

**Palaeoecology and population demographics
of the extinct New Zealand moa (Aves: Dinornithiformes)**

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Abstract

The cause(s) of the worldwide Late Pleistocene megafaunal extinctions and their effects on modern ecosystems has been debated by the scientific community since the widespread discovery of megafaunal fossils in the nineteenth century. New Zealand is a good case study because of its geographical isolation, resulting in the late colonisation of New Zealand by Polynesians in about 1280 AD. The subsequent extinction of New Zealand's megafauna, including the moa (Aves: Dinornithiformes), took place at a time of relative climatic stability, and is thought to be due to over-hunting and habitat destruction. The aim of this thesis, using moa as a case study, is to conduct a detailed examination of a megafaunal palaeoecosystem prior to the introduction of humans.

In this thesis, Chapter One reviews the literature concerning the causes and consequences of the Late Pleistocene megafaunal extinctions; the evolution of moa; New Zealand ecology; ancient DNA and its applications; and coalescent theory. The aims and structure of the thesis is then outlined.

To investigate the New Zealand palaeoecosystem using moa, it is first necessary to examine the quality of the recent moa fossil record. This is especially important because specimens used in temporal population demographic analyses need to be interpreted in the correct depositional context and timeframe. There have been a number of theories proposed to explain the deposition mechanisms of swamp deposits, or, more correctly, miring bone deposits, including large floods and stampeding during wildfires. Chapter Two discusses the taphonomy of three different New Zealand swamp deposits that were reconstructed using a novel ARC-GIS methodology specifically designed for this study. It concludes that the reconstructions are consistent with non-catastrophic periodic miring of individual moa.

To gain an insight into the faunal composition of North Canterbury, New Zealand in the Late Glacial period (10,000-14,000 years ago), and how moa responded to climate and habitat change, I led a team that re-excavated the Late Glacial Glencrieff miring bone deposit and reconstructed the palaeofauna. The analysis presented in Chapter Three shows the Glencrieff fauna was a characteristic glacial fauna, despite extensive climatic and habitat change during this period.

A new opportunity to examine moa palaeoecology has been presented by the discovery of moa coprolites. Previous reconstructions of moa diet have concluded that moa were predominantly browsers of trees and shrubs. There is considerable debate over the role of moa in the evolution of ‘anti-browsing’ growth characteristics found in many of the New Zealand flora. Chapter Four discusses the analysis of newly discovered coprolite deposits and subsequent reconstructions of moa diet. The results challenge historical perceptions of moa diet, showing there was considerable overlap in dietary preferences between different moa species, despite differences in skull and bill morphology, with the majority of plants eaten being less than 30 cm in height. In addition, plants with ‘anti-browsing’ growth characteristics were found in the coprolites, consistent with the moa anti-browsing hypothesis.

To further study moa ecology I led a genetic investigation of moa appearance using moa feathers. The current knowledge of moa plumage is limited because the majority of moa feathers are recovered as isolated specimens in caves and rockshelters, and cannot be related to specific species. In Chapter Five, ancient DNA (aDNA) is extracted from isolated sub-fossil feathers and used to identify species. Digital techniques used to reconstruct moa plumage indicate that four species of moa were characterised by either a plain brown slightly streaky plumage or a speckled plumage, with considerable overlap in plumage between species. The overlap may be due to convergent evolution of feather colour for camouflage against aerial predators as observed in many other New Zealand bird species, for example kiwi (*Apteryx* spp.), kakapo (*Strigops habroptilus*), kea (*Nestor notabilis*), takahe (*Porphyrio hochstetteri*) and weka (*Gallirallus australis*).

In Chapters Six and Seven I analyse how moa species have responded to changes in climate and habitat since the Last Glacial Maximum (LGM; 29-19 Kya in New Zealand). Ancient DNA and fossil records are used to examine the responses of the extinct crested moa (*Pachyornis australis*) and heavy-footed moa (*Pachyornis elephantopus*) to climate and habitat change. I show that crested moa tracked changes in its sub-alpine habitat since the LGM due to warming climate with little effect on population size. Concurrently, climate and habitat change promoted phylogeographic structuring and allometric size variation within heavy-footed moa. Importantly, while climate and habitat change had an effect on moa, it did not cause their ultimate extinction.

Chapter Eight further investigates the temporal population demographic methods used in Chapters Six and Seven. I discuss how sampling biases common to most aDNA datasets affect the robustness of the Bayesian Skyline Plot (BSP), a commonly used analytical method for inferring the past population demographic history of species or populations. The analyses indicate that sampling biases produced large variations in the BSP of Beringian Steppe Bison and *Pachyornis* moa, when the datasets were re-examined and re-sampled to simulate sampling biases. Importantly, this reveals the BSP may not accurately reflect the true demographic history of a species or population when analysing contemporary genetic data alone.

Finally, the thesis concludes with a discussion drawing together, and interpreting the outcomes and significance of the research and argues that the results of this research represent a significant addition to our present knowledge of the pre-human New Zealand megafaunal palaeoecosystem.

Declaration

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text.

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Gongora *et al.* 2008. Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. *Proceedings of the National Academy of Sciences of the USA* **105**: 10318-10313.

Gongora *et al.* 2008. Correction: Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA Correction. *Proceedings of the National Academy of Sciences of the USA* **105**: 14234.

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This thesis is dedicated to my late father

Grant William Rawlence

(1946-1995)

No moa, no moa,
In old Ao-tea-roa.
Can't get 'em.
They've et 'em;
They've gone and there aint no moa!

A popular New Zealand song.