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RESEARCH

Reconstructing ecological niche and feeding ecology of pre-contact New Zealand avifauna from Harwood, Otago Peninsula

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Abstract: Over 25% of endemic bird species have become extinct since the time of the first human settlement of Aotearoa | New Zealand in the mid-13th century CE. This has been attributed to multiple factors, including human impact from over-hunting, habitat loss, and the introduction of successive waves of novel mammalian predators. In this study, we analyse carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values from bulk bone collagen of 19 positively identified living and extinct bird species from the coastal pre-contact (i.e. before 1769 CE) subfossil site at Harwood (831–1534 CE, $n = 39$) on Otago Peninsula in the southeastern South Island. We compare the $\delta^{13}C$ and $\delta^{15}N$ values to the broadly contemporaneous coastal early Māori archaeological site at Wairau Bar (1288–1320 CE, $n = 48$) in the northeastern South Island, and the modern-day known feeding ecology of living species. A number of the extant birds analysed displayed $\delta^{13}C$ and $\delta^{15}N$ values that supported a diet similar to their known modern-day feeding ecology. However, a few species, such as the pārera | grey duck (*Anas superciliosa*), pūtangitangi | paradise shelduck (*Tadorna variegata*), tarāpuka | black-billed gull (*Chroicocephalus bulleri*), and tarāpunga | red-billed gull (*Chroicocephalus novaehollandiae*), may have had different regional feeding ecologies prior to human arrival. Our research is significant because it is one of the first comprehensive investigations of the pre-contact diet of birds in Aotearoa.

Keywords: avian diet; carbon and nitrogen stable isotopes; extinct; Wairau Bar

Introduction

Dietary studies using stable isotope analyses of ancient animal remains can provide information about species palaeoecology (Kelly 2000; Boecklen et al. 2011), including that of species that are now extinct (e.g. Domingo et al. 2012; Williams et al. 2012; Metcalfe et al. 2013; Rawlence et al. 2016; Wood et al. 2017a). This information can be used to investigate feeding behaviour, niche construction, and adaptation over time, especially in response to environmental changes caused by climate change and human impact (e.g. Barnosky et al. 2004; Rawlence et al. 2012; Holdaway et al. 2014; Sandom et al. 2014).

In Aotearoa | New Zealand human settlement began c. 1250–1300 CE with the arrival of East Polynesian voyagers (Bunbury et al. 2022). A second wave of colonisation began in the mid-17th century with the voyages of Abel Tasman and James Cook, which was followed by European colonisation from 1769 CE (Anderson 2018). The relatively late human settlement of Aotearoa makes it a unique geographical setting to test for the impact of both pre-human climate-induced and anthropogenic environmental change on endemic species (Worthy 1999; Worthy & Holdaway 2002; Allentoft et al. 2014; Rawlence et al. 2019a).

The extensive Late Quaternary fossil record spanning 60 000 years shows that the pre-human ecosystem of Aotearoa was dominated by large flightless avian megafauna, including nine species of now extinct moa (Aves: Dinornithiformes) (Miskelly et al. 2024). Both Polynesian and European settlement affected

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the environment and biodiversity through habitat loss, over-hunting, and the introduction of mammalian predators such as cats (*Felis catus*), dogs (*Canis familiaris*), rats (*Rattus exulans, Rattus rattus*, and *Rattus norvegicus*), stoats (*Mustela erminea*), and possums (*Trichosurus vulpecula*) (Duncan & Blackburn 2004; Tennyson & Martinson 2007; Greig & Rawlence 2019; Robertson et al. 2021). A high precision radiocarbon chronology has helped to determine that moa became extinct within c. 150 years of human settlement (Holdaway et al. 2014; Perry et al. 2014; Tomlinson et al. 2024). A number of other native bird species, including the world's largest known eagle, Haast's eagle (*Aquila moorei*), followed the same fate as the moa (Holdaway 1989; Holdaway et al. 2002; Bunce et al. 2005; Rawlence et al. 2022). Estimates indicate that at least 64 avian taxa have become extinct since human arrival, with 178 living birds threatened or at risk of extinction today (Tennyson & Martinson 2007; Greig & Rawlence 2019; Robertson et al. 2021; Rawlence et al. 2022; Miskelly et al. 2024).

Since the arrival of humans, a number of native and exotic birds have filled ecological niches that were either once occupied by now extinct birds or previously supported larger populations of a diverse range of species (Cassey 2001; Lee et al. 2010; Rawlence et al. 2015a, 2017, 2019a). Investigating the paleoecology of living and extinct species can help us understand how avifauna coped with anthropogenic environmental change and potentially provide evidence as to how birds may respond to future pressures (Innes et al. 2010; Wood et al. 2017b, c).

Carbon and nitrogen stable isotopes (δ^{13}C and δ^{15}N) are regularly used to investigate past food web structures and temporal changes in the diet of vertebrate species (e.g. Hilton et al. 2006; Misarti et al. 2009; Rawlence et al. 2012; Williams et al. 2012; Holdaway et al. 2013; Grecian et al. 2016; Wood et al. 2017a; Salvador et al. 2021; Schultz et al. 2021, 2023). In Aotearoa, this method has primarily been used to reconstruct the feeding ecology and ecological niches of birds, and more recently, marine mammals (Wing et al. 2025a, b). Isotopic studies of moa have shown regional and habitat-specific inter-species dietary preferences and how direct (e.g. coprolites, gizzard contents) and indirect (e.g. stable isotopes) methods of dietary reconstruction can differ due to sample type, aridity, water use, and canopy effects (Worthy & Holdaway 2002; Rawlence et al. 2012, 2016; Wood et al. 2017a).

Wood et al. (2017a) examined a range of living and extinct species from different trophic levels at two subfossil sites (Harwood and Finsch's Folly Cave in southern Aotearoa) to reconstruct the high trophic level diet of the extinct ngutu hahau | South Island adzebill (*Aptornis defossor*) (see also Worthy & Holdaway 2002). Carbon and nitrogen stable isotopes have shown that, in some geographic regions, the extinct manutahora | Finsch's duck (*Chenonetta finschi*) may have been foraging under dense forest canopy (Holdaway et al. 2002; Worthy & Holdaway 2002; Wood et al. 2017a). Williams et al. (2012) used stable isotope analysis of subfossil bones and historical museum skins to reconstruct the diet and feeding environment of the extinct mergansers (*Mergus* spp.) from the New Zealand region. They found that while the Chatham Island merganser (*Mergus milleneri*) fed on marine prey (Williams et al. 2014), and *Mergus* spp. from Rakiura | Stewart Island and mainland Aotearoa (Miskelly et al. 2024; Rawlence et al. 2024) were likely to have mainly inhabited freshwater ecosystems, the miuweka | Auckland Islands merganser (*Mergus australis*) had a mixed marine and freshwater-based diet.

Carbon and nitrogen isotopes have also been used to investigate temporal changes in food web structures and diets of extant sea birds. Rayner et al. (2021) used stable dietary isotopes on a time-series of extant birds dating back to the 19th century CE from the Hauraki Gulf in northern Aotearoa and showed that kawau tikitiki | spotted shags (*Phalacrocorax punctatus*) changed their diet from fish to squid, and their foraging grounds from inshore to offshore. The trophic position of kāruhiruhi | pied shag (*Phalacrocorax varius*) and kororā | little penguin (*Eudyptula minor minor*) did not change, but like spotted shags, they changed foraging grounds. No significant changes in δ^{13}C and δ^{15}N values were seen in tara | white-fronted tern (*Sterna striata*) or tarāpunga | red-billed gull (*Chroicocephalus novaehollandiae*). Galbraith et al. (2025) used stable dietary isotopes on a time series of karoro | southern black-backed gull (*Larus dominicanus*) comprising pre-human subfossil bones, historical skins, and modern specimens to show that in the Hauraki Gulf, their niche has changed from a coastal marine predator or scavenger with a high trophic position to a lower trophic level terrestrial-based diet.

Wing et al. (2025a, b) used a time series of pakake | New Zealand sea lions (*Phocarctos hookeri*) and kekeno | New Zealand fur seals (*Arctocephalus forsteri*) dating from East Polynesian settlement to the present to show that subantarctic populations of these species maintained high trophic positions through time but recently diverged in ecological niche due to resource limitation. In contrast, sea lions and fur seals on mainland Aotearoa (including Rakiura | Stewart Island) declined in trophic position, and either maintained ecological partitioning or recently converged on the same niche due to a reduced diversity of available prey species.

Despite this preliminary research, there is a knowledge gap in our understanding of the feeding ecology of pre-contact freshwater, coastal, and marine birds in Aotearoa. These birds represent around 64% of the total bird species found in Aotearoa in recent times. Many species have gone extinct or were locally extirpated, and of those that survived, many underwent significant range contractions and population bottlenecks, surviving only in relictual populations in regions that may not reflect their pre-human habitat preferences (e.g. Verry et al. 2022; Tomlinson et al. 2024). It is important to understand how these avian species may have been impacted by human arrival and settlement, and how they adapted, or failed to adapt, to these pressures.

In this study, we used δ^{13}C and δ^{15}N values to reconstruct the past diet, trophic level, and feeding ecology of living and extinct birds from the coastal pre-contact subfossil site at Harwood, located on the Otago Peninsula in southeastern Aotearoa (Fig. 1). The δ^{13}C values represent the feeding habitat (marine, terrestrial, or freshwater) but can be affected by water use effects (i.e. high and low rainfall), canopy effects (i.e. light levels in open habitat/forest canopy versus under a closed canopy) (Rawlence et al. 2016), and distance offshore (e.g. Carpenter-Kling et al. 2020). The δ^{15}N values reflect an animal's trophic position but can be equally affected by the nitrogen source such that ecosystems with marine nitrogen input (e.g. bird guano, beach cast detritus) have significantly higher δ^{15}N values (Schoeninger & DeNiro 1984). This includes those in Aotearoa where widespread pre-contact and contemporary coastal seabird populations occur (Holdaway et al. 2007; Kinaston et al. 2013; Hawke et al. 2017; Wood et al. 2017a).

The isotopic data generated in this study are statistically compared to previously published data from morphologically reidentified avian specimens from the broadly contemporaneous early Māori archaeological site of Wairau Bar in the northern

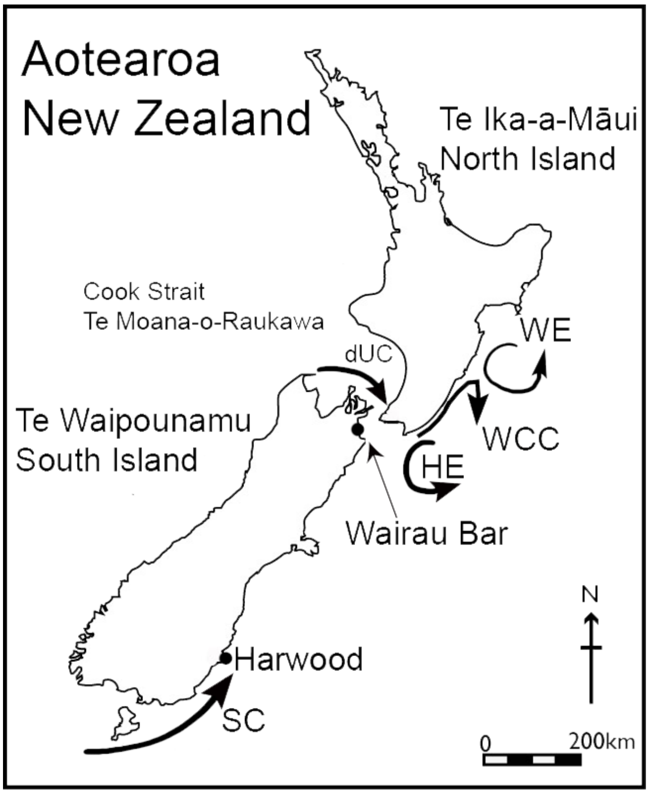

Figure 1. Map of Aotearoa New Zealand showing the location of the Harwood subfossil and Wairau Bar archaeological deposits. Abbreviations: dUC: D'Urville Current; HE: Hikurangi Eddy; SC: Southland Current; WCC: Waiarapa Coastal Current; WE: Waiarapa Eddy.

South Island (Fig. 1). We also compare inferences from isotopic data with the known modern-day feeding ecology of the same species and discuss the possible reasons for any observed variation in dietary isotopic values between sites and time-periods, such as environmental conditions or differences in feeding behaviours.

Depositional and geographic setting

Harwood

Harwood is a subfossil site with pre-human and early Māori era faunal remains. The site is located in Otago Harbour (i.e. inside the Otago Peninsula) on wide marine intertidal sand flats (mid-way down the harbour on the southeast side and seaward of two intra-harbour islands) in an area 300 m by 20 m, parallel to low dunes on the nearby shore on Otago Peninsula (45°48′47″ S, 170°40′17″ E; Fig. 1) (Lalas et al. 2014). Although not an in situ deposit per se, its exact nature is unknown. The bones were found ex situ and may have eroded from the nearby sand dunes (Wood et al. 2017a) upslope of the site or from peat swamps behind these dunes due to marine inundation. There is evidence of peat beneath the intertidal sand flats (CL pers. obs.) and subfossil moa bones have been found historically, eroding from peat deposits along the Harwood and nearby Ōtākou foreshore (West 2017). Given Harwood's sheltered location well-inside Otago Harbour, and the terrestrial avifauna at the site, it is probable that only a small minority of individuals in the deposit originated from beach-cast material. Likewise, it is equally unlikely that individuals were transported to the site from the only permanent freshwater stream (Leith Stream) draining into the head of the harbour over ten kilometres away. The abundant local detritovore populations (e.g. crabs) would have also aided decomposition and therefore reduced the likelihood of carcases being transported long distances and deposited at Harwood. The absence of archaeological material (e.g. burnt bone, bones with cut marks, stone tools, or human bone) suggests that Harwood was not an archaeological midden, but the presence of kurī | Polynesian dog (*Canis familiaris*) indicates that at least part of the deposit was created after human arrival from the mid-13th century CE.

Accelerator Mass Spectrometer radiocarbon dates from two moa (large- and small-bodied), one South Island adzebill, two Polynesian dogs, one Waitaha penguin (*Megadyptes antipodes waitaha*; confirmed through genetic analysis), five matapu | New Zealand swans (*Cygnus sumnerensis sumnerensis*), and four matapo | Otago shags (*Leucocarbo chalconotus*) indicate that the bones at Harwood were deposited over a short time period from 831 to 1534 CE (Rawlence et al. 2015a, b, 2017). One rat-gnawed mataī seed (*Prumnopitys taxifolia*) found in the same deposit has been dated to 1400–1499 CE, while two pieces of kānuka wood (*Kunzea robusta*) have been dated to 681–1268 CE, though inbuilt age may have resulted in older dates (Rawlence et al. 2015a, b; Wood et al. 2017a). All previously published conventional radiocarbon ages from Harwood were calibrated in the original studies using OxCal v4.2 (Bronk-Ramsey 2009), the SHCal13 (Hogg et al. 2013) and Marine13 calibration curves (Reimer et al. 2013), and local ΔR values of 41 ± 39 SD rather than maximum values for Aotearoa (Petchey et al. 2008).

Palaeobotanical remains indicate the terrestrial environment around Harwood was dominated by diverse podocarp forests including mataī (Wood et al. 2017a), a species that provided important food resources for moa, especially moariki | little bush moa (*Anomalopteryx didiformis*) and moa nunui | South Island giant moa (*Dinornis robustus*) (Wood 2007; Rawlence et al. 2011).

The Southland Current carries highly modified subtropical water, originating from the East Australia Current, from south to north past Otago Peninsula (Stevens et al. 2021) (Fig. 1). This subtropical water is restricted to shelf areas, while subantarctic waters are found offshore (Stevens et al. 2021). Banks Peninsula and the Chatham Rise, off the eastern South Island, act as a marine barrier between subtropical and subantarctic waters (Stevens et al. 2021), and their associated current systems (Fig. 1), resulting in biogeographic splits in some species (e.g. northern and southern lineages of Waitaha penguin; Boessenkool et al. 2009). These current systems, their influence on the wider ecosystems and food webs at Harwood and Wairau Bar (see below), and the abundance of marine bird species in both deposits highlight the need to analyse these sites separately to avoid any geographical effects on the biological interpretation of isotope values (e.g. Rawlence et al. 2012, 2016; Wood et al. 2017a).

Wairau Bar

Wairau Bar is located on the north-eastern coast of the South Island (41°30′25.9″ S, 174°03′43.8″ E; Fig. 1). It is one of the earliest archaeological sites found in Aotearoa and dates to the late 13th and early 14th centuries CE (1288–1320 CE) (Higham et al. 1999; Jacomb et al. 2014). A number of human burials (kōiwi tangata) were found during excavations in the mid-20th century (Duff 1977; Brooks et al. 2011). The faunal specimens morphologically reidentified for comparative isotopic purposes in this study were sampled from the zooarchaeological collection unearthed during the most recent (2008 and 2009) excavations in preparation for the repatriation and reburial of the kōiwi (Brooks et al. 2009; Buckley et al. 2010). The faunal remains were found in a midden that filled a stone-lined earth oven (umu) and likely represent the remains of animals that were eaten during one large communal cooking event (Brooks et al. 2009). This fauna may not all have been locally sourced and could have come from the surrounding areas.

Wairau Bar is located on a rocky spit bordered by the Wairau Estuary and Cook Strait. The site is adjacent to different marine current systems than Harwood. The main marine features near Wairau Bar include Cook Strait, which separates the North and South Islands of Aotearoa. Highly modified subtropical water, from the East Australia Current, is carried into the region by the D'Urville Current that flows through Cook Strait from west to east, and by the Wairarapa Eddy that flows southwards along the eastern North Island into Cook Strait, before combining with the D'Urville Current to form the Hikurangi Eddy (Stevens et al. 2021) (Fig. 1).

Methods

Specimens, collagen extraction, and isotopic analysis from Harwood

Subfossil bones from Harwood were initially identified by JH to species through comparison to the reference collection at the Department of Archaeology, University of Otago. Identical bone elements were photographed (ventral and dorsal) and sampled from each bird species to avoid sampling the same individual twice, unless there were variations in size that clearly indicated different individuals.

Bulk collagen was extracted from the bones following Longin (1971) with modifications by Brown et al. (1988) and Collins and Galley (1998), described in detail in Kinaston et al. (2013). The purified collagen was analysed by EA-IRMS at Iso-Analytical (Cheshire, UK) (Appendix S1 in Supplementary Material). Analytical precision was determined through repeated analysis of laboratory standards IA-R038 (L-alanine), IA-R069 (tuna protein), IA-R046/IAEA-C7 (mixture of ammonium sulphate and oxalic acid), and duplicate samples. Analytical error, calculated from replicate measurements of samples, was ± 0.2 ‰ for δ^{13}C and ± 0.2 ‰ for δ^{15}N (1 SD, $n = 38$ for Harwood and $n = 50$ for Wairau Bar). Collagen quality indicators were used to determine which samples were adequately preserved. If samples displayed C:N ratios outside the range of 2.9 to 3.6, %C < 30%, or %N < 11%, they were removed from further analysis (DeNiro 1985; van Klinken 1999). All fauna were from the pre-industrial era and therefore we did not correct for the Suess effect, a world-wide depletion in ^{13}C (and ^{14}C) as a result of burning fossil fuel (Dombrosky 2020). The following interpretations focused on the comparison of only pre-industrial fauna, but if comparisons are made with stable isotope values of modern fauna in the future, correction for the Suess effect should be made. Stable dietary isotope values of South Island adzebill and kurī from Harwood were sourced from Wood et al. (2017a) as ecological baselines (e.g. high trophic position fauna).

Comparative isotopic data from Wairau Bar

Comparative δ^{13}C and δ^{15}N data from avifauna at Wairau Bar was sourced from Kinaston et al. (2013), where bones had been initially identified to species through comparison to the reference collection at the Department of Archaeology, University of Otago. The δ^{13}C and δ^{15}N values of marine predators (adult New Zealand fur seal and adult New Zealand sea lion), marine fish (pelagic kahawai [*Arripis trutta*] and barracouta [*Thyrsites atun*]), terrestrial omnivores (kiore | Pacific rat [*R. exulans*] and kurī), and a terrestrial frugivore (kererū | New Zealand pigeon [*Hemiphaga novaeseelandiae*]) were included in the analysis to provide ecological baselines at Wairau Bar only (Kinaston et al. 2013). The use of these isotopic values as ecological baselines for Harwood was negated due to (1) potential marine and/or terrestrial variation in isotopic signals along the east coast of the South Island (e.g. Rawlence et al. 2016; Wood et al. 2017a), (2) differences in omnivore diet and foraging patterns of animals between sites, and (3) the absence of some taxa in Otago during the pre-contact period (e.g. kahawai; Smith 2013).

Data analysis

To control for geographical variation in isotopic signals, we examined Harwood in isolation, even though it is broadly contemporaneous to Wairau Bar. Species were initially compared across sites, to assess whether any observed differences in isotopic values may be related to environmental factors (including marine and/or terrestrial carbon and nitrogen influences) and/or temporal or geographic dietary shifts. Isotopic values were plotted in R version 4.4.1 (R Core Team 2025), with summary statistics (mean, standard deviation) calculated for each species/site using Stata.

For bird specimens from Harwood and Wairau Bar with potential outlier δ^{13}C and δ^{15}N values, we morphologically reidentified these bones, and then due to the high number of initial misidentifications, all remaining bones (regardless of outlier status) were reidentified by AJDT (curator of birds and palaeontology) using the extensive comparative reference collections at the Museum of New Zealand Te Papa Tongarewa. Morphological reidentifications were undertaken using the ventral and dorsal photographs of each bone. The original bones were not available as they had been either partially or entirely used for the isotopic analysis. This was primarily because sulphur stable isotope analysis (data not shown) was also conducted for the Harwood and Wairau Bar samples. The sulphur analysis used significantly larger sample sizes than δ^{13}C and δ^{15}N analyses. If avifaunal specimens could not be accurately reidentified to species they were discarded from the analyses.

Isotopic values were plotted in R, along with the recalculation of summary statistics. Where sample sizes allowed, we conducted statistical analyses (F tests and two tailed t-tests assuming [un]equal variances) using Stata to test for inter-species differences between taxa at Harwood, and intra-species differences between taxa in both Harwood and Wairau Bar.

Māori and English vernacular names, scientific names, and taxonomic order of birds follow Miskelly et al. (2024).

Results and discussion

Morphological reidentification of comparative Wairau Bar avifauna

Morphological reassessment of bird bones from Wairau Bar resulted in taxonomic reidentifications of some of those presented in Kinaston et al. (2013). The following new identifications should be noted: WF41 is a pārera | grey duck (*Anas superciliosa*) (previously kererū); WF55 is a pūtangitangi | paradise shelduck (*Tadorna variegata*) (previously grey duck); WF64 is a grey duck (previously pāpango | NZ scaup [*Aythya novaeseelandiae*]); WF70 is a South Island kākā *Nestor meridionalis meridionalis* (previously kawaupaka | little shag [*Microcarbo melanoleucos*]); and WF72 is a *Thalassarche* sp. albatross (previously southern black-backed gull). The following fragmentary specimens were excluded from the analysis as their morphological identifications could not be verified: WF65 and WF66 are now indeterminate small ducks (previously New Zealand scaup); WF39 (previously kererū), WF62 (previously paradise shelduck), WF67 (previously New Zealand scaup), and WF71 (previously kawau pāteketeke | New Zealand king shag [*Leucocarbo carunculatus*]) are all unknown species. The morphological reidentifications listed above do not change the human dietary interpretations noted in Kinaston et al. (2013) because some outliers were removed and avifaunal remains were only used for broad ecological baselines to interpret human diet.

Trophic positions, feeding ecology, and niches of birds at Harwood and Wairau Bar

The full dataset and summary tables for δ^{13}C and δ^{15}N values of morphologically confirmed birds from Harwood and Wairau Bar are presented in Table 1, Figs. 2 and 3, and Appendices S1–S5. The C:N ratios and the %C and %N of bone collagen from all Harwood specimens were within the range of well-preserved collagen (Table 1; Appendix S1) (van Klinken 1999).

Dinornithiformes: Moa

The moa from Harwood displayed δ^{13}C values that ranged between −21.0 ‰ and −25.1 ‰ and δ^{15}N values that ranged between 4.5 ‰ and 9.3 ‰ (Table 1, Fig. 2; Appendices S1–S3). For the little bush moa (n = 1, δ^{13}C −21.0 ‰, δ^{15}N 5.8 ‰), the stable isotope values were comparable with individuals from Wairau Bar (Table 1, Fig. 3; Appendices S1, S4, & S5). In contrast, the South Island giant moa (n = 1, δ^{13}C −25.1 ‰, δ^{15}N 4.5 ‰) displayed lower δ^{13}C and δ^{15}N values than individuals from Wairau Bar (Table 1, Fig. 3; Appendices S1, S4, & S5), which could have been influenced by dietary differences between individuals of different sexes (Wood et al. 2012, 2013, 2020). Two bones were identified as medium-sized moa: one displayed the highest δ^{15}N value (9.3 ‰) of all the moa analysed, while the other displayed a lower δ^{15}N value (4.6 ‰). Both these individuals displayed similar δ^{13}C values (−23.8 ‰ and −23.1 ‰, respectively; Table 1, Fig. 2; Appendices S1–S3). It is probable that these medium-sized moa represent different species, given the ecological niche

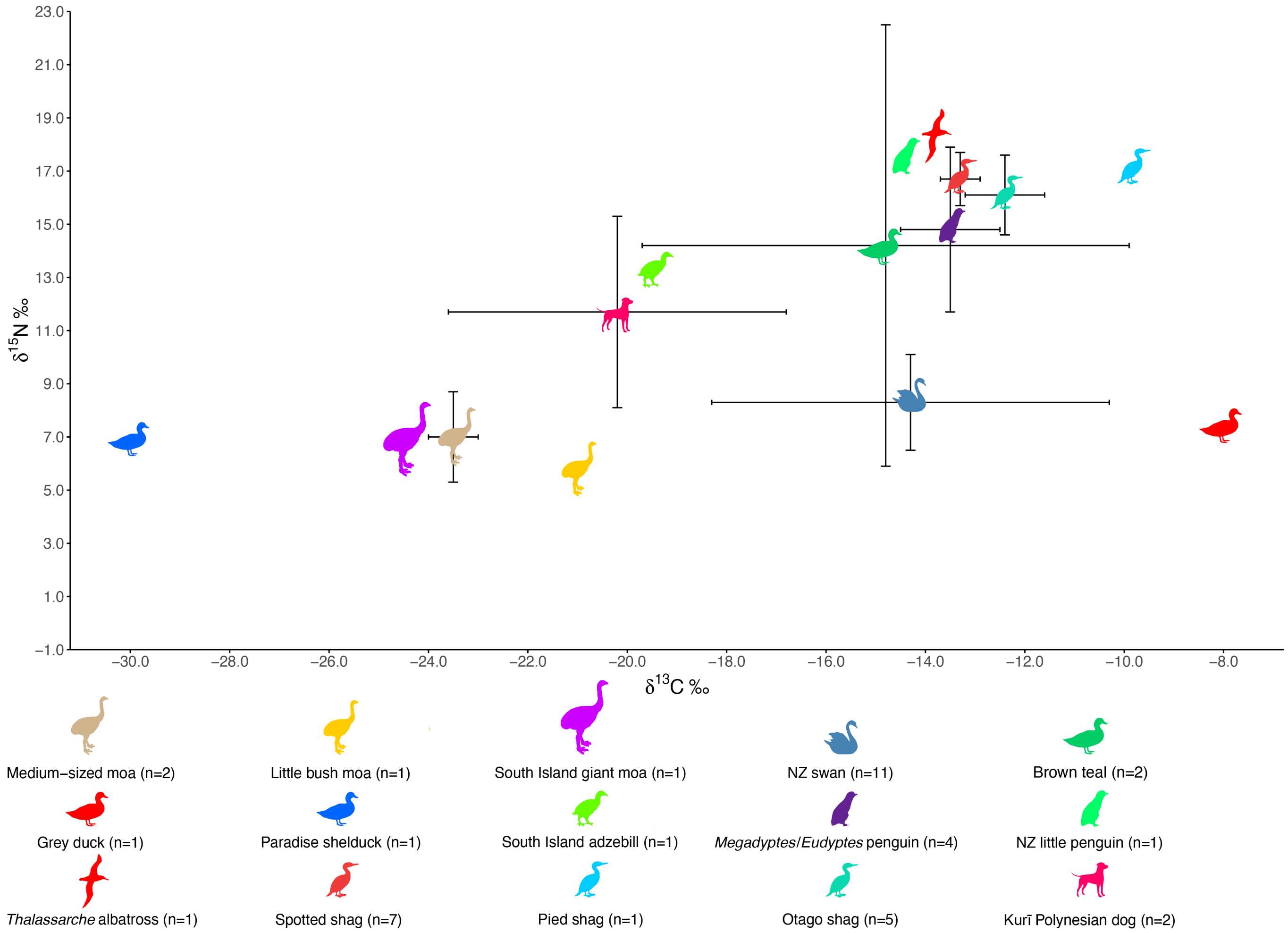

Figure 2. Summary schematic stable isotope bi-plot showing mean (± 1 SD) δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Harwood subfossil deposit. For bi-plots showing summary and raw stable isotope data see Appendices S1–S2.

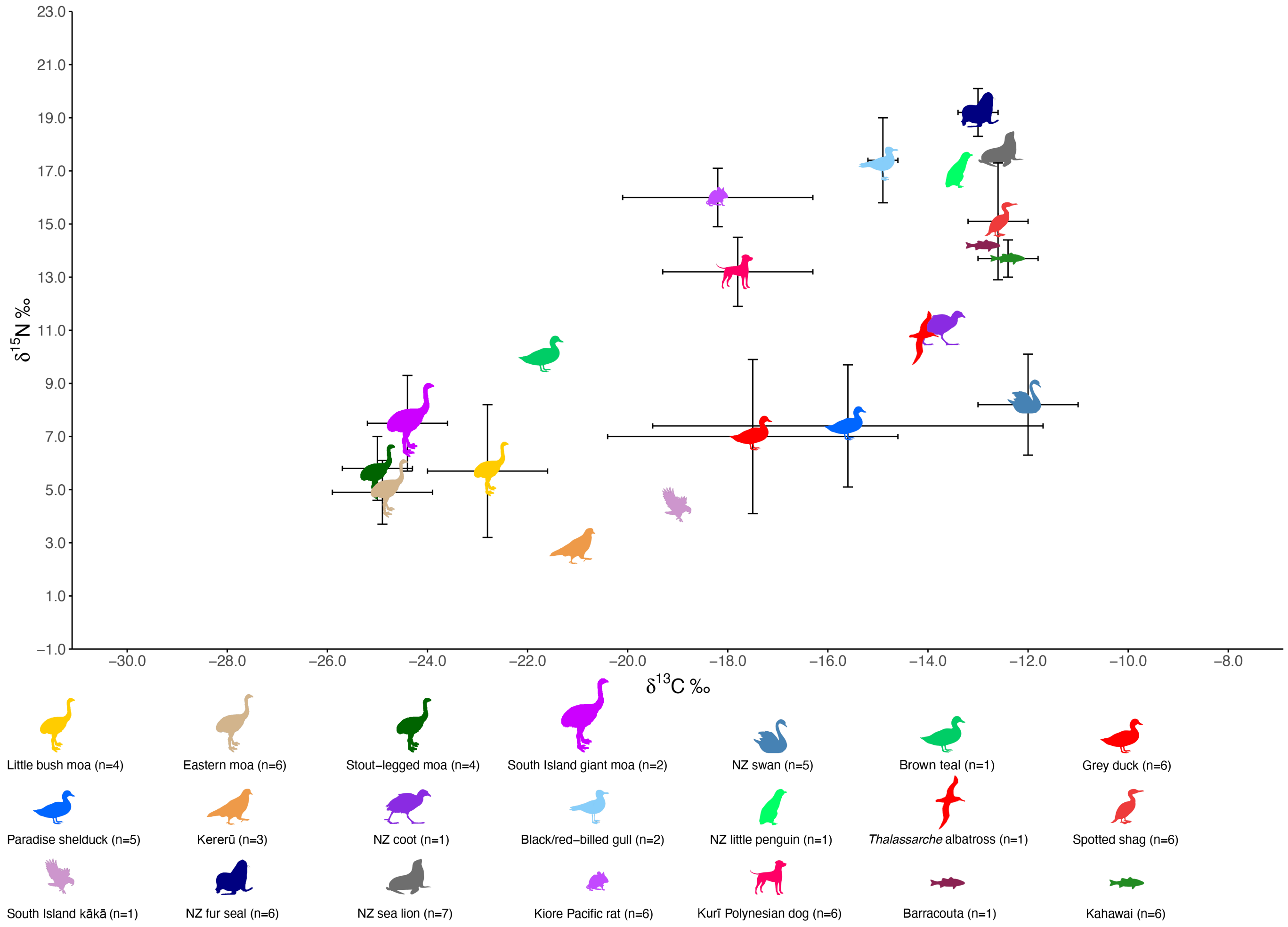

Figure 3. Summary schematic stable isotope bi-plot showing mean (± 1 SD) δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Wairau Bar archaeological deposit. For bi-plots showing summary and raw stable isotope data see Appendices S3–S4.

partitioning seen between moa species (Wood et al. 2020). The stable isotope values of moa from Harwood were comparable to the values of two individuals analysed by Wood et al. (2017a): a large-sized moa (δ^{13}C −24.68 ‰, δ^{15}N 8.63 ‰), which was likely to have been either moa waewae taumaha | heavy-footed moa (*Pachyornis elephantopus*) or South Island giant moa, and a small-sized moa (δ^{13}C −21.56 ‰, δ^{15}N 6.16), which was likely to have been either moa pukepuke | upland moa (*Megalapteryx didinus*) or little bush moa.

Moa species displayed the most terrestrial δ^{13}C values of the fauna analysed from Wairau Bar (Table 1, Fig. 3; Appendices S1, S4, & S5). The Wairau Bar δ^{13}C values were similar for the South Island giant moa (n = 2, −25.0 ‰ to −24.0 ‰), the moa hakahaka | stout-legged moa (*Euryapteryx curtus gravis*) (n = 4, −25.8.0 ‰ to −24.0 ‰), and the moa mōmona | eastern moa (*Emeus crassus*) (n = 6, −26.0 ‰ to −23.8 ‰), but higher for the little bush moa (n = 4, −23.4 ‰ to −21.7 ‰). The δ^{15}N values of the Wairau Bar moa had wide intra- and inter-species ranges, but most mean δ^{15}N values were between 4.9 ‰ and 5.8 ‰, with the exception of the South Island giant moa, which displayed a higher value (7.5 ‰ ± 1.8 ‰ SD). As with the δ^{13}C results, the little bush moa displayed the most variable δ^{15}N values (5.7 ‰ ± 2.5 ‰ SD).

Previous stable isotope analyses of moa from other Aotearoa subfossil sites suggested that δ^{13}C values of −25.0 ‰ to −30.0 ‰ were broadly indicative of moa inhabiting closed canopy forest, compared to values of −20.0 ‰ to −25.0 ‰ which reflected open grassland-shrubland habitat (Worthy & Holdaway 2002; Rawlence et al. 2012). Likewise, given that moa were herbivores, Rawlence et al. (2012) suggested that δ^{15}N values for moa are inversely correlated to rainfall (i.e. aridity). Otiran Glacial to Late Glacial (c. 70–10 k.y.a.) moa koukou | crested moa (*Pachyornis australis*) from the northwest South Island exhibited δ^{15}N values lower than 4.0 ‰ (coinciding with a period of high rainfall). In contrast, Late Glacial to Holocene (c. 14–0.5 k.y.a.) heavy-footed moa from the eastern South Island displayed δ^{15}N values higher than 4.0 ‰ (coinciding with a period of lower rainfall). The introduction of marine nitrogen into terrestrial ecosystems, such as from living or extirpated seabird colonies, can similarly increase δ^{15}N values (Holdaway et al. 2007; Hawke et al. 2017). Dietary plants can also have different δ^{15}N values within and between sites, potentially due to differences in nitrogen preference, onset of spring growth, rooting depth, and variation in symbiont mycorrhizal fungus nitrogen supply and/or signatures (Hawke et al. 2017). Rawlence et al. (2016) compared direct dietary evidence from moa coprolites and gizzards to indirect evidence from bone collagen stable isotope values and found that complexities in isotope systems (especially δ^{13}C) made it difficult to determine feeding ecology and habitat use for

Table 1: Summary statistics of δ^{13}C and δ^{15}N values for species analysed from the Harwood subfossil and Wairau Bar archaeological deposits.

Site	Scientific name	Common name	*n* =	*δ*15N	1 SD	*δ*15N min	*δ*15N max	*δ*13C	1 SD	*δ*13C min	*δ*13C max
Harwood	*Anomalopteryx didiformis*	Little bush moa	1	5.8				−21.0			
Harwood	*Dinornis robustus*	South Island giant moa	1	4.5				−25.1			
Harwood	*Dinornithiformes*	Medium sized moa	2	7.0	1.7	11.7	14.1	−23.5	0.5	−23.8	−23.1
Harwood	*Cygnus sumnerensis sumnerensis*	New Zealand swan	11	8.3	1.8	6.3	13.2	−14.3	4.0	−24.2	−8.8
Harwood	*Anas chlorotis*	Brown teal	2	14.2	8.3	8.3	20.0	−14.8	4.9	−18.3	−11.3
Harwood	*Anas superciliosa*	Grey duck	1	7.3				−8.0			
Harwood	*Tadorna variegata*	Paradise shelduck	1	6.8				−30.0			
Harwood	*Megadyptes/Eudyptes* sp.	*Megadyptes/Eudyptes* penguin	4	14.8	3.1	11.4	17.6	−13.5	1.0	−15.0	−12.8
Harwood	*Eudyptula minor minor*	New Zealand little penguin	1	17.5				−14.4			
Harwood	*Thalassarche* sp.	*Thalassarche* albatross	1	18.4				−13.8			
Harwood	*Phalacrocorax punctatus*	Spotted shag	7	16.7	1.0	15.2	18.4	−13.3	0.4	−13.8	−12.9
Harwood	*Phalacrocorax varius*	Pied shag	1	17.1				−9.8			
Harwood	*Leucocarbo chalconotus*	Otago shag	5	16.1	1.5	14.3	18.2	-−12.4	0.8	−13.0	−11.0
Harwood	*Aptornis defossor*	South Island adzebill	1	13.3				−19.5			
Harwood	*Canis familiaris*	Kurī (Polynesian dog)	2	11.7	3.6	9.2	14.3	−20.2	3.4	−22.6	−17.8
Wairau	*Anomalopteryx didiformis*	Little bush moa	4	5.7	2.5	2.8	8.2	−22.8	1.2	−24.3	−21.7
Wairau	*Dinornis robustus*	South Island giant moa	2	7.5	1.8	6.2	8.7	−24.4	0.8	−25.0	−23.8
Wairau	*Euryapteryx curtus gravis*	Stout-legged moa	4	5.8	1.2	4.5	7.4	−25.0	0.7	−25.8	−24.1
Wairau	*Emeus crassus*	Eastern moa	6	4.9	1.2	3.0	6.3	−24.9	1.0	−26.0	−23.8
Wairau	*Cygnus sumnerensis sumnerensis*	New Zealand swan	5	8.2	1.9	6.4	10.5	−12.0	1.0	−13.6	−10.9
Wairau	*Anas chlorotis*	Brown teal	1	10.0				−21.7			
Wairau	*Anas superciliosa*	Grey duck	6	7.0	2.9	1.9	10.0	−17.5	2.9	−20.5	−14.5
Wairau	*Tadorna variegata*	Paradise shelduck	5	7.4	2.3	4.2	10.5	−15.6	3.9	−21.4	−11.7
Wairau	*Hemiphaga novaeseelandiae*	Kererū (New Zealand pigeon)	3	2.8	0.3	2.5	3.0	−21.0	0.2	−21.2	−20.8
Wairau	*Eudyptula minor minor*	New Zealand little penguin	1	17.0				−13.4			
Wairau	*Thalassarche* sp.	*Thalassarche* albatross	1	10.8				−14.1			
Wairau	*Phalacrocorax punctatus*	Spotted shag	6	15.1	2.2	12.2	16.8	−12.6	0.6	−13.5	−12.0
Wairau	*Fulica prisca*	New Zealand coot	1	11.2				−13.9			
Wairau	*Chroicocephalus* sp.	Black/red-billed gull	2	17.4	1.6	16.2	18.5	−14.9	0.3	−15.1	−14.7
Wairau	*Nestor meridionalis meridionalis*	South Island kaka	1	4.4				−19.0			
Wairau	*Arctocephalus forsteri*	New Zealand fur seal	6	19.2	0.9	18	20.3	−13.0	0.4	−13.4	−12.4
Wairau	*Phocarctos hookeri*	New Zealand sea lion	7	17.6	0.3	17.3	18.2	−12.6	0.2	−12.9	−12.3
Wairau	*Rattus exulans*	Kiore (Pacific rat)	6	16.0	1.1	14.9	17.4	−18.2	1.9	−20.9	−16.1
Wairau	*Canis familiaris*	Kurī (Polynesian dog)	6	13.2	1.3	11.0	14.7	−17.8	1.5	−20.2	−16.2
Wairau	*Arripis trutta*	Kahawai	6	13.7	0.7	13.1	15.0	−12.4	0.6	−13.0	−11.6
Wairau	*Thyrsites atun*	Barracouta	1	14.2				−12.9			

specific moa species when analysing isotopes in isolation. This study observed geographical differences in moa bone collagen δ^{15}N values, supporting previous research; these differences were attributed to variation in plant water use efficiency (especially in more arid areas) and soil nitrogen availability. Variation from expected moa δ^{13}C values may have been due to a diet that incorporated leaves and fruit falling from the forest canopy, which had not been affected by the canopy effect; the discrepancy may also have been influenced by variations in the proportion of seeds versus leaves in the diet, and their differing δ^{13}C values (Rawlence et al. 2016).

The moa stable isotope results from Harwood and Wairau Bar (Table 1, Figs. 2 & 3; Appendices S1–S5) did not follow a consistent pattern based on species, habitat, or geographic location. Instead, the variation is likely to be due to variations in environmental factors outlined by Rawlence et al. (2016). The δ^{15}N values did not clearly distinguish between the moa from Harwood and Wairau Bar, but this may be a result of similar regional weather patterns, as both areas have a mean annual rainfall of 600–700 mm, which would have been at a similar level in the Late Holocene.

The greater variation in moa stable isotope values at Wairau Bar may also be a result of the depositional history of this site. The fauna recovered from the umu (oven) was likely deposited in a single communal eating event; many species would likely have been sourced locally, but some may have been brought in from hunting camps farther afield, which were common at the time (Brookes et al. 2009). Isotopic variation could also be due to cryptic differences in foraging behaviour over the lifetime of moa, especially in osteologically mature individuals where age at death is not known, and δ^{13}C and δ^{15}N represent a lifetime average. Indeed, analysis of direct dietary evidence from moa coprolites has shown seasonal, sexual, and potential ontogenetic intraspecific variation in reconstructed diets (Wood et al. 2012, 2013, 2020).

Anatidae: Swans and ducks

The Anatidae at Harwood (and to a lesser extent at Wairau Bar) had a wide range of δ^{13}C and δ^{15}N values (Table 1, Figs. 2 & 3; Appendices S1–S3) that were distributed over a large proportion of the available isotopic space, reflecting the species' diverse habitat preferences and diets. The New Zealand swan, grey duck, pāteke | New Zealand brown teal (*Anas chlorotis*), and paradise shelduck displayed variable diets, including between Harwood and Wairau Bar (Table 1, Fig. 3; Appendices S1, S4, & S5), indicating different feeding ecologies that may reflect environmental differences between sites at the time of human arrival.

The New Zealand swan has been identified through geometric morphometric and ancient DNA analyses (Rawlence et al. 2017). This endemic species is thought to have been larger, flight-reduced, and potentially more terrestrial than the Australian black swan (*Cygnus atratus*). The New Zealand swan went extinct around the 15th century CE. It was not until the mid-late 19th century that its Australian congener was translocated to Aotearoa (and may also have colonised naturally) (Rawlence et al. 2017). The radiocarbon dates for Harwood and Wairau Bar (see Depositional and geographic setting) and ancient DNA analysis of swans from these sites indicated that the birds analysed here were the New Zealand swan.

The range in δ^{13}C and δ^{15}N values of New Zealand swans at Harwood (n = 11; Table 1, Fig. 2; Appendices S1–S3) indicates that they predominantly used marine and estuarine habitats (n = 10) rather than freshwater habitats (n = 1). They displayed highly variable δ^{13}C values, ranging from −8.8 ‰ to −24.2 ‰, and δ^{15}N values that ranged from 6.3 ‰ to 13.2 ‰, slightly lower than the values for the swans at Wairau Bar (n = 5; Table 1, Fig. 3; Appendices S1, S4, & S5). Those from Wairau Bar displayed lower δ^{15}N values (6.4 ‰–10.5 ‰) indicating a lower trophic level marine diet that corresponds with the known feeding ecology of the living Australian black swan: freshwater or estuarine plants, especially *Zostera* spp. (Marchant & Higgins 1990b). From the marine δ^{13}C values (−11.0 ‰ to −13.6 ‰), it can be suggested that New Zealand swans at Wairau Bar fed mostly on estuarine plants, such as those found in the nearby Wairau estuary. However, any differences in isotopic signatures between Harwood and Wairau Bar were statistically non-significant (δ^{13}C: df = 14, $t = -1.31$, $P = > 0.05$; δ^{15}N: df = 15, $t = 0.019$, $P = > 0.05$). As such, the current isotopic evidence suggests that the ecological feeding niche of the extinct New Zealand swan was varied and overlapped with the foraging habitats of the Australian black swan. As with the moa, cryptic differences in foraging behaviour over the lifetime of swans, especially in osteologically mature individuals, could also have contributed to variation in isotopic values.

New Zealand brown teal are currently restricted to the North Island. Remains of Holocene pre-contact brown teal have been found in a wide range of aquatic (e.g. lacustrine, coastal dunes, swamps), and terrestrial (e.g. inland forests, including wet and seasonally dry podocarp forests and montane silver beech) habitats, indicating that this species had a generalist foraging strategy prior to human arrival (Worthy 2002; Holdaway et al. 2013; Salvador et al. 2021). Contemporary individuals have diverse diets that span all these habitats and can include plants, fungi, insects, crustaceans, molluscs, and polychaete worms (Moore et al. 2006). The brown teal from Harwood (n = 2) displayed variable δ^{13}C and δ^{15}N values (δ^{13}C −11.3 ‰, δ^{15}N 20.0 ‰ for the first individual and δ^{13}C −18.3 ‰, δ^{15}N 8.3 ‰ for the second individual), indicating that both individuals inhabited marine and/or freshwater habitats, but fed at different trophic levels, with the former being primarily predatory and the latter being primarily vegetarian. The δ^{13}C and δ^{15}N values of a brown teal from Wairau Bar (n = 1, −27.1 ‰ and 10.0 ‰ respectively), also provide evidence for a highly variable generalist diet, indicating that this individual was feeding from terrestrial and/or freshwater habitats. Our isotopic results are consistent with those of Holdaway et al. (2013) who used δ^{13}C and δ^{15}N values to show that the riparian and estuarine wetland habitat of remaining North Island brown teal populations is a fraction of the pre-human habitat preferences of this species.

Grey ducks have a widespread distribution in the Holocene fossil record but are now largely restricted to undisturbed remote lakes and the headwaters of rivers; they are also endangered due to hybridisation with the introduced mallard (*Anas platyrhynchos*) (Miskelly et al. 2024). Contemporary grey ducks are known to be low trophic level omnivores (e.g. aquatic plants, invertebrates, crustaceans, and molluscs; Marchant & Higgins 1990b). The grey duck from Harwood (n = 1) displayed δ^{13}C and δ^{15}N values of −8.0 ‰ and 7.3 ‰, respectively, compared to variable values from Wairau Bar (n = 6; δ^{13}C −20.5 ‰ to −14.5 ‰; δ^{15}N 1.9 ‰ to 10.0 ‰). The variation in stable isotope values at Harwood and Wairau Bar suggests that grey ducks historically had a more generalist feeding behaviour than they do now, potentially associated with their wider pre-contact distribution (Salvador et al. 2021). It is also possible that the variation results from differences in foraging behaviour over the lifetime of the individuals analysed.

There was only one paradise shelduck analysed from Harwood, and it displayed the lowest δ^{13}C value (−30.0 ‰) of all the avifauna sampled, so should be treated as an outlier. Combined with the δ^{15}N value (6.8 ‰), this δ^{13}C value would traditionally be indicative of this bird foraging on lower trophic level terrestrial plants and invertebrates in sub-canopy habitat of dense forest where there was a depletion in ^{13}C (i.e. the canopy effect; van der Merwe & Medina 1989, 1991) rather than in more open habitats, which would be reflected in δ^{13}C values > −25.0 ‰ (Rawlence et al. 2012, 2016). Similar low δ^{13}C values for Finsch's ducks from Finsch's Folly Tomo (c. 2000–1000 k.y.a.) have been observed (Wood et al. 2017a) and some researchers have attributed this to a feeding habitat under a dense forest canopy (Worthy & Holdaway 2002). At Wairau Bar, the δ^{13}C values of the paradise shelducks (n = 5) ranged from −21.4 ‰ to −11.7 ‰ and the δ^{15}N values from 4.2 ‰ to 10.5 ‰. This substantial intra-species variation indicates wide-ranging habitat use that reflects that observed for contemporary paradise shelducks, including wetlands, riverbeds, and open terrestrial habitats (Marchant & Higgins 1990b). Given the isotopic space of paradise shelducks at Wairau Bar, the potential inferred behaviour of the individual from Harwood is unusual. With only a single specimen, further research is needed to clarify this result.

Sphenisciformes: Penguins

At the time of human arrival, the tawaki | Fiordland crested penguin (*Eudyptes pachyrhynchus*) was widespread across the South Island and the lower half of the North Island, while pokotiwha | Snares crested penguin (*Eudyptes robustus*), tawaki nana hī | erect-crested penguin (*Eudyptes sclateri*), and Warham's crested penguin (*Eudyptes warhami*) were vagrants to the eastern South Island (Rawlence et al. 2015a; Cole et al. 2018, 2019). The extinct Waitaha penguin, including some genetically confirmed individuals, was resident at Harwood (Rawlence et al. 2015a). Rare vagrant hoiho | yellow-eyed penguins (*Megadyptes antipodes antipodes*) have been found in early Māori archaeological sites in Otago, but they did not colonise the mainland of Aotearoa until after the extinction of Waitaha penguin (Boessenkool et al. 2009; Rawlence et al. 2015a; Waters et al. 2017). The large penguins from Harwood (*n* = 4; δ^{13}C −15.0 ‰ to −12.8 ‰, δ^{15}N 11.4 ‰ to 17.6 ‰) were all *Eudyptes* or *Megadyptes* spp., which are difficult to distinguish osteologically (Rawlence et al. 2019b; Thomas et al. 2020). *Eudyptes* spp. are offshore pelagic foragers, while *Megadyptes* spp. are inshore and offshore pelagic and demersal foragers (Marchant & Higgins 1990a). Our results, and previous carbon isotopic values from Harwood (e.g. Waitaha penguin −14.1 ‰; Table 1, Fig. 2; Appendices S1–S3; Rawlence et al. 2015a), are consistent with this range of foraging niches.

Little penguins at Harwood (*n* = 1; δ^{13}C −14.4 ‰, δ^{15}N 17.5 ‰) and Wairau Bar (*n* = 1; δ^{13}C −13.4 ‰, δ^{15}N 17.0 ‰) foraged in nearshore pelagic zones. Little penguins in Otago are now predominantly the Australian subspecies *Eudyptula minor novaehollandiae*, while those in pre-contact sites, including genetically confirmed individuals at Harwood, are *E. m. minor* (Grosser et al. 2016, 2017).

The isotopic values of penguins from Harwood are comparable to those of contemporaneous marine predators such as New Zealand sea lions from early Māori (1250–1450 CE) coastal archaeological sites in Otago (*n* = 9; δ^{13}C: −12.2 ‰ to −15.7 ‰, mean −13.4 ‰, SD 1.0; δ^{15}N: 13.6 ‰ to 19.3 ‰, mean 16.6 ‰, SD 2.0) (Wing et al. 2025a, b).

Diomedeidae: Thalassarche *albatrosses*

Thalassarche spp. albatrosses (toroa) feed in waters on the continental shelf (e.g. white-capped albatross [*Thalassarche cauta*] and Buller's albatross [*Thalassarche bulleri*]) or the shelf edge/upper slope (e.g. black-browed albatross [*Thalassarche melanophris*]). These albatrosses are scavengers who consume fish and dead deep-sea squid/octopuses from surface waters (up to a few metres depth) of the open ocean (Marchant & Higgins 1990a). One bone from Harwood was identified as a *Thalassarche* sp. albatross with δ^{13}C −13.8 ‰ and δ^{15}N 18.5 ‰ (Table 1, Fig. 2; Appendices S1–S3), indicating a marine diet at a higher trophic level than those of marine divers like penguins and shags (see below), and New Zealand sea lions (Wing et al. 2025a, b). This is at least two trophic levels higher than the single *Thalassarche* sp. albatross from Wairau Bar, which had δ^{13}C −14.1 ‰ and δ^{15}N 10.8 ‰ (Table 1, Fig. 3; Appendices S1, S4, & S5). The discrepancy could reflect our small sample size coinciding with large differences between individuals or an individual bias towards scavenging larger prey compared to predating smaller prey. The δ^{13}C and δ^{15}N values match contemporary dietary assessments and identify these birds as open-ocean surface feeders and shallow-divers.

Phalacrocoracidae: Shags

The majority of isotopic values for shags at Harwood (spotted shag [*n* = 7], Otago shag [*n* = 5], and pied shag [*n* = 1]) were consistent with these species having been marine divers, as shown by their δ^{13}C values (−13.8 ‰ to −9.8 ‰) and relatively high δ^{15}N values (14.3 ‰ to 18.4 ‰), which indicate that they fed on marine prey with high δ^{15}N values (Table 1, Fig. 2; Appendices S1–S3; see also Wing et al. 2025a, b). The δ^{13}C values of Otago shags from Harwood were consistent with those previously analysed from the same site (−11.2 ‰ to −12.5 ‰; Rawlence et al. 2015a). At both Harwood and Wairau Bar, there was overlap in the δ^{13}C isotopic space of shags and New Zealand swans, potentially reflecting utilisation of the same estuarine and marine environments at these sites, as occurs with shags and Australian swans today.

Contemporary spotted shag populations in Aotearoa are nearshore pelagic foragers across the continental shelf. Their known diet consists of planktonic crustaceans, small fish, gastropod molluscs, and algae (Marchant & Higgins 1990b). Statistical analysis of spotted shags from Harwood (*n* = 7) and Wairau Bar (*n* = 6) showed significant differences in δ^{13}C values (df = 11, *t* = −2.89, *P* = 0.01) but not δ^{15}N values (df = 7, *t* = 1.56, *P* = > 0.05). The lower δ^{13}C values for individuals from Harwood indicate that spotted shags foraged further offshore (despite Harwood being situated in a shallow marine harbour) than those at Wairau Bar, while the similar δ^{15}N values indicate that the average trophic level of marine prey was similar at both sites. The differences in δ^{13}C values indicate inter-regional differences between foraging locations at the time of human arrival in Aotearoa. However, due to the small sample sizes analysed these statistical results should be interpreted with caution.

Pied shag bones are increasingly being identified in the archaeological record in Otago through palaeogenetic reidentification of bones that had been morphologically misidentified as Otago shag (NJR pers. obs.). Numbers of extant individuals are increasing in the region today (Robertson et al. 2007) after the species likely suffered large population declines and local extinctions due to human impact. While no detailed study of pied shag diet has been conducted, they feed mainly on fish, and occasionally crustaceans (Marchant & Higgins 1990b; Rayner et al. 2021).

Contemporary Otago shag populations are nearshore benthic foragers (up to 15 km from the coast on the continental shelf at depths of 1–30 m), feeding on fish and marine invertebrates (such as crabs, octopuses, and polychaete worms; Marchant & Higgins 1990b). Otago shags and the generally pelagic spotted shags are ecologically partitioned in the region today. However, the observable isotopic differences in niche space between these shags in Harwood (Otago, *n* = 5; spotted, *n* = 7; Fig. 2; Appendices S2–S3) are not statistically significant (δ^{13}C: df = 5, *t* = 2.24, *P* = > 0.05; δ^{15}N: df = 10, *t* = −0.83, *P* = > 0.05), suggesting that these marine predators may have had overlapping foraging zones in the past, targeting prey at similar trophic levels. However, due to the small sample sizes analysed these statistical results should be interpreted with caution.

Further discussion on trophic positions, feeding ecology and niches of birds at Wairau Bar

Rallidae: New Zealand coot

The extinct New Zealand coot (*Fulica prisca*) was twice the weight of extant coots (e.g. Australian coot *Fulica atra australis*), and remains have been found in forested, subalpine, and coastal regions, indicating a generalist habitat for this species (Worthy & Holdaway 2002; Tennyson & Martinson

2007). The New Zealand coot from Wairau Bar ($n = 1$) displayed a marine δ^{13}C value (−13.9 ‰) and a δ^{15}N value (11.2 ‰) that was higher than those for most of the Anatidae analysed at the site (Table 1, Fig. 3; Appendices S1, S4, & S5). If the New Zealand swans from Wairau Bar are used as a baseline for marine/estuarine herbivores, the δ^{13}C and δ^{15}N values of the coot from this site indicate that it fed on estuarine and marine invertebrates. The closely related Australian coot, which is also present in New Zealand, is mainly a herbivore but will also feed on invertebrates, including aquatic insects, molluscs, and crustaceans (Marchant & Higgins 1993).

Larinae: gulls

Black-billed gulls and red-billed gulls were present in the archaeological record at Wairau Bar. Black and red billed gulls cannot easily be differentiated based on bone morphology alone (Worthy & Holdaway 2002). These gulls (n = 2) displayed marine δ^{13}C (−14.7 ‰ to −15.1 ‰), and δ^{15}N (16.2 ‰ to 18.6 ‰) values that may be indicative of the capture of live prey (Table 1, Fig. 3; Appendices S1, S4, & S5). Red-billed gulls are a coastal species and mainly consume krill, but in anthropogenically modified environments can also consume terrestrial food (McClatchie et al. 1989; Higgins & Davies 1996; O'Driscoll et al. 1998). In contrast, black-billed gulls nest on inland braided rivers, and predominantly feed on freshwater and terrestrial invertebrates and freshwater fish. In the non-breeding season they also feed in marine environments on fish and invertebrates (Higgins & Davies 1996).

The δ^{13}C and δ^{15}N isotopic signatures of black-billed/red-billed gulls from Wairau Bar show that these individuals were feeding on much higher trophic level foods that resemble those of marine divers, especially penguins, contrary to the at-sea diet seen today of lower trophic level plankton. This may reflect our small sample size, an individual bias towards scavenging larger prey compared to predating smaller prey, or a change in feeding ecology and ecological niche over time. This last explanation is particularly likely for black-billed/red-billed gulls that feed at sea, as the marine environment has been increasingly modified (Wood et al. 2017b, c).

Conclusions

Our stable dietary isotopic analyses are a start to reconstructing the diet of avifauna in Aotearoa at the time of human settlement (e.g. Rawlence et al. 2012; Wood et al. 2017a), how it varied across geography and habitats, and how it may have changed with time. There are limitations, however, that need to be addressed with future research. Due to taphonomic processes and the nature of the subfossil and archaeological record, our sample sizes for some species are small, and any conclusions drawn should be treated as preliminary and with caution.

Accurate morphological and/or genetic identification of bones using ancient DNA or collagen fingerprinting (e.g. ZooMS; Richter et al. 2022) are key to reconstructing the palaeoecology of living and extinct species into the future (e.g. Rawlence et al. 2012; Holdaway & Rowe 2020). Special care needs to be taken with fragmentary bones and with taxa that are difficult to tell apart morphologically (e.g. moa, ducks, *Eudyptes* and *Megadyptes* penguins, albatrosses). It is important to use extensive, taxonomically confirmed, comparative reference collections (like those at large museums with curatorial expertise in avian skeletal anatomy) and to embrace conservative morphological identifications, especially for fragmentary bones. Several of the bones initially identified from Harwood and those previously published from Wairau Bar (Kinaston et al. 2013) were morphologically reidentified upon comparison to the extensive Museum of New Zealand Te Papa Tongarewa reference collections (e.g. little shag changed to South Island kākā at Wairau Bar). A significant number of bones from both Harwood and Wairau Bar were too fragmentary for re-identification from their photos.

Pre-human ecological baselines, using bulk and compound-specific isotopic analyses of subfossil specimens, if available (e.g. Wood et al. 2017a; Galbraith et al. 2025), from the local area are needed to determine whether archaeological specimens represent locally or distantly foraged food (e.g. moa from Wairau Bar). Likewise, local isotopic baselines are needed for living bird species around Aotearoa, so that direct temporal comparisons at varying timescales can be conducted (e.g. Rayner et al. 2021; Galbraith et al. 2025). It should be noted that comparisons between modern and pre-industrial faunas need to account for the Suess effect (Dombrosky 2020).

With these caveats in mind, our stable isotope analysis of many of the pre-contact period bird species from Aotearoa matched what would be expected for their modern descendants, indicating similar feeding ecologies and niches over time. Some notable exceptions to this trend were identified, including the grey duck, whose former widespread range (and inferred generalist diet) has largely contracted to relictual habitats around remote lakes and headwaters of rivers. Our analyses also suggest that the extinct New Zealand swan had a similar feeding ecology to its Australian congener, with the latter filling a similar feeding niche to the endemic species, despite pronounced morphometric differences between the two species.

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Additional information and declarations

Author contributions: RLK conceived the study, analysed the data and co-wrote the manuscript; NJR analysed the data and co-wrote the manuscript; CL collected bones from Harwood; JH recorded, collected, and identified the bones from Harwood and co-wrote the manuscript; NJR and AJDT conducted morphological reidentifications; ALA analysed the data; RW led the 2008–2009 Wairau Bar excavations; and MR conducted the isotopic analyses. All authors edited and approved the manuscript.

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Supplementary material

Additional supporting information may be found in the online version of this article.

Appendix S1. δ^{13}C and δ^{15}N values for species represented in the Harwood subfossil and Wairau Bar archaeological deposits.

Appendix S2. Stable isotope bi-plot showing mean (± 1 SD) δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Harwood subfossil deposit.

Appendix S3. Stable isotope bi-plot showing δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Harwood subfossil deposit.

Appendix S4. Stable isotope bi-plot showing mean (± 1 SD) δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Wairau Bar archaeological deposit.

Appendix S5. Stable isotope bi-plot showing δ^{13}C and δ^{15}N values of bone collagen from fauna analysed from the Wairau Bar archaeological deposit.