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Ancient DNA analyses of early archaeological sites in New Zealand reveal extreme exploitation of moa (*Aves: Dinornithiformes*) at all life stages

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Abstract

The human colonisation of New Zealand in the late thirteenth century led to catastrophic impacts on the local biota and is among the most compelling examples of human over-exploitation of native fauna, including megafauna. Nearly half of the species in New Zealand's pre-human avifauna are now extinct, including all nine species of large, flightless moa (Aves: Dinornithiformes). The abundance of moa in early archaeological sites demonstrates the significance of these megaherbivores in the diet of the first New Zealanders. Combining moa assemblage data, based on DNA identification of eggshell and bone, with morphological identification of bone (literature and museum catalogued specimens), we present the most comprehensive audit of moa to date from several significant 13th–15th century archaeological deposits across the east coast of the South Island. Mitochondrial DNA (mtDNA) was amplified from 251 of 323 (78%) eggshell fragments and 22 of 27 (88%) bone samples, and the analyses revealed the presence of four moa species: *Anomalopteryx didiformis*; *Dinornis robustus*; *Emeus crassus* and *Euryapteryx curtus*. The mtDNA, along with polymorphic microsatellite markers, enabled an estimate of the minimum number of individual eggs consumed at each site. Remarkably, in one deposit over 50 individual eggs were identified – a number that likely represents a considerable proportion of the total reproductive output of moa in the area and emphasises that human predation of all life stages of moa was intense. Molecular sexing was conducted on bones ($n = 11$). Contrary to previous ancient DNA studies from natural sites that consistently report an excess of female moa, we observed an excess of males (2.7:1), suggestive that males were preferential targets. This could be related to different behaviour between the two highly size-dimorphic sexes in moa. Lastly, we investigated the moa species from recovered skeletal and eggshell remains from seven Wairau Bar burials, and identified the presence of only the larger species of moa, *E. curtus* and *D. robustus*.

Keywords: Ancient DNA; Fossil eggshell; Moa; Archaeology; Faunal extinction; Megafauna; Midden; Human burial

Introduction

In the late thirteenth century AD, Polynesians in the final phase of Austronesian expansion arrived in New Zealand. The timing of this arrival makes New Zealand the last major temperate landmass to be settled by humans. Archaeological deposits and dating of archaeological sites suggest a rapid expansion along the east coast of New Zealand's South Island (Fig. 1) (Higham et al., 1999; Walter et al., 2010). These earliest inhabitants would have encountered a heavily forested landscape, well provisioned with wild food resources. At the time of human contact, New Zealand was home to ~245 avian species, many of which were flightless (Holdaway et al., 2001). Within a century or so, many birds were hunted to extinction, including the megafaunal ratites, the moa (Holdaway and Jacomb, 2000). Often coexisting, there were nine species of moa in six genera (Bunce et al., 2009), ranging in height from 50 cm to 200 cm at their back. Unlike the extinction debates involving Northern Hemisphere or Australian megafauna (Koch and Barnosky, 2006; Roberts and Brook, 2010; Lorenzen et al., 2011; Prescott et al., 2012) there is very little controversy that moa were driven to extinction by a combination of direct hunting (Holdaway and Jacomb, 2000) and the indirect effects of anthropogenic fires (McWethy et al., 2009a, 2009b). However, the specifics of moa hunting are scarce, with speculation that snares, nooses, spears, and possibly dogs, were used (Anderson, 1989). Also, despite the importance of moa in the diet of the first New Zealanders, there is a paucity of information on which species were hunted during the first contact phase.

Until now, moa remains from archaeological assemblages have been identified using skeletal morphology. However, much of the archaeological bone is fragmented, reworked, burnt, or from incomplete skeletons, and these conditions can make definitive identifications difficult (Baker et al., 2005; Allentoft et al., 2010). Eggshell is even more challenging (see Oskam et al., 2010), although the large quantity of unassigned moa eggshell fragments in museum collections represents a major source for new insights on the diet of the colonisers. For some bone specimens (especially those damaged or from juveniles), and for all fragments of eggshell analysed, accurate species identification can only be obtained by DNA profiling (Allentoft et al., 2010; Oskam et al., 2010, 2011).

Polynesians rapidly explored New Zealand and its offshore islands and concentrated their settlements near the coast where they had immediate access to land and sea resources (Walter et al., 2010). The first settlements were often large (>5 ha) but were probably short-lived; radiocarbon dates suggest that occupation lasted no longer than a generation (Anderson and Smith, 1992) or 20–50 years (Anderson and Smith, 1996). Arguably the most significant, and certainly one of the earliest archaeological sites in New Zealand, is Wairau Bar (Fig. 1), from which large quantities of moa bone and eggshell have been excavated in several periods of study. Additionally, skeletal remains (*koiwi tangata*) from over 40 Polynesian humans have been discovered (Duff, 1950; Buckley et al., 2010), representing the burials of some of the first people in New Zealand. The inclusion of moa bones and eggs in the human burials at Wairau Bar reflects the value placed on moa (Oppenheim, 1973; Anderson, 1989).

In this study, we report the representation of moa in geographically dispersed archaeological deposits. The aims of this study are threefold: 1) To estimate the total numbers of individual

moa present and the relative species representations. This should result in insights on the ecological impact of the initial contact between humans and moa. 2) To test for differences in species representation based on DNA results from bone and eggshell in Wairau Bar. This could provide information on moa hunting practices and moa biology. 3) To identify the moa remains from human burial sites and, for example, report any species preference as funerary offerings.

Materials and methods

Site information, moa eggshell and bone sampling

Moa eggshell ($n = 323$) and bone ($n = 27$) were sampled from ovens, middens and burials excavated at seven significant archaeological deposits along the east coast of the South Island of New Zealand: Wairau Bar (P28/21) (Marlborough); Fyffe's (O31/30) and Waiopuka (O31/80) (Kaikoura); Moa-bone Point Cave (M36/25), Monck's Cave (M36/47), and Redcliffs Flat (M36/24) (Christchurch); and Pounaweia (H47/1) (South Otago) (Fig. 1). Moa specimens were provided from the from a recent archaeological excavation conducted at Wairau Bar in 2009 (see Oskam et al., 2010). Eggshell and bone were sampled and powdered following ancient DNA (aDNA) protocols of Oskam et al. (2010) and Allentoft et al. (2009) at the Department of Anthropology and Archaeology, University of Otago, New Zealand.

Human burial description

Human skeletal remains of what are likely to be the first generation or two of Polynesian settlers in New Zealand were found buried at Wairau Bar (Anderson, 1989). Three cemeteries have been identified at this archaeological site. Burials 1–44 have previously been grouped

based on their location and grave good contents. Group 1 (burials 1–7) comprised ‘superiorly ranked’ human remains, almost exclusively young to mid-adult males (Buckley et al., 2010) and were richly furnished plots containing adzes, necklaces and avifauna remains (Duff, 1950; Oppenheim, 1973). Groups 2 and 3 (burials 8–11 and 12–44 respectively) have markedly fewer funerary artefacts and have been described as a ‘common resting place’ that contain a mixture of age and sex (Duff, 1950; Buckley et al., 2010). In this study, we investigate the moa remains (bone $n = 8$; egg $n = 4$) excavated from seven burials from groups 1–3 (see Fig. 2 and S1; Table S1).

Molecular analyses of moa eggshell and bone

DNA was extracted from 100 mg and 200 mg aliquots of moa eggshell and bone powder, respectively, as described in Oskam et al. (2010, 2011) and Allentoft et al. (2009).

Polymerase chain reactions (PCR) were carried out in conjunction with multiple extraction controls and non-template controls throughout the study. Quantitative PCR (qPCR) assay using mitochondrial DNA (mtDNA) control region primers (primer pairs CR262F/441R along with CR185F/294R) were carried out in both eggshell and bone for species assignment (Oskam et al., 2011). Amplicons were then sent for sequencing at a commercial facility, Macrogen (Seoul, South Korea). In order to assign each sampled element to a species level, the obtained sequences were compared with >700 reference moa mtDNA sequences available on GenBank (see Allentoft and Rawlence, 2012) using Geneious 5.4.3 (Biomatters, New Zealand) and were then deposited on GenBank (accession numbers JF927651–JF927706 and JX271058–JX271274).

Minimum number of individual eggs

An estimate of the minimum number of individuals (MNI) within a zooarchaeological assemblage is important in estimating the hunting pressure exercised by colonisers but pseudo replication can be problematic, especially when analysing eggshell. Unlike bone, where duplication can be eliminated by consistently sampling either a right or left skeletal element (Allentoft et al., 2010), eggshells are more challenging, usually being fragmented and lacking species-specific eggshell morphologies (Oskam et al., 2011). However, the recent development of highly polymorphic microsatellite markers developed exclusively for moa (Allentoft et al., 2009, 2011a), provides an opportunity to effectively discriminate between individuals and hence determine the minimum number of individual eggs (MNIE).

A two-step approach was employed to determine the MNIE (Oskam et al., 2011); first using mtDNA signatures; and second, using microsatellite variability, resulting in a higher resolution. Both DNA damage and allelic dropout were taken into consideration when determining MNIE. Mitochondrial sequences were aligned and analysed using Geneious 5.4.3 and haplotype assignment was based upon reliable differences observed in the mtDNA sequence; sequences with ambiguous bases or rare haplotypes were either resequenced or the PCR was repeated and resequenced. Conscious of potential DNA damage artefacts, eggshell fragments displaying different mtDNA sequences would have been laid by a different female. In addition, to further discriminate between different individuals, when eggshell fragments presented indistinguishable mtDNA haplotypes, the allelic combination from nuclear markers was used. These five moa-specific microsatellite markers were amplified and genotyped according to methods presented in Allentoft et al. (2009, 2011a). We acknowledged remains

to be from different individuals only when different mtDNA profiles and/or different microsatellite profiles from eggshell fragments, were identified.

Working with aDNA presents challenges, and this study was no exception. Preservation issues in eggshells excavated from midden material, also observed in Oskam et al. (2011), led to high allelic dropout and often incomplete multi-locus genotypes for eggshell fragments even when multiple PCR repetitions and re-extractions were performed. However, although we were mindful of the established criteria for data fidelity set out by Allentoft et al. (2011a), our principal intention was not to generate a high fidelity dataset for advanced population genetic analyses, but simply to use these microsatellite allele calls for discriminating between individual eggshell fragments only. We therefore relaxed the criteria pertaining to samples not being genotyped for all microsatellite primers.

Molecular sexing of moa bones

To investigate the skeletal remains from Wairau Bar, moa bones were sexed according to the protocols established by Bunce et al. (2003) and Huynen et al. (2003), with robust modifications outlined by Allentoft et al. (2010), using two independent primer pairs (Moa1-FAM/Moa2 and KW1F/KW1R-FAM). The addition of the fluorescent FAM dye, to one primer of each pair, allowed for PCR products to be accurately separated using an ABI 3730 genetic analyser (Applied Biosystems, Foster City, CA). The sex of the bone was then determined by scoring the DNA fragments manually using GENEMARKER v 1.5 (Soft Genetics, State College, PA).

Moa assemblage comparisons between archaeological deposits

Moa assemblage compositions between archaeological deposits were compared using χ^2 tests using PASW Statistics 18.0 (IL, USA). However, when sites contained species with $n < 5$, the χ^2 likelihood ratio was used.

Sex ratios between paleontological and archaeological sites were analysed using the Fisher's exact test (PASW Statistics 18.0). Combined sex ratios from adult *Euryapteryx curtus* and *Emeus crassus* bone specimens in this study (archaeological sites) were compared with sex ratios from adult *E. curtus* and *E. crassus* bone specimens reported in Huynen et al. (2003) and Allentoft et al. (2010), representing the paleontological sites. Juvenile skeletal remains are rare at the Wairau Bar site and to eliminate any potential bias observed by Allentoft et al. (2010), who observed that juvenile sex ratios are significantly different to those present in adults, we only analysed the adult sex ratios. Furthermore, data from the Pyramid Valley site were not included here due to the extreme excess there of female moa, resulting from a depositional bias – likely linked to moa behaviour (Allentoft et al., 2010). Statistical significance was assigned at the $P < 0.05$ level.

Results and discussion

Moa assemblages in archaeological sites of the South Island

Here we present an analysis of moa eggshell and moa bone remains from some of the most significant 13th–15th century archaeological deposits in the South Island of New Zealand (Figs. 1 and 3). The samples were primarily sourced from midden material (bone $n = 19$; eggshell $n = 318$), but also included material from human burials (bone $n = 8$; egg $n = 5$).

Mitochondrial DNA was successfully isolated and characterised from 251 (78%) eggshell fragments and 22 (81%) bone remains. Nuclear microsatellites could be amplified in 56% of the eggshells ($n = 140$) and 50% of the bones ($n = 11$) that worked for mtDNA.

Fig. 3 illustrates the moa assemblages, genetically identified from moa bone and eggshell. Along with the genetic results from this study, Table 1 collates all the archaeological moa assemblage data based on morphological identification of bone (literature and museum catalogued specimens). The multi-site assemblages compiled here therefore represent the most comprehensive audit of moa conducted to date.

Across all of the four regions (Marlborough; Kaikoura; Christchurch; South Otago) *E. curtus* (mass = 40–109 kg, height = 80–103 cm (Worthy and Holdaway, 2002)) was the most abundant moa species. Because of the rapid pace of moa extinction (Holdaway and Jacomb, 2000), it is difficult to disentangle extinction timelines for each of the moa species. However, based on this dataset the predation pressure on *E. curtus* was likely to have been extreme. Duff (1950) theorised that the giant moa *Dinornis robustus* (mass = 56–249 kg; height = 90–200 cm) would have been rare at the time of Polynesian arrival but the data presented here suggest otherwise. For example, 43 *D. robustus* eggshell fragments from at least 14 individuals were identified at Wairau Bar (Fig. 3). Moa remains morphologically assigned to *E. crassus* (mass = 36–79 kg; height = 73–99 cm (Worthy and Holdaway, 2002)) have been well documented throughout the coastal archaeological and paleontological sites, with an abundance of *E. crassus* at the Christchurch and Kaikoura sites (Table 1). Therefore, the absence of *E. crassus* eggshells in this study from the Christchurch sites was unexpected. With the exception of *E. crassus*, the presence of *D. robustus*, *E. curtus* and *Anomalopteryx*

didiformis are consistent with moa distributions as reported previously (Worthy, 2009). The lack of *Pachyornis elephantopus* eggshell in the coastal sites, and the observation of minimal skeletal remains in the areas where *P. elephantopus* is known to have been present (Worthy and Holdaway, 2002), may reflect its relative rarity in many areas in the mid- to late Holocene (Allentoft et al., 2011b). We also note that eggs would only be present within archaeological sites if moa were reproducing at the time of moa hunting in that particular area, implying that potential interspecies differences in breeding times could bias the results.

An overall χ^2 test rejected with high significance the null hypothesis that the seven archaeological sites had the same relative representation of moa species ($\chi^2_{\text{likelihood ratio}} = 67.8$, df 18, $P < 0.0005$). However, because some of the sites had species with small sample sizes ($n < 5$), this result should be interpreted with caution. To partly overcome this limitation, sites within close proximity were combined into regions (see Fig. 1), reducing this sample size issue, but the significant differences in moa representation remained ($\chi^2_{\text{likelihood ratio}} = 41.0$, df 9, $P < 0.0005$). This result reflects previous findings of moa representation differences in natural sites (Allentoft et al., 2011b) and suggests that moa hunters were not preferentially targeting certain species, but rather exploited whatever was available in their region.

One problematic factor evident from using eggshells when comparing sites, and even reconstructing zooarchaeological assemblages, is potential error associated with pseudo replication. However, by combining haplotypes, determined from the mtDNA sequences together with microsatellite profiles, we eliminated this potential problem and were able to identify a minimum of 105 individual moa eggs from the 251 eggshell fragments (Fig. 3).

With the MNIE at each archaeological site determined, the level of moa exploitation can be further investigated.

In addition, χ^2 tests using the MNIE data showed that irrespective of whether the total number of eggshell fragments or MNIE data were used, significant differences of moa assemblages between regions were still maintained ($\chi^2_{\text{likelihood ratio MNIE}} = 22.6$, df 9, $P < 0.007$). Additional pairwise comparisons between the four regions illustrate differences between Marlborough and Kaikoura, Marlborough and Christchurch and Christchurch and South Otago ($0.0005 < P < 0.015$).

Moa bones from Wairau Bar were genetically assigned to the species *D. robustus* ($n = 1$), *E. crassus* ($n = 4$) and *E. curtus* ($n = 17$) (Fig. 3). The single *D. robustus* bone was associated with the human burial site (see Discussion below). Species comparisons from morphologically identified bone (assembled from often ambiguous and incomplete museum catalogues and literature) and genetically identified eggshell fragments illustrate slight differences in assemblage (Table 1). These differences could reflect how Polynesians utilised different moa remains. For example, besides being a valuable source of nutrition, bone was often carved into jewellery or to make tools (Duff, 1950; Dell and Falla, 1972), and whole eggs were also perforated at one end for possible use as water containers (Duff, 1950; Anderson, 1989). The time of site occupation could play a role in the species composition and the egg to bone ratio because, as opposed to the birds themselves, eggs were only present during moa breeding season.

The difference between eggshell-derived species identifications and those estimated from bone signifies the advantage in using novel sampling methods, when reconstructing zooarchaeological assemblages. Although morphological species assignment of intact adult moa bones has been shown to be reasonably reliable (91.3% reported in Allentoft et al. (2010)), problems can arise with fragmented or worked bone commonly encountered at archaeological sites. For example, 26 of the 27 Wairau Bar bones had a taxonomic assignment associated with them based solely on morphology (Tables S1 and S2). aDNA analyses showed that only 76% of these were accurate (16 of the 22 that yielded sufficient DNA for species identification). The problem becomes even more noticeable with eggshell, and our previous work (Oskam et al., 2011) has demonstrated that morphometrics of eggshell (specifically thickness) is a poor predictor of species identification. The accuracy afforded by genetic approaches means that the data compiled here provides the best opportunity yet to study moa exploitation during first human contact period in New Zealand.

Moa hunting practices

The MNIE values, as shown in Table 1 and Fig. 3, demonstrate a heavy exploitation of moa eggs. Eggs from at least 105 individuals were identified from the seven archaeological sites including fifty eggs identified from a single site (Wairau Bar). Moa were large, long-lived ratites and were most likely slow reproducers with small clutches (i.e. K-selected species) (Holdaway and Jacomb, 2000). The level of exploitation observed could have put the moa under extreme and unsustainable reproductive stress. An extensive dating program (currently underway) may assist in further resolving the relative contribution of predation on moa birds and eggs to the study of extinction dynamics.

For the first time, sex ratios were examined from archaeological moa bones. Of the 18 bones excavated from a single earth oven at Wairau Bar, 11 (61%) had sufficient DNA preservation for molecular sexing (Table S2). In contrast to natural fossils sites, where Bunce et al. (2003), Huynen et al. (2003) and Allentoft et al. (2010) have all consistently recorded more females than males, averaging 1 male per 2.4 females (Table 2 and S3), the bones from this oven feature showed a skewed sex ratio of 5(♂):3(♀) (1.7:1) in favour of *E. curtus* males. Also, the three bones assigned to *E. crassus* were all male and suggests that the harvest of adult moa may have been gender-biased. With the excess of male skeletal remains observed here, the null hypothesis that sex ratios are the same at paleontological and archaeological sites is rejected ($P = 0.014$) (Table 2). The excess of males may indicate an easier access to this sex. There could be several reasons for this, including males being slower, smaller and perhaps less timid. An alternative explanation is that as with other ratites (Handford, 1985), male moa were likely the primary incubators of the egg(s) (Huynen et al., 2010) and would therefore have been extremely vulnerable to predation from the moa-hunters. Allentoft et al. (2010) suggested that the lack of males found within natural fossil deposits around North Canterbury could be partly due to the males being occupied with incubation and rearing of young elsewhere. Also, it could be argued that paternal incubation was favoured in moa in order to reduce the risk of accidental egg breakage (Birchard and Deeming, 2009; Huynen et al., 2010), given that female moa were up to 200% heavier than their male counterparts (Bunce et al., 2003; Huynen et al., 2003). Considering that this is the first time that moa sex ratios have been analysed from archaeological sites, the male excess we observed is intriguing, but additional bones from other archaeological sites will need to be sexed and dated to confirm if males were indeed preferential targets.

To understand how moa hunters gathered food, it is important to address the geographical extent of their hunting grounds. To explore if the mtDNA data encoded information on the range of the moa hunters, we generated a BEAST v1.6.2 (Drummond and Rambaut, 2007) phylogenetic tree for each genus (*Dinornis*, *Emeus* and *Euryapteryx*; see Fig S2 for *Dinornis*), comprising mitochondrial control region sequences obtained from this study, along with those freely available on GenBank. No obvious genetic structuring along the east coast of the South Island is evident within the two emeids (*Emeus* and *Euryapteryx*) (data not shown), but Figure S2 illustrates a strong phylogeographic pattern in *D. robustus*, where genetic distances separate mtDNA into West Coast (WC), North and Central East Coast (NCEC) and South East Coast (SEC) clades (Fig. S2). *D. robustus* from Pounaweia (SEC) (Fig. S2, clade 2) groups closely with South and Central Otago samples (~120 km) demonstrating a geographically restricted lineage, whereas the next closest moa samples geographically from North Otago (~200 km), are mixed within the homogeneous NCEC moa. We cannot ascertain if moa within NCEC were hunted afar due to the geographically homogenous genepool in the region, but it is clear that the high genetic affiliation of the Pounaweia samples with other SEC individuals illustrate that these moa had been locally sourced. Microsatellite data and/or stable isotopic profiles from eggshell may provide a greater resolution and assist in differentiating between geographical regions.

Moa remains in human burials

In combination with diagnostic Polynesian artefacts (Brooks et al., 2009), moa remains (both eggshell and bone) found as burial offerings suggest that these remains had a high cultural value. Mitochondrial DNA species assignment was achieved in three eggshell fragments and four bone samples (including one juvenile bone) from seven burials at Wairau Bar (Fig. 2). *E.*

curtus was the dominant taxa found across the three burial groups and was identified from bone and eggshell. Interestingly, the smaller of the moa taxa, *E. crassus*, found within the midden material at Wairau Bar, was absent from the burials. In contrast, a single *D. robustus* bone was found in burial 6. This is only the second appearance of a *D. robustus* skeletal element at Wairau Bar (in burial or midden; Scofield et al., 2003). This scarcity among midden material could be because bone from the largest moa species was preferentially reworked into tools and jewellery (see Section 3.1) or, as seen here, as a high status item buried with the apparently high-ranked Group 1 burials.

Concluding remarks

The combination of both mtDNA haplotypes and polymorphic microsatellite markers from over 250 moa eggshell fragments and 18 moa bones has added significantly to our understanding of the interaction between the first New Zealand colonisers and the local megafauna they encountered. The level of detail described here regarding species composition, number of individual eggs consumed and moa sex ratios could not have been achieved without DNA technology. The intensity of moa egg collection presented here shows that moa were exploited heavily at all life stages, combining to accelerate their extinction.

The cause and timing of megafaunal extinctions are often challenging to pinpoint, as clear examples of human over-exploitation are rare. However, archaeological sites in New Zealand, in particular Wairau Bar, presented an exceptional opportunity to examine the level of exploitation of extinct megafauna. A multidisciplinary approach, combining robust radiocarbon dates and stable isotopic profiles (ongoing study) with genetically identified

eggshells (present study), will allow new insight into the interaction between the first humans in New Zealand and megafauna and will contribute to a better understanding of the process and timing of moa extinction.

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Fig. 1. Trotter, 1975 and Jacomb, 2008 and descriptions of seven significant 13th–15th century ad archaeological deposits, grouped into four ‘regions’, along the east coast of Trotter and McCulloch, 1993 and Trotter and McCulloch, 1993.

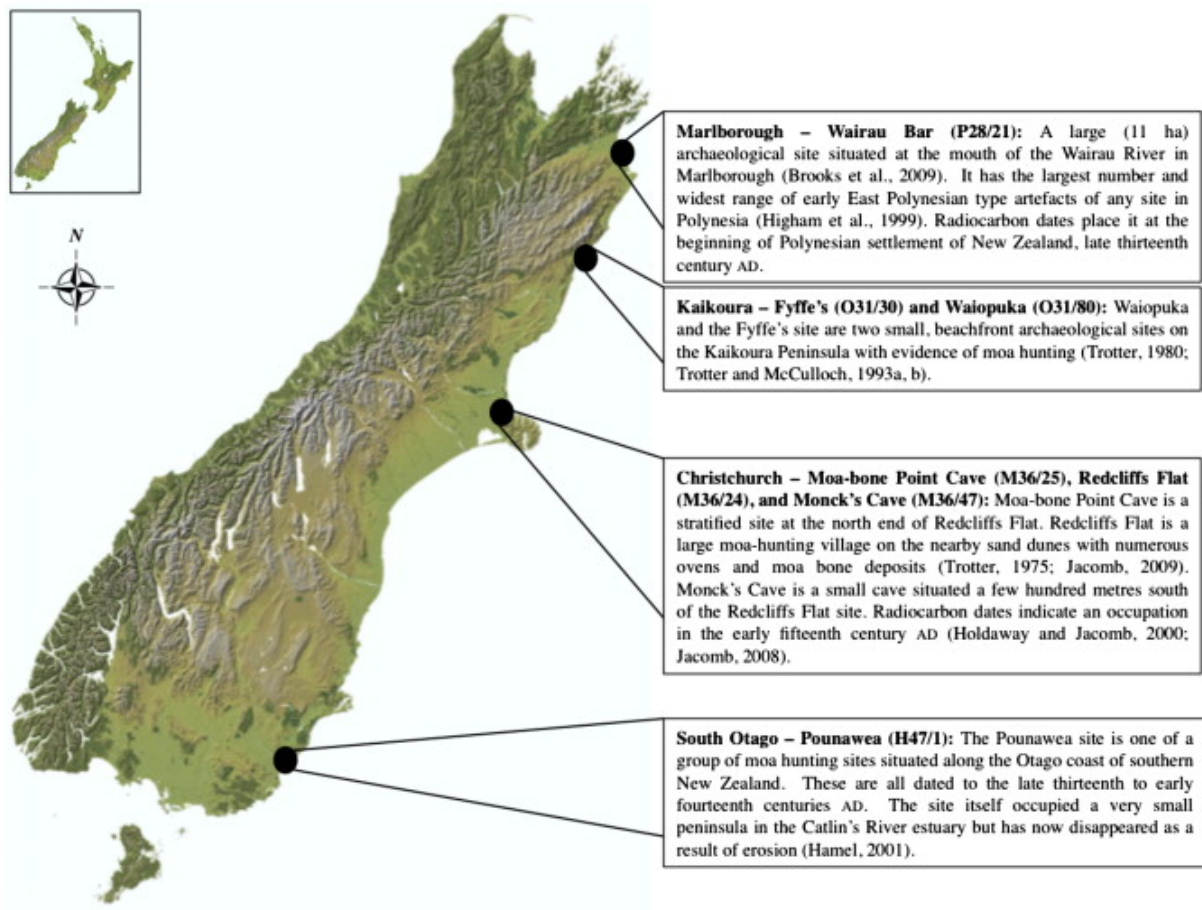


Fig. 2. Human burials at the thirteenth century ad Wairau Bar archaeological site. A) Aerial schematic of the three known cemeteries. B) Burials I–VII from burial group 1. Moa eggshell and bone icons represent specimens analysed in this study from burials III–VII. Black egg or bone = *Euryapteryx curtus*. Light Grey bone = *Dinornis robustus*. White egg or bone = undetermined. Burial VII, fragmented human and moa remains. Modified from Eyles (2007).

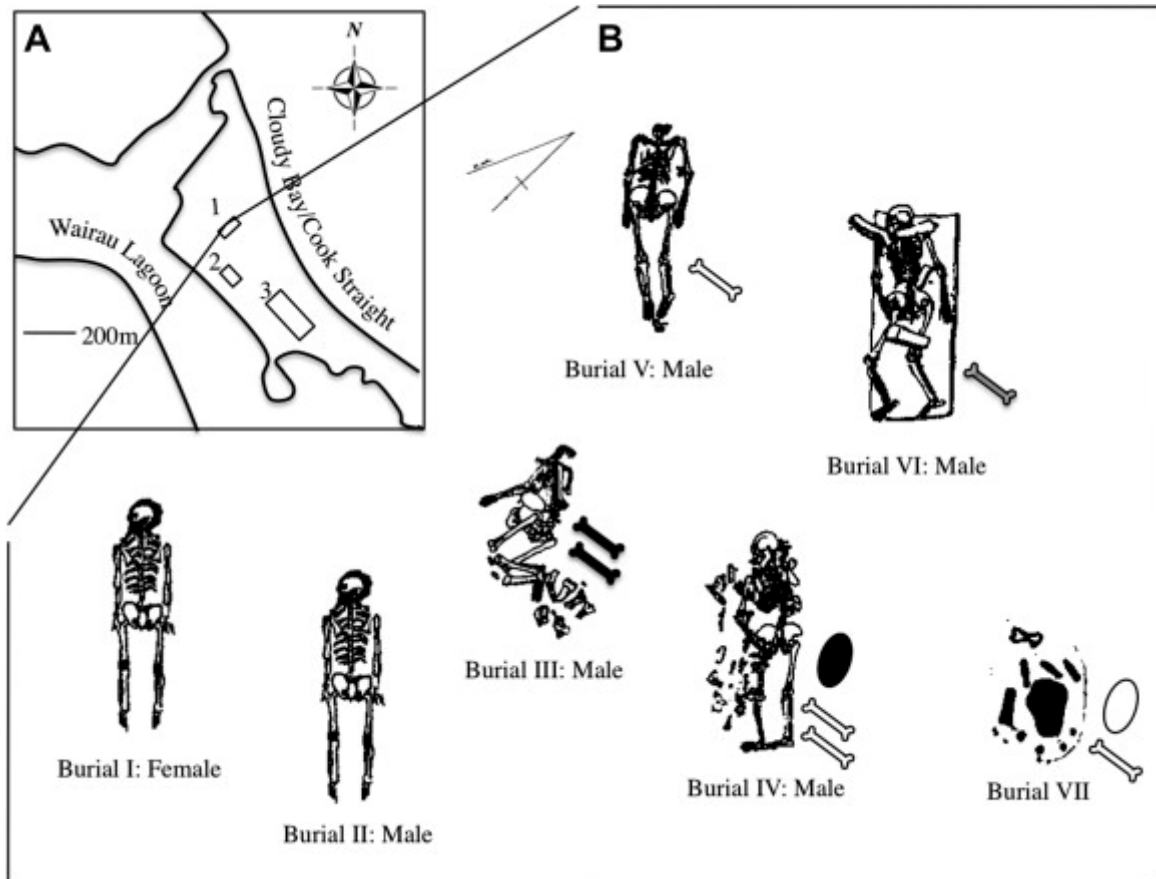


Fig. 3. Moa assemblages reconstructed through mtDNA analyses from the four key archaeological regions. Minimum number of individual eggs (MNIE) estimated using a combination of mtDNA haplotypes and polymorphic microsatellite markers. A) Marlborough. i, Eggshell; ii, Bone. B) Kaikoura. C) Christchurch. D) South Otago. Inserted key: The four represented moa taxa in this study.

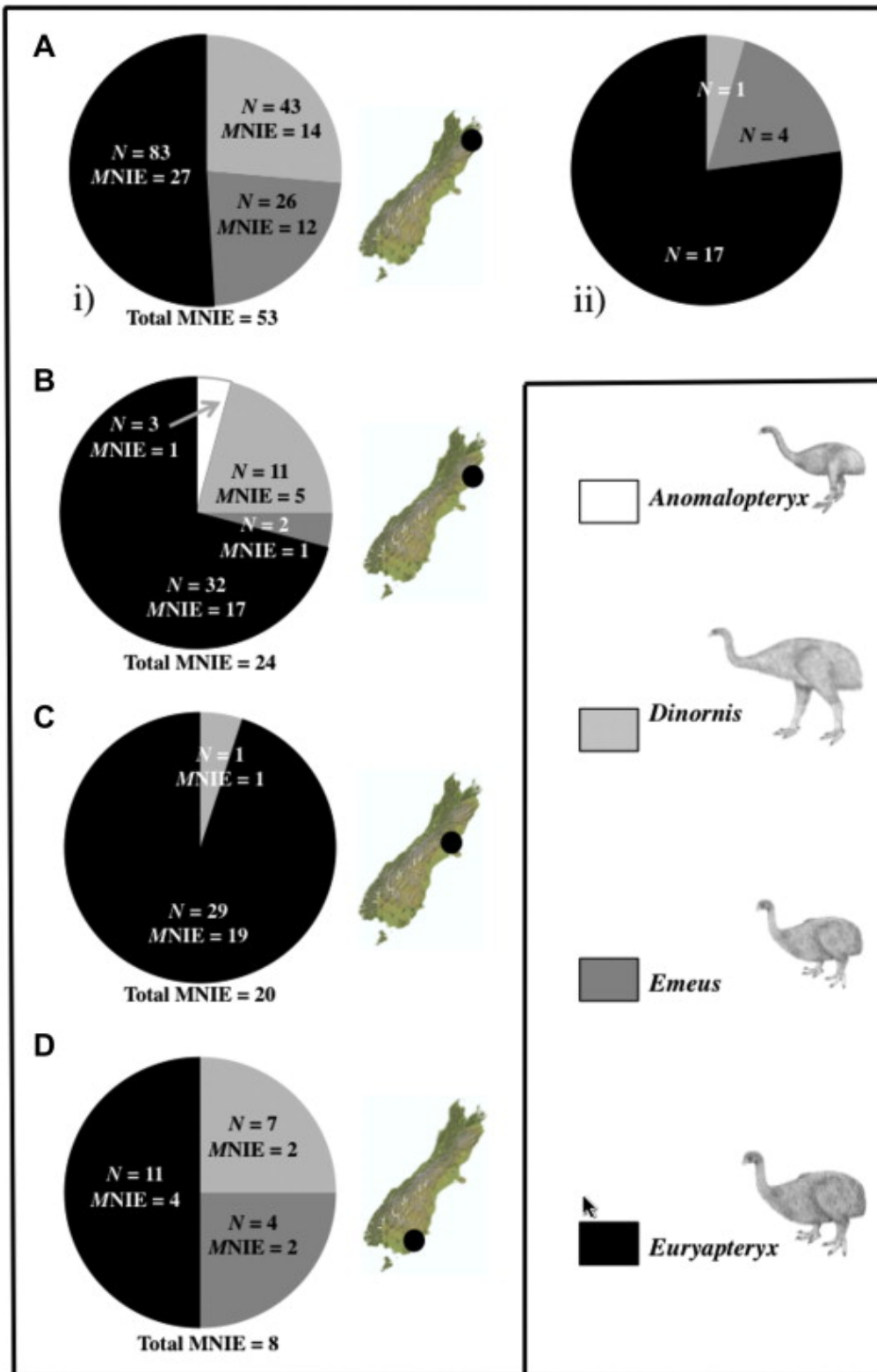


Table 1. Moa assemblages and distribution from the four key archaeological regions, determined from morphological identification of bone (literature and museum catalogued specimens) and aDNA assigned eggshell and bone (shaded).

Region	<i>Anomalopteryx</i>	<i>Dinornis</i>	<i>Emeus</i>	<i>Euryapteryx</i>	<i>Megalapteryx</i>	<i>Pachyornis</i>	Reference
Marlborough	2	1	9	36	1	1	(Scofield et al., 2003)
	–	1 (14)	4 (12)	17 (27)	–	–	– This study; (Oskam et al., 2011)
Kaikoura	X	–	X	X	–	–	– (Trotter, 1980; Anderson, 1989; Challis, 1991), CMC
	-1	-5	-1	-17	–	–	– This study
Christchurch	X	X	X	X	–	–	X (Anderson, 1989; Challis, 1995; Jacomb, 2009)
	–	-1	1	-19	–	–	– This study; (Oskam et al., 2010)
South Otago	2	–	5	3	2	1	1 (Hamel, 2001)
	–	-2	-2	-4	–	–	– This study

CMC, Canterbury Museum Catalogue. X, abundant, x, present. Values in parentheses are the minimum number of individual (MNI) eggs. Other numbers are the MNI as estimated by the original author(s).

Table 2. Moa sex ratios obtained from published paleontological deposit studies and from the present archaeological study.

Site	Reference	<i>Emeus crassus</i>			<i>Euryapteryx curtus</i>			Total		
		♂	♀	♂:♀	♂	♀	♂:♀	♂	♀	♂:♀
	Paleontological							14	33	1:2.4b
	Huynen et al. (2003)	–	–	–	6	7	1:1.13			
	Allentoft et al. (2010)	2	11	1:5.5	6	15	1:2.5			
	Archaeological							8	3	2.7:1b
	This study	3	–	–	5	3	1.7:1			