



A high-precision chronology for the rapid extinction of New Zealand moa (Aves, Dinornithiformes)



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ABSTRACT

Mega faunal extinction followed the prehistoric human settlement of islands across the globe, but the exact duration and dynamics of the extinction processes are difficult to determine. The New Zealand moa (Aves, Dinornithiformes) are a prime example, where, despite an extensive fossil and archaeological record, debate continues about their extinction chronology and how extinction timings varied among regions and species. We apply probabilistic sightings methods to 111 high-quality radiocarbon dates (from a pool of 653 dates) on moa remains from natural and archaeological sites to provide a high-resolution spatio-temporal chronology of moa extinction. We interpret this alongside an estimated time for the onset of hunting pressure, obtained by applying the same methods to the most reliable proxies for initial human settlement of New Zealand: coprolites and seeds gnawed by the commensal Pacific rat (*Rattus exulans*). By comparing local and national extinction times, we discriminate between the point at which hunting stopped (economic extinction) and the total extinction of moa (ca 150 and 200 years after settlement, respectively). Extinction occurred contemporaneously at sites separated by hundreds of kilometres. There was little difference between the extinction times of the smallest (20–50 kg) and largest (200+ kg) moa species. Our results demonstrate how rapidly megafauna were exterminated from even large, topographically- and ecologically-diverse islands such as New Zealand, and highlight the fragility of such ecosystems in the face of human impacts.

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1. Introduction

The late Holocene settlement of oceanic islands resulted in abrupt and dramatic ecological transformations (Rick et al., 2014). Nowhere is this better exemplified than on the recently settled islands of east Polynesia (Rolett and Diamond, 2004), where hunting by humans, predation by the introduced commensal Pacific rat (*Rattus exulans*), and the destruction of large tracts of forest by anthropogenic fire resulted in severe post-settlement faunal extinctions (Steadman, 1995). Across all east Polynesian islands, an estimated at least 1000 species of non-passerine land birds suffered extinction during the prehistoric period (Duncan et al., 2013), representing losses not only of community components, but also of functional diversity (Hansen and Galetti, 2009; Boyer and Jetz, 2014). Small ground-dwelling species (i.e. those vulnerable to

predation from introduced mammals) and large-bodied species (i.e. those targeted by hunters) were most susceptible to extinction (Duncan and Blackburn, 2004; Boyer, 2008).

New Zealand represents the southernmost island group of east Polynesia and was settled during the final phase of Polynesian expansion in the late 13th century CE (Wilmshurst et al., 2008, 2011), at a time of relative climatic stability (Wilmshurst et al., 2007), and probably with a founding population of 50–100 females (based on mtDNA diversity) (Murray-McIntosh et al., 1998). As with other islands across east Polynesia, the settlement of New Zealand was accompanied by a rapid fire-driven reduction in forest cover (McGlone and Wilmshurst, 1999; McWethy et al., 2009) and a wave of faunal extinctions (Worthy and Holdaway, 2002; Duncan and Blackburn, 2004). Before European settlement (c. 1800 CE), three frogs, at least one reptile, and 30 bird species went extinct (Wood, 2013). With a recent human settlement (and the associated faunal extinctions) and extensive radiocarbon dated material from natural and archaeological deposits, New Zealand presents an ideal situation for constructing a high-precision chronology of the prehistoric extinction of island megafauna.

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The flightless ratite moa (Aves, Dinornithiformes) were the largest of New Zealand's extinct avian fauna. At the time of human settlement, nine species (six genera) of moa (Bunce et al., 2009) occurred across New Zealand. These ecologically diverse herbivores (Wood et al., 2013) ranged in body mass from 20 to 250 kg, with pronounced sexual dimorphism in some taxa (Worthy and Holdaway, 2002; Worthy and Scofield, 2012). Moa had a dominantly K-selected demography, characterised by prolonged pre-reproductive periods, long lifespans and a low reproductive output (Turvey and Holdaway, 2005; Werner and Griebeler, 2012). The total moa population at the time of initial human settlement was likely on the order of 50,000–100,000 individuals (SI text), with densities possibly higher in the South than the North Island (Anderson, 1989b) due to greater levels of sympatry (Figs. S1 and S2). Moa bones are abundant in prehistoric butchery sites across New Zealand (Anderson, 1989b). Both eggs and adults appear to have been predated, with ancient DNA (aDNA) analyses of midden bones providing evidence for hunting targeting incubating males (Oskam et al., 2012). The phylogenetic structure revealed by aDNA from moa bones at individual butchery sites suggest that hunting was relatively localised (Oskam et al., 2012), although dietary reconstructions from stable isotopes are more ambiguous (Kinaston et al., 2013). Recent phylogenetic analyses suggest that moa populations were stable during the period immediately preceding human settlement (Rawlence et al., 2012), and that populations of some taxa may even have been expanding in size during the late Holocene (Allentoft et al., 2014).

While there is little doubt that human activity drove the moa to extinction (Allentoft et al., 2014), the exact mechanisms behind this extinction event and its spatio-temporal dynamics remain unresolved and continue to be debated. Population models based on best-guess estimates for moa and human demographics, and moa hunting rates, suggest the extinction window (i.e. the period from human arrival to moa extinction) may have been as short as 100 years (Holdaway and Jacomb, 2000b). Other estimates, however, suggest a more prolonged extinction window (400–500 years) after an initially intensive exploitation phase (Anderson, 1983, 1989b). It is also unclear whether all moa species shared similar extinction windows (Anderson, 1989c), or if the windows varied due to a selective hunting strategy. Extinction seems to have loosely followed the 'overkill' model (Martin, 1967) but whether it occurred contemporaneously throughout New Zealand or followed a 'blitzkrieg' rolling extinction front is again less clear (Anderson, 1989c).

Sightings methods (Rivadeneira et al., 2009) use a temporal record of historical observations to estimate the probability of extinction at some point in time, and have been applied in palaeontology to estimate extinction times for various fauna (Roberts and Solow, 2003; Solow et al., 2006; Bradshaw et al., 2012; Lima-Ribeiro and Diniz-Filho, 2014). Here, we critically examine the date of moa extinction by applying sightings methods to a georeferenced set of high-quality (based on criteria outlined in the Methods section) radiocarbon dates on moa remains from natural and archaeological deposits. We apply the same methods to high-quality radiocarbon dates on Pacific Rat coprolites and gnawed seeds (Wilmschurst et al., 2008, 2011) to estimate the time of initial human settlement for New Zealand. When combined these two estimates enable us to determine the time taken for moa to have been driven to extinction. The application of these methods allows us to evaluate moa extinction patterns in space and time (synchronicity across New Zealand) and across taxa (with respect to different body masses). By estimating the timing of initial settlement and final extinction, and taking into consideration radiocarbon dating errors via calibrated calendar distributions of radiocarbon dates, we provide the highest-precision chronology yet for the prehistoric extinction of an entire island megafaunal

guild and provide new insights into offtake rates by early moa hunters.

2. Materials and methods

2.1. Radiocarbon dates and quality control

We compiled a database of 653 radiocarbon dates from moa remains, with associated metadata including the species, locality, context, dating method, dated fraction, and citation of data source (Table S1). The remains were categorised (after Worthy and Scofield, 2012) into two adult body mass classes of 20–50 kg (*Megalapteryx didinus*, *Pachyornis geranoides*, *Anomalopteryx didiformis*) and 200+ kg (*Pachyornis elephantopus* and *Dinornis* spp.) representing the extreme ends of the body mass spectrum. We also compiled a database of radiocarbon dates on Pacific rat coprolites ($n = 5$) and rat-gnawed seeds ($n = 56$) (Table S2). To ensure that our results were not biased by the inclusion of poor-quality or imprecise dates, radiocarbon dates were only included in subsequent analyses if they met the following quality criteria: 1) the dates had not previously been categorised as poor-quality by Petchey (1997) (relates to the moa dates only); 2) the samples had been analysed using accelerator mass spectrometry (AMS); 3) the dates were on materials other than carbonate, bulk-collagen or unspecified bone fractions; and 4) the measurement error was <10% of the radiocarbon age. A large proportion of the radiocarbon dates that passed these criteria was produced since 2000, when the last quantitative estimate of moa extinction was published (Holdaway and Jacomb, 2000b), over which period there has been a marked increase in the quality and precision of radiocarbon dates from moa remains (Fig. S4). All radiocarbon dates were calibrated using the R package BChron (Parnell, 2013) and the SHCal 13 calibration curve (Hogg, 2013); all calibrated dates are reported as Cal CE and BP refers to years before 1950 AD.

2.2. Sightings methods

Sightings methods (SM) are probabilistic tools for estimating extinction or introduction dates based on a series of temporal observations. Some SM directly estimate the time of extinction or introduction (e.g. Roberts and Solow, 2003), while others (e.g. Bradshaw et al., 2012) estimate the probability of a sighting at some time in the future or past (requiring a predetermined threshold (α) for declaring a species extinct or introduced; in our analyses we use $\alpha = 0.05$). SM provide a statistically robust alternative to summing calibrated radiocarbon dates, a method that is widely used in the archaeological literature but one which has been questioned on statistical grounds (Williams, 2012). When applying SM to a fossil or archaeological record, quantifiable uncertainty exists around the timing of each 'sighting' (i.e. radiocarbon error). We dealt with this uncertainty by resampling from the 68th (1 σ) and 95th (2 σ) percentiles of the calibrated age distributions of each date under consideration to generate a large number ($n = 2500$) of synthetic sighting records. This approach accounts for uncertainties both in the age of each individual sample and the set of samples used; note that the set of calibrated 'sightings' used in each of the 2,500 records will vary, as will the date attached to each. We used two sampling ranges (68th and 95th percentiles of calibrated age ranges) to provide both narrow and conservative estimates of extinction and introduction times. We generated our synthetic sightings records using dates where the minimum boundary of the 95% calibrated age range was <1000 years BP (i.e. significantly earlier than human settlement of NZ in the 13th century). A total of 111 radiocarbon dates met both this temporal cut-off point, and the

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