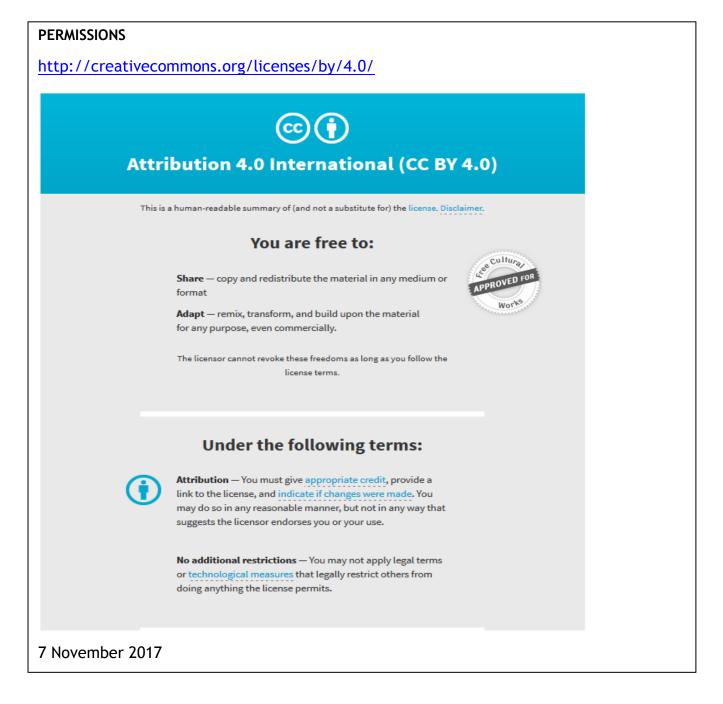
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Origin and timing of New Zealand's earliest domestic chickens: Polynesian commensals or European introductions?

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Human settlers transported chickens (Gallus gallus domesticus) to most East Polynesian archipelagos between AD 1000 and 1300; however, it has long been assumed that New Zealand was an exception. Despite the fact that chicken bones have been recovered from localities of early archaeological middens in New Zealand, their age and genetic relationships have never been critically assessed. Here, we test the assumption that chickens were not introduced to New Zealand during prehistory through ancient DNA and radiocarbon analyses of chicken bones from sites of Māori middens containing prehistoric material. The chickens belong to the widespread mitochondrial control region haplogroup E. Radiocarbon dating reveals that the bones are not prehistoric, but are still the earliest chicken remains known from New Zealand. Two of the bones pre-date permanent European settlement (ca 1803s onwards) but overlap with the arrival of James Cook's second voyage (1773-1774), and, therefore, they are likely to be chickens, or progeny thereof, liberated during that voyage. Our results support the idea that chickens were first introduced to New Zealand by Europeans, and provide new insights into Maori uptake and integration of resources introduced during the early post-European period.

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1. Introduction

The colonization of the remote islands of East Polynesia from the AD eleventh to thirteenth centuries was the last major migration of modern humans to habitable lands [1,2]. During this dispersal, voyagers transported a variety of cultigens and commensal species throughout the East Polynesian archipelagos, including taro (Colocasia esculenta), bottle gourd (Lagenaria siceraria), paper mulberry (Broussonetia papyrifera), Pacific rat (Rattus exulans), pig (Sus scrofa) and chicken (Gallus gallus domesticus) [3–7]. Previous studies have demonstrated how the analysis of the distribution, morphology, genetics and age of these translocated species can provide important insights into the timing and origins of prehistoric movements of people throughout the Pacific (e.g. [1,8–15]). Prehistoric bones indicate that some commensal species, such as the Pacific rat, were nearly ubiquitous throughout East Polynesia [8,9]. However, the distribution of other species remains poorly resolved [3,6]. For example, prehistoric chicken bones have been excavated from early Polynesian middens on some of the most remote islands in the region, including Rapa Nui/Easter Island and Hawai'i [14], yet they remain conspicuously absent from the equally remote but cooler subtropic and temperate southern islands of Polynesia (including New Zealand, and the Chatham, Auckland, Kermadec and Norfolk Islands) [3,6]. The apparent absence of prehistoric chicken remains on these islands raises many questions [3]. For example, were chickens introduced by the first Polynesian settlers but then subsequently lost to disease, low propagule pressure, competition and predation or because there was no need to sustain domestic chickens in the presence of abundant large native flightless birds? Were they never taken in the first place [16–19]? Or, have chicken bones in prehistoric middens been overlooked as recent contamination? Answering these questions will help to resolve broader questions regarding the frequency and longevity of inter-island voyaging following initial settlement. This is of particular relevance on Pacific islands, where large prey species were hunted to extinction relatively quickly and human population growth meant food resources soon became limited. In such scenarios, returning to ancestral islands to source chickens (or other food resources) would clearly be desirable if long-distance inter-island travel was still feasible. For example, in Tonga, radiocarbon dating suggests that chickens were only introduced after the large native megapode (Megapodius alimentum) and iguana (Brachylophus sp.) had become extinct [3].

In the light of these long-debated and unresolved questions, it is perhaps surprising that the prehistoric presence of chickens in New Zealand has never been critically examined, especially given that the lack of evidence for their former absence is somewhat misleading. In fact, chicken bones have been excavated from several localities of prehistoric Polynesian (Māori) middens throughout New Zealand, including potentially archaic sites (e.g. [20–26]). Chicken bones in Māori middens are usually assumed to represent disturbance and incorporation of recent material into older layers (e.g. [26]). In some sites, this is likely, especially where stratigraphy is disturbed, and/or where other items, such as sheep (*Ovis aries*) bones or glass, are also present (e.g. [23,24]). However, such dogma creates the potential for genuine prehistoric chicken remains to be overlooked.

Here, we provide the first radiocarbon and ancient DNA analyses of chicken bones from sites of Māori middens containing prehistoric material. We focus on bones from three different sites along the northeast coast of New Zealand's South Island (figure 1). The sites were selected as ideal candidates for finding potentially prehistoric chicken specimens, as they also contained pre-European faunal assemblages (electronic supplementary material), including bones of moa and other large birds (such as South Island adzebill (*Aptornis defossor*) and South Island goose (*Cnemiornis calcitrans*)) that became extinct within 200 years of initial human settlement [27–29].

2. Results

2.1. Radiocarbon dating

Gelatin fractions from the three bones studied fell within the required mass range for standard accelerator mass spectrometry (AMS) dating. The oldest bone was from Redcliffs School Site (RSS), returning an age of 226 ± 25 14C years before present (BP) (median age = AD 1756; 95.4% calibrated confidence range = AD 1650–1805; table 1 and figure 2). The bone from Mussel Point (MP) was only slightly younger at 211 ± 23 14C years BP (median age = AD 1757; 92.6% calibrated confidence range = AD 1652–1810; table 1 and figure 2). The bone from Fyffe's Site (FS) was dated at 164 ± 23 14C years BP (median age = AD 1840; 95.4% calibrated confidence range = AD 1675–1950; table 1 and figure 2).

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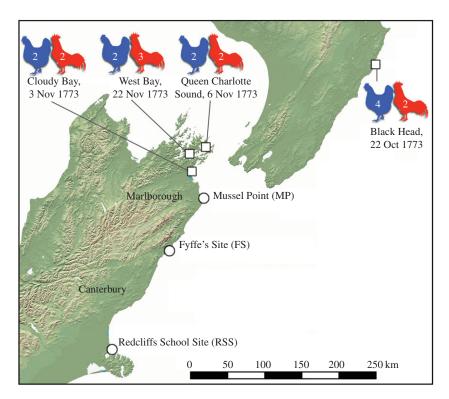


Figure 1. Locations (squares) and number of live chickens liberated or gifted to Maori tribes on Captain Cook's second voyage to New Zealand in 1773 (male red, female blue). The locations of the three chicken bones from Maori middens examined in this study are marked by circles.

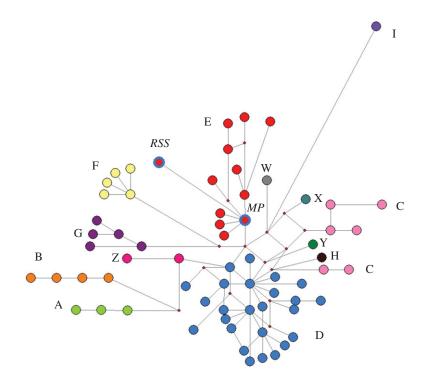


Figure 2. Haplotype network for chickens based on a 200 bp sequence of mitochondrial control region. Both the Redcliffs School Site (RSS) and Mussel Point (MP) specimens are within the widespread haplogroup E.

2.2. Ancient DNA

Ancient DNA (200–201 bp of mitochondrial control region) was amplified and sequenced from the two oldest chicken bones (from RSS and MP), but was not obtained from the younger bone (from FS).

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1. Wk, Waikato Radiocarbon Dating Laboratory code; CM, Canterbury Museum; CRA, conventional Radiocarbon Age. Owing to small	carbon dates have therefore been corrected for isotopic fractionation. All isotope values measured on bone gelatin.
Table 1. Radiocarbon dates for archaeological chicken bones from South Island, New Zealand. Wk, We	sample sizes, d13C was measured on prepared graphite using the AMS spectrometer. The radiocarbon da

- - - -	2 sigma calibrated ranges	AD 1675–1738 (29.8%)	AD 1797—1950 (65.6%)				AD 1650–1690 (23.4%)	AD 1726–1805 (72.0%)	AD 1652–1700 (22.3%)	AD 1721–1810 (70.3%)	AD 1836–1844 (0.9%)	AD 1866–1878 (1.5%)	AD 1932–1938 (0.5%)
	T sigma calibrated ranges	AD 1684—1711 (16.2%)	AD 1719–1730 (5.9%)	AD 1803-1813 (5.4%)	AD 1837–1883 (24.2%)	AD 1925 – (16.5%)	AD 1666–1675 (8.3%)	AD 1739–1797 (59.9%)	AD 1670–1679 (8.9%)	AD 1733–1785 (53%)	AD 1794–1801 (6.4%)		
	error	23					25		23				
	CKA	164					226		211				
Ţ	C:N	3.37					3.36		3.39				
1541	d ^{1,} N	7.66					6.73		8.04				
gelatin	yıeld (%)	7.5					4.1		9.5				
powdered	mass (g)	0.18					0.22		0.2				
:	site	Fyffe's Site, Kaikoura					Redcliffs School Site,	Christchurch	Mussel Point, Cape Campbell				
-	CM number	Av33059					Av23181		Av17724				
-	Wk number	Wk38085					Wk38086		Wk38088				

The two sequences (Genbank accession nos. KX394444 and KX394445) varied by four nucleotides, all being G–A or C–T transitions. Both sequences fall within the widespread chicken mitochondrial control region haplogroup E (figure 2). The sequence from the RSS bone represents a previously unsequenced haplotype (confirmed by nearest BLAST match having 99% identity), while the sequence from the MP bone represents a widespread haplotype previously reported in chickens from Africa, Asia, Europe, South America and the Pacific.

3. Discussion

3.1. Age and origin of the chickens

The calibrated age ranges of the radiocarbon-dated chicken bones from two sites (RSS and MP) suggest they pre-date permanent European settlement (1830s). Although there are multiple probability distributions for the calibrated dates, the highest probabilities on the age ranges for these sites (table 1) occur before the 1830s, with the median age of *ca* AD 1760, meaning these are the earliest chicken remains known from New Zealand. The bone from FS is somewhat younger, although still relatively early (median age of AD 1840), yet the major probability distributions are bimodal, split between AD 1837 and 1883 (1 sigma). There is no significant difference between the ages of the three bones (test statistic T = 3.75; χ^2 (0.5) = 5.99; 2 d.f.).

The potential for marine carbon to skew the radiocarbon age of archaeological chicken bones has previously been examined with regard to pre-Columbian chicken bones from Chile [11,14,30–34]. Owing to the small sample sizes, the d13C from the New Zealand chicken bones was measured on prepared graphite. However, all three bones reported here had d15N values (table 1) consistent with an entirely terrestrial diet (F. Petchey 2014, personal communication), and the radiocarbon dates are, therefore, unlikely to have been influenced by the marine reservoir effect. Although the accuracy of the dates appears to be robust, the precision of the dates is affected by a plateau in the radiocarbon calibration curve after *ca* AD 1800, meaning that there are wide confidence intervals around calibrated ages within this time period. However, the bones from RSS and MP are just old enough so as not to be affected by this plateau to the same degree as the FS specimen. The confidence ranges for the ages of the two older bones (more than 90% before 1810) appear to rule out early European settlers (who began arriving *en masse* from the 1830s onwards) as a source. However, as we discuss below, several other transient European visitors were visiting the New Zealand coastline prior to the 1830s, and their potential as sources for the chickens requires critical assessment.

The first of the early European (pre-1830) visitors to New Zealand were sealing gangs, who visited and explored the coastal areas of New Zealand in the late eighteenth and early nineteenth centuries. However, the calibrated age ranges for the RSS and MP chicken bones, together with what is known about the timing and location of sealing expeditions to New Zealand [35], appear to rule out sealers as a likely source. Only two sealing voyages to New Zealand can be confirmed prior to the main period of sealing between 1803 and 1840 [35]. The earliest phase of sealing (1803–1807) was concentrated along the Fiordland and Stewart Island coastlines in the far south of the South Island [35], and there is no evidence that sealing took place along the eastern South Island coastline north of Dunedin (the location of our chicken bones) at this time. Although there were some port visits by sealers in Canterbury (including Banks Peninsula) from 1809 to 1829 [35], these visits are too late to represent a likely source for the RSS and MP chicken bones.

Whalers also operated around the New Zealand coastline from the late eighteenth century, but can be ruled out as a likely source of the chickens. Most early whaling was concentrated around the northern North Island (e.g. Bay of Islands) [36]. Whalers do not appear to have made cruises down the South Island until the 1830s, with visits to Banks Peninsula from 1835 onwards [37].

Several cruises were made around the New Zealand coastline by exploration expeditions between the time of New Zealand's discovery by Europeans (Abel Tasman in 1642) and the beginning of sealing and whaling in the late eighteenth to early nineteenth centuries (e.g. Vancouver in 1791, Malaspina in 1793). However, there is no evidence to suggest that chickens were released onshore during these voyages [38]. Other early, yet unrecorded, expeditions may have shipwrecked upon the New Zealand coast, with the potential for live cargo to have escaped ashore [39]. However, just one expedition provides clear evidence for chickens having been liberated in New Zealand, with dates that coincide with our earliest dated specimens: that of Captain James Cook's second voyage to New Zealand in 1773. Therefore, in the light of the evidence outlined above, we suggest that the ages of the RSS and MP chicken bones are most

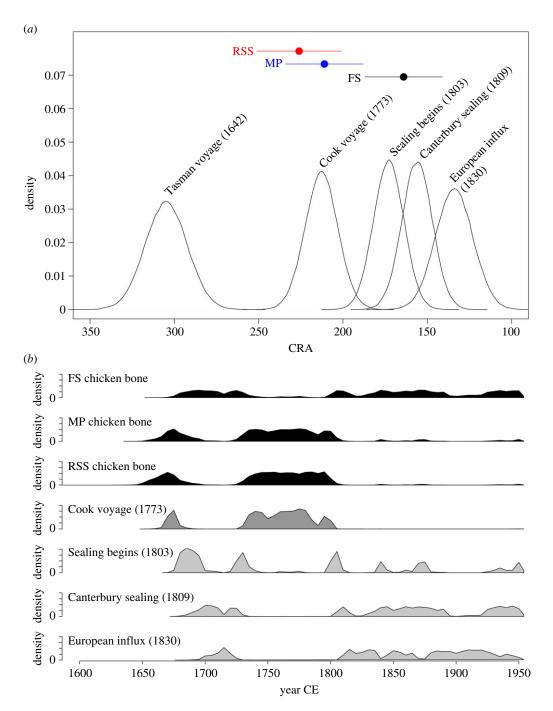


Figure 3. (*a*) Median and 2σ ranges for conventional radiocarbon ages (CRA) of chicken bones from Redcliffs School Site (RSS), Mussel Point (MP) and Fyffe's Site (FS), South Island, New Zealand, compared with distributions of the CRAs corresponding to calendar years for key events in the early European-contact period; (*b*) calibrated age distributions for New Zealand chicken bones compared with those for CRAs relating to key events in the early European-contact period.

consistent with them representing chickens, or near descendants thereof, brought to New Zealand on Cook's 1773 expedition (figures 2 and 3).

DNA sequences from both the RSS and MP chicken bones were from the globally distributed E-haplogroup, and so did not provide any information on the potential place of origin. The chickens released by Cook's expedition in New Zealand may have had mixed origins, as they definitely acquired chickens during a stop at the Cape Verde Islands ([40], p. 27), but may also have had chickens sourced from England, South Africa (during a stop there en route to New Zealand) and Tahiti/Tonga (chickens were not liberated in New Zealand until the expedition had returned from these islands).

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3.1.1. Ethnographic evidence for early uptake of introduced chickens by Maori

The occurrence of chicken bones in Maori middens from the South Island that date from before the main period of European settlement (after which chickens could be widely sourced) provides new insights into the adoption, spread and use of novel species by Maori during the early post-European-contact era. The fate of Captain Cook's chickens, or how long they may have persisted, has never been known. Cook himself appears to have felt that the chickens had slim chances of survival. For example, on 3 November 1773 he gave two cocks and two hens to a local of the Cloudy Bay/Port Underwood area, noting that these 'he received with such indifferency, as gave me little hopes that proper care would be taken of them' ([40], p. 285). Cook also recorded that upon gifting two cocks and four hens to a Maori chief near Black Head, south of Cape Kidnappers, on 22 October 1773 the chief appeared unimpressed with the birds ([40], p. 279). From these records, it might seem unlikely that Cook's chickens would have persisted long enough to form self-sustaining populations. However, there were some instances where it seems that they did. For example, Cook liberated chickens at West Bay in the Marlborough Sounds, northern South Island, in 1773, and upon returning the following year a fresh hen's egg was discovered in the forest, suggesting at least one of the females had survived ([40], p. 291 and 573). It appears that a large number of chickens were also liberated by Tobias Furneaux (Captain of Adventure, the second ship on Cook's second voyage) in the Marlborough Sounds, although the exact details of these were not recorded. Of them, Cook stated 'More Cocks and Hens are left behind than I know of as several of our people had of these as well as my self, some of which they put on shore and others they sold to the Natives, whom we found took care enough of them' ([40], p. 296).

Previously, there has been no record of what became of the chickens Cook left in New Zealand, yet the bones examined here suggest they may have bred and been transported by Māori moving along the east coast of the South Island, and were possibly traded between groups. Further evidence supporting mobility of Māori and transport of European goods along this coast during the early post-contact era comes from the discovery locations of medals that were gifted by Cook to Māori living in the Marlborough Sounds, also on his second voyage. At least a dozen of these medals have since been discovered in association with sites of Māori settlement, mainly in the Marlborough Sounds and along the east coast of the South Island [41,42] (figure 4).

3.1.2. Significance of historic introduction of chicken

The apparent rapid uptake of chickens by Māori in the late eighteenth century and their dispersal around New Zealand has parallels with a number of other food items introduced by early European visitors to New Zealand, such as white potatoes, turnips, carrots and cabbages [43,44]. Māori were quick to realize the potential of these new resources [17] and rapidly integrated them into their livelihoods, often resulting in significant changes to their society and economy [17,43,44]. This rapid uptake and dispersal of new food commodities is consistent with the idea that food resources were limited for Māori populations during the initial European-contact era, and had been so for several centuries prior to this time [17].

At the time of initial settlement in the AD thirteenth century [1], New Zealand's terrestrial fauna was dominated by large, flightless and naive birds, and abundant land-breeding seabirds and pinnipeds, which provided a rich source of easily hunted animal protein that helped to sustain early population growth [17]. However, in less than two centuries, intense hunting pressure [27] and forest clearance by fire [45–47] caused massive and widespread extinctions and a reduction in large easily harvested prey species. This in turn led to changes to Maori society (e.g. increased warfare) and economy (e.g. construction of fortified villages and cidatels) [17]. If chickens had not been introduced or successfully established in New Zealand at the time of initial settlement, it is reasonable to assume that by AD 1450 (when extinction of megafauna occurred and other protein sources were in decline), that given the ability, Maori would have made return voyages to their ancestral Polynesian islands to source chickens (and other protein resources such as pigs) [3,17]. The nearest archipelagos to New Zealand that had chickens (and pigs) at this time were the southern Cook Islands [6], only several weeks of open-ocean voyaging away to the northeast [48]. However, the New Zealand archaeological record lacks any evidence for material cultural exchange with East Polynesia after ca AD 1450, suggesting long-distance inter-island voyaging had ceased by this time. This concurs with the finding more generally in East Polynesia for a marked decline in long-distance voyaging and inter-island exchanges after AD 1450 [49].

Chicken bones are relatively rare in pre-1830s New Zealand archaeological middens, and the chicken bones from the three sites we selected for our analyses represent a significant proportion of the total chicken remains known from such sites. For this reason, and the fact that the chicken bones were

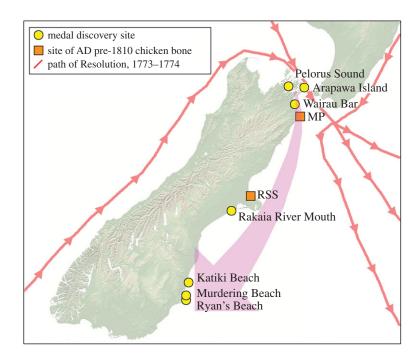


Figure 4. The path of Captain Cook's ship *Resolution* through New Zealand waters on his second voyage (1773–1774), with locations where medals associated with this voyage have been found, and where the two chicken bones in this study that pre-dated AD 1810 were excavated (MP, Mussel Point; RSS, Redcliffs School Site).

from sites that also contained bones of large bird species that went extinct in the first 200 years after initial settlement, we targeted our analyses towards specimens offering the greatest likelihood of being prehistoric chickens. Although the dates for the chicken bones make them the oldest known chicken remains from New Zealand, the fact they are all eighteenth century or younger strongly suggests that chickens were either not introduced prehistorically, or if they were, they did not persist long enough to leave a trace in the archaeological record. If chickens had been established in New Zealand by the first settlers, we believe chicken bones would be more abundant and widespread in middens throughout the country, as they tend to be on other Polynesian islands where they were introduced and successfully established during prehistory [3]. Although it is speculative and difficult to prove, it seems probable that when the first Polynesians arrived in New Zealand and found an abundance of large, easily hunted, flightless birds, efforts to establish the domestic chicken, which required a certain amount of husbandry, may have been rapidly abandoned. The same explanation may apply to other Pacific archipelagos with apparent anomalous absences of prehistoric commensals [17]. For example, in New Caledonia, pigs were not introduced prehistorically, despite the relatively close proximity to source islands (Vanuatu) [3]. As with New Zealand, the first settlers to New Caledonia would have encountered large animals, including giant bats, turtles and flightless birds such as Sylviornis neocaledoniae, which would have provided easy hunting in the initial settlement period.

4. Conclusion

We have radiocarbon dated and sequenced DNA from the three most likely candidates for prehistoric chicken bones from New Zealand. Our results demonstrate that all were deposited during the early European-contact era. This finding strongly supports the hypotheses that chickens were either not brought to New Zealand by the first Polynesian settlers, or did not persist for very long following their introduction, due to the abundance of large native animals that could easily be hunted. However, sources of large native animals had become depleted by the time Captain Cook introduced chickens in 1773, after which chickens became readily integrated into Māori livelihoods, and were moved around New Zealand by Māori at this time. The fact that chickens (and other commensals such as pigs) were not introduced to New Zealand soon after the AD fifteenth century extinction of megafauna, such as occurred in Tonga, provides compelling evidence for the idea that Māori had lost the ability/knowledge for long-distance inter-island voyaging by this time.

5. Methods

5.1. Sites and samples

Chicken bones from three Māori midden deposits were selected for study: RSS, Christchurch (NZ Archaeological Association site number M36/24); Mussel Point, Marlborough (NZ Archaeological Association site number Q29/1) and Fyffe's site, Avoca Point, Kaikoura (NZ Archaeological Association site number S49/46). Although the bones had been collected some decades prior to this study, and there were no exact details on stratigraphic contexts available, faunal remains, artefacts and radiocarbon dates from the same localities show that each of the sites included occupation layers from the earliest phase of human settlement. Faunal assemblages from these sites also include significant proportions of bird species that became extinct prior to European settlement (electronic supplementary material, figure S1). Archaeological sites on Redcliffs Flat (which includes the RSS) span from the earliest phase of human settlement in New Zealand to recent times [23]. Further details of the study sites are presented in the electronic supplementary material.

5.2. Radiocarbon dating

Subsamples of chicken bones were submitted to the Waikato Radiocarbon Dating Laboratory in New Zealand for analysis. The samples were cleaned and ground, decalcified in 2% HCl, rinsed and dried. The remaining fraction was gelatinized in HCl (pH 3.0) at 90°C for 4 h before being ultrafiltered and freeze-dried, and dated using accelerator mass spectrometry (AMS). Radiocarbon dates were calibrated using the ShCal13 curve [50] via OXCAL 4.2 [51].

5.3. Ancient DNA

Ancient DNA extractions and the setting up of PCR reactions were performed in a dedicated, purposebuilt ancient DNA facility at Landcare Research, Lincoln, New Zealand. DNA was extracted from 22 to 31 mg samples of bone by incubation overnight at 55°C in 945 µl of 0.5 M EDTA (pH 8.0), 20 µl of 10% SDS and 35 μ l of 20 mg ml⁻¹ Proteinase-K, followed by extraction of the supernatant using the DNeasy Blood & Tissue Kit (Qiagen). Two microlitres of carrier RNA were added along with the AL buffer. A variable and globally well-characterized fragment of the chicken mitochondrial control region was amplified using the primers GG144 (5'-ACCCATTATATGTATACGGGCATTAA-3') and GG387 (5'-CGAGCATAACCAAATGGGTTAGA-3') [14]. PCR reactions (final volume 25 μ l) contained 1 mg ml⁻¹ bovine serum albumin, $1 \times$ PCR buffer, 2 mM MgSO₄, 200 μ M dNTP, 1 μ M each primer, 1 U Platinum HiFi Taq (Invitrogen), 0.5 U shrimp DNase (Affymetrix) and 2 µl of DNA extract. The PCR master mix was incubated at 37°C for 15 min and 65°C for 15 min, prior to addition of the DNA template to allow the shrimp DNase to digest double-stranded DNA contaminants in the reagents. This was an essential step, as chicken DNA is a known contaminant of some PCR reagents, and can result in the amplification of non-endogenous products when working with ancient chicken DNA extracts [14,52]. PCR products were visualized on a 3% agarose gel, and amplified products were purified using ExoSAP-IT (Affymetrix) following the manufacturer's protocol, and bidirectionally sequenced using BigDye terminator technology on a capillary sequencer. The RSS and MP sequences were aligned with available whole mitochondrial genomes representing all-known chicken mitochondrial haplogroups (electronic supplementary material, table S1) using MUSCLE algorithm in GENIOUS v. 7.1.2. The alignment was truncated to 200 bp corresponding to the ancient DNA fragment. To identify the haplogroup assignment of the NZ sequences, a phylogenetic network was estimated via median-joining network [53] using NETWORK v. 4.6.1 (from fluxus-engineering.com). Following this, the RSS and MP sequences were aligned to a dataset comprising chicken mitochondrial control region sequences with known haplogroup and geographical assignments.

Ethics. Permission to sample chicken bones for this study was provided by Canterbury Museum, Christchurch, New Zealand.

Data accessibility. DNA sequences from the New Zealand chicken bones are available from GenBank (accession nos. KX394444 and KX394445). All other data are presented in the paper or electronic supplementary material.

Authors' contributions. J.R.W., R.P.S. and J.M.W. designed the study. R.P.S. selected specimens for the study. J.R.W. performed molecular analyses and submitted samples for radiocarbon analysis. J.R.W., M.J.B.H. and J.M.W. analysed the data. J.R.W., M.J.B.H., R.P.S. and J.M.W. interpreted the results and wrote the manuscript. All authors gave final approval for publication.

Competing interests. The authors declare no competing interests.

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