Regional Comparisons of the Thickness of Moa Eggshell Fragments (Aves: Dinornithiformes)

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ABSTRACT. Samples of moa eggshell fragments from eight sites throughout New Zealand were measured to investigate the usefulness of the graphed distribution of eggshell-thicknesses in reflecting the moa fauna of the site. Assuming larger moa species laid eggs with thicker eggshells, a frequency histogram of eggshell thicknesses for each site seems to mirror what is known (from bones) of the incidence and relative abundance of large and small moa species at the site. This is particularly so for North Island sites which had lower moa diversity than South Island sites. At North Cape and Tokerau Beach abundant thin eggshell (mode at 0.90–0.94 mm) was probably produced by *Euryapteryx “curtus-gravis”* and *Pachyornis geranoides*, and rarer thick eggshell (mostly 1.2–1.7 mm) by *Dinornis novaeseelandiae*. At both Puketitiri and Castle Point there were broadly unimodal distributions of thin to medium-thickness eggshell, with thick eggshell almost absent. At Puketitiri the eggshell is assumed to be mainly from *Anomalopteryx didiformis*, and the slightly smaller *P. geranoides*, and averages thicker with a broader range than at Castle Point where the assumed identity of the eggshell lies with two small species (*P. geranoides* and *Eu. “curtus-gravis”*). At the four South Island sites the correlation to species is less clear. The modal thicknesses at Wairau Bar, Oamaru, Chatto Creek and Shag River are all in the range 1.15–1.44 mm and probably largely attributable to *Eu. “curtus-gravis”* which has a large form in the South Island and dominates the bones at all four sites. However, several other moas could have contributed the thinnest and thickest eggshells in most of the South Island samples. Archaeological sites had similar large ranges of eggshell-thickness to natural sites, suggesting that Maoris collected moa eggs from all available species and not just the largest ones. The study demonstrates the usefulness of eggshell-thickness histograms at particular sites as an adjunct to, or surrogate for, information on the relative abundance of moa bones, especially for North Island sites.


Fossil bones and eggshell fragments are the main evidence of the former presence in New Zealand of moas (Dinornithiformes), the extinct large ratite birds currently thought to number 10 species (nomenclature after Worthy & Holdaway, 2002; Bunce *et al.*, 2003; Worthy, 2005). Moa eggshell fragments are common, often in large quantities, in various archaeological and Holocene fossil sites throughout New Zealand. However, there has been little research on the nature and characteristics of moa eggshell fragments, and reports of archaeological and paleontological excavations typically and unhelpfully record “moa eggshell”, without further analysis. One aim of my recent work on moa eggs and eggshell (Gill, 2000, 2006, 2007) has been to seek a better understanding of unassociated, broken moa eggshell.
Materials and methods

Sites. I examined samples of moa eggshell fragments at eight sites or geographic areas chosen because they had yielded large samples held in museum collections, and the sites were spread latitudinally throughout New Zealand (Fig. 1). Five are natural sites, known (or assumed) to be of Holocene age, i.e. no older than 10,000 years before present. Three archaeological sites, all in the South Island, are assumed to date from within 100–200 years of first human settlement of New Zealand (which was ca. 1250 A.D.; Anderson, 1991; Wilmshurst et al., 2008). The sites were as follows (see Table 3 for latitudes and sample sizes; see Appendix for museum registration numbers):

- North Cape, Northland (natural sites)
- Tokerau Beach, Northland (natural sites; same sample analysed in Gill, 2000)
- Puketitiri, Hawke’s Bay (natural sites)
- Castle Point region, Wairarapa Coast (natural sites)
- Wairau Bar, Marlborough (archaeological site)
- Oamaru, North Otago (archaeological site)
- Chatto Creek, Central Otago (natural sites)
- Shag River mouth, Otago (archaeological site)

Samples. Eggshell fragments from the selected sites were examined closely and any with significant signs of surface-wear were rejected. For each acceptable fragment (n = 3565), one measurement of eggshell thickness was made to the nearest 0.01 mm (with vernier callipers or a screw micrometer) at an undamaged point on the edge of the fragment. Thicknesses were plotted as histograms with 0.05 mm intervals to give a very finely-divided spread of thickness classes (0.50–0.54, 0.55–0.59, 0.60–0.64 etc.). All fragments were white (or shades close to white) except for six of the 79 fragments in OM AV7477, which were green. Green eggshell belongs to Megalapteryx didinus (see Gill, 2007), but the identity of white eggshell is open to conjecture.

Moa faunas. The moa faunas at each site are known from the identity and relative abundance of bones. The taxonomy and nomenclature of moas is still under review. Bunce et al. (2003) showed that instead of three species of giant moas Dinornis throughout New Zealand there is just one North Island species (D. novaezelandiae) and one South Island species (D. robustus). This has simplified the moa fauna at most sites. Worthy (2005) showed that the stout-legged moa, previously called Euryapteryx geranoides, should now be called Eu. gravis, and that Mappin’s moa Pachyornis mappini is now P. geranoides.

It is also likely that Eu. gravis (North and South Islands) and Eu. curtus (North Island only) are conspecific, with size-differences in the bone samples reflecting various combinations of temporal, geographic and sexual variation (Tennyson & Martinson, 2006: 36, 146; T.H. Worthy, pers. comm. 2008). For example, Eu. gravis is recorded from Tokerau Beach but such bones probably belonged to the biggest of the larger (female) individuals of Euryapteryx at that site. Worthy (1987) showed that histograms of bone-lengths of Euryapteryx from Tokerau Beach were all bimodal, and he considered the different size-classes to reflect sexual dimorphism. The Holocene bones of Euryapteryx vary clinally in size, tending larger towards the south (Worthy, 1987). The two nominal species are referred...
Table 1. Presumed relative abundance of moa taxa (based on bones) at North Island sites where eggshell thickness was assessed. *** predominant, ** present, * rare, — absent.

<table>
<thead>
<tr>
<th>Site</th>
<th>Euryapteryx</th>
<th>P. geranoides</th>
<th>A. didiformis</th>
<th>D. novaezealandiae</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Cape</td>
<td>***</td>
<td>**</td>
<td>—</td>
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</tr>
<tr>
<td>Tokerau Beach</td>
<td>***</td>
<td>**</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Puketitiri</td>
<td>—</td>
<td>**</td>
<td>***</td>
<td>•</td>
</tr>
<tr>
<td>Castle Point</td>
<td>***</td>
<td>***</td>
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<td>**</td>
</tr>
</tbody>
</table>

Table 2. Presumed relative abundance of moa taxa (based on bones) at South Island sites where eggshell thickness was assessed. *** predominant, ** present, * rare, — absent.

<table>
<thead>
<tr>
<th>Site</th>
<th>Euryapteryx</th>
<th>P. elephantopus</th>
<th>A. didiformis</th>
<th>E. crassus</th>
<th>M. didinus</th>
<th>D. robustus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wairau Bar</td>
<td>***</td>
<td>•</td>
<td>*</td>
<td>**</td>
<td>*</td>
<td>•</td>
</tr>
<tr>
<td>Oamaru</td>
<td>***</td>
<td>**</td>
<td>?</td>
<td>**</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Chatto Creek</td>
<td>***</td>
<td>**</td>
<td>—</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
</tbody>
</table>

Figure 2. Regressions of mean eggshell thickness on latitude for the eight geographic samples in this study (Table 3) and for the 20 whole moa eggs for which measurements of eggshell thickness are possible (Gill, 2007). For eggshell fragments (open circles), the four North Island data-points are at bottom left and the four South Island ones at middle right. The regression lines and correlation coefficients are: $y = 0.028x + 0.027, r = 0.75$ (fragments; lower line); $y = 0.034x - 0.17, r = 0.44$ (whole eggs; upper line).

Results

Table 3 summarizes thickness for the samples of eggshell fragments at the eight sites in this study, and for whole moa eggs, and shows that minimum, mean and maximum thicknesses tend to be higher for South Island than for North Island samples. Fig. 2 shows the relationship between mean thickness and latitude for the eight broken eggshell samples (open circles). The eggshell thicknesses of whole eggs (Fig. 2; closed circles) show a very similar regression to the eggshell fragments, though data for the North Island are few.

Figures 3–10 show the histograms of moa eggshell thickness for each of the eight sites. North Cape (Fig. 3) and Tokerau Beach (Fig. 4) show a similar pattern—a broadly bimodal distribution with a spread of numerous thin eggshell fragments (mode at 0.90–0.94 mm) and a second spread of rarer thicker fragments (mostly 1.2–1.7 mm thick). The thin eggshell was presumably produced by Euryapteryx “curtus-gravis” with a lesser contribution by Pachyornis geranoides. Both are small moas, and the former is particularly small in the north (Worthy, 1987). The latter species would have had a
Figures 3–6. Histograms of moa eggshell thicknesses for samples of (Fig. 3) 612 fragments from North Cape, Northland; (Fig. 4) 1042 fragments from Tokerau Beach, Northland; (Fig. 5) 273 fragments from Puketitiri, Hawke’s Bay; and (Fig. 6) 431 fragments from Castle Point, Wairarapa.
Figures 7–10. Histograms of moa eggshell thicknesses for samples of (Fig. 7) 340 fragments from the Wairau Bar archaeological site, Marlborough; (Fig. 8) 595 fragments from the Oamaru archaeological site; (Fig. 9) 147 fragments from Chatto Creek, Central Otago; and (Fig. 10) 125 fragments from the Shag River archaeological site, Otago.
minor contribution at Tokerau Beach and a greater contribution at North Cape, according to the relative abundance of bones at these sites, but the eggshells of the two species seem inseparable in the histograms. The thick eggshell at the two northern sites (Figs. 3, 4) was presumably produced by Dinornis novaezealandiae, the only large moa present.

Puketitiri (Fig. 5) and Castle Point (Fig. 6) show broadly unimodal thickness histograms of thin to medium-thickness eggshell, with thick eggshell almost absent. At Puketitiri the eggshell is assumed to be mainly from the small species Anomalopteryx didiformis and the even smaller P. geranoides. At Castle Point the assumption is that the eggshell is a mixed sample attributable largely to P. geranoides and Eu. “curtus-gravis”, as at North Cape and Tokerau Beach. Indeed, the frequency distribution at Castle Point, with a mode at about 1.0 mm, is very like that of thin eggshell at the two northern-most sites. Anomalopteryx didiformis probably had thicker eggshell than P. geranoides, being larger, and this may be reflected in the thicker eggshell overall at Puketitiri than at Castle Point. Some of the thickest eggshell at Puketitiri, and the few pieces in the 1.40–1.49 mm range at Castle Point, may belong to Dinornis.

The four South Island samples are all broadly unimodal and towards the thicker end of the spectrum. Very thin eggshell is rare. The modal thicknesses at Wairau Bar (Fig. 7), Chatto Creek (Fig. 9) and Shag River (Fig. 10) are all at 1.35–1.44 mm. Oamaru (Fig. 8) has a lower mode (1.15–1.19 mm) but greater modal thickness than for the two North Island unimodal samples (Puketitiri and Castle Point). Eu. “curtus-gravis” dominated the bones at all four South Island sites, and much of the eggshell presumably belongs to this moa, which is large-statured in the South Island.

However, the South Island situation is complicated by a greater diversity of moas at each site (usually 4–6 spp.; Table 2) than in the North Island (3–4 spp.; Table 1). Emeus crassus, Anomalopteryx didiformis and Megalapteryx didinus could have contributed the thinnest eggshells in most of the South Island samples, and Pachyornis elephantopus and Dinornis robustus were present at most sites to contribute the thickest eggshell fragments.

A few fragments from Chatto Creek (4%) were green, i.e. attributable to M. didinus, and all were 0.89–1.13 mm thick, placing them at the very left-hand tail of the histogram (Fig. 9). White eggshell in that thickness range was also present, which at Chatto Creek could be Megalapteryx eggshell that has faded to white (see Gill, 2007), or attributable to E. crassus.

North Cape and Tokerau Beach have larger ranges of eggshell thicknesses (1.17 mm, 1.13 mm; Table 3) than all other sites except Wairau Bar (1.16 mm; Table 3). However, the thickness range at Wairau is exaggerated by one outlying thin fragment in the 0.65–0.69 mm range (Fig. 7) which could conceivably belong to a large bird other than a moa.

### Discussion

The latitudinal trend in moa eggshell thickness, with thicker eggshells in the south (Fig. 2), has two probable explanations. One underlying factor will be the presence of certain large moa species in the South Island (most notably Pachyornis elephantopus) that are absent in the North Island. However, Bergmann’s Rule may also be involved. For New Zealand birds, this predicts that where a species varies geographically in size, individuals in cooler (e.g., southern) areas will be larger. Bergmann’s Rule is thought to have operated in Holocene populations of various moas, e.g., Euryapteryx (Worthy, 1987, 1992) and Dinornis (Worthy et al., 2005), whose populations are present in both islands. If the birds of these species varied clinally in body-size, then so too may the size of their eggs and the thickness of their eggshells.

In general, the histograms of moa eggshell thickness seem to mirror closely what is known of the diversity and relative abundance of moas at the sites. For example, the bimodally distributed thick and thin eggshell at the two northern-most sites (Figs 3, 4) seem to fit with the indication from bones of numerous small moas (Euryapteryx “curtus-gravis” and Pachyornis geranoides) and rarer large moas (Dinornis novaezealandiae). The extreme spread of eggshell thicknesses at each of the two northernmost sites must reflect the presence there of moas of extreme sizes—the smallest known members

<table>
<thead>
<tr>
<th>locality</th>
<th>mean</th>
<th>n</th>
<th>s.d.</th>
<th>range</th>
<th>latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Island</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>North Cape</td>
<td>1.08</td>
<td>612</td>
<td>0.287</td>
<td>0.54–1.71 (1.17)</td>
<td>34.4</td>
</tr>
<tr>
<td>Tokerau Beach</td>
<td>0.96</td>
<td>1042</td>
<td>0.210</td>
<td>0.56–1.69 (1.13)</td>
<td>34.9</td>
</tr>
<tr>
<td>Puketitiri</td>
<td>1.08</td>
<td>273</td>
<td>0.129</td>
<td>0.65–1.41 (0.76)</td>
<td>39.3</td>
</tr>
<tr>
<td>Castle Point</td>
<td>0.97</td>
<td>431</td>
<td>0.109</td>
<td>0.70–1.48 (0.78)</td>
<td>41.0</td>
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<tr>
<td>South Island</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Wairau Bar</td>
<td>1.31</td>
<td>340</td>
<td>0.188</td>
<td>0.66–1.82 (1.16)</td>
<td>41.5</td>
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<tr>
<td>Oamaru</td>
<td>1.21</td>
<td>595</td>
<td>0.156</td>
<td>0.77–1.73 (0.96)</td>
<td>45.1</td>
</tr>
<tr>
<td>Chatto Creek</td>
<td>1.37</td>
<td>147</td>
<td>0.161</td>
<td>0.89–1.65 (0.76)</td>
<td>45.1</td>
</tr>
<tr>
<td>Shag River</td>
<td>1.35</td>
<td>125</td>
<td>0.167</td>
<td>0.83–1.69 (0.86)</td>
<td>45.5</td>
</tr>
<tr>
<td>fragments (overall)</td>
<td></td>
<td></td>
<td></td>
<td>0.66–1.82</td>
<td></td>
</tr>
<tr>
<td>whole eggs</td>
<td></td>
<td></td>
<td></td>
<td>1.02–1.89</td>
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</table>
of the *Euryapteryx* “curtus-gravis” complex and a *Dinornis*. The situation is now much simpler and clearer than when three species of *Dinornis* and two of *Euryapteryx* were thought to occur at Tokerau Beach (Gill, 2000).

We can infer from the histograms that both *Euryapteryx* “curtus-gravis” and *Pachyornis geranoides* had eggshell roughly 0.5–1.2 mm thick at North Cape (Fig. 3) and 0.6–1.1 mm at Tokerau Beach (Fig. 4). A whole egg from Tokerau Beach thought to belong to *Eu. “curtus-gravis”* (Gill, 2006: Egg 2) has eggshell about 0.9 mm thick (Archey, 1931), which places it at the mode in both thickness histograms and in the centre of the spread of thin eggshell fragments. The same histograms suggest that the eggshell of *Dinornis novaeezalandiae* was approximately 1.1–1.7 mm thick but there is no information from whole eggs on eggshell thickness in this species. The largest North Island egg (Gill, 2006: Egg 5, Waitomo) is probably *Dinornis* but the eggshell fragments are assembled in a way that prevents their thickness being measured. The thickest eggshell measured from North Island whole eggs is only 1.5 mm (Table 3) and thickness being measured. The thickest eggshell measured from the North Island whole eggs is only 1.5 mm (Table 3) and was attributed to *Anomalopteryx* (Gill, 2006: Egg 8).

We can predict from Fig. 5 (Puketitiri) that *P. geranoides* had eggshell from about 0.7 mm thick to an unknown maximum, and that A. didiformis at the same site had eggshell from an unknown minimum to 1.4 mm thick. No whole eggs of *P. geranoides* are known but four whole eggs from inland North Island sites and most likely attributable to *A. didiformis* have data on eggshell thickness (Gill, 2006, 2007: Eggs 7, 8, 13 and 14). The attribution of the eggs to *Anomalopteryx* is based on that small species dominating at the inland sites where the eggshells were found and on the eggshell being small (i.e. 152–175 mm long). Thirty-five eggshell thickness measurements from these four eggs had a range of 1.1–1.5 mm. This supports the notion that at least the thicker eggshell at Puketitiri belonged to *A. didiformis*. By elimination, much of the thinner eggshell at Puketitiri, especially in the range 0.7–1.0 mm, must belong to *P. geranoides*. At Castle Point, where the small and similarly-sized *P. geranoides* and *Eu. “curtus-gravis”* dominated (on bone evidence), most of the eggshell was indeed in that range (Fig. 6).

Given that the large South Island form of *Eu. “curtus-gravis”* dominated the bones at all four South Island sites, the frequency bars in the histograms suggest that its eggshell was about 1.1–1.5 mm thick at Wairau Bar (Fig. 7), 1.0–1.3 mm at Oamaru (Fig. 8), 1.3–1.5 mm at Chatto Creek (Fig. 9) and 1.2–1.6 mm at Shag River (Fig. 10), or roughly 1.0–1.6 mm for the South Island in general. Considering whole eggs, there are seven South Island eggs possibly attributable to *Euryapteryx* (Gill, 2006, 2007): Eggs 16 and 18–21 from the same Wairau Bar site as the eggshell fragments (Fig. 7) and Eggs 11 and 32 from the same Oamaru site as in Fig. 8. These eggs are not objectively linked to *Euryapteryx*, but they are medium-sized (i.e. 194–215 mm long) and assumed to belong to the medium-sized moa that dominates bones at the sites. Fifty-three thickness measurements from these seven eggs had a range of 1.1–1.7 mm. This close agreement in thickness between the broken eggshell and whole eggs reinforces the conjecture that the bulk of the eggshell fragments at Wairau Bar, Oamaru, Chatto Creek and Shag River are from medium-sized eggs that were probably *Euryapteryx*.

Green eggshell fragments at Chatto Creek were thin (0.89–1.13 mm) and signal the presence of *Megalapteryx didinus*. Three whole green eggs, two from Chatto Creek (Gill, 2006: Eggs 22 and 23) and one from Mt Aspiring National Park (Egg 29), had similarly thin eggshell (1.1–1.2 mm thick; Gill, 2007). A whole egg from the Shag River site has an eggshell-thickness of 1.73–1.89 mm (Gill, 2007: Egg 27), the thickest moa eggshell ever recorded, and thought to belong to *P. elephantopus*. This extreme thickness was not represented in the broken eggshell sample from that site (Fig. 10); the sample of 125 fragments was clearly not large enough. However, the Shag River sample has a big peak at 1.60–1.64 mm, more so than for any other sample. These thickest fragments in the Shag River sample may be attributable to *P. elephantopus*.

The archaeological eggshell samples at Wairau Bar, Oamaru and Shag River are presumably biased towards the moa eggs that local Maoris collected and discarded. Yet the range of eggshell thicknesses at these midden sites is very large, and seems no different from the range of thicknesses at natural sites (Table 3). This suggests that moa eggs of all available sizes (i.e. from all available species) were collected for human use, not just the largest ones.

This study suggests a usefulness in histograms of moa eggshell thicknesses generated for specific paleontological and archaeological sites. Moa eggshell thickness profiles seem broadly to reflect the moa faunas at the sites, and may be a helpful adjunct to, or surrogate for, information on the relative abundance of moa bones at sites. This is especially so in the North Island where moas are usually less diverse at a site than in the South Island.

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References


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Appendix

Museum registration numbers of the samples from which moa eggshell fragments were measured for thickness (number of fragments measured shown in brackets). Where the number measured was not the entire sample, fragments were chosen at random. Museum codes: UO, Anthropology Department, University of Otago, Dunedin; AIM, Auckland Museum, Auckland; CMC, Canterbury Museum, Christchurch; HBM, Hawke’s Bay Museum, Napier; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington; OM, Otago Museum, Dunedin.


Tokerau Beach (97 samples, 1,042 fragments). See Gill (2000: Appendix 1).


Castle Point (11 samples, 431 fragments). Samples collected 1934–2000 by E. Barton, T. Cairns, T. Duff, R. Danderman, E. Smith and A.J.D. Tennyson.—Coast between Mataikona and Whakatāki: NMNZ S23166 (52), S23167 (15), S36733 (3), S37690 (20), S37910 (13), S37913 (92), S37923 (23), S38403 (97), S38441 (56), S38460 (10), S40676 (50).


Oamaru (23 samples, 595 fragments). Archaeological excavations by W.B.D. Mantell ca. 1852.

The Mantell collection at AIM (LB4014) is a large assemblage of eggshell fragments believed to have been collected from a Maori midden site at Awanui, near Oamaru, North Otago (Archev, 1941: 74). Mantell grouped the fragments on some basis. Within each group, numerous fragments are joined in an attempt to reconstruct sections of the original eggs, but thickness varies greatly within most of these groupings so they cannot represent separate individual eggs.

Boxes A–D (20), Box E (1), Boxes F–G (2), Box H (56), Box I (23), Boxes J–K (20), Box L (17), Boxes M–N (23), Box O (21), Box P (17), Box Q (20), Box R (30), Box S (27), Box 4014/1 (56), Box 4014/2 (43), Box 4014/3 (92), Box 4014/4 (22).

Chatto Creek (2 samples, 147 fragments). Samples collected ca. 1954 (collector not recorded). OM AV7376 (68), AV7477 (79).