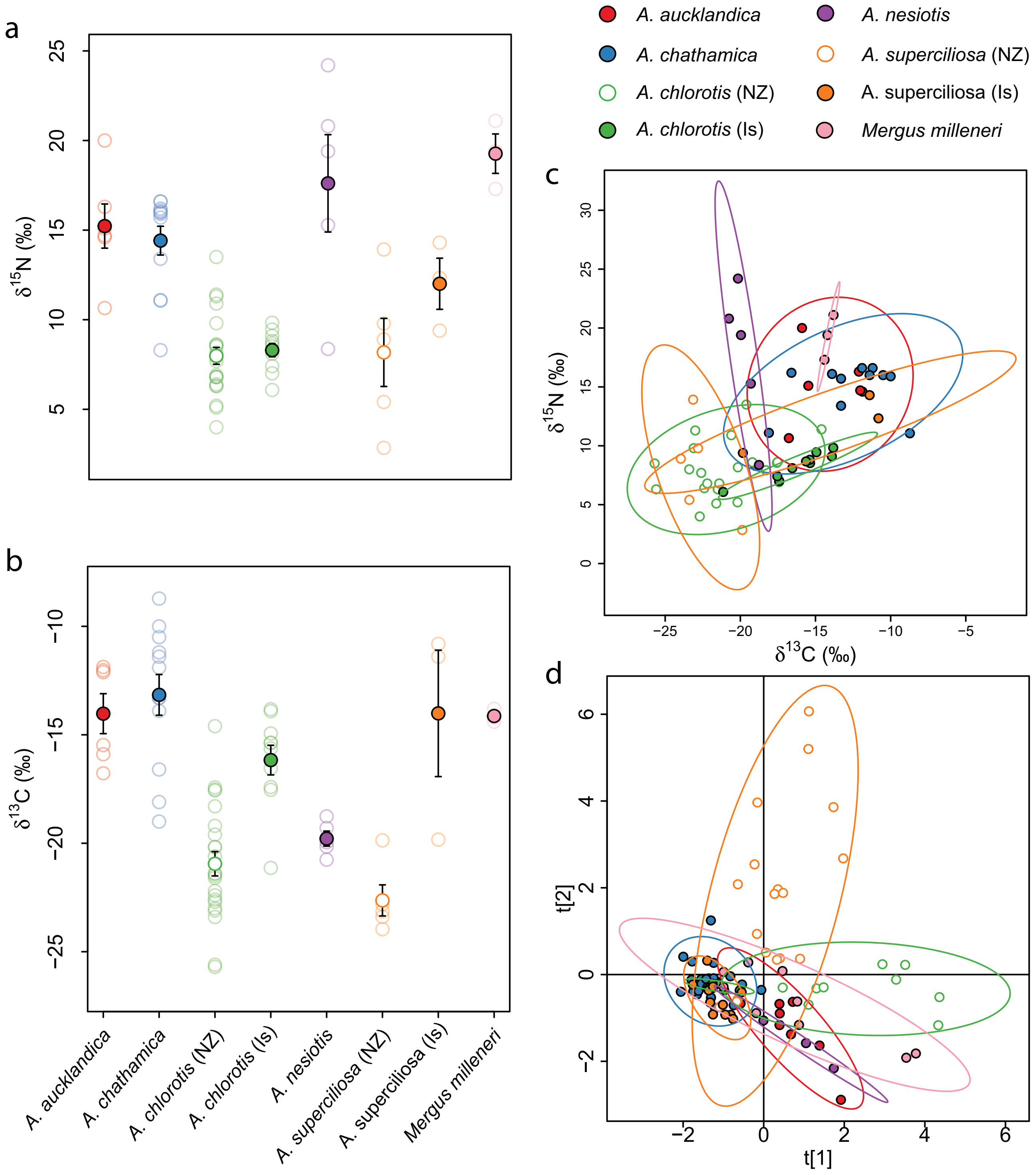

Figure 2. (a) δ^{15}N values for all species, with mean and standard error bars. (b) δ^{13}C values for all species, with mean and standard error bars. (c) δ^{13}C and δ^{15}N biplot showing the difference in isotopic niche of each species. Each point represents a single specimen. (d) Scores scatter plot of components t1 and t2 resulting from the OPLS-DA analysis of the pXRF data. Brown Teal (*A. chlorotis*) and Grey Duck (*A. superciliosa*) are divided into mainland (NZ) and island specimens (Is).

negative in the mainland specimens, the latter reflecting a terrestrially influenced basal food web ($F = 4.75$; $p < 0.01$) (Figure 2(b,c)). The post hoc comparison revealed significantly less negative δ^{13}C values for *A. chathamica* (−13.2 ± 0.9 ‰) than mainland *A. chlorotis* (−20.9 ± 0.6 ‰), mainland *A. superciliosa* (−22.6 ± 0.4 ‰) and *A. nesiotis* (−22.6 ± 0.7 ‰), but no difference between *A. chathamica* and *A. aucklandica* (−14.0 ± 0.9 ‰), island

A. chlorotis (−16.2 ± 0.7 ‰), island *A. superciliosa* (−14.0 ± 2.9 ‰) or *M. milleneri* (−14.1 ± 0. ‰). For a full comparison, see Supplementary Material (Tables S2, S4).

The OPLS-DA analysis of pXRF data clustered different species and their associated habitat (island or mainland) into different regions based on their elemental composition. The clustering accuracy, which combined two latent variables (t1 and t2), accounts for 48% of the species separation, respectively highlighting that some species overlap and do not cluster well into their classes (Figure 2(d); total classification accuracy R2X(cum) = 63.9%). The classification performance of the OPLS-DA model was evaluated by the cumulative contribution of latent variables (R2Y; only 24.1% for t1 and t2) and goodness of fit (Q2; = 15.1%); this suggests that there are too many scattered outliers to cluster each species according to a predictive model.

The significant chemical elements (VIP >1.0) contributing to t1 (Figure S1) were magnesium, calcium, aluminium; iron was borderline (0.98). In t2 (Figure S2), the elements were iron, silica, magnesium, zinc, calcium, aluminium; strontium was borderline (0.99). With very few exceptions, samples lying in the negative region for t1 are related to islands, while positive values are more indicative of the mainland. No clear relation between species and environment could be established based on t2, although most samples clustering in the upper left quadrant (negative t1 and positive t2) are from the Chatham Islands. Figure S3 shows the loadings scatter plot resulting from the pXRF displaying the relationship between the elements, the species and their habitat. In this plot, elements close to the centre of the quadrant have lower discriminatory powers. *Anas chathamica* plots closely to the island representatives of *A. superciliosa* and *A. chlorotis*, which is expected given that the latter are almost exclusively from the Chatham Islands (Table S1). *Mergus milleneri, A. nesiotis* and *A. aucklandica* plot close to one another, forming a second cluster. Mainland samples of *A. superciliosa* and *A. chlorotis* plot the farthest away from the other species.

Discussion

Stable isotope results and morpho-anatomical features are in line with one another, indicating that *A. chathamica* had a marine diet and habit, even to a greater extent than previously hypothesised. Results from pXRF analysis showed that this methodology can produce data of ecological interest, although it is of rather restricted use when compared to stable isotope and morpho-anatomical data.

Trophic level and diet

Holdaway (1989) posited a diet entirely made up of crustaceans and molluscs for *Anas chathamica*. On the other hand, Mitchell *et al.* (2014) proposed a mostly herbivorous diet, which was later questioned by Williams (2015b) based on the brackish and marine environment predominant in the Chathams. Our results are consistent with a carnivorous diet based on invertebrates

Our results show very similar high δ^{15}N values between *A. chathamica, A. aucklandica* and *A. nesiotis* (Figure 2(a, c); Table S1) indicating a diet rich in marine invertebrates (marine invertebrates are enriched in ^{15}N compared to freshwater ones; France 1994). Both teals inhabit islands (and thus are in comparable ^{15}N-enriched habitats; see below) and are mostly carnivorous (Williams 1995; Williams and Robertson 1996). For *A. nesiotis*, higher δ^{15}N values allied to more negative δ^{13}C values (see below) support the hypothesis they are eating from a food web with a detrital base that may be affected by bird guano, or they are possibly insectivorous feeders. Less negative δ^{13}C values support that *A. aucklandica* feed more on marine invertebrates (cf. Williams 1995; Williams and Robertson 1996). *Anas chlorotis* and *A. superciliosa* typically have lower δ^{15}N and more negative δ^{13}C values than the other species, in line with their omnivorous diet with a larger freshwater plant component (Moore *et al.* 2006).

Notably, the nitrogen isotope values obtained for *A. chathamica* were not significantly different from those of the piscivorous *M. milleneri* (Figure 2(a,c); Table S1). On average, both species had relatively high δ^{15}N values with a non-significantly higher average δ^{15}N value for *M. milleneri*. However, the low number of *M. milleneri* samples analysed may misrepresent the isotope variability of this species and bias the statistics, given that the average value for the species is much higher than that of *A. chathamica*. A difference of ca. 3–4‰ is typically considered a change of one trophic level (Mizutani *et al.* 1992; Post 2002; McCutchan *et al.* 2003), so we could expect the piscivorous *M. milleneri* to be on a trophic level above *A. chathamica*.

As alluded to above, islands (especially small oceanic ones) usually have a marked enrichment in ^{15}N due to the presence of large numbers of seabirds (Hobson *et al.* 1994; Caut *et al.* 2012). That is due to ^{15}N-enriched bird guano (coming from ^{15}N-enriched marine prey) leaching into primary food (plants) and water sources (Hobson *et al.* 1994; Erskine *et al.* 1998; Ellis *et al.*

2006; Caut *et al.* 2012). The Chatham Islands are a global hotspot for seabirds, so heightened background levels of ^{15}N could be expected there. This would affect nitrogen isotope values for animals feeding in terrestrial and freshwater environments on the islands (marine environments are already naturally enriched in ^{15}N). For instance, enrichment in ^{15}N has already been observed for the Chatham Island snipe *Coenocorypha pusilla* (Buller, 1869), which forages in the soil for invertebrates, as well as other snipes on oceanic islands around New Zealand (Hawke and Miskelly 2009). Nevertheless, an enrichment in ^{15}N was not observed when comparing mainland New Zealand and island *A. chlorotis* and *A. superciliosa* (both almost exclusively from the Chathams; Figure 2(a), Table S1). However, the small sample size of island-dwelling *A. superciliosa* might have biased the results for this species, as their island average was much higher than that of their mainland counterparts, despite not being statistically significant.

Habitat

The carbon isotope values obtained for *A. chathamica* are in line with those of *M. milleneri* (Figure 2(b,c); Table S1), indicating a similar marine environment. They differ greatly from the δ^{13}C values of the freshwater-feeding *A. chlorotis* and *A. nesiotis* (Williams and Robertson 1996; Holdaway *et al.* 2013), but are similar to those of *A. aucklandica*, which feeds among kelp on protected shorelines (Williams 1995).

Williams (2015a) considered that *A. chathamica* would inhabit marine edges, sheltered reaches or coves, like *A. aucklandica*. The latter has very small salt glands and can spend a lot of time away from the sea in runnels and among tussock (Williams 2015b). The larger salt glands of *A. chathamica* (Figure 1) indicate more obligatory marine habits, including the island's large brackish Te Whanga Lagoon, which would offer more sheltered habitats and has also been postulated as the prime habitat of *M. milleneri* (Williams *et al.* 2012, 2014). Furthermore, until a few millennia ago, the Chathams were a single large island, in all likelihood with a much more extensive shoreline (Campbell 2008) able to support a larger *A. chathamica* population.

From the OPLS-DA analysis of the pXRF values (Figures 2(d), S1–S3), it can be seen that habitat is a strong determinant of the bone's elemental composition, given that *A. chathamica* plotted together with island-dwelling *A. superciliosa*, which are all from the Chathams, and island-dwelling *A. chlorotis*, mostly from the Chathams (Table S1). In the scatter plot (Figure S3), it can also be seen that the three values obtained for the three above-mentioned species cluster close to the elemental loading values of phosphorus and zircon. Phosphorus is elevated in island duck species due to concentrated and localised bird guano deposits from the marine diet ingested by these birds (e.g. Landis and Craw 2003; Irick *et al.* 2015). Mineralogy of the Chatham Island sediments has shown they are rich in detrital zircon from the Permian-Triassic Torlesse greywacke equivalent (and also in Sr, U, and Rb in basement rocks; Adams *et al.* 2008). Values from the mainland *A. superciliosa* and *A. chlorotis* plot far away from P and Zr (Figure S3) due to different regional geology, and higher geographical dispersal and mobility of the birds than on the Chathams.

Morphology

Morpho-anatomical features observed in *A. chathamica* also offer ecological information to complement the results of the chemical analyses. First and foremost, the large impressions on the skull indicate the presence of well-developed salt glands (Figure 1; Williams 2015a), which is an important adaptation to marine life in birds (Schmidt-Nielsen 1960). Thus, this feature provides further evidence of a marine (or strongly marine-influenced) feeding environment for *A. chathamica*.

Anas chathamica was flightless (Williams 2015b; Watanabe 2017), indicating sessile habits in an environment which was productive and predictable, i.e. an island with food supply all year round (Williams 2015a, 2015b). In particular, *A. chathamica* is the largest species in the genus, which led Williams (2015a, 2015b) to propose that it became large-bodied after colonising the Chatham Islands. It is the only island-dwelling *Anas* species that has done so (though a similar scenario is known from the Hawaiian moa-nalos; Sorenson *et al.* 1999), and that author hypothesised it was due to higher predation risk in the more exposed and open shoreline environments of the Chathams. It is hard to ascertain the validity of that hypothesis based on current evidence, especially given that other explanations for large size are apparent in other anatid lineages.

A similar increase in size and flightlessness can be seen, for instance, in South American marine streamer ducks (*Tachyeres* spp.) and in the extinct coastal duck *Chendytes lawi* Miller, 1925 from California and the Channel Islands; all those species feed/fed on marine invertebrates (Miller *et al.* 1961; Fulton *et al.* 2012; Buckner *et al.* 2018). In *C. lawi*, the increase in size is hypothesised to be related to locomotion, diving, and access to larger (possibly sessile) invertebrate prey (Miller *et al.* 1961; Buckner *et al.* 2018). In *Tachyeres*, the increase in size is hypothesised to be related to improved locomotion on the water, diving, thermoregulation, defence and wing-assisted combat (Livezey and Humphrey 1986).

A strong territorialism is implied in *A. chathamica* by their carpal weaponry, which is proportionally the largest in Anseriformes (Williams 2015a). Thus, we suggest that a more likely explanation for their increase in size is related to territorialism, aggressive behaviour display and wing-assisted combat, as proposed for streamer ducks (Livezey and Humphrey 1986). Similar cases of flightlessness accompanied by carpal weaponry are known from unrelated avian taxa, such as the Rodrigues solitaire *Pezophaps solitaria* (Gmelin, 1789) (Columbidae) and the Jamaican ibis *Xenicibis xympithecus* Olson & Steadman, 1977 (Threskiornithidae), both now extinct (Livezey 1993; Longrich and Olson 2011; Hume and Steel 2013).

Conclusion

The ability to investigate the ecology of extinct species is necessarily more limited than investigating living taxa, so using multiple lines of evidence helps to achieve stronger interpretations (Grimes *et al.* 2003; Rasser *et al.* 2019). Herein, we combined stable isotope analysis and morphoanatomical data to achieve a better understanding of the ecology of the extinct *Anas chathamica*. We show that it had a more fully marine diet than previously hypothesised, mainly composed of invertebrates but likely containing a minor plant component. The large body size of *A. chathamica* is possibly related to territoriality and combat, as suggested by the presence of carpal weaponry. Finally, we also highlight that, while non-destructive techniques such as pXRF are important in cases where few specimens exist, they are rather limited in what they can achieve. As such, destructive sampling (e.g. isotope analysis and DNA extraction) will remain necessary in most cases.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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References

Adams, C. J., Campbell, H. J., and Griffin, W. J. (2008). Age and provenance of basement rocks of the Chatham Islands: An outpost of Zealandia. *New Zealand Journal of Geology and Geophysics* **51**, 245–259. doi:10.1080/00288300809509863

Adan-Bayewitz, D., Asaro, F., and Giauque, R. D. (2007). Determining pottery provenance: Application of a new high-precision X-ray fluorescence method and comparison with instrumental neutron activation analysis. *Archaeometry* **41**, 1–24. doi:10.1111/j.1475-4754.1999.tb00849.x

Bond, A. L., and Jones, I. L. (2009). A practical introduction to stable-isotope analysis for seabird biologists: Approaches, cautions and caveats. *Marine Ornithology* **37**, 183–188.

Buckner, J. C., Ellingson, R., Gold, D. A., Jones, T. L., and Jacobs, D. K. (2018). Mitogenomics supports an unexpected taxonomic relationship for the extinct diving duck *Chendytes lawi* and definitively places the extinct Labrador Duck. *Molecular Phylogenetics and Evolution* **122**, 102–109. doi:10.1016/j.ympev.2017.12.008

Byrnes, J. F., and Bush, P. J. (2016). Practical considerations in trace element analysis of bone by portable X-Ray Fluorescence. *Journal of Forensic Sciences* **61**, 1041–1045. doi:10.1111/1556-4029.13103

Campbell, H. J. (2008). Geology. In 'Chatham Islands: Heritage and Conservation.' (Ed. C. M. Miskelly.) pp. 35–52. (Canterbury University Press: Christchurch.)

Caut, S., Angulo, E., Pisanu, B., Ruffino, L., Faulquier, L., Lorvelec, O., Chapuis, J.-L., *et al.* (2012). Seabird modulations of isotopic nitrogen on islands. *PLoS ONE* **7**, e39125. doi:10.1371/journal.pone.0039125

Coplen, T. B. (2011). Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid Communications in Mass Spectrometry* **25**(17), 2538–2560. doi:10.1002/rcm.5129

DeNiro, M. J., and Epstein, S. (1981). Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* **45**, 341–351. doi:10.1016/0016-7037(81)90244-1

Ellis, J. C., Farina, J. M., and Witman, J. D. (2006). Nutrient transfer from sea to land: The case of gulls and cormorants in the Gulf of Maine. *Journal of Animal Ecology* **75**, 565–574. doi:10.1111/j.1365-2656.2006.01077.x

Erskine, P. D., Bergstrom, D. M., Schmidt, S., Stewart, G. R., Tweedie, C. E., and Shaw, J. D. (1998). Subantarctic Macquarie Island — A model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. *Oecologia* **117**, 187–193. doi:10.1007/s004420050647

Fox, A. D., and Bearhop, S. (2008). The use of stable-isotope ratios in ornithology. *British Birds* **101**, 112–130.

France, R. L. (1994). Nitrogen isotopic composition of marine and freshwater invertebrates. *Marine Ecology Progress Series* **115**, 205–207. doi:10.3354/meps115205

Fry, B. (2006). ‘Stable Isotope Ecology.’ (Springer: New York.)

Fulton, T. L., Letts, B., and Shapiro, B. (2012). Multiple losses of flight and recent speciation in steamer ducks. *Proceedings of the Royal Society B* **279**, 2339–2346. doi:10.1098/rspb.2011.2599

Grimes, S. T., Mattey, D. P., Hooker, J. J., and Collinson, M. E. (2003). Paleogene paleoclimate reconstruction using oxygen isotopes from land and freshwater organisms: The use of multiple paleoproxies. *Geochimica et Cosmochimica Acta* **67**, 4033–4047. doi:10.1016/S0016-7037(03)00173-X

Hawke, D. J., and Miskelly, C. M. (2009). ^{13}C and ^{15}N enrichment in snipe (*Coenocorypha* spp.) from islands across the New Zealand biogeographic region. *Journal of the Royal Society of New Zealand* **39**, 35–42. doi:10.1080/03014220909510562

Hobson, K. A., and Clark, R. G. (1992). Assessing avian diets using stable isotopes I: Turnover of δ^{13}C in tissues. *Condor* **94**, 181–188. doi:10.2307/1368807

Hobson, K. A., Piatt, J. F., and Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* **63**, 786–798. doi:10.2307/5256

Holdaway, R. N. (1989). New Zealand’s pre-human avifauna and its vulnerability. *New Zealand Journal of Ecology* **12** (suppl.), 11–25.

Holdaway, R. N., and Beavan, N. R. (1999). Reliable ^{14}C AMS dates on bird and Pacific rat *Rattus exulans* bone gelatin, from a $CaCO_3$-rich deposit. *Journal of the Royal Society of New Zealand* **29**, 185–211. doi:10.1080/03014223.1999.9517592

Holdaway, R. N., Williams, M., and Hawke, D. J. (2013). A comparison of the pre-human and present isotopic niches of brown teal (*Anas chlorotis*): Implications for conservation. *Notornis* **60**, 233–244.

Hume, J. P., and Steel, L. (2013). Fight club: A unique weapon in the wing of the solitaire, *Pezophaps solitaria* (Aves: Columbidae), an extinct flightless bird from Rodrigues, Mascarene Islands. *Biological Journal of the Linnean Society* **110**, 32–44. doi:10.1111/bij.12087

Inger, R., and Bearhop, S. (2008). Applications of stable isotope analyses to avian ecology. *Ibis* **150**, 447–461. doi:10.1111/j.1474-919X.2008.00839.x

Irick, D. L., Gu, B., Li, Y. C., Inglett, P. W., Frederick, P. C., Ross, M. S., Wright, A. L., *et al.* (2015). Wading bird guano enrichment of soil nutrients in tree islands of the Florida Everglades. *Science of the Total Environment* **532**, 40–47. doi:10.1016/j.scitotenv.2015.05.097

Keeling, C. D. (1979). The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. *Environment International* **2**, 229–300. doi:10.1016/0160-4120(79)90005-9

Kelly, J. F. (2000). Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* **78**, 1–27. doi:10.1139/z99-165

LaBrecque, J. J., Vaz, J. E., Cruxent, J. M., and Rosales, P. A. (1998). A simple radioisotope X-ray fluorescence method for provenance studies of archaeological ceramics employing principal component analysis. *Spectrochimica Acta B* **53**, 95–100. doi:10.1016/S0584-8547(97)00115-8

Landis, C. A., and Craw, D. (2003). Phosphate minerals formed by reaction of bird guano with basalt at Cooks Head Rock and Green Island, Otago, New Zealand. *Journal of the Royal Society of New Zealand* **33**, 487–495. doi:10.1080/03014223.2003.9517739

Livezey, B. C. (1993). An ecomorphological review of the dodo (*Raphus cucullatus*) and solitaire (*Pezophaps solitaria)*, flightless Columbiformes of the Mascarene Islands. *Journal of Zoology* **230**, 247–292.

Livezey, B. C., and Humphrey, P. S. (1986). Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): Its morphological bases and probable evolution. *Evolution* **40**, 540–558. doi:10.1111/j.1558-5646.1986.tb00506.x

Longrich, N. R., and Olson, S. L. (2011). The bizarre wing of the Jamaican flightless ibis *Xenicibis xympithecus*: A unique vertebrate adaptation. *Proceedings of the Royal Society B* **278**, 2333–2337. doi:10.1098/rspb.2010.2117

Marshall, Y. M., Scarlett, R. J., and Sutton, D. G. (1987). Bird species present on the Southwest coast of Chatham Island in the 16th Century A.D. *Working Papers in Anthropology, Archaeology, Linguistics and Maori Studies* **76**, 1–25.

McCutchan, J. H., Lewis, W. M., Kendall, C., and McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios for carbon, nitrogen, and sulphur. *Oikos* **102**, 378–390. doi:10.1034/j.1600-0706.2003.12098.x

Meineke, E. K., Davies, T. J., Daru, B. H., and Davis, C. C. (2018). Biological collections for understanding biodiversity in the Anthropocene. *Philosophical Transactions of the Royal Society B* **374**, 20170386. doi:10.1098/rstb.2017.0386

Millener, P. R. (1999). The history of the Chatham Island’s bird fauna of the last 7,000 years – A chronicle of change and extinction. *Smithsonian Contributions to Paleobiology* **89**, 85–109.

Miller, L., Mitchell, E. D., and Lipps, J. H. (1961). New light on the flightless goose *Chendytes lawi*. *Los Angeles County Museum Contribution in Science* **43**, 3–10.

Minagawa, M., and Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between ^{15}N and animal age. *Geochimica et Cosmochimica Acta* **48**, 1135–1140. doi:10.1016/0016-7037(84)90204-7

Miskelly, C. M. (2008). Birds and lizard. In ‘Chatham Islands: Heritage and Conservation.’ (Ed. C. M. Miskelly.) pp. 125–139. (Canterbury University Press: Christchurch.)

Mitchell, K. J., Wood, J. R., Scofield, R. P., Llamas, B., and Cooper, A. (2014). Ancient mitochondrial genome reveals unsuspected taxonomic affinity of the extinct Chatham duck (*Pachyanas chathamica*) and resolves divergence times for New Zealand and sub-Antarctic brown teals. *Molecular Phylogenetics and Evolution* **70**, 420–428. doi:10.1016/j.ympev.2013.08.017

Mizutani, H., Fukuda, M., and Kabaya, Y. (1992). ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. *Ecology* **73**, 1391–1395. doi:10.2307/1940684

Moore, S. J., Battley, P. F., Henderson, I. M., and Webb, C. J. (2006). The diet of brown teal (*Anas chlorotis*). *New Zealand Journal of Ecology* **30**, 397–403.

Oliver, W. R. B. (1955). ‘New Zealand Birds,’ 2nd edn. (A.H. & A. W. Reed: Wellington.)

Peinado, F. M., Ruano, S. M., González, M. G. B., and Molina, C. E. (2010). A rapid field procedure for screening trace elements in polluted soil using portable X-ray fluorescence (PXRF). *Geoderma* **159**, 76–82. doi:10.1016/j.geoderma.2010.06.019

Peterson, B. J., and Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**, 293–320. doi:10.1146/annurev.es.18.110187.001453

Plummer, T. W., Kinyua, A. M., and Potts, R. (1994). Provenancing of hominid and mammalian fossils from Kanjera, Kenya, using EDXRF. *Journal of Archaeological Science* **21**, 553–563. doi:10.1006/jasc.1994.1054

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods and assumptions. *Ecology* **83**, 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Radu, T., and Diamond, D. (2009). Comparison of soil pollution concentrations determined using AAS and portable XRF techniques. *Journal of Hazardous Materials* **171**, 1168–1171. doi:10.1016/j.jhazmat.2009.06.062

Rasser, M. W., Höltke, O., and Salvador, R. B. (2019). Gastropod paleohabitats of Miocene Lake Randeck Maar and its hinterland defined by an actualistic genus-level approach. *Lethaia* **53**, 229–241. doi:10.1111/let.12353

Rogers, K. M. (2019). Provenance, authentication and residue analysis of some Māori taonga using portable X-ray fluorescence. *Tuhinga* **30**, 256–268.

Salvador, R. B., and Cunha, C. M. (2020). Natural history collections and the future legacy of ecological research. *Oecologia* **192**, 641–646. doi:10.1007/s00442-020-04620-0

Schmidt-Nielsen, K. (1960). The salt-secreting gland of marine birds. *Circulation* **21**, 955–967. doi:10.1161/01.CIR.21.5.955

Schmitt, C. J., Cook, J. A., Zamudio, K., and Edwards, S. V. (2018). Museum specimens of terrestrial vertebrates are sensitive indicators of environmental change in the Anthropocene. *Philosophical Transactions of the Royal Society B* **374**, 20170387. doi:10.1098/rstb.2017.0387

Sorenson, M. D., Cooper, A., Paxinos, E. E., Quinn, T. W., James, H. F., Olson, S. L., and Fleischer, R. C. (1999). Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. *Proceedings of the Royal Society B* **266**(1434), 2187–2193.

Tennyson, A., and Martinson, P. (2007). 'Extinct Birds of New Zealand.' (Te Papa Press: Wellington.)

Verburg, P. (2007). The need to correct for the Suess effect in the application of δ^{13}C in sediment of autotrophic Lake Tanganyika, as a productivity proxy in the Anthropocene. *Journal of Paleolimnology* **37**, 591–602. doi:10.1007/s10933-006-9056-z

Watanabe, J. (2017). Quantitative discrimination of flightlessness in fossil Anatidae from skeletal proportions. *The Auk* **134**, 672–695. doi:10.1642/AUK-17-23.1

Webster, M. S. (2017). The extended specimen. In 'The Extended Specimen: Emerging Frontiers in Collections-based Ornithological Research.' (Ed. M. S. Webster.) pp. 1–10. (CRC Press: Boca Raton.)

Williams, G. R. (1964). Extinction of the Anatidae of New Zealand. In 'The Wildfowl Trust Fifteenth Annual Report.' (Eds H. Boyd and P. Scott.) pp. 140–146. (Tillotsons: Bolton.)

Williams, M. (1995). Social structure, dispersion and breeding of the Auckland Island teal. *Notornis* **42**, 219–262.

Williams, M. (2015a). Formidable carpal weaponry of *Anas chathamica*, Chatham Island's extinct flightless duck. *Notornis* **62**, 113–120.

Williams, M. (2015b). Size and flight capability of *Anas chathamica*, an extinct duck from Chatham Island, New Zealand. *Wildfowl* **65**, 75–99.

Williams, M., Holdaway, R. N., and Rogers, K. M. (2012). Feeding environments of New Zealand's extinct merganser revealed by stable isotope analyses. *Wildfowl* **62**, 190–203.

Williams, M., and Robertson, C. J. R. (1996). The Campbell Island teal *Anas nesiotis*: History and review. *Wildfowl* **47**, 134–165.

Williams, M., Tennyson, A. J. D., and Sim, D. (2014). Island differentiation of New Zealand's extinct mergansers (Anatidae: Mergini), with description of a new species from Chatham Island. *Wildfowl* **64**, 3–34.

Young, H. G., Tonge, S. J., and Hume, J. P. (1996). Review of Holocene wildfowl extinctions. *Wildfowl* **47**, 166–180.

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.