

Character displacement as a mechanism for coexistence in moa (Aves: Dinornithiformes)

Nicholas Anning

Palaeobiology Laboratory, Department of Biology

Macquarie University

Supervisor: Dr John Alroy

Submission Date: 10th October 2014

Journal Style: Paleobiology

Style Guidelines (<http://www.paleosoc.org/content/AuthorContribInstr.html>)

Table of Contents

ABSTRACT.....	4
ACKNOWLEDGEMENTS.....	5
INTRODUCTION.....	6
1.1 <i>The moa</i>	6
1.2 <i>Character displacement</i>	6
1.3 <i>Hypothesis</i>	7
1.4 <i>Criteria for character displacement</i>	8
LITERATURE REVIEW	10
2.1 <i>Morphological variation in moa</i>	10
2.2 <i>Moa diet and ecology</i>	11
2.3 <i>Development of modern concepts of character displacement</i>	13
2.4 <i>Character displacement in fossil communities</i>	14
METHODOLOGY.....	17
3.1 <i>Collecting size data</i>	17
3.2 <i>Statistical analysis</i>	19
RESULTS.....	20
4.1 <i>Sites and moa species diversity</i>	20
4.2 <i>Statistical testing</i>	23
DISCUSSION.....	37
5.1 <i>Body size and femur bones</i>	37
5.2 <i>Statistical tests and fossils</i>	37
5.3 <i>Niche partitioning through habitat preference</i>	38
5.4 <i>Savannah grazers: possible analogue for moa?</i>	40
5.5 <i>Savannah strategies and their applications for moa ecology</i>	41
CONCLUSIONS.....	44
REFERENCES.....	45
APPENDIX: WILCOXON RANK-SUM TESTS.....	48

Abstract

The moa (Aves: Dinornithiformes) are an extinct group of ratite birds endemic to New Zealand. They were the dominant herbivores prior to human arrival. Analysis of coprolite data showed that moa diet varied little between species in the same area, despite each one being inhabited by three or more moa species. Many hypotheses have been proposed to explain how moa utilised niche partitioning. I aimed to test for evidence of character displacement in body size, which would influence feeding height among other ecologically significant factors. Moa were morphologically diverse in body size, which may have been partly related to displacement. Measurements of femur length and width at midshaft and distal end were taken and used as a proxy for body size. The log-transformed results were then analysed using the V statistic. Results showed that sizes were randomly distributed and not indicative of character displacement. Moa therefore did not evolve character displacement in body size. Niche partitioning may have been accomplished through the evolution of other traits, such as bite dimensions or habitat preferences.

Keywords: Palaeoecology, moa, New Zealand

Acknowledgements

To John Alroy, Nick Chan, Hayley Bell and the other members of the Macquarie University Palaeobiology Lab for their invaluable help in assembling this thesis, whether it was through supervising (thanks John!), helping me with the more technical aspects of R , sharing useful papers, proofreading, or through many, many other ways.

This study would not have been possible without the help of Paul Scofield, Kyle Davies and the staff of the Canterbury Museum, as well as Emma Burns and the staff of the Otago Museum, who allowed me to look through their respective museum collections. I would not have been able to test my methods without the help of Ross Pogson, who let me practice on the moa collection of the Australian Museum.

Finally, much thanks to my friends and family, for supporting me every step of the way.

Chapter 1: Introduction

1.1 The moa

The moa (Aves: Dinornithiformes) are an extinct group of birds that were endemic to New Zealand. Classified within the Palaeognathae, the moa are in fact most closely related to the tinamou, a group of South American birds capable of flight (Phillips et al. 2009). Ratites therefore appear to have independently lost flight multiple times, rather than sharing a flightless common ancestor (Phillips et al. 2009). Of the ratites, the moa had the most extreme adaptations for a flightless lifestyle, lacking wings or a wishbone (Worthy and Holdaway 2002). Molecular data indicates that moa underwent rapid morphological diversification around 5 Ma, coinciding with a period of geological uplift that generated increased habitat diversity across New Zealand (Bunce et al. 2009). Moa diversification appears to have been a response to new habitat types. Within these habitats the moa filled the large herbivore niche, exploiting a range of plant types (Wood *et al.*, 2012b). Evidence of their diets can be found in preserve coprolites and gizzards and will be discussed later. In turn the moa were preyed upon by the giant eagle *Aquila moorei*, their only predator until the arrival of humans (Worthy and Holdaway 2002). Along with many other bird species, the moa died out soon after human arrival. Given that the climate at the time was stable, and that there is archaeological evidence for large-scale moa hunting, humans were directly responsible for the extinction of moa (Rawlence et al. 2012).

Moa species could overlap significantly in terms of the types of plants they ate (Wood *et al.* 2008). Furthermore, fossil deposits reveal that three or more moa species coexisted in ecological communities throughout New Zealand (Worthy 1990). The overlapping diets and species density indicate that some form of niche partitioning should have occurred amongst the moa where this overlap occurred.

1.2 Character Displacement

One form of niche partitioning is character displacement, also sometimes referred to as competitive displacement. First described by Brown and Wilson (1956), character displacement is an evolutionary phenomenon found in ecological guilds worldwide. According to their definition, character displacement occurs when populations of two or more similar species that make use of the same resources are sympatric with each other (Brown and Wilson 1956). When this occurs, the populations of these species will diverge along paths that enable them to coexist,

such as evolving distinct differences in morphology that permit them to exploit different food sources (Brown and Wilson 1956). When the populations are allopatric they will more closely resemble the other species (Brown and Wilson 1956). Brown and Wilson (1956) observed this phenomenon across multiple taxa, including finches, frogs, and insects. Later studies further developed the concept of character displacement. Hutchinson (1959) suggested that there was a minimum difference in trait size that permitted sympatric populations of similar species to coexist. Hutchinson measured traits from mammals and birds that were involved in trophic interactions, such as skull length. He found that the mean ratio of the smaller forms to the larger forms was 1.3, and tentatively suggested that this was an example of the difference required for species to occur sympatrically at the same trophic level (Hutchinson 1959). Similarly, it was suggested that the mean sizes of species within the same ecological guild would be overdispersed, resulting in size ratios that were more equal than expected. This pattern was termed 'community-wide character displacement' (Strong et al. 1979).

The study of character displacement has evolved significantly in the years since the Brown and Wilson (1956). In addition, there have been several studies of character displacement within palaeocommunities. Both of these points will be discussed further in chapter 2.

1.3 Hypothesis

I hypothesise that moa species were able to coexist through size-based character displacement. As discussed above, moa varied in body size both temporally and geographically. Populations influenced by character displacement vary significantly from allopatric populations of the same species (Brown and Wilson 1956). Therefore, some of the variation in moa body size may be related to character displacement. In addition, dietary evidence suggests that moa feeding habits overlapped, sometimes to significant extents such as that found by Wood *et al.* (2008). Thus, some form of niche partitioning would have been required for moa species to coexist as they did. Niche partitioning has been previously suggested for moa by Atkinson and Greenwood (1989). However, it does not seem to have been seriously tested.

As part of a larger study on moa and their relationships with native plant taxa, Atkinson and Greenwood (1989) calculated moa body sizes. They found that the size difference between four species of *Dinornis*, also known as the giant moa, fell within

the expected ranges for Hutchinson's Ratio. This result suggested that *Dinornis* species coexisted through niche partitioning. However, more recent discoveries have made this conclusion problematic. The data used by Atkinson and Greenwood (1989) came from several sites throughout New Zealand. As moa are now known to have been varied in size between sites, this may have affected the data and produced misleading average values. Revisions of moa taxonomy have also affected these results. It is now known that *Dinornis* contains only two species, *D. novaezealandiae* and *D. robustus*, with all other previously described species being morphological variations or particular sexes (Worthy and Holdaway 2002; Olson and Tuvey 2013). This does lead to the potentially interesting conclusion that *Dinornis* may have evolved its extreme sexual dimorphism due to ecological reasons such as those discussed by Shine (1989).

Genetic data has also indicated a phylogeographic structuring of moa species (Allentoft and Rawlence 2011). This suggests that the potential for character displacement in moa species does exist.

1.4 Criteria for character displacement

As part of their study of character displacement in three-spined sticklebacks, Schluter and McPhail (1992) listed six criteria for determining whether character displacement exists.

1. Observed patterns could not occur by chance.
2. Phenotypic differences between populations must have a genetic basis.
3. Differences between sympatric species should be due to evolutionary shifts and not the inability of species to coexist.
4. Phenotypic differences should reflect differences in resource use.
5. Sites of sympatry and allopatry should not be significantly different in terms of available resources.
6. Independent evidence should be obtained to demonstrate competition.

Though designed for extant communities, it is possible to address most of the criteria in relation to the moa. The number of species in a single site, and the long evolutionary history of the moa, account for the first criterion, and the extensive work on moa phylogeny, using genetic analysis, evidence for (2) and (3) (Bunce *et al.* 2009). (4) is difficult to answer as moa resource use cannot be observed directly for obvious reasons, though it can be inferred that differences in body size could permit

moa species to feed at different heights (Atkinson and Greenwood 1989).

Palaeoenvironmental reconstructions can account for (5), but evidence for (6) is difficult, if not impossible, to acquire for extinct organisms. Despite the difficulty involved in fulfilling these criteria, most of them can be applied to this study.

Therefore, it seems very much possible that moa could have utilised body size as a means of niche partitioning.

Chapter 2: Literature review

2.1 Morphological variation in moa

There is evidence to suggest that moa species varied in size through time. Several species experienced post-Pleistocene dwarfing. In particular, moa that frequented open environments changed size as temperatures rose and fell (Worthy and Holdaway 2002). This is in accordance with Bergman's Rule, i.e., that the mean size of endothermic animals increases as they move down a temperature gradient (Worthy and Holdaway 2002). Geographic variation is also evident in moa between and within the islands of New Zealand (Worthy and Holdaway 2002).

Recent studies have found that moa also displayed sexual dimorphism. Extant ratites are sexually dimorphic, but evidence for its occurrence in moa was first found by Worthy (1987). His measurements of moa bones found that they fell into a strong bimodal distribution, implying sexual dimorphism. Ratites display reversed sexual dimorphism, where the female is larger than the male, leading Worthy (1987) to interpret the larger set of bones as female. Huynen *et al.* (2003) confirmed this interpretation through molecular analysis of DNA recovered from moa femur bones. Their results showed that the W chromosome, indicative of female birds, was consistently found in the larger bones (Huynen *et al.* 2003.). In addition to establishing that moa possessed reversed sexual dimorphism, Huynen *et al.* (2003) also found significant differences in size between male and female moa. In particular, *Dinornis* females were sometimes nearly 300% larger than the males, though this difference was not abnormal based on allometric scaling of ratite species (Olson and Turvey 2013).

Initial classifications of moa genera and species were based purely on morphology (Worthy 1988). Many species were erected based on small differences in size, resulting in 37 described moa species and a not insignificant amount of taxonomic confusion (Worthy 1988). Later studies reduced the number of moa species through studies of morphology and then later genetics (Huynen *et al.* 2003; Worthy 1988). Moa taxonomy has thus been significantly revised over the 20th century; the most current model of moa phylogeny can be seen in fig. 1. Given their taxonomic history, it is therefore important for studies into moa morphology to take into account the potential for variation.

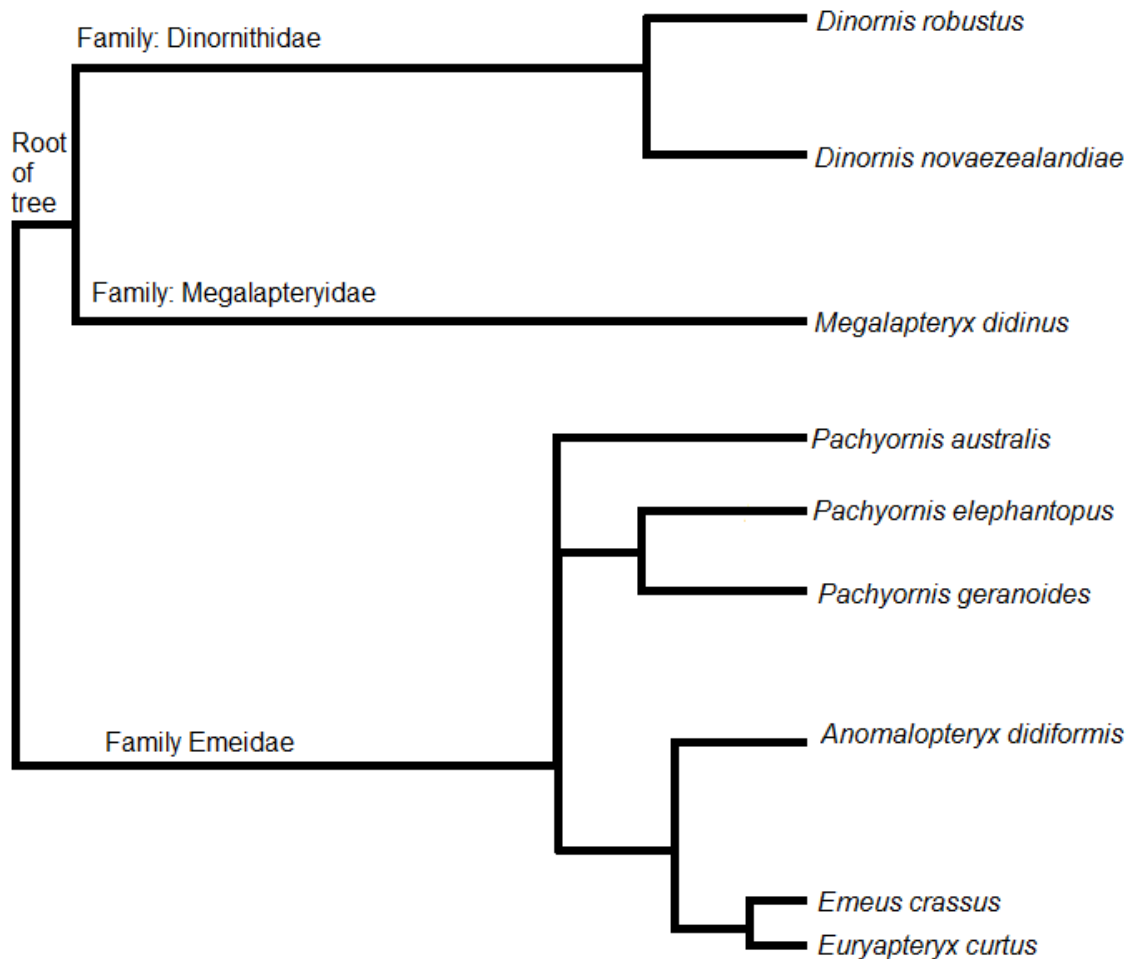


Figure 1: Modern moa phylogeny, constructed via mitochondrial control sequences. Modified from the phylogeny in Bunce *et al.* (2009).

2.2 Moa diet and ecology

The moa were the largest herbivores of the pre-human New Zealand ecosystem. Direct evidence for their diets comes from coprolites and remains of moa gizzards preserved in moa that died while mired in swamps (Worthy and Holdaway 2002). Initial studies of moa diet were controversial. They were initially inferred to have been grazers based on their body shape and size (Worthy and Holdaway 2002). Additionally, early moa workers assumed that the open environments that covered much of New Zealand were natural, rather than the result of centuries of Polynesian logging (Worthy and Holdaway 2002). In contrast to the grazing hypothesis, preserved gizzards discovered in swamp deposits held the remains of woody material, leaves and fruits, indicative of a browsing diet (Wood 2007; Wood *et al.* 2008). The contents of gizzards are potentially biased towards plant species that would have been in reach of a mired moa before its death (Wood 2007). Coprolites attributed to moa contain plant remains that indicate a broad diet including both

browsing and grazing behaviour. Moa therefore appear to have been generalist browsers and grazers, feeding on a wide variety of plants including trees, shrubs and herbs (Wood et al. 2012b). A generalist diet may have been a key reason for their success. It permitted moa to exploit different habitats and subsequently attain a wide distribution across New Zealand. Data from coprolites attributed to the upland moa *Megalapteryx didinus* support this hypothesis, as they suggest that this moa fed in the open environments of the subalpine zone during the summer and migrated to forests at lower elevations during the winter (Wood et al. 2012a).

As the largest herbivores in pre-human New Zealand, moa would have had significant evolutionary interactions with the plants they fed upon. Wood *et al.* (2012a) found intact seeds in the coprolites attributed to *M. didinus*, suggesting that moa may have also played an important role in the dispersal of some plant species. Moa may have also influenced the evolution of plant defences, as many characteristic modes of plant growth, such as divaricating branching patterns, are found across a diverse range of plant taxa native to New Zealand (Atkinson and Greenwood 1989). These have been suggested to have evolved in response to moa grazing. They could also have evolved in adaptation to environmental conditions during the Pleistocene, though Wood *et al.* (2008) note that these traits are often found on islands where birds are the dominant herbivores. It therefore appears that moa had complex relationships with native plant species. As moa became extinct only recently compared to other megafauna, their effects on native plant evolution should still be evident: taxa that relied on moa for pollination and dispersal could still be present in extant New Zealand ecosystems (Wood *et al.* 2012a). Therefore, studies of moa diet and ecology create a unique opportunity for palaeoecological reconstruction.

Curiously, despite being generalists, moa within the same area may have fed largely on the same types of plants. Wood *et al.* (2008) examined moa coprolites found in the Otago region of the South Island. The coprolites came from two broad ecological zones. The Dart river valley features a mixture of grassland, shrubland and *Nothofagus* forest, and has not changed significantly since human settlement (Wood et al. 2008). The second zone, in the central Otago region, has been heavily modified by European settlers into grazing land but was previously characterised by scrubland featuring a diverse herb flora (Wood *et al.* 2008). Neither of these areas had been altered significantly since human settlement (Wood *et al.* 2008). Three

species of moa were identified from DNA fragments found in coprolites: *D. robustus*, *M. didinus*, and the heavy-footed moa *Pachyornis elephantopus* (Wood *et al.* 2008). The data showed that while these moa consumed a wide variety of plants, the majority of their diets were composed of mostly the same species of herbs and subshrubs in similar proportions (shown in fig. 2) (Wood *et al.* 2008). More variation in moa diet occurred between sites than between species within the same site (Wood *et al.* 2008). A later analysis of pollen samples found in coprolites from the coastal moa *Euryapteryx curtus* and *P. elephantopus* indicated that, while both generalist herbivores, *E. curtus* was predominantly a browser while *P. elephantopus* was mostly a grazer (Wood and Wilmshurst 2012). There is however still significant overlap in the types of plants eaten by the other species in Wood *et al.* (2008). Dietary overlap has also been identified between the little bush moa *Anomalopteryx didiformis*, *M. didinus*, and *D. robustus* (Wood *et al.* 2012a).

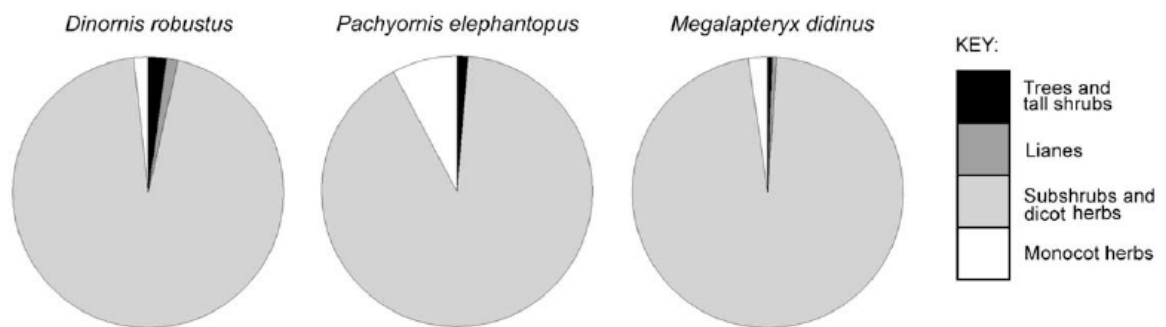


Figure 2: Diets of three sympatric moa species from the Dart River Valley, South Island. From Wood *et al.* (2008).

That moa have significantly similar diets, particularly at sites where multiple species coexisted, suggests that some other form of niche partitioning may have existed to enable this situation. It is possible that some species favoured different feeding modes, as reported by Wood and Wilmshurst (2012). Wood *et al.* (2008) suggest that niche partitioning may not have been required until food became scarce. Considering the degree of dietary overlap described by Wood *et al.* (2008), this seems unlikely. Niche partitioning has also been proposed by other authors such as Atkinson and Greenwood (1989), though it does not seem to have been seriously investigated. The lack of obvious niche partitioning in moa therefore raises significant questions about their palaeoecology.

2.3 Development of modern concepts of character displacement

Following the publication of Hutchinson (1959), many more studies appeared to recognise the 1.3 ratio, termed Hutchinson's Ratio or Rule, as a biological

constant, finding it in a diverse range of organisms (Roth 1981). The liberal application of the ratio in ecological studies led in part to criticism of Hutchinson's Ratio as a concept. In a review, Roth (1981) found that studies of the Hutchinson Ratio often liberally applied the rule without sufficiently explaining what it actually meant, resulting in a wide variety of contradictory definitions that failed to be useful. He also criticised some studies for measuring features without regard for their ecological meaning. Measuring trilobite head length, for example, had no clear relevance as the trilobites in question were inferred to have been detritus feeders (Roth 1981). Simberloff and Boecklen (1981) also found that there was insufficient evidence for elevating the 1.3 ratio to an ecological rule. It therefore appeared that Hutchinson's Ratio, and by extension character displacement, was not an ecological rule after all. MacNally (1988) suggested that the popularity of the ratio was due to its simplicity: taking measurements is significantly easier than defining concepts such as resource overlap.

The criticism of the Ratio led to the development of the modern concept of character displacement, with more rigorous procedures for testing, such as the six criteria proposed by Schluter and McPhail (1992) presented above in chapter 1.4. Schluter and McPhail (1992) were able to meet the first five criteria, though they did not yet possess the data to meet the sixth. In all other respects, however, their study found clear evidence for character displacement in their target populations. They found that in sympatric populations of sticklebacks each species exploited a different level of the water column but would feed at all depths when allopatric (Schluter and McPhail 1992). This suggests that fulfilling all six criteria may not be required to prove the existence of character displacement, and may actually be impractical (Robinson and Wilson 1994). However this does not mean that character displacement studies can simply get away with ignoring most of them, as they provide a coherent framework for study (Dayan and Simberloff 2005). Modern studies of character displacement must therefore be more rigorous in their methodologies than earlier examples.

2.4 Character displacement in fossil communities

Though the majority of character displacement studies have been performed on extant communities, several have examined fossil communities. Subjects of these studies have included Bermudan land snails (Schindel and Gould 1977), Israeli canids (Dayan et al. 1992), hyaenids (Werdelin 1996; Stynder 2009), hominids

(Schaffer 1968), trilobites (Eldredge 1974) and North American carnivores (Van Valkenburgh 1988). Studies such as these can reveal the structuring and evolution of palaeocommunities and can also be important in demonstrating the evolution of character displacement if extant species are represented in a palaeocommunity. For example, Dayan *et al.* (1992) used the canine sizes of Palaeolithic canids to infer that they were affected by different selective pressures than their extant populations.

Character displacement studies of fossils have to deal with most of the same issues as studies of extant populations, such as justifying the significance of the traits to be measured. The lack of such justification in the earliest studies was a point of much criticism (Roth 1981). Schindel and Gould (1977), looking at shell morphology in Bermudan land snails, admitted that they had no evidence explaining how shell morphology would give an ecological advantage; the features used were chosen only because they were reasonable descriptors of the overall form. Their results suggested that the snails exhibited character displacement, so shell morphology was inferred to have been of ecological significance. In particular, one extinct species exhibited significant changes in morphology compared to a species that is still extant, suggesting to Schindel and Gould (1977) that the latter was a superior competitor. After the revitalisation of the character displacement field following its eclipse in the 1980s, more rigorous justification is required for examining morphological differences than that used by Schindel and Gould (1977). In his study of Miocene hyaenids, Werdelin (1996) argued convincingly that character displacement patterns similar to modern canids should be found in the hyaenids as they filled the same niche as canids in modern ecosystems. Modern ecological studies therefore have the capacity to inform palaeoecological studies in regards to what constitutes ecologically significant features.

However, studies of character displacement in fossil species have to deal with issues inherent in palaeontological studies. There is the unfortunate fact that the fossil record is unable to offer a complete view of a community. Schindel and Gould (1977) were very fortunate to have a relatively complete series of fossils to study. It is more common to have a small sample size, often because of issues associated with the selective nature of preservation. Werdelin (1996) limited his analyses to fossil sites that contained at least four species and substantial amounts of material to create a significant sample size. Sample size can also be restricted by a lack of data on the fossils themselves. Werdelin (1996) found that some of his samples lacked

specific information on locality or position within their formation, and was forced to pool the available material into one sample. He argued that this solution was suitable as there was no evidence of significant community or environmental change over the depositional history of the site, so pooling the material should not have had significant effects on the data (Werdelin 1996). Similarly, though the ages for most of the hominids examined by Schaffer (1968) were generally agreed upon, he noted that some were in dispute. Thus a lack of data on samples is as much of an issue for palaeontological studies as a lack of actual samples.

Studies of character displacement in fossil communities can be potentially useful for reconstructing palaeoecology and the evolution of character displacement in extant communities. However, researchers need to consider that in addition to the typical aspects of character displacement studies, such as the six criteria defined by Schluter and McPhail (1992), the fossil record presents significant issues that greatly affect the feasibility of studying communities or populations, such as the selective nature of preservation.

Chapter 3: Methodology

3.1 Collecting size data

Size data were obtained through measurements of moa femur bones, based on the methods used by Worthy (1987), on the theory that femur size is a suitable proxy for body size. Length measurements were taken with tape measure and width measurements were taken with digital callipers. Measurements were taken to the nearest centimetre. Traditional callipers were used as a backup after the digital callipers failed during data collection. In addition to measuring length, two measurements of width were taken: at the midpoint and the distal end of the femur, respectively representing the thinnest and thickest parts of the bone. Figures 1 and 2 demonstrate these measurements. When femur bones were found in pairs only the right femur was used. Femora that were broken or significantly worn were not measured. A 'trial run' of this method was undertaken using moa bones in the collection of the Australian Museum (Sydney, Australia). The results were not included in the final analysis as no specific locality data were associated with the specimens.



Figure 3: Length measurement of moa femur.



Figure 4: Width measurements of moa femur bones.

To minimise the effects of temporal variation on moa body size, only material excavated from swamp deposits was used, as swamps preserve remains from only a short period of time compared to other deposits such as caves. The sites included in this study are generally within the middle to late Holocene, with the swamps having accumulated remains for periods ranging from at least 2000 years to a maximum of 5000 years (Worthy and Holdaway 1996; Worthy 1998).

There is still a preservation bias in that swamp deposits are far more frequent in lowland areas than higher altitudes (Atkinson and Greenwood 1989). The moa species in this study therefore represent species found at low altitudes, though some may have been occasional migrants, such as *M. didinus*.

Swamp sites were selected if they were known to include three or more moa species. Data were obtained from six sites: Pyramid Valley, Kapua Swamp, Glenmark Swamp, O'Malley's Swamp, Hamilton's Swamp and Enfield Swamp. Material was sourced from collections held in the Canterbury Museum in Christchurch and the Otago Museum in Dunedin, New Zealand. Material from some sites collected by the Canterbury Museum, in particular Pyramid Valley and Kapua

Swamp, had been distributed to other museums in the past. Sufficient material was still held at Canterbury to permit analysis.

For the purpose of this study, it was assumed that species were contemporaries within the confines of each site. Stratigraphic and radiocarbon dating at many sites suggests that the known species of moa did coexist (Wood et al. 2013), so this assumption is reasonable.

Sexual dimorphism within populations also needs to be addressed. This could have potentially important effects on the data, such as masking signals of character displacement. Sexual dimorphism can also be related to ecology and thus potentially character displacement (Shine 1989). There was regrettably no available means of sexing most of the genera used in this study, as DNA analysis was not an option and no values for specific male or female sizes could be obtained from the literature. An exception was *D. robustus*, which had been given sex-based cutoff values by Worthy (2005). Male and female *D. robustus* were identified as male or female based on these values and were treated as separate morphotypes. Worthy (2005) did not include any values for *D. robustus* bones from Hamilton's Swamp or O'Malley's Swamp. *D. robustus* from these sites were thus treated as one morphotype. The low numbers of *D. robustus* specimens from these two sites should mean that effects of dimorphism should be minimised.

It should be noted that femur length is negatively allometric to body size (Cracraft 1976).

3.2 Statistical analysis

Analysis of moa size data was performed using the statistical program R, with some equations performed with Microsoft Excel. The mean, standard deviation and coefficient of variation were calculated for the populations of each individual species at each site. Analysis was also performed for every combination of species pairs from each site. The data were log transformed before performing calculations.

Width data, while collected and calculated, was ultimately not used as it did not provide additional useful information compared to the length data.

The *V* statistic, originally proposed under the name *Var* by Poole *et al.* (1979) and refined by Williams (1995), was used to test for character displacement within moa populations and species pairs at each site. This statistic has been used

previously in studying community-wide character displacement in fossil communities by Stynder (2009). It has proven to be more likely than other tests (e.g. Barton-David) to detect displacement in terms of even spacing between species and less likely to misidentify displacement in clumped or random distributions (Stynder 2009). The V statistic is calculated with the following equation:

$$V = \frac{SS}{(n-1) \times (\text{Range}^2)}$$

Where SS is the sum of squared deviations from the mean of the distances between values, *n* is sample size, and *range* refers to the highest and lowest distances between values.

The resulting value is then compared with the table in Williams (1995) shown in figure 5, to determine the probability of obtaining that value and therefore the likelihood of the data given the existence of character displacement. This test assumes as a null hypothesis that the body size distribution is uniform.

Num- ber of spe- cies	.001	.0025	.005	.01	.025	.05	.10	.90	.95	.975	.99	.995	.9975	.999
3	.06500	.0312	.0125	.0500	.0312	.00125	.00500	.405	.451	.475	.490	.495	.498	.499
4	.03137	.0347	.03688	.00139	.00345	.00689	.0138	.179	.218	.249	.279	.294	.305	.316
5	.03601	.00113	.00179	.00286	.00528	.00839	.0130	.0985	.123	.145	.169	.185	.197	.211
6	.00116	.00179	.00247	.00345	.00540	.00767	.0109	.0625	.0772	.0922	.110	.122	.135	.148
7	.00137	.00196	.00259	.00342	.00494	.00654	.00868	.0432	.0530	.0631	.0762	.0853	.0939	.105
8	.00148	.00201	.00254	.00320	.00426	.00551	.00707	.0316	.0386	.0457	.0553	.0625	.0692	.0776
9	.00149	.00194	.00238	.00289	.00378	.00466	.00586	.0241	.0292	.0346	.0419	.0474	.0530	.0597
10	.00147	.00184	.00219	.00259	.00330	.00399	.00493	.0189	.0228	.0270	.0325	.0368	.0412	.0470

Figure 5: Table of values from Williams (1995). Where the value falls in the lower portion of the table indicates the significance, or not, of the result.

Chapter 4: Results

4.1 Sites and moa species diversity

Moa populations were drawn from six swamp deposits, details of which can be found in Table 1. At least four moa species occur at any given site, with at least three species – *Dinornis robustus*, *Emeus crassus* and *Pachyornis elephantopus* – occurring together at every site.

Site name	Pyramid Valley	Kapua Swamp	Hamilton's Swamp	Glenmark Swamp	Enfield Swamp	O'Malley's Swamp
Museum collection	CM	CM	CM/OM	CM/OM	CM/OM	OM
<i>Anomalopteryx didiformis</i>	-	2	1	-	-	-
<i>Dinornis robustus</i>	47	15	3	5	7	1
<i>Emeus crassus</i>	61	25	30	7	65	2
<i>Euryapteryx curtus</i>	15	-	10	4	3	13
<i>Megalapteryx didinus</i>	-	3	-	2	-	-
<i>Pachyornis elephantopus</i>	11	13	4	6	12	79
<i>Pachyornis geranoides</i>	-	-	6	-	-	14
Total individuals	134	58	54	24	87	109

Table 1: Site data, including moa species and sample sizes at each site. CM denotes Canterbury Museum, OM denotes Otago Museum.

Site	Males	Females
Enfield	5	2
Glenmark	3	2
Kapua	6	9
Pyramid Valley	9	38

Table 1: Division of sexes of *D. robustus* using the data from Worthy (2005). O'Malley's Swamp and Hamilton's Swamp were not included in Worthy's analysis, and so were left out of this analysis

4.2 Statistical testing

Site/Species	Mean
ENFIELD	
<i>D. robustus F</i>	3.637586
<i>D. robustus M</i>	3.465161
<i>E. crassus</i>	3.253307
<i>E. curtus</i>	3.343902
<i>P. elephantopus</i>	3.377885
GLENMARK	
<i>D. robustus F</i>	3.687628
<i>D. robustus M</i>	3.39852
<i>E. crassus</i>	3.234539
<i>E. curtus</i>	3.191319
<i>M. didinus</i>	3.177185
<i>P. elephantopus</i>	3.261279
HAMILTON'S SWAMP	
<i>A. didiformis</i>	3.258097
<i>D. robustus</i>	3.525205
<i>E. crassus</i>	3.270552
<i>E. curtus</i>	3.23945
<i>P. geranoides</i>	3.287926
<i>P. elephantopus</i>	3.213645
KAPUA	
<i>A. didiformis</i>	3.198465
<i>D. robustus F</i>	3.619166
<i>D. robustus M</i>	3.343689
<i>E. crassus</i>	3.270246
<i>M. didinus</i>	3.147151
<i>P. elephantopus</i>	3.378051
O'MALLEY'S SWAMP	
<i>D. robustus</i>	3.295833

<i>E. crassus</i>	3.276967
<i>E. curtus</i>	3.372952
<i>P. geranoides</i>	3.392084
<i>P. elephantopus</i>	3.397722
PYRAMID VALLEY	
<i>D. robustus F</i>	3.669993
<i>D. robustus M</i>	3.522077
<i>E. crassus</i>	3.271612
<i>E. curtus</i>	3.295375
<i>P. elephantopus</i>	3.382063

Table 2: Means of log-transformed measurements for each species.

Site/Species	Std. Dev.
ENFIELD	
<i>D. robustus F</i>	X
<i>D. robustus M</i>	0.0377149
<i>E. crassus</i>	0.119696
<i>E. curtus</i>	0.02025998
<i>P. elephantopus</i>	0.0894426
GLENMARK	
<i>D. robustus F</i>	0.07076969
<i>D. robustus M</i>	0.09033196
<i>E. crassus</i>	0.05624011
<i>E. curtus</i>	0.2838603
<i>M. didinus</i>	0.0589597
<i>P. elephantopus</i>	0.1546014
HAMILTON'S SWAMP	
<i>A. didiformis</i>	X
<i>D. robustus</i>	0.05890002
<i>E. crassus</i>	0.0767067
<i>E. curtus</i>	0.08202407
<i>P. geranoides</i>	0.06425946
<i>P. elephantopus</i>	0.1182523
KAPUA	
<i>A. didiformis</i>	0.02886551
<i>D. robustus F</i>	0.04031507
<i>D. robustus M</i>	0.02907047
<i>E. crassus</i>	0.08193223
<i>M. didinus</i>	0.09119226
<i>P. elephantopus</i>	0.07287539
O'MALLEY'S SWAMP	
<i>D. robustus</i>	X
<i>E. crassus</i>	0.02668644
<i>E. curtus</i>	0.1032158

<i>P. geranoides</i>	0.06544868
<i>P. elephantopus</i>	0.06023761
PYRAMID VALLEY	
<i>D. robustus F</i>	0.06856175
<i>D. robustus M</i>	0.05362504
<i>E. crassus</i>	0.06630676
<i>E. curtus</i>	0.08034751
<i>P. elephantopus</i>	0.04175137

Table 3: Standard deviations of log-transformed moa data. Rows marked with X indicate the standard deviation could not be calculated, due to insufficient numbers of specimens for that species or morphotype.

The Shapiro-Wilk test for the distribution of femur sizes showed that the femur sizes from all sites were not normally distributed. Subsequently, a Wilcoxon rank-sum test was performed on each pair of species in each site, which showed that the majority of moa pairs were of different sizes (Appendix). Of particular interest is the Pyramid Valley site, which showed a more significant degree of interspecies size differences than the other sites.

Site/Species	Test statistic	P-value
ENFIELD		
<i>D. robustus F</i>	X	X
<i>D. robustus M</i>	0.8382	0.16
<i>E. crassus</i>	0.7947	4.096e-08
<i>E. curtus</i>	0.75	<2.2e-16
<i>P. elephantopus</i>	0.9164	0.2896
GLENMARK		
<i>D. robustus F</i>	NA	NA
<i>D. robustus M</i>	0.8844	0.3374
<i>E. crassus</i>	0.7947	4.096e-08
<i>E. curtus</i>	0.75	<2.2e-16
<i>M. didinus</i>	NA	NA
<i>P. elephantopus</i>	0.8755	0.249
HAMILTON'S SWAMP		
<i>A. didiformis</i>	NA	NA
<i>D. robustus</i>	0.9997	0.9676
<i>E. crassus</i>	0.8849	0.003668
<i>E. curtus</i>	0.7694	0.006144
<i>P. geranoides</i>	0.8669	0.214
<i>P. elephantopus</i>	0.8825	0.3495
KAPUA		
<i>A. didiformis</i>	NA	NA

<i>D. robustus F</i>	0.898	0.2406
<i>D. robustus M</i>	0.8208	0.08975
<i>E. crassus</i>	0.8527	0.001979
<i>M. didinus</i>	0.9139	0.4311
<i>P. elephantopus</i>	0.948	0.5682
O'MALLEY'S SWAMP		
<i>D. robustus</i>	NA	NA
<i>E. crassus</i>	NA	NA
<i>E. curtus</i>	0.9531	0.6455
<i>P. geranoides</i>	0.8907	0.08273
<i>P. elephantopus</i>	0.9512	0.004345
PYRAMID VALLEY		
<i>D. robustus F</i>	0.9698	0.3862
<i>D. robustus M</i>	0.6998	0.0008758
<i>E. crassus</i>	0.8985	0.0001021
<i>E. curtus</i>	0.8695	0.03313
<i>P. elephantopus</i>	0.9107	0.2483

Table 4: Shapiro-Wilks test results, showing femur size distributions within each species. Rows marked NA indicate where the test could not be applied due to insufficient data.

The V statistics for each site are shown below. While some are suggestive of competitive displacement, no coherent patterns could be observed. Some sites are contradictory: results for Enfield show both clumped and dispersed measurements, depending on which measurement is employed.

Site/species no.	V statistic	Corresponding P value on Williams (1995) table
Enfield (5 species*)	0.049	.10/.90
Glenmark (6 species)*	0.153	.999.
Hamilton's swamp (6 species)	0.007 (.025/.05)	.025/.05
Kapua (6 species)*	0.129	.995/.9975
O'Malley's Swamp (5 species)	0.084 (.10/.90)	.10/.90
Pyramid Valley (5 species)*	0.184	.99/.995

Table 5: V statistics for each site. An asterisk denotes sites where *Dinornis* was split into two morphotypes.

It is possible that the results for Pyramid Valley were influenced by the significant skew towards females in the *D. robustus* population at that site, as they were significantly larger than the males. To acquire a more even distribution of the sexes, the four sites from the Canterbury region (Pyramid Valley, Enfield, Glenmark, and Kapua) were compiled into a single dataset. Wilcoxon rank-sum tests were then applied for moa within the Canterbury region and between moa species from Canterbury and outside the Canterbury region (Hamilton's Swamp and O'Malley's Swamp). The results are shown in the appendix. Of these, *P. elephantopus* and *P. geranoides* showed particularly significant results, as illustrated in the graphs below. After the initial tests, distal width was determined to not be a useful measurement in part because *P. elephantopus* was heavily built in general, which may have masked any signs of displacement. Later tests only examined length and midshaft width.

As *D. robustus*, *E. crassus* and *P. elephantopus* were consistently found together at each site, V statistics were calculated for these three species. As *D. robustus* was included, the Canterbury region dataset was used to obtain a more

even distribution of moa sexes. The results for these three species also showed a random distribution of body sizes.

Site	Canterbury	Hamilton's Swamp	O'Malley's Swamp
Femoral length (Williams value)	0.25 (.10/.90)	0.89 (.10/.90)	0.25 (.10/.90)

Table 6: V statistic values for *D. robustus*, *E. crassus* and *P. elephantopus*.

Chapter 5: Discussion

5.1 Body size and femur bones

In this study femur bones were used as a proxy for moa body size. Femur size has been shown to correlate to body size for many groups of vertebrates, including birds (Campione and Evans 2012; Hone *et al.* 2008; Sookias *et al.* 2012). Body size was chosen because the high levels of variation in moa size made it seem possible that this trait was affected by character displacement. Character displacement of body size as a means of lessening competition has been suggested by previous studies. Specifically, it might be a mechanism for allowing different feeding heights (Atkinson and Greenwood 1989). The scaling relationship between body size, metabolic rate and gut capacity also makes it seem possible that this trait could be influenced by character displacement (Kleynhans *et al.* 2011). As the results showed, this was not the case.

Femora were chosen as these bones are relatively numerous compared to other elements of the moa skeleton. As discussed above, the incomplete nature of the fossil record is a major problem for palaeoecological studies. Fossil communities are rarely preserved completely; a rare exception is the snails examined by Schindel and Gould (1977). Researchers attempting to examine palaeoecology must therefore deal with issues such as lower sample sizes. Werdelin (1996) encountered such problems in their study of fossil hyaenids. He was unable to acquire complete material for canine size data, which would have been a key part of his study, leading to his use of the third premolar as a replacement. Furthermore, some of the assemblages were not complete or there was no data on the provenance of remains, which also necessitated the substitution of species data from other areas or the pooling of all species from an area where data on age was lacking (Werdelin 1996). This demonstrates the types of problems and limitations that face any study of the community dynamics and evolution of fossil organisms. Moa femur bones, as the most commonly available parts of the moa skeleton, thus represented the best available means for finding evidence of character displacement.

5.2 Statistical testing

Given the diversity of moa species and their apparent dietary overlap (Wood *et al.* 2008), competitive displacement should have been present within these communities. In contrast to expectations, the V statistic indicated that there was no

competitive displacement. Size distributions were instead largely random. Some results were significant, but on the whole the results were not indicative of competitive displacement among moa.

It is possible that competitive displacement did occur, but not in terms of body size. Atkinson and Greenwood (1989) suggest that displacement may have also occurred in factors such as beak size and gizzard development. Attempting to examine these features for displacement would, however, present problems, not the least of which is sample size. Though moa remains are numerous throughout New Zealand, not all parts of the skeleton are represented equally. Robust bones such as femora and other elements of the leg are more likely to survive intact than other parts, the skull in particular.

5.3 Niche partitioning through habitat preference

As body size appears to have been of no significance in niche partitioning, moa coexistence may have been enabled by other means.

It is possible that each moa species preferred different habitat types or different feeding modes. As discussed above, Wood and Wilmshurst (2012) found that *E. curtus* and *P. elephantopus* preferred browsing and grazing, respectively, and so would have preferred different types of habitat. Habitat preferences in moa would have been particularly pronounced during the Pleistocene, when forests were restricted to higher elevations and much of New Zealand was covered in scrub and grassland (Wood *et al.* 2008). Smaller moa such as *E. curtus* would have been common in the latter habitats, while *Dinornis* species would have been restricted to the forests (Worthy and Holdaway 2002). Similarly, during the Holocene *M. didinus* lived mostly at higher elevations, but it would descend to the lowland forests during the winter as revealed by coprolite data (Wood *et al.* 2012a). Therefore, it cannot be counted as a member of the local fauna at most sites, with the exception of the Kauana swamp site from the Pleistocene where it was a permanent resident (Tennyson and Martinson 2006).

However, it would appear that moa ranges often overlapped. At least four species were found in each of the swamp sites that were used in this study, and three or four seems to have been the number of moa species commonly found at fossil sites in general (Tennyson and Martinson, 2006). Atkinson and Greenwood (1989) claim that all moa could have overlapped with each other, within the confines

imposed by the North and South Islands, and this seems to have been true even for *M. didinus*, which shared its upland environment with *D. robustus* and *Pachyornis australis* (Worthy and Holdaway 2002).

Moa may have been forced to overlap by climate changes across the Pleistocene and Holocene. Pleistocene New Zealand was dominated by scrub and grassland, but became mostly forested during the Holocene with only small pockets of open habitat (Wood *et al.* 2008). Moa that were previously separated by habitat type may have been forced to coexist, suggested by the consistent association of *D. robustus*, a forest-dwelling moa, with *E. crassus* and *P. elephantopus*, two moa that preferred the open lowlands (Tennyson and Martin 2005). This fact suggested that these three species may have evolved character displacement in relation to each other. However the V statistic for these three species at each site reveals that their sizes were just as randomly distributed as in every other set of moa species. These species would have only begun coexisting relatively recently as New Zealand became more forested during the Holocene. However it still seems likely that some form of character displacement would have evolved as it has been observed to manifest in only a few decades of two populations commencing competition (Grant and Grant 2006).

However, evidence suggests that most moa utilised forest habitats. Analysis of both natural deposits and moa-hunting sites indicate that these were formed in areas that were forested (Anderson 1984). Most of New Zealand was also covered in forest prior to human arrival. Therefore, any moa species could have been at least partially forest-dwelling (Atkinson and Greenwood 1989). Among extant ratites, moa morphology was also most similar to that of the cassowary, an extant ratite that lives in dense rainforest (Worthy and Holdaway 2002). In particular, the neck vertebrae were relatively short and the head would have been held at the level of the back (Worthy and Holdaway 2002). This posture has been suggested as an adaptation for pushing through dense forest growth (Atkinson and Greenwood 1989). It is possible that this morphology is an artefact of a preference for forests in moa ancestors, but given the high density of forest cover in the Holocene it seems likely that it would have been used for this function. Morphological and palaeoenvironmental evidence therefore suggests that all moa species not only utilised forest habitats but also coexisted with each other in these areas.

The evidence discussed above suggests that we can rule out habitat preference as a means of niche partitioning for moa.

5.4 Savannah grazers: possible analogue for moa?

Several hypotheses have been formed to explain moa niche partitioning, such as differences in feeding height (Atkinson and Greenwood 1989). We are unable to test these hypotheses through observations of moa and their ecological relationships, for obvious reasons. Therefore, modern ecosystems that feature multiple species living off the same general resource may provide clues as to how moa communities functioned. One such ecosystem is the African savannah.

The African savannah is an ecosystem characterised by a diverse array of herbivores that mostly feed upon grass. How these herbivores partition this resource has been a subject of extensive study. It has been suggested that resources were partitioned via body size, given the scaling relationship between body size, metabolic rate and gut capacity (Kleynhans *et al.* 2011). Larger animals require more food but are able to live off low-quality graze, whereas smaller herbivores require less but need higher quality food (Cromsigt and Orloff 2006). Variation in food quality was also attributed mainly to variation in plant height (Cromsigt and Orloff 2006). Additionally, large herbivores forage at coarser scales than smaller herbivores (Cromsigt and Orloff 2006). Observations of grazing herbivores in the Serengeti appeared to support this idea: as grass swards are steadily grazed down, the larger herbivores like African buffalo move away while smaller animals like gazelle remain behind (Arsenault and Owen-Smith 2008).

Evidence suggests that niche partitioning on the savannah is more complex than just being a function of body size or grass height. Savannah grazers may also partition resources based on patch size and quality (Cromsigt and Orloff 2006). As reported by Cromsigt and Orloff (2006), warthog and impala prefer shorter grasses with coarser grains, while white rhino and zebra are not observed to have a specific preference. Spatial heterogeneity could therefore be a means for herbivore niche partitioning, potentially moreso than grass or herbivore height. Similarly, Arsenault and Owen-Smith (2008) reported that observations of grazing herbivores did not follow their expected patterns of body size influencing grass height. The white rhino, despite being the largest herbivore observed by Arsenault and Owen-Smith (2008), consistently utilised the shortest grasses, while the smallest herbivore, the impala, ate at heights intermediate between those used by zebra and wildebeest. Arsenault

and Owen-Smith (2008) propose that the scaling of the bite dimensions (effective bite width divided by the cube root of the body mass) may be a more important factor for niche partitioning than body size; the wide muzzles of rhino allow them to feed efficiently on short grass, while smaller grazers with narrow mouths selectively pluck individual leaves from grass tufts (Arsenault and Owen-Smith 2008).

5.5 Savannah strategies and their application for moa

Spatial heterogeneity may have been a factor in moa niche partitioning. The term 'forest' does not indicate a single type of environment (Worthy and Holdaway 2002). Variations in forests exist, and so forest-dwelling moa species may have employed spatial heterogeneity. However, it is essentially impossible to examine this idea without being able to observe living animals, which naturally limits its application to studies of extinct species. The landscape and environments of New Zealand have also changed significantly since human settlement. The extensive forests that moa would have inhabited have been mostly cleared away by Polynesian and European settlers (Worthy and Holdaway 2002). The patches that still exist therefore may not be representative of the forest types that moa inhabited.

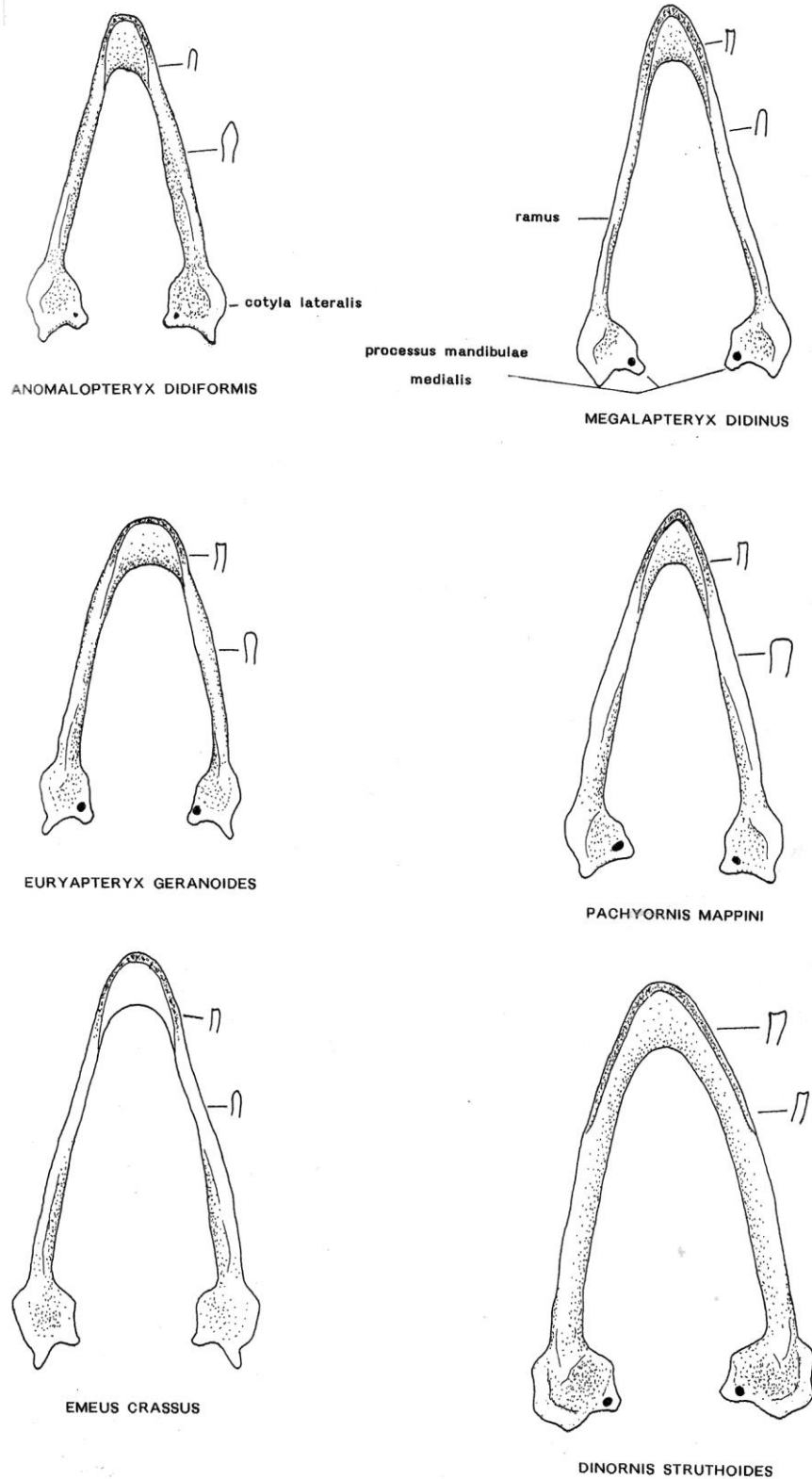


Figure 6: Mandibles from each of the six moa genera, scaled to each other to better show differences in morphology.

Note that *E. geranoides*, *P. mappini* and *D. struthoides* are now classified as *P. geranoides*, *E. curtus* and *D.*

novaezealandiae, respectively. From Worthy and Holdaway (2002).

However, it is possible to look at bite dimensions and beak structure, which may have played a role in niche partitioning among moa. Mandibles from representatives of each genus are shown in fig. 1. Only one rhamphotheca is known, from *M. didinus*, so the cutting edge of most moa beaks has to be inferred from the edges of the maxilla and mandible (Worthy and Holdaway 2002). *A. didiformis* had a short, stout beak theorised to possess a sharp cutting edge, which may have permitted it to feed on the woody, hardier parts of plants unavailable to other moa (Tennyson and Martinson 2005). Many other moa species also seem to have specialised in fibrous material (Tennyson and Martinson 2005). An exception was *E. crassus*, which had a more delicate beak than most moa (Tennyson and Martinson 2005). Gizzards from *E. crassus* contain remains of fruit and leaves, showing that it preferred soft plants (Tennyson and Martinson 2005). However, many moa still overlapped in their preference for tough plant material, in addition to the high degree of overlap reported by Wood *et al.* (2008). Given the overlap, bite dimensions may have permitted niche partitioning through allowing moa to selectively feed on different parts of plants. This hypothesis may represent an intriguing opportunity for future research. In addition to examining bite dimensions, the plant remains from coprolites and gizzards may indicate preferences for particular plant parts, but showing whether this is true depends on the remains being identifiable.

Chapter 6: Conclusions

The moa were generalist herbivores that overlapped in range and diet. In extant populations, this situation has been observed to result in character displacement, where ordered differences in trait sizes allow coexisting populations to utilise different resources and thus avoid competing. Given the noted variation in moa body size, I hypothesised that moa species could have evolved character displacement within this trait. However, applying the V statistic to measurements from moa femur bones, used as a proxy for body size, demonstrated that their sizes were randomly distributed and not indicative of competitive displacement.

As moa species overlapped in range and diet to the extent that character displacement could have evolved, niche partitioning, if it existed in moa species, must have occurred in a trait other than body size. It is unlikely to have been related to environmental preference as moa ranged widely and could essentially be found in any habitat throughout New Zealand. Examples of extant environments with many herbivores feeding on essentially the same plant types, such as the African savannah, indicate that niche partitioning could have occurred via spatial heterogeneity of patches or through different bite dimensions permitting selective feeding.

References

- Allentoft, M.E. and N.J. Rawlence. 2011. Moa's Ark or volant ghosts of Gondwana? Insights from nineteen years of ancient DNA research on the extinct moa (Aves: Dinornithiformes) of New Zealand. *Annals of Anatomy - Anatomischer Anzeiger*, 194 (1). pp. 36-51.
- Anderson, A. 1984. The Extinction of Moa in Southern New Zealand. *In* P. S. Martin, and R. G. Klein, eds. *Quaternary Extinctions*. The University of Arizona Press, Tucson.
- Arsenault, R., and N. Owen-Smith. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos* 117:1711-1717.
- Atkinson, I. A. E., and R. M. Greenwood. 1989. Relationships between moa and plants. *New Zealand Journal of Zoology* 12:67-96.
- Brown, W. L., and E. O. Wilson. 1956. Character Displacement. *Systematic Zoology* 5(2):49-64.
- Bunce, M., T. H. Worthy, M. J. Phillips, R. N. W. Holdaway, E., J. Haile, B. Shapiro, R. P. Scofield, A. Drummon, P. J. J. Kamp, and A. Cooper. 2009. The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. *PNAS* 106(49):20646-20651.
- Campione, N. E., and D. C. Evans. 2012. A universal scaling relationship between body mass and proximal limb bone dimensions in quadrupedal terrestrial tetrapods. *BMC Biology* 10(60):1-21.
- Cracraft, J. 1976. Covariation Patterns in the Postcranial Skeleton of Moas (Aves, Dinornithidae): A Factor Analytic Study. *Paleobiology* 2(2): 166-173.
- Cromsigt, J. P. G. M., and H. Olff. 2006. Resource partitioning among savannah grazers mediated by local heterogeneity: an experimental approach. *Ecology* 87(6):1532-1541.
- Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters* 8:875-894.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society* 45(315-331).
- Eldredge, N. 1974. Character Displacement in Evolutionary Time. *American Zoology* 14:1083-1097.
- Grant, P. R., and B. R. Grant. 2006. Evolution of Character Displacement in Darwin's Finches. *Science* 313(5784):224-226.
- Hone, D. W. E., G. J. Dyke, M. Haden, and M. J. Benton. 2008. Body size evolution in Mesozoic birds. *Journal of Evolutionary Biology* 21:618-624.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? *The American Naturalist* 93(870):145-159.
- Huynen, L., C. D. Millar, R. P. Scofield, and D. M. Lambert. 2003. Nuclear DNA sequences detect species limits in ancient moa. *Nature* 425:175-178.
- Kleynhans, E. J., A. E. Jolles, M. R. E. Bos, and H. Olff. 2010. Resource partitioning along multiple niche dimensions in differently sized African savannah grazers. *Oikos* 120(4):591-600.
- MacNally, R. C. 1988. On the Statistical Significance of the Hutchinsonian Size-Ratio Parameter. *Ecology* 69(6):1974-1982.
- Olson, V. A., and S. T. Turvey. 2013. The evolution of sexual dimorphism in New Zealand giant moa (*Dinornis*) and other ratites. *Proceedings of the Royal Society B* 280.
- Phillips, M. J., G. C. Gibb, E. A. Crimp, and D. Penny. 2009. Tinamous and Moa Flock Together: Mitochondrial Genome Sequence Analysis Reveals

- Independent Losses of Flight among Ratites. *Systematic Biology* 59(1):90-107.
- Poole, R. W., B. J. Rathcke, and F. G. Stiles. 1979. Regularity, Randomness and Aggregation in Flowering Phenologies. *Science* 203(4379):470-471.
- Rawlence, N. J., J. L. Metcalf, J. R. Wood, T. H. Worthy, J. J. Austin, and A. Cooper. 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.
- Robinson, B. W., and D. S. Wilson. 1994. Character release and displacement in fish: a neglected literature. *American Society of Naturalists* 144(4):596-627.
- Roth, V. L. 1981. Constancy in the size ratios of sympatric species. *The American Naturalist* 118(3):394-404.
- Schaffer, W. M. 1968. Character Displacement and the Evolution of the Hominidae. *The American Naturalist* 102:559-571.
- Schindel, D. E., and S. J. Gould. 1977. Biological Interaction between Fossil Species: Character Displacement in Bermudian Land Snails. *Paleobiology* 3(3):259-269.
- Shine, R. 1989. Ecological Causes for the Evolution of Sexual Dimorphism: A Review of the Evidence. *The Quarterly Review of Biology* 64(4): 419-461.
- Schluter, D., and J. D. McPhail. 1992. Ecological character displacement and speciation in sticklebacks. *The American Naturalist* 140(1):85-108.
- Simberloff, D., and W. Boeklen. 1981. Santa Rosalia reconsidered: size ratios and competition. *Evolution* 35(6):1206-1228.
- Sookias, R. B., R. J. Butler, and R. B. J. Benson. 2012. Rise of dinosaurs reveals major body-size transitions are driven by passive processes of trait evolution. *Proceedings of the Royal Society B* 279:2180-2187.
- Strong, D. R., Jr., L. A. Szyska, and D. S. Simberloff. 1979. Test of Community-Wide Character Displacement Against Null Hypotheses. *Evolution* 33(3):897-913.
- Stynder, D. 2009. Tooth crown form as an indicator of niche partitioning among Late Miocene/Early Pliocene hyenas from 'E' Quarry, Langebaanweg, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* 283:148-159.
- Tennyson, A., and P. Martinson. 2006. *Extinct Birds of New Zealand*. Te Papa Press, Wellington.
- Van Valkenburgh, B. 1988. Trophic diversity in past and present guilds of large predatory mammals. *Paleobiology* 14(2):155-173.
- Werdelin, L. 1996. Community-wide character displacement in Miocene hyaenas. *Lethaia* 29:97-106.
- Williams, M. R. 1995. Critical Values of a Statistic to Detect Competitive Displacement. *Ecology* 76(2):646-647.
- Wood, J. R. 2007. Moa Gizzard Content Analyses: further information on the diets of *Dinornis robustus* and *Emeus crassus*, and the first evidence for the diet of *Pachyornis elephantopus* (Aves: Dinornithiformes). *Records of the Canterbury Museum* 21:27-39.
- Wood, J. R., N. J. Rawlence, G. M. Rogers, J. J. Austin, T. H. Worthy, and A. Cooper. 2008. Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). *Quaternary Science Reviews* 27:2593-2602.
- Wood, J. R., and J. M. Wilmshurst. 2012. Pollen analysis of coprolites reveals dietary details of heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) from Central Otago. *New Zealand Journal of Ecology* 37(1):151-155.
- Wood, J. R., J. M. Wilmshurst, S. J. Wagstaff, T. H. Worthy, N. J. Rawlence, and A. Cooper. 2012a. High-Resolution Coproecology: Using Coprolites to

- Reconstruct the Habits and Habitats of New Zealand's Extinct Upland Moa (*Megalapteryx didinus*). PLoS One 7(6):e40025
- Wood, J. R., J. M. Wilmshurst, T. H. Worthy, and A. Cooper. 2012b. First coprolite evidence for the diet of *Anomalopteryx didiformis*, an extinct forest ratite from New Zealand. *New Zealand Journal of Ecology* 36(2):164-170.
- Wood, J.R., J.M. Wilmshurst, S.J. Richardson, N.J. Rawlence, S.J. Wagstaff, T.H. Worthy and A. Cooper. 2013. Resolving lost herbivore community structure using coprolites of four sympatric moa species (Aves: Dinornithiformes). *PNAS* 110(42): 16910-16915
- Worthy, T. H. 1987. Sexual dimorphism and temporal variation in the North Island moa species *Euryapteryx curtus* (Owen) and *Pachyornis mappini* Archey. . *National Museum of New Zealand Records* 3(6):59-70.
- Worthy, T. H. 1988. A re-examination of the moa genus *Megalapteryx*. . *Notornis* 35:99-108.
- Worthy, T. H. 1990. An analysis of the distribution and relative abundance of moa species (Aves: Dinornithiformes). *New Zealand Journal of Zoology* 17:213-241.
- Worthy, T. H., M. Bunce, A. Cooper, and R. P. Scofield, eds. 2005. *Dinornis*-an insular oddity, a taxonomic conundrum reviewed.
- Worthy, T. H., and R. N. Holdaway. 2002. *The Lost World of the Moa: Prehistoric Life of New Zealand*. Indiana University Press.

Appendix

Wilcoxon rank-sum tests between species pairs within sites

Enfield

Species	<i>D. robustus</i>		<i>E. crassus</i>	<i>E. curtus</i>	<i>P. elephantopus</i>
<i>D. robustus</i>	X		455/1.307e-05	21/0.02104	71.5/0.01341
<i>E. crassus</i>	455/1.307e-05		X	0/1.457e-09	156.5/0.0009239
<i>E. curtus</i>	21/0.02104		0/1.457e-09	X	14.5/0.6544
<i>P. elephantopus</i>	71.5/0.01341		156.5/0.0009239	14.5/0.6544	X

Glenmark

Species	<i>D. robustus</i>	<i>E. crassus</i>	<i>E. curtus</i>	<i>M. didinus</i>	<i>P. elephantopus</i>
<i>D. robustus</i>	X	34.5/0.006283	18/0.06506	10/0.09524	27/0.03534
<i>E. crassus</i>	34.5/0.006283	X	10/0.4868	11.5/0.2192	15.5/0.4612
<i>E. curtus</i>	18/0.06506	10/0.4868	X	6/0.4811	10.5/0.8253
<i>M. didinus</i>	10/0.09524	11.5/0.2192	11.5/0.2192	X	3/0.4018
<i>P. elephantopus</i>	27/0.03534	15.5/0.4612	10.5/0.8253	3/0.4018	X

Hamilton

Species	<i>A. didiformis</i>	<i>D. robustus</i>	<i>E. crassus</i>	<i>E. curtus</i>	<i>P. elephantopus</i>	<i>P. geranoides</i>
<i>A. didiformis</i>	X	0/0.5	10.5/0.6463	0./01175	2/1	2.5/1
<i>D. robustus</i>	0/0.5	X	90/0.004471	30/0.01231	12/0.05714	18/0.02688
<i>E. crassus</i>	10.5/0.6463	90/0.004471	X	194/0.1672	78/0.3375	77.5/0.6016
<i>E. curtus</i>	0./01175	30/0.01231	194/0.1672	X	23/0.7138	15/0.1072
<i>P. elephantopus</i>	2/1	12/0.05714	78/0.3375	23/0.7138	X	17/0.3299
<i>P. geranoides</i>	2.5/1	18/0.02688	77.5/0.6016	15/0.1072	17/0.3299	X

Kapua

Species	<i>A. didiformis</i>	<i>D. robustus</i>	<i>E. crassus</i>	<i>M. didinus</i>	<i>P. elephantopus</i>
<i>A. didiformis</i>	X	0/0.02954	8.5/0.1291	4/0.7609	0.5/0.03865
<i>D. robustus</i>	0/0.02954	X	348.5/5.63e-06	45/0.008761	141/0.04573
<i>E. crassus</i>	8.5/0.1291	348.5/5.63e-06	X	66/0.03353	46.5/0.0003103
<i>M. didinus</i>	4/0.7609	45/0.008761	66/0.03353	X	0.5/0.01178
<i>P. elephantopus</i>	0.5/0.03865	141/0.04573	46.5/0.0003103	0.5/0.01178	X

O'Malley's Swamp

Species	<i>D. robustus</i>	<i>E. crassus</i>	<i>E. curtus</i>	<i>P. elephantopus</i>	<i>P. geranoides</i>
<i>D. robustus</i>	X	1.5/1	3.5/0.5329	3.5/0.1195	1/0.1928
<i>E. crassus</i>	1.5/1	X	6/0.267	4.5/0.02262	2/0.006282
<i>E. curtus</i>	3.5/0.5329	6/0.267	X	445.5/0.441	84/0.7493
<i>P. elephantopus</i>	3.5/0.1195	4.5/0.02262	445.5/0.441	X	560.5/0.9392
<i>P. geranoides</i>	1/0.1928	2/0.006282	84/0.7493	560.5/0.9392	X

Pyramid Valley

Species	<i>D. robustus</i>	<i>E. crassus</i>	<i>E. curtus</i>	<i>P. elephantopus</i>
<i>D. robustus</i>	X	2867/<2.2e-16	705/6.609e-09	517/2.879e-07
<i>E. crassus</i>	2867/<2.2e-16	X	338/0.1126	0/1.059e-07
<i>E. curtus</i>	705/6.609e-09	338/0.1126	X	23.5/0.001998
<i>P. elephantopus</i>	517/2.879e-07	0/1.059e-07	23.5/0.001998	X

Canterbury region

Length

Species	<i>A. didiformis</i>	<i>D. robustus</i>	<i>E. crassus</i>	<i>E. curtus</i>	<i>M. didinus</i>	<i>P. elephantopus</i>
<i>A. didiformis</i>	X	0/0.01831	74/0.1936	5.5/0.08643	6.5/0.6849	4.5/0.03512
<i>D. robustus</i>	0/0.01831	X	11449/<2.2e-16	1568.5/4.439e-11	370/0.0001951	2861/5.283e-14
<i>E. crassus</i>	74/0.1936	11449/<2.2e-16	X	1248.5/0.03033	657/0.01078	1167/7.056e-11
<i>E. curtus</i>	5.5/0.08643	1568.5/4.439e-11	1248.5/0.03033	X	98/0.006832	242.5/0.001697
<i>M. didinus</i>	6.5/0.6849	370/0.0001951	657/0.01078	98/0.006832	X	9.5/0.000943
<i>P. elephantopus</i>	4.5/0.03512	2861/5.283e-14	1167/7.056e-11	242.5/0.001697	9.5/0.000943	X

Wilcoxon rank sum tests for same species from different sites

Anomalopteryx didiformis

	Length (W/P)	
Canterbury v Hamilton's Swamp	0 / 0.6667	

Dinornis robustus

		Length (W/P)
Canterbury v Hamilton's Swamp		160 / 0.2002
Canterbury v O'Malley's Swamp		73 / 0.09993
Hamilton's Swamp v O'Malley's Swamp		1.5 / 1

Emeus crassus

	Length (W/P)	
Canterbury v Hamilton's Swamp	2355 / 0.957	
Canterbury v O'Malley's Swamp	165 / 0.9194	
Hamilton's Swamp v O'Malley's Swamp	33.5 / 0.8107	

Euryapteryx curtus

	Length (W/P)	
Canterbury v Hamilton's Swamp	164.5 / 0.02594	
Canterbury v O'Malley's Swamp	82 / 0.03636	
Hamilton's Swamp v O'Malley's Swamp	19 / 0.004371	

Megalapteryx didinus

	Length (W/P)	
Glenmark vs Kapua	3.5 / 1	

Pachyornis elephantopus

	Length (W/P)	
Canterbury v Hamilton's Swamp	1299 / 0.04756	
Canterbury v O'Malley's Swamp	148 / 0.01239	
Hamilton's Swamp v O'Malley's Swamp	300 / 0.002328	

Pachyornis geranoides

	Length (W/P)	
Hamilton's Swamp vs O'Malley's Swamp	8.5 / 0.005734	