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Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes)

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ABSTRACT

The discovery in New Zealand of Late Holocene deposits of coprolites from extinct avian megaherbivores has provided a unique opportunity to gain a detailed insight into the ecology of these birds across ecologically diverse habitats. Macrofossil analysis of 116 coprolites of the giant ratite moa (Aves, Dinornithiformes) reveals a diverse diet of herbs and low shrubs in both semi-arid and high rainfall ecological zones, overturning previous models of moa as dominantly browsers of trees and shrubs. Ancient DNA analysis identified coprolites from four moa species (South Island giant moa, *Dinornis robustus*; upland moa, *Megalapteryx didinus*; heavy-footed moa, *Pachyornis elephantopus* and stout-legged moa, *Euryapteryx gravis*), revealing a larger dietary variation between habitat types than between species. The new data confirm that moa fed on a variety of endemic plant taxa with unusual growth forms previously suggested to have co-evolved with moa. Lastly, the feeding ecologies of moa are shown to be widely different to introduced mammalian herbivores.

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1. Introduction

The ecological consequences of the extinction of the Pleistocene megafauna (MacPhee, 1999; Owen-Smith, 1987) remain a contentious topic, along with the potential co-evolutionary role of megafauna in the origin of plant growth and reproduction traits (Atkinson and Greenwood, 1989; Bond and Silander, 2007; Bond et al., 2004; Burns and Dawson, 2006). Both issues have major implications for interpreting and conserving modern ecosystems, and the potential for their re-wilding (Donlan et al., 2005). However, a lack of detailed dietary evidence for nearly all extinct megaherbivore species has prevented detailed testing of these issues, or even of general palaeoecological reconstructions that might aid re-wilding attempts to reconstruct pre-human ecosystems.

New Zealand provides a unique opportunity to analyse a recently extinct megafaunal ecosystem in detail, and to test the accuracy of current approaches to palaeoecological reconstruction. The terrestrial fauna was free of mammals (except for three species

of bat) (Worthy and Holdaway, 2002), and dominated by 10 species of avian megaherbivore, the ratite moa (Aves, Dinornithiformes). There has been much debate about the palaeoecology of the different moa taxa, and their potential role in the evolution of a range of distinctive plant growth characteristics found across a taxonomically diverse range of the New Zealand flora (Atkinson and Greenwood, 1989). These unusual forms include divarication, mimicry, and heteroblasty amongst others. In contrast, hypotheses of moa-plant co-evolution have been described as “ghost stories” (McGlone and Clarkson, 1993), with at least two of the most notable growth forms (divarication and heteroblasty) also suggested to be responses to cold, arid and windy climatic conditions during the Late Pleistocene (Day, 1998; Howell et al., 2002; Rattenbury, 1962). However, it also has been noted that these forms are well represented on other islands where birds were dominant herbivores (Bond and Silander, 2007; Burns and Dawson, 2006). Because of their large, robust bodies, moa were originally interpreted as grassland grazers (as reviewed by Worthy, 1991), but analyses of several gizzard contents excavated from swamps has led to the current view that at least some genera (*Dinornis*, *Emeus*, *Euryapteryx*, *Pachyornis*) were browsers of trees and shrubs along forest margins (Burrows et al., 1981; Wood, 2007). However, the gizzards are biased towards diets in wetland and lowland forest habitats, or potentially vegetation within reach of a mired bird (Wood, 2007), and other direct evidence of diet is sparse.

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Coprolites have previously been used in palaeodietary studies of several extinct megaherbivores, but generally only for relatively low-resolution macrofossil analyses (e.g. Davis et al., 1984; Horrocks et al., 2004; James and Burney, 1997; Mead et al., 1986). Ancient DNA (aDNA) analysis provides the opportunity to identify both the defecating species and the dietary components, but the few studies of megafaunal coprolites have featured limited numbers of samples and have generally only been able to resolve floral components to order or family level (Hofreiter et al., 2000, 2003; Poinar et al., 1998). The only two palaeodietary studies of extinct avian herbivore coprolites (Horrocks et al., 2004; James and Burney, 1997) were limited by small sample sizes, and did not use aDNA so could only infer the identity of the defecating species. In New Zealand, Late Holocene coprolites of the extant kakapo (*Strigops habroptilus*), a large flightless parrot, have also been studied (Horrocks et al., 2008).

Moa coprolites could potentially provide dietary information across a broad range of habitats for the ten currently recognised moa species, but have only been rarely reported. We excavated rockshelter and cave sites from across southern New Zealand and recovered almost 2000 avian coprolites across a broad geographic area. From a subset of these we used plant macrofossils and aDNA to analyse the dietary specialisations of three sympatric moa species in two distinct ecological zones, in order to complement current moa palaeoecological reconstructions and investigate the issue of moa-plant co-evolution.

2. Regional setting

The newly identified coprolite deposits are located in the Otago region, South Island, New Zealand (Fig. 1). These occur in two broad ecological zones. First, Daley's Flat is situated in the Dart River Valley, a glacially-carved valley in West Otago, that receives >1.5 m mean annual rainfall (Tait et al., 2001). The coprolites were collected from dry shelters beneath large boulders (within a ca 60 ha rockfall deposit) in closed canopy silver beech (*Nothofagus menziesii*) forest, although grassland and patchy scrub occur in places on the valley floor. Despite a lack of palaeovegetation data from West Otago, other evidence suggests the vegetation is

relatively unmodified compared to the pre-settlement situation. Pollen records from similar montane valley sites along central South Island (Burrows and Russell, 1990; McGlone et al., 1997, 2004; Moar, 1971, 1973) indicate a non-synchronous but repeated pattern of post-glacial shrubland establishment (14,000–10,000 years BP), followed by spread of tall podocarp forest (13,600–7500 years BP) and later expansion of *Nothofagus* dominated forest (>7500–2000 years BP). Present forest patterns in the mid- to upper-valley (around Daley's Flat) (Mark, 1977) suggest little or no post-settlement loss of forest, which is characteristic of central and eastern regions of South Island (e.g. McGlone, 2001; McGlone and Moar, 1998), although some reduction of palatable plant species in the forest understorey is likely due to introduced mammalian herbivores. In contrast, Central Otago is non-glaciated and has a semi-arid climate. Coprolites were excavated from four rockshelters (Sawers', Kawarau, Roxburgh Gorge B and Roxburgh Gorge C) (Fig. 1), located in river gorges that receive <500 mm mean annual rainfall (Tait et al., 2001). The present vegetation of Central Otago is highly modified due to anthropogenic burning, widespread land clearing for pastoralism in the 19th Century, and a suite of introduced grasses and weeds. Pre-settlement vegetation in the Central Otago lowlands was characterised by low shrubland and diverse herbs (McGlone and Moar, 1998; Wood and Walker, 2008).

3. Materials and methods

3.1. DNA extraction, PCR and sequencing

DNA extractions were carried out on a sub-sample of 43 of the coprolites on which macrofossil analysis was performed (22 from Dart River Valley and 21 from Central Otago), in the physically isolated, dedicated ancient DNA facility at ACAD (Australian Centre for Ancient DNA, University of Adelaide) following standard ancient DNA procedures (Cooper and Poinar, 2000). Coprolite pieces were ground to a fine powder using a Mikrodismembrater (Braun) and tungsten ball bearings. The powder was hydrated for 24 h in 10 mL of 10 mM Tris–HCl, pH 8.0. DNA was extracted from up to 0.6 g of hydrated powder using the MoBio Power Soil Kit following the

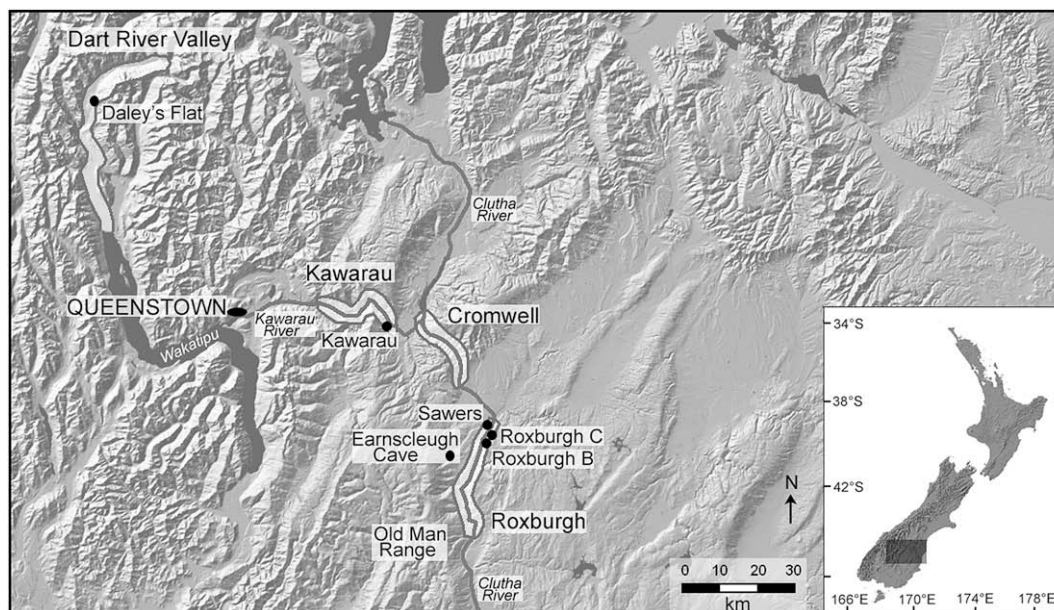


Fig. 1. The Otago region, South Island, New Zealand, showing the location of moa coprolite deposits studied, and the three Central Otago river gorges (Kawarau, Cromwell and Roxburgh).

manufacturer's instructions. Multiple negative extraction controls were included with each batch of extractions. Repeat extractions of a subset of the coprolites were performed to confirm that sequence results and specific status of the defecator was authentic. The defecating moa species were identified using mitochondrial DNA control region sequences (see Supplementary data), following PCR amplification of fragments of 200 bp, 48 bp, 31 bp or 11 bp in length (excluding primers) from each coprolite DNA extract. Moa nomenclature used here is based on that of Worthy and Holdaway (2002), incorporating subsequent revisions (Bunce et al., 2003; Huynen et al., 2003; Worthy, 2005).

PCR reactions were conducted in 25 µL volumes containing 2 mg/mL RSA (Sigma), 1× PCR buffer (Platinum, Invitrogen), 2 mM MgSO₄, 200 µM dNTPs, 1 µM each primer, 1 unit Platinum Taq HiFi (Invitrogen), 1–2 µL DNA. PCR reactions were set up in the ancient DNA facility at ACAD. Multiple negative PCR controls were included with each batch of PCR amplifications. PCR conditions were as follows: 94 °C 3 min; 55 cycles of 94 °C 30 s, 55 °C 30 s and 68 °C 45 s; followed by 68 °C 10 min, then holding at 15 °C. The PCR amplification reaction and all downstream procedures were carried out in the ACAD post-PCR lab on the main campus of the University of Adelaide.

PCR products were visualised on 4% 1× TBE agarose gel. PCR products >100 bp (including primers) were purified using the AMPURE magnetic bead system (Agencourt) following the manufacturer's instructions. Those <100 bp (including primers) were purified using EXOSAP (4 units Exo1, 0.6 units SAP) by incubation at 37 °C for 30 min and 80 °C 15 min.

PCR products were sequenced in both directions using the M13USP, M13RSP or PCR primers (see Supplementary data) using Big Dye Terminator technology (BigDye v3.1) and separated on an ABI 3130XC capillary sequencer. Sequences obtained from the coprolites have been deposited in the GenBank database (accession numbers FJ214598–FJ214618), and are provided in the supplementary information.

3.2. Macrofossil analysis

Plant taxa browsed by moa were determined from macrofossils preserved within coprolites. A sample of 116 coprolites (81 from Dart River Valley and 35 from Central Otago), identified as likely belonging to moa due to their large size, were selected for macrofossil analysis. Approximately 10–20% of each coprolite was removed for DNA analysis. The remaining portion was softened in a standard household detergent solution for 2–3 weeks and then disaggregated by gentle mashing. Sediment from each disaggregated coprolite was examined in a Petri dish under a dissecting microscope at 10–40× magnification. All seeds, leaf cuticle fragments and invertebrate remains were picked from the dish with fine forceps and stored in glass vials of 70% ethanol. Seeds were identified using reference images (Webb and Simpson, 2001), and by comparison with specimens in the Otago Regional Herbarium, New Zealand. Where greater detail was required for identification, seeds were examined using a Cambridge scanning electron microscope. Leaf cuticles were mounted in glycerol on glass slides, and identified by comparison with the Allan Herbarium cuticle photograph reference collection, Lincoln, New Zealand. Remaining coprolite sediment residues and associated plant macrofossils are held at Otago Museum, Dunedin, New Zealand (OM Av10656–10767).

3.3. ¹⁴C age determination

AMS radiocarbon dates were obtained for coprolites or contemporaneous organic sediment from three rockshelters. Samples underwent standard ABA pre-treatment and

graphitisation at Waikato Radiocarbon Dating Laboratory, and were analysed at Rafter Radiocarbon Laboratory. Radiocarbon dates were calibrated using the Southern Hemisphere calibration curve (McCormac et al., 2004).

3.4. Statistical analyses

Differences in coprolite seed assemblages between moa species in Dart River Valley, and between Central Otago and Dart River Valley, were assessed using the general linear model function of the statistical program Minitab v.15. Seed count data (see Supplementary information) were log₁₀-transformed prior to analysis and residuals were plotted to ensure normality. Potential moa preferences for different plant types (differences between percentage of seeds in coprolites and bulk rockshelter sediments) were assessed by two-sample *t*-test.

4. Results

4.1. DNA identification

Of the 43 coprolites analysed for moa DNA, 24 were positively identified as moa (Fig. 2). Extractions of the remaining 19 either failed to amplify, or amplified DNA fragments of the incorrect length. It was noted that the majority of coprolites that gave amplifiable moa DNA had relatively hard exteriors, and this, along with constant aridity of the deposition site, may be important factors for DNA preservation in coprolites. A single clean sequence

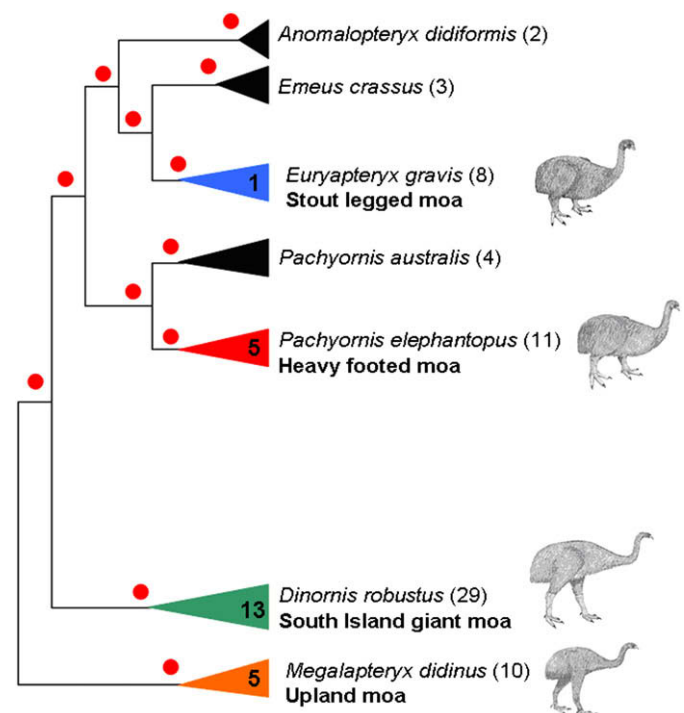


Fig. 2. Maximum parsimony strict consensus phylogeny (ten random sequence addition replications, 500 bootstrap replicates) of reference moa (2914 bp of concatenated CR, 12S, COIII, ATP6, Cyt b, ND3, ND4, ND5, tRNA Lys or 379 bp CR data depending on specimen) constructed using PAUP*4.0b10. All major branches and clades in the phylogeny below have bootstrap values greater than 90% (represented by red dots above the relevant branches/clades. See Supplementary figure 2 for phylogeny). To determine specific defecator status, partial control region sequences from moa coprolites were placed onto this phylogeny using a full heuristic maximum parsimony search with the bootstrap phylogeny as a backbone constraint. Highlighted clades contain sequences from moa coprolites, with the number in the clade representing the number of coprolite sequences obtained. Numbers in brackets next to the species designation for each clade represent the number of sequences within a given clade.

(i.e. not multiple sequences, indicative of more than one PCR product the same size) was obtained from each coprolite sample, and sequences from repeat extractions and PCRs were identical to the initial results. Comparison of the sequences against a comprehensive database of moa control region sequences (77 published and 300 unpublished sequences, encompassing the entire geographic range of each species in the South Island) was sufficient to identify the moa species which had deposited each coprolite. Because only a single sequence was obtained from each sample, and the samples were taken from the coprolite interior, the results are assumed to be from the depositing individual, rather than the result of contamination within the rockshelter sediments.

DNA sequences identified coprolites from four moa species: *Dinornis robustus* (South Island giant moa, $n = 13$), *Megalapteryx didinus* (upland moa, $n = 5$), *Pachyornis elephantopus* (heavy-footed moa, $n = 5$), and *Euryapteryx gravis* (stout-legged moa, $n = 1$). The single *E. gravis* coprolite provided only an 11 bp sequence that is identical in both *E. gravis* and little bush moa (*Anomalopteryx didiformis*), but was identified as the former species because bones of *A. didiformis* are not known from Central Otago (Worthy, 1998; Wood, 2008a). This tentative identification is not important in the interpretation of the results. The other 92 coprolites could be attributed to moa on the basis of size and morphological similarity with the identified specimens, although as no inter-specific variation in coprolite morphology was detectable (Fig. 3) these could not be assigned to species. The species identifications obtained for coprolites by aDNA analysis fit those expected from known Holocene moa distributions, based on analysis of fossil bone deposits. Coprolites of *D. robustus*, *P. elephantopus* and *M. didinus* were identified from Dart River Valley, and bones of all three species were found beneath rockshelters in the immediate

area. Coprolites of *P. elephantopus*, *M. didinus* and *E. gravis* were identified from Central Otago, and were all common in the region during the Holocene (Worthy, 1998).

4.2. Macrofossils

Coprolites were mostly comprised of amorphous organic material interpreted as digested leaf, fruit or woody tissues. Identifiable plant macrofossils (Table 1) were dominated by seeds (recognised in 58.6% of coprolites examined), although intact leaves, leaf margins, thorns and cuticle fragments were also present. Few wood fragments were recovered, and none were large enough to identify by microstructural analysis. Frequent intact seeds permitted high resolution (typically to species) analysis of the taxonomic diversity and composition of plant taxa eaten. Remains of at least 18 plant taxa were identified in coprolites from Dart River Valley, and at least 19 in the coprolites from Central Otago, with 7 taxa common between both regions (Table 1). Invertebrate remains were also present in the coprolites, but were not frequent enough to dismiss their accidental ingestion with vegetation. Identified remains included fragments of beetle, oribatid mites, and post-depositional fly exuviae.

4.3. Coprolite ages

All calibrated radiocarbon ages of coprolite horizons in Central Otago rockshelters were < 3500 years BP (Table 2) and the similar stratigraphy observed in undated sites suggests contemporaneity (Wood and Walker, 2008). The exact age of the coprolites from Dart River Valley is not known, although they must post-date the retreat

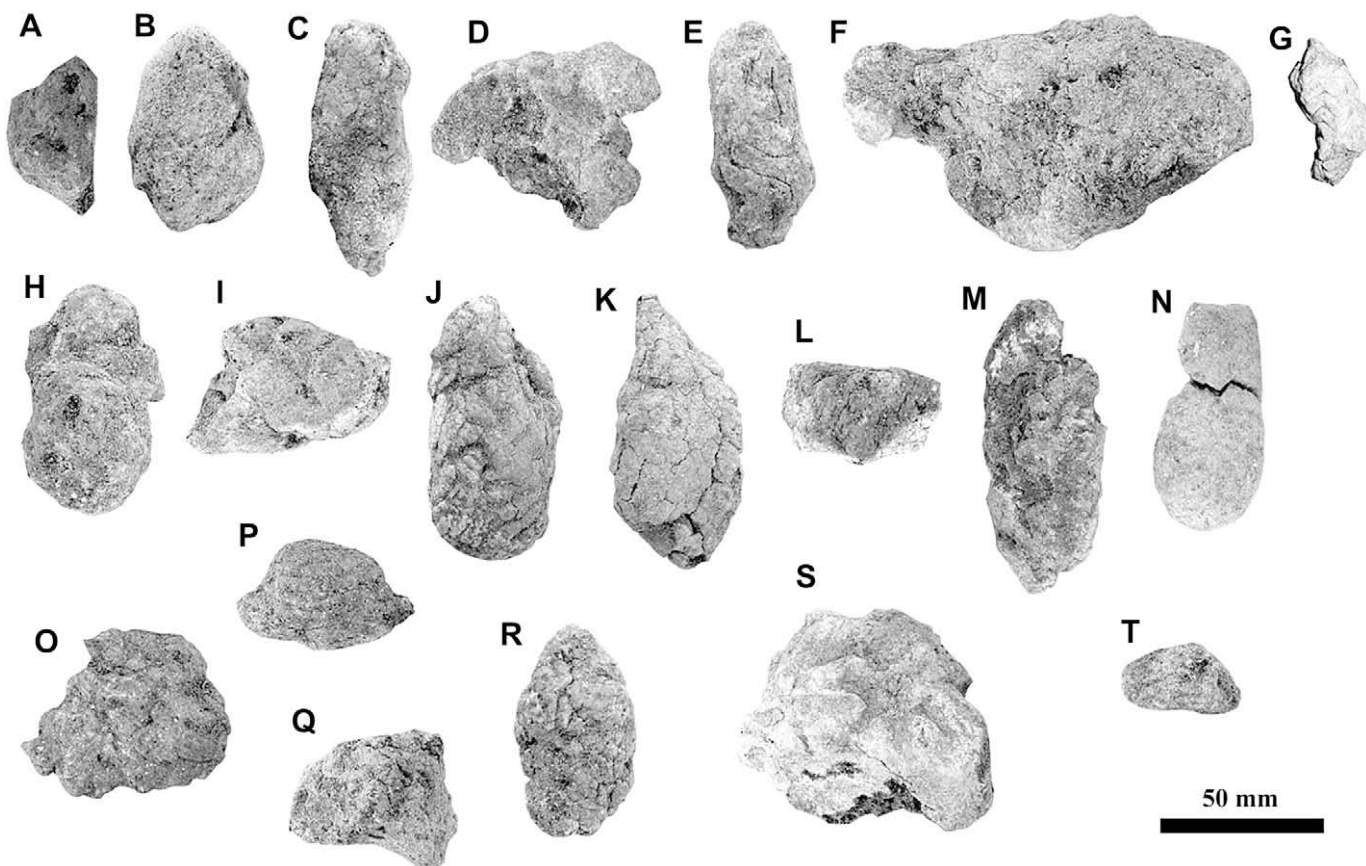


Fig. 3. Morphology of coprolites from three moa species identified from a DNA analysis: A–C, *Pachyornis elephantopus*; D–H, *Megalapteryx didinus*; I–T, *Dinornis robustus*. All coprolites shown are from Dart River Valley, except G (from Old Man Range, Central Otago).

Table 1
Summary of macroremains identified from moa coprolites

Plant taxa	Dart River Valley				Central Otago			
	<i>Diro</i>	<i>Pael</i>	<i>Medi</i>	Unid.	<i>Pael</i>	<i>Medi</i>	<i>Eugr</i>	Unid.
	(n = 13)	(n = 3)	(n = 4)	(n = 61)	(n = 2)	(n = 1)	(n = 1)	(n = 31)
Trees and tall shrubs								
<i>Carmichaelia</i> sp.	–	–	–	0.02 s	–	–	–	–
<i>Coprosma</i> spp.	0.46 s	0.67 s	0.25 s	0.20 s 0.07 l	0.5 l	–	–	0.03 s
<i>Coprosma</i> or <i>Olearia</i>	–	–	–	–	4 l	–	1 l	0.10 l
<i>Hebe</i> sp.	–	–	–	–	–	–	8 s	–
<i>Meliccytus</i> sp.	–	–	–	–	0.5 s	–	–	0.03 s
<i>Nothofagus menziesii</i>	0.08 l	–	–	0.02 l	–	–	–	–
<i>Olearia</i> sp.	–	–	–	–	–	–	1 s	–
Gymnosperm	–	0.33 s	–	0.05 s 0.02 l	–	–	–	–
	0.46 s 0.08 l	1 s	0.25 s	0.27 s 0.11 l	0.5 s 4.5 l	–	9 s 1 l	0.06 s 0.10 l
Lianes								
<i>Muehlenbeckia axillaris</i>	0.31 s	–	0.25 s	0.18 s	1.5 s	–	–	0.55 s
<i>Rubus</i> sp.	–	–	–	–	–	–	–	0.6 s 0.32t
	0.31 s	–	0.25 s	0.18 s	1.5 s	–	–	1.15 s 0.32t
Subshrubs and dicot herbs								
<i>Ceratocephala pungens</i>	–	–	–	–	0.5 s	–	–	0.48 s
<i>Colobanthus</i> sp.	–	–	–	–	–	–	–	0.06 s
<i>Coprosma petriei</i>	5.77 s	6 s	11.75 s	1.34 s	–	–	–	–
<i>Coriaria plumosa</i>	5.23 s	–	1.5 s	0.23 s	–	–	–	–
<i>Einadia triandra</i>	–	–	–	–	3 s	–	–	0.48 s
Chenopodiaceae cf. <i>E. allanii</i>	–	–	–	–	–	–	–	1.68 s
<i>Gaultheria crassa</i>	1 s	–	0.5 s	1.82 s	–	–	–	–
<i>Gonocarpus aggregatus</i>	0.38 s	0.67 s	0.5 s	0.11 s	–	–	–	–
<i>Lagenifera pumila</i>	0.08 s	1.33 s	0.25 s	0.13 s	–	–	–	–
<i>Leucopogon fraseri</i>	1.69 s 3.85 l	4.33 s 11 l	10.5 s 5.25 l	1.85 s 2.16 l	–	–	–	0.06 l
<i>Myosotis pygmaea</i> s.l.	–	–	–	–	–	–	–	0.03 s
<i>Myosurus minimus novae-zelandiae</i>	–	–	–	–	–	–	–	0.58 s
<i>Oxalis exilis</i>	–	–	–	–	–	–	–	0.71 s
<i>Pratia angulata</i>	0.08 s	–	0.25 s	0.15 s	–	–	–	–
<i>Ranunculus gracilipes</i>	0.46 s	77 s	16.5 s	1.7 s	–	–	–	–
<i>Ranunculus</i> sp.	1.23 s	3 s	1 s	0.13 s	–	1 s	–	–
<i>Urtica incisa</i>	0.15 s	1.33 s	0.5 s	0.7 s	–	–	–	–
<i>Wahlenbergia pygmaea</i>	0.23 s	–	0.25 s	0.15 s	–	–	–	–
Unidentified	–	–	–	–	–	c	–	c
	16.3 s 3.85 l	93.66 s 11 l	43.5 s 5.25 l	8.31 s 2.16 l	3.5 s	1 s	–	4.02 s 0.06 l
Monocot herbs								
<i>Carex</i> sp.	0.38 s	7.67 s	1 s	0.25 s	–	–	–	0.58 s
<i>Juncus</i> sp.	–	0.33 s	–	0.02 s	–	–	–	1.35 s
Poaceae	–	–	–	–	1.5 s	–	–	0.06 s
Unidentified	–	–	–	–	–	c	–	c
	0.38 s	8.0 s	1 s	0.27 s	1.5 s	–	–	1.99 s
Invertebrate fragments								
	0.15	1.67	–	1.10	2	3	–	0.61

Data are mean number per coprolite; bold numbers are totals. Moa species are: *Diro*, *Dinornis robustus*; *Pael*, *Pachyornis elephantopus*; *Medi*, *Megalapteryx didinus*; *Eugr*, *Euryapteryx gravis*; Unid., unidentified. Macroremains are: s, seeds; l, leaves; t, thorns; c, leaf cuticle.

Table 2
Radiocarbon dates from sites associated with moa coprolites examined in this study

Lab. no.	Site	Material dated	$\delta^{13}\text{C}$ (‰)	$\delta^{14}\text{C}$	% modern	Radiocarbon age, years BP	Calibrated age (2 s.d.), years BP
Wk-16348	Kawarau Gorge rockshelter	Coprolite (27 cm depth)	-29.1 ± 0.2	-122.9 ± 3.3	88.1 ± 0.4	1017 ± 34	954–795
Wk-16382	Roxburgh Gorge rockshelter B	Plant material from coprolite layer	-26.0 ± 0.2	-306.8 ± 8.6	69.5 ± 0.9	2928 ± 100	3319–2778
Wk-19082	Sawyers' rockshelter	Plant material from coprolite layer	-27.8 ± 0.2	-205.7 ± 3.0	79.5 ± 0.3	1843 ± 35	1823–1605
NZA-4615	Earnsclough Cave	<i>Euryapteryx gravis</i> bone	-24.37	?	?	2176 ± 76	2322–1930
NZA-4596	Earnsclough Cave	<i>Sceloglaux albifacies</i> bone	-19.78	?	?	1552 ± 68	1528–1295

Ages are calibrated using Southern Hemisphere Calibration Curve (McCormac et al., 2004). Dates for Kawarau Gorge, Roxburgh Gorge and Sawyers' rockshelters from Wood and Walker (2008), and Earnsclough Cave from Clark et al. (1996).

of the Dart Glacier beyond Daley's Flat, and therefore are probably also of mid to late Holocene age.

4.4. Moa diet and habitat

The coprolite contents show that all the moa taxa consumed a diverse range of plants (at least 30 taxa) with a strong dominance of herbs and subshrubs (<1 m tall) (Table 1, Fig. 4). Overall, different moa species within the same habitat type appeared to eat a very similar range of plant species (Table 1). The relative abundances of different plant types (i.e. trees and tall shrubs, lianes, subshrubs and dicot herbs, and monocot herbs) also did not vary greatly between species; there was no significant variation seen in the types of plants eaten by three sympatric moa species in the Dart River Valley ($F = 1.93$, $P = 0.088$) (Fig. 4), where the number of identified coprolites was sufficient to allow such a comparison. The smaller number of identified coprolites ($n = 4$, of three species) from Central Otago prevented a similar comparison between species. Surprisingly, variation between the seed assemblages of coprolites from Dart River Valley and Central Otago ($F = 4.17$, $P = 0.006$) exceeded the interspecific variation observed in the Dart River Valley alone (Fig. 4), and is presumed to reflect a strong habitat influence. Plant species identified in coprolites from Central Otago are typical of the shrubland with herb-rich understoreys that existed throughout the Central Otago river gorges during the late Holocene (Wood and Walker, 2008). Plant species identified in coprolites from the Dart River Valley are characteristic of moraine and rockfall habitats, and valley floor grasslands, of West Otago (Mark, 1977).

Seed assemblages in bulk sediment from coprolite-bearing horizons in three Central Otago rockshelters (Wood and Walker, 2008) provide a proxy for palaeovegetation communities, and therefore a unique opportunity to assess plant taxa preferences of moa. The data appear to suggest that not only did subshrubs and herbs form a larger part of the diet of moa in Central Otago, but that they were preferentially selected for by moa (Fig. 5). However, these potential preferences were not statistically significant (for the

difference between the two preference extremes; monocot herbs and trees/tall shrubs, $t = -2.58$, $P = 0.123$).

5. Discussion

5.1. Moa coprolite deposits

That moa utilised rockshelters and caves, whether for shelter, roosting, or nesting, is supported by numerous moa remains (bones, eggshell, feathers, DNA) obtained from such sites throughout New Zealand (e.g. Ambrose, 1970; Haile et al., 2007; Hamilton, 1894; Hartree, 1999; White, 1877; Wood, 2008b). Large coprolites, putatively identified as being from moa, have previously been reported from caves and rockshelters in southern New Zealand (Duff, 1952; Hamilton, 1894; Ritchie, 1982; Trotter, 1970; White, 1877). For the first time, our study has confirmed that some coprolites found in such sites are attributable to moa. Evidence from Central Otago suggests that some coprolites may be associated with nesting sites (Wood, 2008b).

The range of size and morphology seen in coprolites recovered suggests that other extinct birds may also be represented in the deposits, including South Island goose (*Cnemiornis calcitrans*) and Finsch's duck (*Chenonetta finschi*).

Desiccation of organic matter, such as coprolites, is dependent on a consistently arid microclimate in the site of deposition, preventing decay by fungi and invertebrates (Hansen, 2001). Whereas published radiocarbon ages of fossil remains from Central Otago sites that are not strictly dependant on aridity for preservation (e.g. swamps, loess, colluvium) have a relatively even temporal distribution throughout the Late Pleistocene and Holocene, radiocarbon ages of remains from dry caves and rockshelters (including the coprolite deposits reported on here) are clustered in the late Holocene (Wood 2008). This reflects the most intense period of ENSO (El Niño Southern Oscillation) cycling within the last 150,000 years (Johnson, 2006), which led to the mid-Holocene aridification of the Central Otago region (McGlone and Moar, 1998). This increased aridity may have directly influenced coprolite

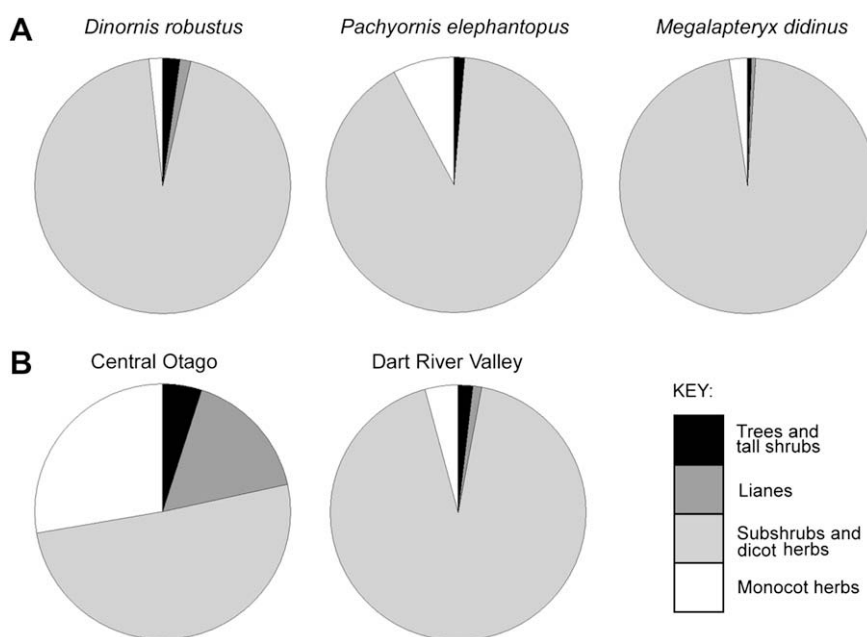


Fig. 4. Diet variation in moa represented by percentage of seeds in coprolites. (A) Interspecific variation between three sympatric moa species (*Dinornis robustus*, $n = 13$; *Pachyornis elephantopus*, $n = 3$; *Megalapteryx didinus*, $n = 4$) in the Dart River Valley. (B) Geographic- or habitat-related variation between total samples from Central Otago ($n = 35$) and Dart River Valley ($n = 81$).

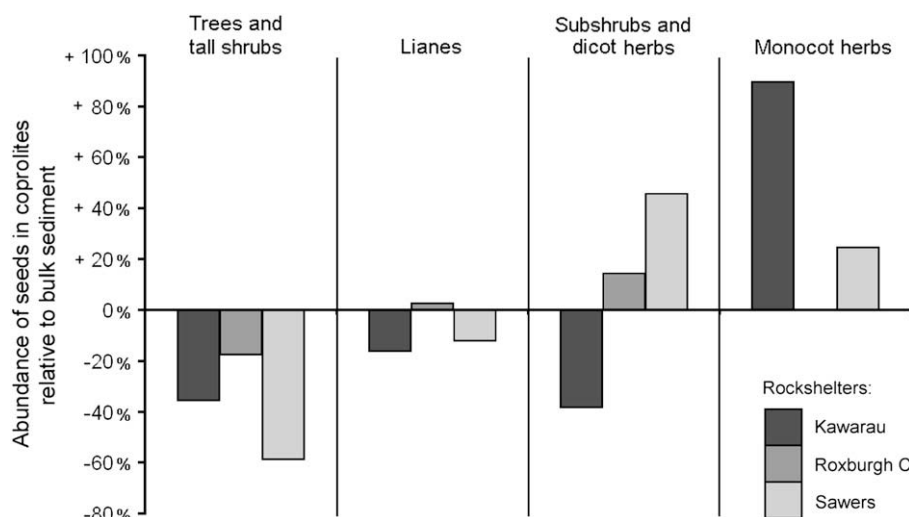


Fig. 5. Selection of plant taxa by moa in Central Otago, represented by comparison of seed assemblages from moa coprolites and bulk-sediment from coprolite-bearing horizons (proxy of local palaeovegetation composition) (Wood and Walker, 2008). Preferential selection by moa is suggested by positive values.

preservation, and therefore, continuous stratigraphic records of desiccated coprolites extending beyond ca 4000 years BP may be rare.

5.2. Moa diet and habitat

We suggest that some of the variation in plant macrofossil content between individual coprolites is possibly due to seasonal diet variation, with fruit/seed being widely available during summer months but less common during winter. A similar seasonal pattern was present in data from a study of Hawaiian moa-nalo coprolites (James and Burney, 1997), where pollen/spore counts were high ($n > 200$) in 33% of coprolites examined (suggesting deposition of these during spring/summer), but were low ($n < 40$) in 67% (suggesting deposition during winter).

While faecal seed analysis is often used to determine diets of primarily frugivorous birds, such as cassowary (*Casuarius* spp.) (e.g. Bradford et al., 2008; Wright, 2005), the correlation with diet of more general herbivores is less well known. A potential bias in our interpretation of moa diet is that amorphous organic material in the coprolites was not able to be identified, and may include plant species not represented by seeds. However, we believe seeds in coprolites are a good indicator of the plant taxa eaten by moa, as they are likely to be ingested whether a bird is feeding on fruit, or incidentally in association with browsing of foliage, twigs or whole plants. In support of this, studies of relatively undigested plant remains from moa gizzards reveal the majority of plant species identified were represented by seeds (87% in Burrows et al., 1981; 72% in Wood, 2007). Although seeds are indicative of plant taxa consumed, they do not necessarily reveal details of the diet such as the parts of plants that are being preferentially eaten. For example, our data indicate that three moa species (*M. didinus*, *D. robustus*, and *P. elephantopus*) were feeding on a very similar range of plants in the Dart River Valley (Fig. 2). However, we cannot resolve whether one of these species was, for example, preferentially feeding on fruit, and another on twigs and leaves. Some variation of this sort might be expected from the morphological variation in moa bills (Atkinson and Greenwood, 1989; Worthy and Holdaway, 2002). We also compare seed assemblages from coprolites and bulk rockshelter sediment to provide an estimate of plant types preferred by moa in Central Otago (Fig. 5). The underlying assumption is that most seeds within the bulk sediment were deposited by falling from vegetation growing around each site. A potential problem is that disaggregated coprolites may contribute

to the bulk sediment, and therefore the seed assemblage within the sediment is not an independent measure of local vegetation. However, any contribution of seeds from coprolites into the bulk sediment is likely to reduce the amount of variation between the two assemblages, and therefore provide an underestimate of any moa preferences.

While the similar dietary preferences between different moa taxa are surprising, there is also a remarkable similarity between moa and several still extant native avian herbivores. For example, the diet of kakapo (*Strigops habroptilus*), an endangered large flightless parrot, includes many of the plants found in moa gizzards and coprolites, including highly fibrous *Olearia* twigs and *Phormium* leaves (Atkinson and Merton, 2006; Horrocks et al., 2008). It is possible that for generalist herbivores the preferential selection of nitrogen-rich food, especially juvenile plants, may result in significant dietary overlap, with plant taxa eaten being differentiated by plant availability and accessibility rather than quality. This is likely to be particularly evident on islands with depauperate floras, but may have also been a factor in continental ecosystems with megafauna.

Seeds provide a good indication of the habitat that the moa were utilising although it is possible that some bias may exist in seeds that pass through into the droppings intact. Larger and denser seeds (e.g. *Prumnopitys*, *Elaeocarpus*) may be retained in the gizzard longer than small seeds (Wilson, 1989), and therefore may be proportionally under-represented in coprolites. However, we do not see this as biasing habitat interpretations, as moa gizzard contents from North Canterbury (Burrows et al., 1981), and coprolites from Dart River Valley, both contained abundant seeds of *Coprosma* spp., yet those in the gizzards were of forest species whereas those in the coprolites were of a non-forest, prostrate species.

Two of the moa species identified from Dart River Valley (*P. elephantopus* and *M. didinus*) are characteristic of open shrubland and low vegetation (Worthy and Holdaway, 2002). The third, *Dinornis robustus*, occurred in these habitats but also in heavily forested regions (Worthy and Holdaway, 2002). Despite the bone assemblage being representative of shrubland or grassland habitat, the lack of forest plant remains in the coprolites was unexpected, as they were excavated from sites currently beneath a closed forest canopy. Three possible explanations exist. First, following the Holocene retreat of glaciers from the valley, forest would likely have had to reinvade from the south (near Lake Wakatipu), and therefore may not have been widespread in the upper valley when

the coprolites were deposited. Second, the coprolites may represent a period soon after the rockfall occurred, and prior to regeneration of forest. Third, moa may have roosted and nested in the rockshelters within the forest, but moved out of the forest to preferentially feed on plants in open habitats. Such movement may have also been altitudinal; however this is unlikely as we did not identify any exclusively subalpine plant taxa in the coprolites.

Remarkably, for such large birds (up to 250 kg and 2 m tall at back), more than half of the identified plant taxa are <30 cm in height. This pattern is in direct contrast to the dietary inferences from the gizzard contents, and current concepts of moa, in particular *Dinornis*, as being dominantly a tree and shrub browser (Burrows et al., 1981; Wood, 2007). One explanation for this discrepancy may involve the extreme sexual dimorphism in *Dinornis*, where females are up to 280% the weight and 150% the height of males (Bunce et al., 2003), which might suggest strong sexual variation in food selection. Examined gizzard contents from *Dinornis* have almost exclusively been from females (Wood, 2007), and therefore the *Dinornis* coprolites from Dart River may represent the varying diet of males. Another alternative is that *Dinornis*, which had a wide distribution across varying habitat types (Worthy and Holdaway, 2002), also had a broad dietary range, and therefore its feeding tier varied with the available vegetation.

The coprolite results, synthesised with previous dietary data, provide an important new assessment of the diet of three moa genera. Our coprolite data reveal that *D. robustus* and *P. elephantopus* were substantial grazers; however, gizzard content analyses (Burrows et al., 1981; Wood, 2007) have indicated that they also browsed trees and tall shrubs along forest margins. Our results suggest that *M. didinus* was predominantly a herb grazer (Fig. 4, Table 1). Some twigs were identified in putative *M. didinus* coprolites by Horrocks et al. (2004), but aDNA identification of these coprolites was not carried out. Therefore, we do not include these in the synthesis on the possibility that they may be from another moa species that existed in the area (e.g. *A. didiformis*, *D. robustus*). We also identified a single coprolite from *E. gravis*, and although few plant remains were identified in this specimen, our

data complement gizzard content analyses that suggest this species fed on leaves and fruit of trees and shrubs (Gregg, 1972).

These feeding differences are reflected in morphology, where *Dinornis* and *Pachyornis* have comparatively robust bills, large temporal fossae and large gizzard stone sets (Wood, 2007; Worthy and Holdaway, 2002), all of which are consistent with diets that feature relatively high proportions of fibrous leaves and twigs. Intriguingly, dietary variation detected between the genera was relatively minor compared to the amount of variation observed between the different ecological zones (Fig. 4). This raises interesting questions about how these megafaunal species partitioned niches in the many areas of apparent sympatry throughout New Zealand, and seems to support the suggestion by Atkinson and Greenwood (1989) that niche partitioning in moa may not have been important until food was scarce, such as during droughts. Further to this, the habitat component of niche partitioning may have been more pronounced during Pleistocene glacial periods when shrubland and grassland habitats would have been widespread (McGlone et al., 1993) and forest was restricted to topographically-sheltered sites. Graviportal and short-statured moa genera (*Pachyornis*, *Euryapteryx*, *Emeus*, *Megalapteryx*) that specialised in utilising such habitats (Worthy and Holdaway, 2002) would have been common, with partitioning of *Dinornis* to more forested habitats. A warming climate led to the ascendancy of forest (McGlone et al., 1993) and, across much of lowland New Zealand, shrubland and grassland habitats were restricted to small pockets edaphic conditions, cold air drainage, or interspersed within a forest matrix and maintained by disturbances such as fire and herbivory (Rogers et al., 2005). Accordingly, *P. elephantopus*, *M. didinus* and *D. robustus* exhibit significant habitat overlap during the Holocene.

5.3. Co-evolution and ecological surrogacy

Coprolites and gizzards are now known to contain plant taxa representing at least eight plant growth forms hypothesised to be responses to moa-browsing (Atkinson and Greenwood, 1989;

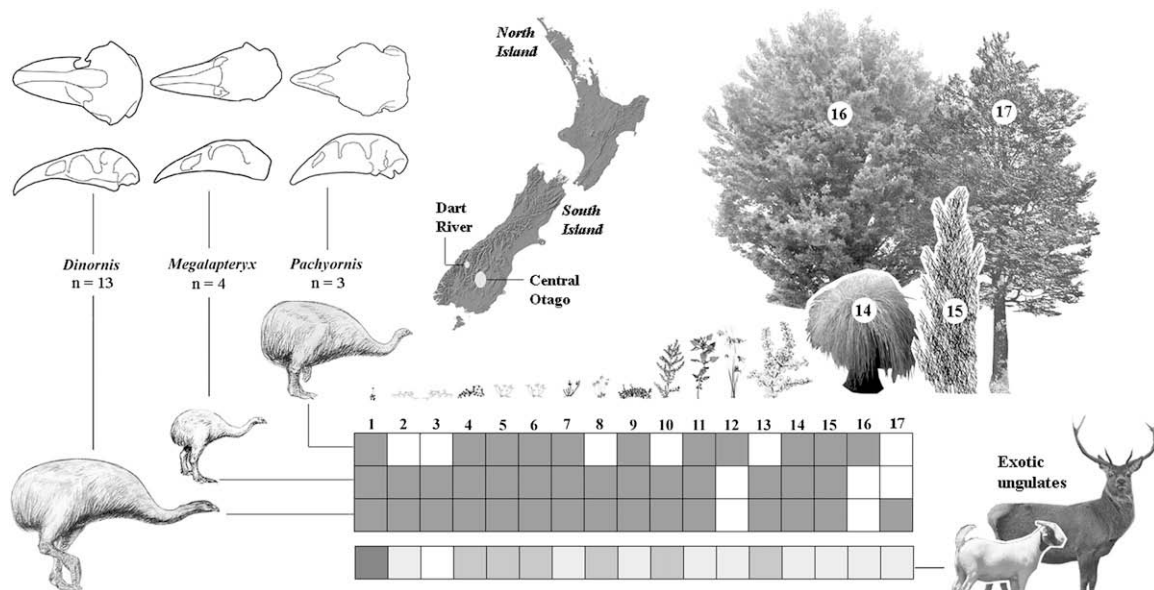


Fig. 6. Similarity in plant taxa eaten by moa species at Dart River and difference with those eaten by exotic ungulates. Plant taxa 1–17 are those identified by macrofossils in moa coprolites, Dart River: 1, *Lagenifera pumila*; 2, *Pratia angulata*; 3, *Muehlenbeckia axillaris*; 4, *Gonocarpus aggregatus*; 5, *Ranunculus* sp.; 6, *R. gracilipes*; 7, *Leucopogon fraseri*; 8, *Wahlenbergia pygmaea*; 9, *Coprosma petriei*; 10, *Coriaria plumosa*; 11, *Urtica incisa*; 12, *Juncus* sp.; 13, *Gaultheria crassa*; 14, *Carex* sp.; 15, *Coprosma* spp.; 16, Gymnosperm; 17, *Nothofagus menziesii*. All plants are shown to scale with moa except 16,17 which are shown approximately 1/5 maximum height. Ungulate diet data (Forsyth et al., 2006) are presented as: dark grey, plant taxa preferred by ungulates; medium grey, plants recorded as being eaten by ungulates; light grey, plant taxa avoided by ungulates; white, no published records of ungulates browsing the plant taxa.

Batcheler, 1989; Greenwood and Atkinson, 1977), including divarication, toxicity, photosynthetic stems, prostrate-filiculate habit, fibrous leaves, stinging hairs and low nutrient status, confirming that plants with these characteristics were indeed part of moa diet, and supporting the co-evolution hypotheses.

In Central Otago, several of the plant species detected in the coprolites are now rare, due to anthropogenically increased fire frequency and pastoralism. New Zealand has four tiny (ca 20 mm diameter) dryland 'spring annual' herbs, including *Ceratocephala pungens* and *Myosurus minimus novae-zelandiae* (Ranunculaceae), both of which are currently endangered and lack dispersers (Rogers et al., 2002, 2007). However, distinctive seeds of these two taxa were unexpectedly common in coprolites from some Central Otago sites, suggesting potential ecological relationships existed between moa and these plants. Although seed dispersal mutualisms are rarely specific to single animal taxa (Herrera, 2002), moa are likely to have played a major role in dispersing the seeds of a range of plants which relied on avian herbivores for dispersal. If so, then reduced avian herbivory is a potentially novel threat-syndrome for New Zealand's herbaceous flora. Furthermore, the presence of spring annuals in the coprolites, as well as a range of other taxa (e.g. *Einadia*, Poaceae) supports the "foliage is the fruit" hypothesis (Janzen, 1984), which posits that herbs with dry indehiscent seeds closely associated with nutritious foliage are adapted for dispersal by large herbivores.

Importantly, the coprolite data strongly refute the idea that modern populations of introduced ungulates (deer and goats) might act as browsing surrogates for moa (Caughley, 1983), as the coprolites show moa ate a high proportion of plant taxa that are avoided by ungulates (Fig. 6), including several that are potentially toxic to mammals (e.g. *Coriaria*, Ranunculaceae) (see Supplementary data). Conversely, the data reveal that in some non-forest habitat types, the feeding ecologies of moa were similar to extant ratites that utilise open habitats (emu, *Dromaius novaehollandiae*; ostrich, *Struthio camelus*; Rhea, *Rhea* spp.). The diets of these birds are comprised mostly of leaves, flowers, fruits and seeds of grasses, dicot herbs and low shrubs (Marchant and Higgins, 1990; Noble, 1991). However, moa gizzard content studies (Burrows et al., 1981; Wood, 2007) and cafeteria experiments (Bond et al., 2004) suggest that, in more forested habitats, some moa species were able to exploit woody twigs to an extent unparalleled by extant ratites. Such data question the suggested suitability of ostriches (*Struthio camelus*) to act as ecological "analogues" of moa (Nicholls, 2006), by filling a similar evolutionary niche. While a similar ecological function may be fulfilled in rare non-forest situations, ostrich, emu and rhea would clearly not be proxies for moa in all indigenous habitat types. Neither would the forest-dwelling cassowary, whose diet consists largely of fallen fruits (Bradford et al., 2008; Wright, 2005). Overall, the new dietary information raises the issue of how many apparently closely related proxy species for Pleistocene rewilding (Donlan et al., 2005) would actually be valid.

6. Conclusions

Our preliminary study, utilising recently discovered late Holocene coprolite deposits, has begun to shed light on the diet and ecology of moa. Importantly, we have shown that (1) some moa species, previously thought of as tree and shrub browsers, in fact had widely varied diets that included grazing on tiny herbs in non-forest habitats; (2) several plant taxa eaten by moa exhibit adaptations that were previously hypothesised to have co-evolved with these birds; and (3) the feeding ecology of moa does not reflect that of introduced ungulates, currently the dominant megaherbivores in New Zealand terrestrial ecosystems. The discovery of the existence of a geographically and ecologically widespread record of megaherbivore coprolites in New Zealand now provides a unique opportunity to reconstruct the first detailed ecological picture of

extinct megafauna, encompassing different habitats, seasonal variation, and species and sexual differences. Future study of this resource, using a range of aDNA, macro- and micropalaeontological techniques, promises to rapidly expand our knowledge of New Zealand's lost avian herbivores.

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Supplemental material

Supplementary information for this manuscript can be downloaded at doi: [10.1016/j.quascirev.2008.09.019](https://doi.org/10.1016/j.quascirev.2008.09.019).

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