



A partial skeleton provides evidence for the former occurrence of moa populations on Rakiura Stewart Island

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Abstract: The pre-human moa fauna of Rakiura Stewart Island is poorly known, and although there is little clear evidence that moa occurred naturally on the island, isolated moa bones are often found associated with archaeological middens. Here we report the discovery and collection of what is likely a naturally deposited partial South Island giant moa (*Dinornis robustus*) skeleton from West Ruggedy Beach, Rakiura, radiocarbon dated to 1297–1395 CE (95.4% CI). The time of death of this moa overlaps with the early occupation of the island by Māori. However, the discovery of this moa skeleton in a dune environment with the presence of an organic rich layer beneath the skeleton, associated gizzard stones, and an absence of archaeological material/features or any cut marks on the bones indicating a cultural association, suggests this individual likely represents a natural subfossil deposit. We discuss the skeleton in the context of other moa remains found on the island and comment on the occurrence of moa populations on Rakiura, ultimately concluding that this skeleton provides additional evidence for the natural occurrence of moa on Rakiura.

Keywords: ancient DNA, archaeology, Dinornithiformes, New Zealand, radiocarbon dating

Introduction

Rakiura/Stewart Island (hereafter: Rakiura) is one of the largest islands in the New Zealand archipelago, currently separated from the southern South Island by Foveaux Strait. During Pleistocene glacial periods, Rakiura would have been connected to the South Island as sea levels were 120 m lower than present (McGlone & Wilson 1996). As a result, the pre-human Rakiura avifauna was likely similar to that of the southern South Island (Worthy 1998a; Wood 2016). However, knowledge of Rakiura's prehuman avifauna may be biased towards certain taxa due to the limited types of local bone deposits (e.g. sand dunes) compared to extensive cave systems and non-acidic swamps which often preserve Late Quaternary subfossils (e.g. Worthy 1993; Holdaway & Worthy 1997). Of particular note is the lack of moa remains in the majority of subfossil sites on the island (Wood 2016). Prior to human arrival (c. 1280 AD; Wilmschurst et al. 2008), moa were found throughout the North and South Islands, with six species represented in the Late Quaternary avifauna of the southern South Island: South Island giant moa (*Dinornis robustus*), upland moa (*Megalapteryx didinus*), heavy-footed moa (*Pachyornis elephantopus*), stout-legged moa (*Euryapteryx curtus*), eastern moa (*Emeus crassus*) and little bush moa (*Anomalopteryx didiformis*) (Worthy 1998b; Bunce et al. 2009). Anthropogenic pressures such as hunting and habitat destruction drove the moa to extinction within 200 years of human settlement (Holdaway et al. 2014; Perry

et al. 2014), and many moa bones can be found in early Māori (c. 1280–1450 CE) middens, where almost all of the moa material known from Rakiura is recorded (Worthy 1998a; Jacomb et al. 2010).

Isolated moa bones morphologically identified as eastern moa, stout-legged moa, and South Island giant moa, are common within the Rakiura midden sites at The Neck (also known as Old Neck; Fig. 1). It has been proposed that these remains may have been transported from the South Island, as major leg bones (femora, tibiotarsi and tarsometatarsi) make up the vast majority of moa remains found within this site (Worthy 1998a). Archaeological excavations and surveys of moa hunting sites have found that such assemblages (e.g. Shag River Mouth, Pleasant River Mouth and Waitaki River Mouth) are dominated by moa leg bones (Anderson 1989; Nagaoka 2001); leg bones contain most of the meat and were therefore more often brought back to settlements after a kill (Anderson 1989). As a result, transportation of moa legs from kill sites around Rakiura to sites such as those found at The Neck, cannot be ruled out. Worthy (1998a) argued that the *Emeus* and *Euryapteryx* individuals (*cf. Dinornis*, see below) did not represent a local population due to an absence of suitable habitat on Rakiura (e.g. shrubland vs wet, dense forests) and that these bones originated from the mainland (Worthy 1998a). It should be noted, however, that moa leg bones, especially of *Emeus* and *Euryapteryx* (e.g. Worthy 1998b), are sometimes morphologically misidentified (e.g. Baker et al. 2005; Rawlence



Figure 1. Map of Rakiura and Foveaux Strait illustrating localities where moa remains have been found.

et al. 2012; Allentoft et al. 2014), and we expect this may be the case here. In addition, little research has been undertaken on the palaeoenvironment of Rakiura to determine whether various species of moa may have naturally occurred there (McGlone & Wilson 1996; Turney et al. 2017), including much needed extensive and systematic excavations of natural dune, rockshelter and cave deposits across Rakiura since those previously conducted over 15 years ago (e.g. Worthy 1998a, 1998b; Wood 2016).

Benham (1910) described two partial moa skeletons at Mason Bay (Fig. 1), found in association with both gizzard stones and stone tools. Bones from one of these skeletons were collected (Otago Museum Av4661), later identified as heavy-footed moa, and radiocarbon dated to 654 ± 56 yrs BP (1285–1421 CE [95.4% CI]; Table 1; Worthy 1998a). Further examination of the bones revealed cut marks consistent with butchery (Wood 2016). Worthy (1998a) stated that the post-human radiocarbon date and associated stone tools suggested these individuals were transported to the location and may not be reflective of a local population. Ancient DNA analysis of the heavy-footed moa remains place it within the southern clade of heavy-footed moa, consistent with a southern New Zealand origin (Rawlence et al. 2012). This does not rule out a local Rakiura origin for these individuals, based on the associated nature of the skeletons, presence of gizzard stones, and the habitat preferences of heavy-footed moa (i.e. open shrubland, and grasslands, including sand dunes in the southern South

Island; Worthy 1998a; Wood et al. 2020). Extensive surveys of Mason Bay (e.g. Worthy 1998c; Wood 2016) have yielded a single additional moa bone (National Museum of New Zealand S.46705), the distal end of a South Island giant moa tibiotarsus, recovered from an eroding sand dune with no evidence of associated archaeological material (Alan Tennyson, Te Papa Tongarewa, pers. comm.), suggesting a possible natural origin. A moa eggshell fragment has also been recorded from the area (Wood 2016), but may be of anthropogenic origin (Gillies unpubl. data; Wood 2016).

The only moa specimen from Rakiura with a suggested natural origin is a partial South Island giant moa skeleton from Native Island (Fig. 1), radiocarbon dated to 1093 ± 69 yrs BP (869–1159 CE [95.4% CI]; Table 1; Worthy 1998a). However, it should be noted that this specimen was dated prior to the now standard use of collagen ultrafiltration to remove high and low molecular weight contaminants (Higham et al. 2006). Seven articulated vertebrae, a partial tibiotarsus, and several other bones were discovered eroding out of dunes and were not associated with any middens (Worthy 1998a), despite the presence of middens on Native Island (Jacomb et al. 2010). The published age of the bones suggests that the moa died prior to the arrival of humans and was not transported to Rakiura from the southern South Island, potentially supporting the notion that moa naturally occurred on the island. Wood (2016) argued that the rarity of pre-human subfossil moa bones in sand-dunes on Rakiura was unusual, as they are common in natural sand

Table 1. Radiocarbon dates and stable dietary isotope values obtained from moa bones found on Rakiura, calibrated using the SHCal20 calibration curve. CM: Canterbury Museum, OM: Otago Museum. Samples CM Av17803 and OM Av4661 were obtained from Worthy 1998a.

Sample	Site	Species	^{14}C age	Calibrated age (SHCal20) 95.4% confidence interval	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$	%C	%N	C:N	% Collagen
West Ruggedy moa	West Ruggedy Beach	<i>Dinornis robustus</i>	672 ± 20	1297–1395 CE	−21.52	3.46	45.03	15.67	3.36	13.5
CM Av17803	Native Island	<i>Dinornis robustus</i>	1093 ± 69	869–1159 CE	−22.3	-	-	-	-	19.2
OM Av4661	Mason Bay	<i>Pachyornis elephantopus</i>	654 ± 56	1285–1421 CE	−22.3	-	-	-	-	5.7

dune deposits on mainland New Zealand (e.g. Worthy 1998a). Based on this, Wood (2016) hypothesised that moa naturally occurred on Rakiura at low population densities.

Here we report the discovery and retrieval of a partial moa skeleton from West Ruggedy Beach, Rakiura (Fig. 1). We use radiocarbon dating and ancient DNA analyses to determine the age and taxonomic identity of the specimen and, based on an analysis of the bones recovered and their context, conclude that the specimen is likely of natural origin.

Depositional Setting and Specimen Details

In March 2020 AJFV and MS travelled to West Ruggedy Beach to excavate a moa skeleton with the aid of Phred Dobbins (Department of Conservation). The skeleton was found c. 500 m inland from the coast at the northern end of West Ruggedy

Beach (Fig. 1), resting within an eroded depression in a large granite boulder (Fig. 2a). The moa remains had been protected through lying in this granite ‘bowl’ and covered in pure quartz sand. Recent storm events had stripped the old dune system down to its underlying granite base exposing the moa remains. There was no evidence of the skeleton being associated with any cultural event or activity (e.g. charcoal or stone tools).

We excavated the skeleton and collected at least eight different elements, including partial left and right tibiotarsus (left shaft fragments and right shaft), right femoral shaft, heavily fragmented pelvis (including sacrum, ilium and ischium, left and right acetabulum i.e. femoral sockets), a single thoracic vertebra, partial rib bones, and several unidentifiable bone fragments (Fig. 2b). A single, isolated left femur (the same size and dimensions as the right femoral shaft) was found on the



Figure 2. Photos of the West Ruggedy Beach (Rakiura) site and subfossil South Island giant moa (*Dinornis robustus*) remains. **a:** The natural site after the skeleton had been excavated. Note the dark brown organic-rich layer in contrast to the surrounding pure quartz sand, and sieved gizzard stones. **b:** The moa skeleton in situ after the top layer of quartz sand had been removed. **c:** Isolated left moa femur found on the dune surface upslope from the skeleton. **d:** Associated gizzard stones and dark organic-rich layer. Abbreviations are as follows: org rich: organic rich layer; pel fem soc: pelvic femoral socket i.e. acetabulum; pel frags: pelvis fragments; pR tt: partial right tibiotarsus; pL fem: partial left femur; Il: ilium and ischium; sac: sacrum (of pelvis); t vert: thoracic vertebra; p rib: partial rib; L tt frags: left tibiotarsus fragments.

dune surface (Fig. 2c), approximately 20 m from the skeleton, likely belonging to the same individual. It is probable that the crania, vertebrae, tarsometarsi, and phalanges were blown or eroded away. Associated gizzard stones were discovered underneath the pelvis in a small tight group, and a dark brown organic-rich layer of sand was found immediately surrounding and underneath the remains. While there is exposed granite in the area, the majority is covered in pure quartz sand, making it improbable that the gizzard stones could represent eroded pebbles that concentrated underneath the pelvis. At West Ruggedy Beach there are patchily distributed organic-rich layers that no doubt represent decomposed plant material as a result of dune movement. However, the depositional setting of this moa skeleton (within a granite bowl surrounded by pure quartz sand) suggests this concentrated organic-rich layer originated from the decomposing moa and gizzard contents (Fig. 2d).

Analysis of the bones did not reveal any butchering marks which may have indicated the moa was killed and processed by humans. Furthermore, the presence of a partial skeleton, associated gizzard stones and organic-rich layer lends support to the hypothesis that the death of this moa was due to natural causes but does not completely rule out the hypothesis this individual was killed by humans and/or transported to the site.

Methods

Ancient DNA

A 1 cm³ cortical bone sample was taken from the partial right tibiotarsus using a Dremel cutting tool. A sub-sample of 0.5 cm³ was sent to the Waikato Radiocarbon Dating Laboratory (University of Waikato) for Accelerator Mass Spectrometry (AMS) radiocarbon dating (see below), while the remainder was transferred to the Otago Palaeogenetics Laboratory (University of Otago) for ancient DNA analysis. The Otago Palaeogenetics Laboratory is dedicated to the manipulation of ancient DNA, physically isolated from other molecular laboratories, and undergoes regular decontamination with bleach (sodium hypochlorite) and UV irradiation. DNA extraction and PCR-setup were undertaken at this facility, while PCR thermocycling and downstream processes were conducted within a separate modern genetics laboratory.

Ancient DNA was extracted following the methodology of Dabney et al. (2013). A negative extraction control was also included, and subjected to the PCR protocols detailed below, which also included a negative PCR control. A 373 bp portion of the hypervariable region one of the mitochondrial control region were amplified in two overlapping fragments using the primer pairs moaCR_185F/moaCR_294R and moaCR_262F/moaCR_441R (Bunce et al. 2003). Each PCR contained 2 µL of DNA, 0.25 µM of each primer, 0.63 mM dNTPs, 4.0 mM MgCl₂, 1 M Betaine, 1 X PCR Buffer II (100 mM Tris-HCl, pH 8.3, 500 mM KCl), and 2 U AmpliTaq Gold (Life Technologies), made up to a total volume of 20 µL with UltraPure double-distilled water (ThermoFisher Scientific). PCR thermocycling conditions consisted of initial denaturation at 94 °C for 5 min, 60 cycles of 94 °C 30 s, 55 °C 45 s, 72 °C 60 s, and a final extension step of 72 °C for 10 min. Successful PCRs were identified via gel electrophoresis on a 2% agarose gel stained with SYBR safe (Thermo Fisher Scientific), visualised under blue light. PCR products were purified using homemade MagNA beads (Rohland & Reich 2012), then sequenced bidirectionally at the University of

Otago using Big Dye terminator technology on an ABI 3730xl capillary sequencer. PCRs were replicated three times, and a majority-rule consensus applied to the independent replicates (Brotherton et al. 2007; Winters et al. 2011) to ensure that the consensus sequence was correct and did not contain errors associated with post-mortem DNA damage (i.e. C→T or G→A transitions). No PCR amplification was observed in the negative DNA extraction or PCR controls.

DNA sequences were checked by eye and trimmed in Geneious Prime (2020.0.4; <https://www.geneious.com>), removing low-quality bases and primer sequences. A BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) search was run (with default parameters) on the resulting consensus sequence to compare it to previously published moa control region sequences.

Radiocarbon Dating

Preparation of the sample for AMS dating followed standard protocols for bone at the Waikato Radiocarbon Dating Laboratory. Initially, the sample was visually inspected, cleaned, and ground to powder. Gelatine was extracted following a modified Longin (1971) protocol, whereby the bone was decalcified in 2% HCl, rinsed with MilliQ water, dried, and gelatinised at 90 °C in weakly acidic water (pH = 3) for 4 hours. The supernatant was removed, ultrafiltered using Centriprep®, Ultracel YM-30 filters, and frozen at -75 °C before freeze-drying. The sample was combusted via oxidation at 800 °C overnight in the presence of pre-baked copper oxide and silver wires, before graphitisation at 550 °C with an iron catalyst. Finally, the resulting graphite was sent to the Keck AMS Radiocarbon Dating Laboratory (UCI Irvine) for AMS dating. The resulting AMS date was calibrated using the SHCal20 calibration curve (Hogg et al. 2020) in OxCal (version 4.4; Bronk Ramsey 2009). We also recalibrated previous radiocarbon dates from moa bones found on Rakiura (Worthy 1998a) in the same manner described above to ensure comparability and accuracy.

Results

Ancient DNA demonstrates that the moa skeleton found at West Ruggedy Beach is that of a South Island giant moa (*Dinornis robustus*). The closest genetic match to the consensus sequence (GenBank accession number: OK077991) obtained from this specimen is that of a South Island giant moa from Glendhu Bay, Wanaka (Canterbury Museum Av20591; Baker et al., 2005) with 99.7% sequence similarity (1 bp difference along the 378 bp of comparable sequence). The absence of a femoral neck on the isolated left femur (not sequenced; Fig. 2c) is consistent with this identification.

The West Ruggedy Beach moa skeleton was dated to 672 ± 20 yrs BP (661–550 cal. yrs BP), corresponding to 1297–1395 CE (95.4% CI), within the time period of the early human occupation of Rakiura.

Discussion

The discovery of a partial South Island giant moa skeleton on Rakiura dating to shortly after human colonisation of the area (Jacomb et al. 2010; Rawlence et al. 2015) represents an important contribution to our knowledge of the avifauna of the islands soon after human arrival.

The available evidence suggests that this individual likely originates from a natural deposit (though an anthropogenic origin cannot be ruled out entirely) and provides additional evidence supporting the probable natural presence of South Island giant moa upon the island. The presence of a dark organic-rich layer immediately surrounding and underneath the remains, alongside associated gizzard stones found underneath the pelvis (Fig. 2d), indicate that the moa likely died near to where it was discovered and was not transported to the site. The depositional setting and nature of the skeleton is similar to the natural pre-human South Island giant moa discovered at Native Island and unlike the isolated legs bones of *Dinornis*, *Emeus* and *Euryapteryx* individuals from The Neck midden (Worthy 1998a). The complete left and partial right femora, and partial right tibiotarsus (missing proximal and distal ends) of the West Ruggedy Beach moa do not exhibit cut marks indicative of butchering like the Mason Bay heavy-footed moa specimen. Furthermore, there were no archaeological features associated with the newly discovered skeleton, unlike those from Mason Bay (i.e. stone tools; Benham 1910) or The Neck (e.g. middens, charred rock, charcoal; Worthy 1998a).

In contrast to the eastern South Island, moa remains are generally rare in archaeological midden deposits in the southern South Island and Foveaux Strait and may not have formed a significant proportion of the diet of early Māori inhabiting the region (Jacomb et al. 2010). As such (and given the evidence discussed above) it is unlikely that the West Ruggedy Beach and partial Mason Bay moa (both with associated gizzard stones) were transported from the southern South Island to Rakiura. This contrasts with the likely transported little bush moa bones found adjacent to a midden on Ruapuke Island in Foveaux Strait (Kyle Davis, Ngāi Tahu, pers. comm.; see also Jacomb et al. 2010 regarding moa eggshell), and the one to two small pieces of transported industrial moa bone from a midden on Whenua Hou off Rakiura's west coast (Richard Walter, University of Otago, pers. comm.). Worthy (1998a) suggested that the bones of eastern moa and stout-legged moa (assuming their morphological identifications are correct) found at The Neck were transported from the southern South Island, as he did not consider these species to form part of the Rakiura fauna.

Of the six moa species known to inhabit the southern South Island, only the generalist South Island giant and open-shrubland/grassland specialist heavy-footed moa may have occurred naturally on Rakiura. The island was connected to the southern South Island during the last glacial period but became isolated due to sea level rise c. 10 000 years ago (McGlone & Wilson 1996; Turney et al. 2017). Pollen data from coastal Southland suggests that the glacial (> 11 700 years ago) habitats on Rakiura were dominated by grasslands (McGlone & Wilson 1996), which could have supported heavy-footed, stout-legged, eastern and South Island giant moa populations – the former three species dominate glacial subfossil deposits in Southland (Worthy 1998a), and at least heavy-footed and eastern moa had refugial populations in the area (Worthy 1998b; Bunce et al. 2009; Rawlence et al. 2012). It is entirely conceivable that little bush and upland moa, whose preferred habitats were closed canopy forest and subalpine areas, respectively (Worthy 1998a; Wood et al. 2020), were not present on Rakiura by the time Foveaux Strait was flooded by rising sea levels, despite the presence of upland moa at low altitudes in Southland during the last glacial period (Worthy 1998b).

The oldest pollen records on Rakiura, dating back to the Pleistocene-Holocene transition c. 11 600 years ago, show that

the area was covered in scrub, ground ferns, tree ferns and rātā (*Metrosideros* spp.), with forest only becoming a feature of the landscape 9000 years ago. Initially dominated by kāmahi (*Weinmannia racemosa*) and southern rātā (*Metrosideros umbellata*), this was followed by a change to predominantly rimu (*Dacrydium cupressinum*) and miro (*Pectinopitys ferruginea*) forest around 5000 years ago (McGlone & Wilson 1996). The common South Island giant moa would have been able to live within this forested landscape (Wood et al. 2020). In contrast, stout-legged, eastern, and heavy-footed moa, who prefer more open habitat (Wood et al. 2020) would have been pushed into dune habitats; these four species dominate late Holocene dune fossil assemblages in coastal Southland (Worthy 1998b). In contrast to these mainland dune deposits, where moa remains are common, they are rare (with the exception of The Neck) in Rakiura dune deposits (which are dominated by seabirds with the near absence of forest birds), suggesting moa occurred at low population densities on the island (Worthy 1998a; Wood 2016).

Our research supports the hypothesis that the South Island giant moa skeleton recovered from West Ruggedy Beach likely originates from a natural deposit. At least this species, and potentially heavy-footed moa, may have occurred naturally on Rakiura at the time of Polynesian arrival. Other moa species may also have occurred there, albeit at low population densities (Wood 2016), based on available habitat. Future subfossil discoveries (including extensive and systematic excavations of sand dune, rockshelter and cave deposits), and genetic and geochemical analyses of moa bones and gizzard stones (e.g. oxygen and strontium isotopes) to determine local versus transported origins, may shed further light on the pre-human avifauna of Rakiura.

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Author contributions

All authors devised the study. AJFV & MS undertook the fieldwork. AJFV conducted the laboratory work and analysed the data. All authors contributed to the interpretation of the data. AJFV and NJR wrote the majority of the manuscript with input from MS.

References

- Allentoft ME, Heller R, Oskam CL, Lorenzen ED, Hale ML, Gilbert MTP, Jacomb C, Holdaway RN, Bunce M 2014. Extinct New Zealand megafauna were not in decline before human colonization. *Proceedings of the National Academy of Sciences* 111: 4922–4927.
- Anderson A 1989. *Prodigious birds: Moas and moa-hunting in New Zealand*. Cambridge UK, Cambridge University Press. 260 p.
- Baker AJ, Huynen LJ, Haddrath O, Millar CD, Lambert DM 2005. Reconstructing the tempo and mode of evolution in an extinct clade of birds with ancient DNA: The giant moas of New Zealand. *Proceedings of the National Academy of Sciences* 102: 8257–8262.
- Benham WB 1910. The discovery of moa remains on Stewart Island. *Transactions and Proceedings of the New Zealand Institute*. 354–356 p.
- Bronk Ramsey C 2009. Bayesian analysis of radiocarbon dates. *Radiocarbon* 51: 337–360.
- Brotherton P, Endicott P, Sanchez JJ, Beaumont M, Barnett R, Austin J, Cooper A 2007. Novel high-resolution characterization of ancient DNA reveals C > U-type base modification events as the sole cause of post mortem miscoding lesions. *Nucleic Acids Research* 35: 5717–5728.
- Bunce M, Worthy TH, Ford T, Hoppitt W, Willerslev E, Drummond A, Cooper A 2003. Extreme reversed sexual size dimorphism in the extinct New Zealand moa *Dinornis*. *Nature* 425: 172–175.
- Bunce M, Worthy TH, Phillips MJ, Holdaway RN, Willerslev E, Haile J, Shapiro B, Scofield RP, Drummond A, Kamp PJJ, Cooper A 2009. The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. *Proceedings of the National Academy of Sciences* 106: 20646–20651.
- Dabney J, Knapp M, Glocke I, Gansauge M-T, Weihmann A, Nickel B, Valdiosera C, García N, Pääbo S, Arsuaga J-L 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proceedings of the National Academy of Sciences* 110: 15758–15763.
- Higham TFG, Jacobi RM, Ramsey CB 2006. AMS radiocarbon dating of ancient bone using ultrafiltration. *Radiocarbon* 48: 179–195.
- Hogg AG, Heaton TJ, Hua Q, Palmer JG, Turney CS, Southon J, Bayliss A, Blackwell PG, Boswijk G, Ramsey CB 2020. SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. *Radiocarbon* 62: 759–778.
- Holdaway RN, Worthy TH 1997. A reappraisal of the late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand. *New Zealand Journal of Zoology* 24: 69–121.
- Holdaway RN, Allentoft ME, Jacomb C, Oskam CL, Beavan NR, Bunce M 2014. An extremely low-density human population exterminated New Zealand moa. *Nature Communications* 5: 5436.
- Jacomb C, Walter R, Jennings C 2010. Review of the archaeology of Foveaux Strait, New Zealand. *The Journal of the Polynesian Society* 119: 25–59.
- Longin R 1971. New method of collagen extraction for radiocarbon dating. *Nature* 230: 241–242.
- McGlone MS, Wilson HD 1996. Holocene vegetation and climate of Stewart Island, New Zealand. *New Zealand Journal of Botany* 34: 369–388.
- Nagaoka L 2001. Using diversity indices to measure changes in prey choice at the Shag River Mouth site, southern New Zealand. *International Journal of Osteoarchaeology* 11: 101–111.
- Perry GLW, Wheeler AB, Wood JR, Wilmshurst JM 2014. A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes). *Quaternary Science Reviews* 105: 126–135.
- Rawlence NJ, Metcalf JL, Wood JR, Worthy TH, Austin JJ, Cooper A 2012. The effect of climate and environmental change on the megafaunal moa of New Zealand in the absence of humans. *Quaternary Science Reviews* 50: 141–153.
- Rawlence NJ, Perry GLW, Smith IWG, Scofield RP, Tennyson AJD, Matisoo-Smith EA, Boessenkool S, Austin JJ, Waters JM 2015. Radiocarbon-dating and ancient DNA reveal rapid replacement of extinct prehistoric penguins. *Quaternary Science Reviews* 112: 59–65.
- Rohland N, Reich D 2012. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. *Genome Research* 22: 939–946.
- Turney CSM, Wilmshurst JM, Jones RT, Wood JR, Palmer JG, Hogg AG, Fenwick P, Crowley SF, Privat K, Thomas Z 2017. Reconstructing atmospheric circulation over southern New Zealand: Establishment of modern westerly airflow 5500 years ago and implications for Southern Hemisphere Holocene climate change. *Quaternary Science Reviews* 159: 77–87.
- Wilmshurst JM, Anderson AJ, Higham TFG, Worthy TH 2008. Dating the late prehistoric dispersal of Polynesians to New Zealand using the commensal Pacific rat. *Proceedings of the National Academy of Sciences* 105: 7676–7680.
- Winters M, Barta JL, Monroe C, Kemp BM 2011. To clone or not to clone: Method analysis for retrieving consensus sequences in ancient DNA samples. *PLoS One* 6: e21247.
- Wood JR 2016. Spatial distribution of late Holocene bird bones in the Mason Bay dune system, Stewart Island, New Zealand. *Journal of the Royal Society of New Zealand* 46: 103–116.
- Wood JR, Richardson SJ, McGlone MS, Wilmshurst JM 2020. The diets of moa (Aves: Dinornithiformes). *New Zealand Journal of Ecology* 44: 1–21.
- Worthy TH 1993. *Fossils of Honeycomb Hill*. Wellington, Te Papa Tongarewa. 56 p.
- Worthy TH 1998a. Fossil avifaunas from Old Neck and Native Island, Stewart Island-Polynesian middens or natural sites. *Records of the Canterbury Museum* 12: 49–82.
- Worthy TH 1998b. The Quaternary fossil avifauna of Southland, South Island, New Zealand. *Journal of the Royal Society of New Zealand* 28: 537–589.
- Worthy TH 1998c. Fossils indicate *Pelecanoides georgicus* had large colonies at Mason Bay, Stewart Island, New Zealand. *Notornis* 45: 229–246.

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