Available on-line at: http://www.newzealandecology.org/nzje/

SHORT COMMUNICATION

Pollen analysis of coprolites reveals dietary details of heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) from Central Otago

Jamie R. Wood* and Janet M. Wilmshurst

Landcare Research, PO Box 40, Lincoln 7640, New Zealand
*Author for correspondence: woodj@landcareresearch.co.nz

Published online: 14 November 2012

Abstract: Palynological analysis of coprolites (preserved dung) can reveal detailed information on the diets and habitats of extinct species. Here, we present pollen assemblages from coprolites of the extinct heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) from the Central Otago region of the South Island, New Zealand. The data complement previous macrofossil (seed and leaf) analyses of the same specimens, and reinforce the interpretation that both species had generalist feeding ecologies. The pollen results reveal a broader selection of plant taxa consumed by both bird species than macrofossils alone, which has helped to discriminate between the predominantly grazing habit of the heavy-footed moa and the browsing habit of the coastal moa.

Keywords: Earnscleugh Cave; extinct species; Kawarau Gorge; Roxburgh Gorge

Introduction

Valuable insights into the ecology of many extinct species have been gained through analysis of coprolites. Most studies of Late Quaternary coprolites have concerned mammals (e.g. Mead et al. 1986; Poinar et al. 1998; Hofreiter et al. 2000), with relatively few focusing on birds (James & Burney 1997; Horrocks et al. 2004; Wood et al. 2008). Recently, several Holocene-age deposits containing desiccated coprolites have been discovered in the southern South Island of New Zealand. Wood et al. (2008) provided ancient DNA identifications for 24 of these coprolites, which included specimens from four species of moa (Aves: Dinornithiformes). Three of these coprolites were from the semi-arid region of Central Otago (Fig. 1), and were identified as having been deposited by heavy-footed moa (*Pachyornis elephantopus*; *n* = 2) and coastal moa (*Euryapteryx curtus*; *n* = 1) (Wood et al. 2008). Here, we present the results of pollen analysis on these three same coprolites, to supplement the identifications of seed and leaf cuticle remains initially provided by Wood et al. (2008), and to further the overall understanding of diet and habitat use by these species. Pollen and macrofossil data from coprolites both assist with dietary interpretation. Pollen offers a greater chance of detecting a wider range of the dietary components than plant macrofossils (seeds and leaf cuticles), which can be biased by taphonomic issues (e.g. over-representation of plant taxa with small, hard seeds and tough leaf tissues) (Wood et al. 2012a). However, macrofossils can be useful in distinguishing the dietary from habitat components of coprolite pollen assemblages.

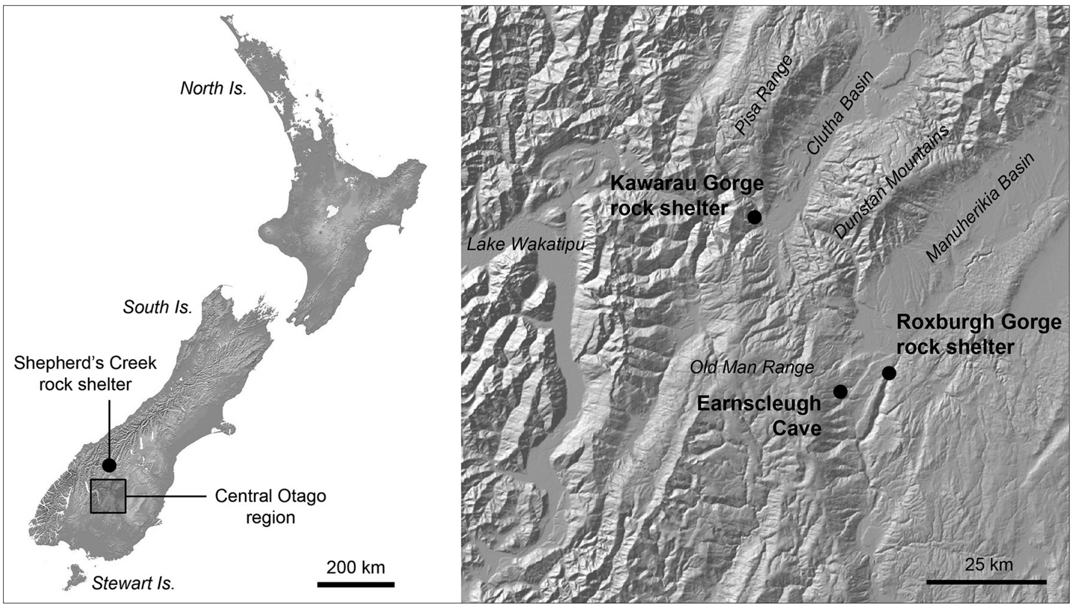

Figure 1. Coprolite localities, Central Otago, New Zealand.

Methods

Study sites

The two heavy-footed moa coprolites are from sheltered sites beneath schist outcrops in the Kawarau (c. 200 m altitude) and Roxburgh gorges (c. 150 m altitude), in the Clutha River catchment (Fig. 1). Descriptions of the sites and their stratigraphies are given by Wood (2007a). The gorges are semi-arid, receiving < 400 mm annual rainfall, and experience significant seasonal temperature ranges (Tait et al. 2001). Radiocarbon dated material from both the Kawarau (moa coprolite, 1017 ± 34 ^{14}C yrs BP) and Roxburgh Gorge sites (plant material from coprolite layer, 2928 ± 100 ^{14}C yrs BP) indicate these samples are of late Holocene age (Wood & Walker 2008).

The coastal moa coprolite is from Earnscleugh Cave, on the eastern slopes of the Old Man Range near Alexandra (Fig. 1). The cave is at a higher altitude (c. 540 m) than the gorge sites and details of the site and stratigraphy are given by Clark et al. (1996). Pollen stratigraphy and dates on bones from Earnscleugh Cave indicate the sediments in the site are also of Late Holocene age (Clark et al. 1996; Worthy 1998). The sampled coprolite is from the Otago Museum collections (Av10436) and is one of several that were probably collected during the original excavations at Earnscleugh Cave in the early 1870s (e.g. Hutton & Coughtrey 1875). Cockburn-Hood (1874) noted, 'The flat ground near had probably been a favourite camping ground, from the quantity of droppings—which are, no doubt, those of the large birds—swept in by the wind.' Based on the stratigraphic description of the cave given by Clark et al. (1996), and the fact moa coprolites usually occur in organic-rich sediment layers, we believe it is most likely that the coprolites were from the organic 'Layer 3', situated stratigraphically above an owl bone dated to 1552 ± 68 ^{14}C yrs BP.

Pollen analysis

Subsamples (1.25 ml) of each coprolite were processed for pollen analysis, using the following methodology: hot KOH for 10 min, HCl wash, acetolysis, float-separation of pollen with lithium polytungstate (specific gravity 2.2), fuchsin-red stain, and mounting on glass microscope slides in glycerol jelly. A known number of exotic *Lycopodium* spores were added to each sample to allow quantification of pollen/spore concentration (Batch no. 483216: 18 583 *Lycopodium* spores per tablet). At least 250 pollen/spore grains were identified and counted from each coprolite. Comparative samples of sediment from the same layers in which the coprolites were collected from the Kawarau and Roxburgh Gorge rock shelters were also prepared using the same method. Differences between paired sediment and coprolite pollen assemblages were examined using the Pearson's chi-squared test function in R (R Development Core Team 2011). Raw pollen count data (rather than percentages) for each identified pollen taxon (the dependent variables) (Fig. 2) were included in these analyses. Sediment and coprolite samples were also plotted based on their entire pollen assemblages using the principal components analysis feature of the program C2 (Juggins 2007).

Results

Pollen content of moa coprolites

Both heavy-footed-moa coprolites contained similar pollen concentrations (138 753 and 114 830 grains ml^{-1}) and assemblages, which were dominated by Chenopodiaceae (61.6% and 34.3% respectively), Poaceae (28.1% and 21.1%), Asteraceae (6.4% and 3.6%) and *Muehlenbeckia* (11. % and 3.9%) (Fig. 2). The coastal-moa coprolite contained relatively low pollen concentrations (8243 grains ml^{-1}) and higher percentages of tree and woody-shrub pollen types compared with the heavy-footed-moa coprolites (Fig. 2). Taxa occurring at greater than trace levels in the coastal-moa coprolite (>2.5% total pollen sum) included Asteraceae (25.1%), *Muehlenbeckia* (20.1%), Cyperaceae (10%), Poaceae (8.3%), *Nothofagus fusca*-type (5.9%), *Pseudopanax* (4.1%), *Coprosma* (3.8%) and *Elaeocarpus* (2.7%).

Difference between coprolite and sediment pollen assemblages

There is a general similarity between the pollen types present in the two heavy-footed-moa coprolites and the associated bulk sediment samples (Fig. 2). However, there are differences in the representation of some pollen types. For example, Chenopodiaceae pollen is more abundant in both coprolites than in the associated sediment samples; and tree and shrub pollen is more abundant in the sediments. There is no sediment sample specifically associated with the coastal-moa coprolite from Earnscleugh Cave. However, we compared the pollen assemblage from this specimen with one previously published for the cave from a layer assumed to be that from which the coprolite originated (soil sample 9; approximately 80 cm depth in the pollen stratigraphy of Clark et al. (1996)). There are major differences in the representation of pollen types in these two assemblages. For example, the coprolite contained more Asteraceae, Cyperaceae and Poaceae pollen, and less *Coprosma* pollen than the sediment sample (Fig. 2). A principal components analysis of the pollen assemblages (Fig. 3) shows the Kawarau Gorge coprolite is more similar to the coprolite and sediment samples from Roxburgh Gorge than to its associated sediment sample. The pollen assemblages from the Kawarau Gorge coprolite and sediment samples were statistically different (χ^2 = 222.25, d.f. = 16, P < 0.001). The Earnscleugh Cave coprolite is more similar to the two unassociated sediment samples than to its associated sediment sample. The Roxburgh Gorge coprolite and sediment sample are the most similar associated pair, but are also statistically different (χ^2 = 71.68, d.f. = 27, P < 0.001). Both the Kawarau and Roxburgh Gorge *Pachyornis* coprolites were significantly different to the Earnscleugh Cave *Euryapteryx* coprolite (χ^2 = 412.1, d.f. = 23, P < 0.001, and χ^2 = 270.84, d.f. = 26, P < 0.001 respectively), and to each other (χ^2 = 80.7, df = 18, P < 0.001).

Discussion

Pollen is perhaps the most widely quantified proxy in coprolite studies globally, and pollen data are often presented in the absence of supporting macrofossil or plant DNA assemblages. Multiproxy analyses can help overcome the biases and issues associated with each proxy individually. For example, pollen assemblages from herbivore coprolites can typically include

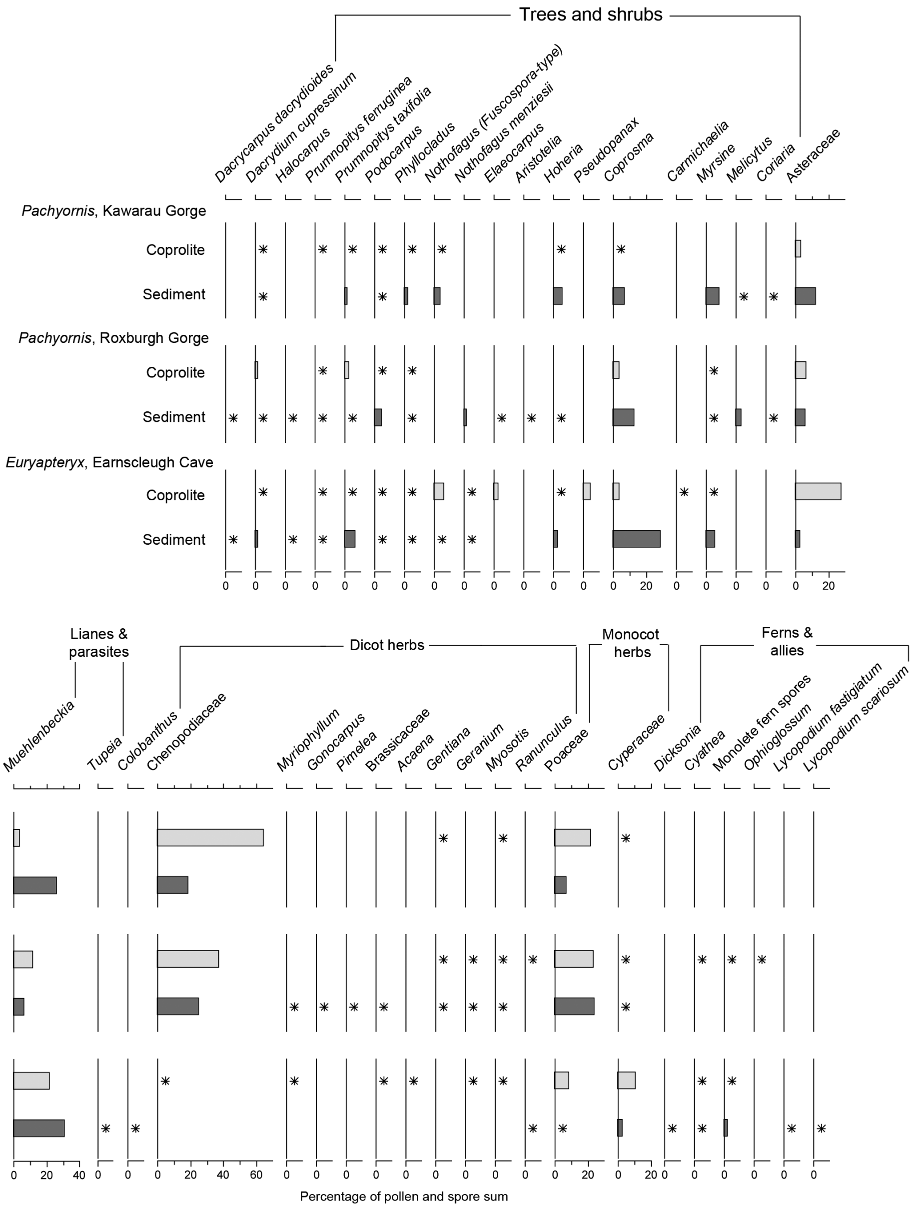

Figure 2. Pollen diagram for coprolites of heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) from Central Otago, South Island, New Zealand, and sediment surrounding the coprolites. Taxa occurring at <2% are represented by asterisks. As no sediment samples are directly associated with the Earnscleugh Cave coprolites, we show the pollen data for soil sample 9 (organic layer 3) in the profile of Clark et al. (1996), which is the most likely layer from which the coprolite originated.

elements reflecting both diet (abundant and dominant pollen types) and habitat (background pollen spectra) (King 1977; Scott & Cooremans 1992). By contrasting pollen content with plant macrofossil or DNA content (more indicative of diet), these two elements can be better distinguished (e.g. Wood et al 2012a).

The two heavy-footed-moa coprolites share remarkably similar pollen assemblages, despite being from sites c. 35 km apart. The four dominant pollen types in the heavy-footed-moa coprolites (Chenopodiaceae, Poaceae, Asteraceae and *Muehlenbeckia*) were also represented by seed and leaf remains (Table 1), suggesting that these plant taxa all formed an important part of the diet of this moa species throughout Central Otago. Macrofossils extracted from the coprolites and rock shelter sediments (Wood & Walker 2008) contained *Olearia* seeds, suggesting that the Asteraceae pollen reported here is highly likely to be from tree daisies (*Olearia*). The coprolite pollen assemblage suggests that both grazing of herbs and browsing of short shrubs and lianes were important parts of the feeding ecology of heavy-footed moa. This conclusion

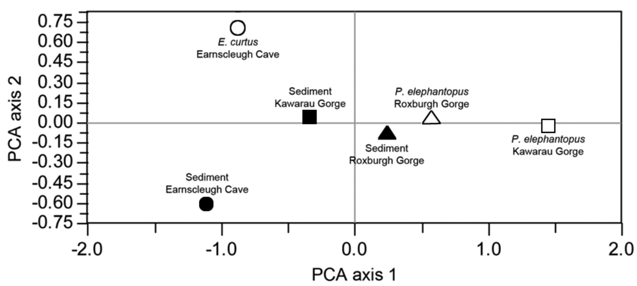

Figure 3. Principal components analysis of pollen assemblages from coprolites of heavy-footed moa (*Pachyornis elephantopus*) and coastal moa (*Euryapteryx curtus*) and associated sediment samples.

Table 1. Plant macrofossils identified in *Pachyornis elephantopus* and *Euryapteryx curtus* coprolites from Central Otago by Wood et al. (2008).

	P. elephantopus (A2074) Kawarau Gorge	*P. elephantopus* (A2069) Roxburgh Gorge	*E. curtus* (A2092) Earnscleugh Cave
Trees/shrubs			
Coprosma/Olearia sp.	1 leaf	8 leaves	1 leaf
Olearia sp.			1 seed
Hebe sp.			1 leaf
Melicytus sp.		1 seed	
Lianes			
Muehlenbeckia axillaris		3 seeds	
Dicot herbs			
Ceratocephala pungens		1 seed	
Einadia triandra	1 seed	5 seeds	
Monocot herbs			
Poaceae	3 seeds		

strengthens previous interpretations based on analyses of coprolites (Wood et al. 2008) and gizzard contents (Wood 2007b).

Less common pollen types in the heavy-footed-moa coprolites were not present in the macrofossil assemblage, and probably represent either very minor dietary components or elements of the habitat in which the birds were living. Many of these plants are known to have grown throughout Central Otago's basin floors and gorges (e.g. *Coprosma, Myrsine, Myosotis, Ranunculus*) (Wood & Walker 2008). Others (e.g. *Dacrydium, Prumnopitys, Podocarpus, Phyllocladus*) reflect vegetation growing on adjacent hillslopes (Clark et al. 1996) with wind-dispersed pollen that has likely just adhered to the leaves of locally consumed plants (Moar et al. 2011). Several of the pollen types present in the coprolites (Fig. 2) are insect- or bird-pollinated, and are not as predominant in sediment records as wind-dispersed pollen types (Moar et al. 2011). Their presence in the coprolites is likely to indicate these plants were directly consumed by moa (Wood et al. 2012a, b). They include *Muehlenbeckia*, *Carmichaelia.* Brassicaceae, *Gentiana, Geranium, Myosotis* and *Ranunculus*.

Although there were differences in the proportions of pollen types in the heavy-footed-moa coprolites and their associated sediment samples, there was a general similarity in the types of pollen present in each (Fig. 2). This may lend support to the idea that a significant component of the organic sediment present in dry rock shelters such as these could originate from decomposed or broken up moa dung (Wood et al. 2008).

The pollen assemblage of the coastal-moa coprolite contained a higher proportion of trees and shrubs than the heavy-footed-moa coprolites, but shared the dominant pollen types of Asteraceae, Poaceae and *Muehlenbeckia*. Overall, the data suggest a similar feeding ecology to heavy-footed moa, with both browsing and grazing components. However, a bias towards tree and shrub macrofossils in the coprolite (Wood et al. 2008) and gizzard content samples (Gregg 1972) of coastal moa suggests this species' feeding habit may have been more towards the browsing end of the herbivory spectrum.

Interestingly, the dominant pollen types in a moa coprolite (depositing species undetermined) from Shepherd's Creek in North Otago (Fig. 1) also included Chenopodiaceae (69%), *Muehlenbeckia* (10%) and Asteraceae (7%) (Trotter 1970). The high representation of these plant taxa in coprolites from three different, widely spaced, rock shelter sites is strong evidence that these were important and favoured food species of moa in the dry rainshadow zone east of the Southern Alps.

Conclusions

The results of pollen analysis of heavy-footed-moa and coastal-moa coprolites from Central Otago support previous inferences about the diets of these species (Wood et al. 2008). Both were probably generalist herbivores within their preferred habitats, but heavy-footed moa appears to have been predominantly a grazer, and coastal moa preferentially a browser. While the pollen analysis has supported the plant macrofossil interpretation, it has also provided a wider selection of the plant taxa consumed by these birds. Analysis of further coprolites is required to gain a more detailed picture of the full dietary breadth of these two moa species, and to discriminate their niches within New Zealand's prehuman ecosystems.

Acknowledgements

We thank Otago Museum (Abigail Blair) for providing the Earnscleugh Cave samples, and Gaye Rattray for sample preparation. Funding was received from the Royal Society of New Zealand Marsden Fund (08-LCR-012-EEB).

References

Clark GR, Petchey P, McGlone MS, Bristow P 1996. Faunal and floral remains from Earnscleugh Cave, Central Otago, New Zealand. Journal of the Royal Society of New Zealand 26: 363–380.

Cockburn-Hood 1874. Letter read to Wellington Philosophical Society 16 January 1874. Transactions and Proceedings of the New Zealand Institute 6: 387–388.

Gregg DR 1972. Holocene stratigraphy and moas at Pyramid Valley, North Canterbury, New Zealand. Records of the Canterbury Museum 9: 151–158.

Hofreiter M, Poinar HN, Spaulding WG, Bauer K, Martin PS, Possnert G, Pääbo S 2000. A molecular analysis of ground sloth diet through the last glaciation. Molecular Ecology 9: 1975–1984.

Horrocks M, D'Costa D, Wallace R, Gardner R, Kondo R 2004. Plant remains in coprolites: diet of a subalpine moa (Dinornithiformes) from southern New Zealand. Emu 104: 149–156.
Hutton FW, Coughtrey M 1875. Notice of the Earnscleugh Cave. With remarks on some of the more remarkable moa remains found in it. Transactions and Proceedings of the New Zealand Institute 7: 138–144.
James HF, Burney DA 1997. The diet and ecology of Hawaii's extinct flightless waterfowl: evidence from coprolites. Biological Journal of the Linnean Society 62: 279–297.
Juggins S 2007. C2 User guide version 1.5: Software for ecological and palaeoecological data analysis and visualisation. Newcastle upon Tyne, University of Newcastle. http://www.staff.ncl.ac.uk/staff/stephen.juggins/software/code/C2.pdf (accessed February 2012).
King FB 1977. An evaluation of the pollen contents of coprolites as environmental indicators. Journal of the Arizona Academy of Science 12: 47–52.
Mead JI, Agenbroad LD, Davis OK, Martin PS 1986. Dung of *Mammuthus* in the arid Southwest, North America. Quaternary Research 25: 121–127.
Moar NT, Wilmshurst JM, McGlone MS 2011. Standardizing names applied to pollen and spores in New Zealand Quaternary palynology. New Zealand Journal of Botany 49: 201–229.
Poinar HN, Hofreiter M, Spaulding WG, Martin PS, Stankiewicz BA, Bland H, Evershed RP, Possnert G, Pääbo S 1998. Molecular coproscopy: Dung and diet of the extinct ground sloth *Nothrotheriops shastensis*. Science 281: 402–406.
R Development Core Team 2011. A language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. http://www.r-project.org.
Scott L, Cooremans B 1992. Pollen in recent *Procavia* (Hyrax), *Petromus* (Dassie rat) and bird dung in South Africa. Journal of Biogeography 19: 205–215.
Tait AB, Basher R, Thompson C, Burgess S, McKenzie R, Mullan B, Porteous A, Salinger J, Shankar U, Wratt D 2001. The climate of Otago: patterns of variation and change / NIWA. Dunedin, Otago Regional Council. 96 p.
Trotter MM 1970. Archaeological investigations in the Aviemore area, South Island. Records of the Canterbury Museum 8: 439–453.
Wood JR 2007a. Pre-settlement paleoecology of Central Otago's semi-arid lowlands, with emphasis on the pre-settlement role of avian herbivory in South Island dryland ecosystems, New Zealand. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand. 432 p.
Wood JR 2007b. 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 JR, Walker S 2008. Macrofossil evidence for pre-settlement vegetation of Central Otago's basin floors and gorges. New Zealand Journal of Botany 46: 239–255.
Wood JR, Rawlence NJ, Rogers GM, Austin JJ, Worthy TH, Cooper A 2008. Coprolite deposits reveal the diet and ecology of the extinct New Zealand megaherbivore moa (Aves, Dinornithiformes). Quaternary Science Reviews 27: 2593–2602.
Wood JR, Wilmshurst JM, Wagstaff SJ, Worthy TH, Rawlence NJ, Cooper A 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. 13 p.
Wood JR, Wilmshurst JM, Worthy TH, Cooper A 2012b. First coprolite evidence for the diet of *Anomalopteryx didiformis*, an extinct forest ratite from New Zealand. New Zealand Journal of Ecology 36: 164–170.
Worthy TH 1998. Quaternary fossil faunas of Otago, South Island, New Zealand. Journal of the Royal Society of New Zealand 28: 421–521.

Editorial Board member: Kevin Burns
Received 23 February 2012; accepted 28 September 2012