The Allometry of Giant Flightless Birds

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology in the Graduate School of Duke University

2007
Abstract

Despite our intuition, birds are no smaller than mammals when the constraints of a flying body plan are taken into account. Nevertheless, the largest mammals are ten times the mass of the largest birds.

Allometric equations generated for anseriforms and ratites suggest mid-shaft femur circumference is the best measure to use in estimating avian body mass. The small sample size of extant ratites makes mass estimate extrapolation to larger extinct species inaccurate. The division of ratites into cursorial and graviportal groups is supported. Aepyornithids do not show atypical femoral shaft asymmetry.

New and more accurate estimates of egg masses, and separate male and female body masses for sexually-dimorphic ratites are generated. Egg mass scaling exponents for individual bird orders differ from that Aves as a whole, probably due to between-taxon effects. Ratite egg mass does not scale with the same exponent as other avian orders, whether kiwi are included or excluded. Total clutch mass in ratites, however, scales similarly to egg mass in other birds, perhaps as a consequence of the extreme variation in ratite clutch size.

Kiwi and elephant bird eggs are consistent with the allometric trend for ratites as a whole, taking clutch size into account. Thus kiwi egg mass is probably an adaptation for a precocial life history, not a side effect of their being a dwarfed descendant of a moa-sized ancestor.

Relatively small body size in ancestral kiwis is consistent with a trans-oceanic dispersal to New Zealand in the Tertiary, as suggested by recent molecular trees. This implies multiple loss of flight in Tertiary ratite lineages, which is supported by biogeographic, molecular, paleontological, and osteological evidence, but which is not the currently prevailing hypothesis.
Acknowledgments

I first and foremost need to thank my patient and encouraging advisor, Louise Roth, for her support and faith when I was ready to give up on the dissertation process, and her tolerance for a graduate student writing a paper on the taxonomy of Big Bird (*Grandicrocavis viasesamensis*). All my committee, especially Dan McShea, have been more than supportive of my desires to pursue a non-standard scientific career. The Roth and McShea lab groups in addition acted as a sounding board for many of the ideas in this dissertation.

It has been said by many that we learn most of what we need in grad school from our fellow students. Fellow Duke Biology students too numerous to name have helped, encouraged, and entertained me over the past eight years, suffered through my presentations, ate my cooking, and listened to me play the ukulele with a straight face, and I look forward to paying them back tenfold in the years to come. Neither would I have reached this point without the support and kind words of Suzanne Kurtzer, Liliana Dávalos, Mary Cromer, and Felicity Turner. My DC friends Mark Mullen and Mary Pickering made it possible for me to spend substantial amounts of time at the Smithsonian, and my visits to the National Museum of Natural History would have have been far less productive were it not for Storrs Olson and Helen James, who stand out among the many generous curators and collection managers around the world that gave me access to rare and precious bones.

As well as the financial support of Duke Biology and Duke OIT, I’m grateful to have been funded by the American Museum of Natural History, the Delaware Museum of Natural History, the Society for Systematic Biology, and the Vienna Institute Summer University program, all of which enabled me to traipse through the bone collections of Europe and Oceania.

As a New Zealander studying flightless birds in a country which has none, I’m often asked why I came to Duke. The quality of Biology departments like Duke’s is one of the reasons kiwis are encouraged to leave their homeland for a Ph.D., and the intellectual environment here is something I’ll remember for the rest of my life. No department, though, however smart its faculty can be truly great without an all-knowing and sympathetic administrator like Anne Lacey, who makes the rough way smooth and earns the devotion of hundreds of grad students in the process.

Without the encouragement of Phil Millener at the Museum of New Zealand I would never have considered abandoning teaching typography to study flightless birds, without my father’s shared passion for natural history I would never have had a childhood dream like this to follow, and without the support of my mother I would never have been able to finish. I thank them all.
1. The Ratite Birds

The Paleognathae are traditionally defined as the avian group comprising both ratites and tinamous (Table 1.1). The ratites include all the Recent giant flightless birds, living and extinct, with two exceptions: *Genyornis* in the Dromornithidae, now in the Anseriformes (Murray and Vickers-Rich, 2004), and *Silviornis* in the Megapodiidae (Poplin and Mourer-Chauviré, 1985), which, along with the similarly-large Tertiary phorusrhacids (Alvarenga and Höfling, 2003), will not be examined in detail here. Ratites share a flat, raft-like (L. *ratis*) sternum, though this character is associated with flightlessness and not unique to the group. They share with the chicken-sized flighted tinamous (Tinamidae) a paleognathous configuration of the palate, in contrast to the neognathous palate of all other modern birds (or neognaths), to which the paleognaths are the sister group, and which together comprise the modern birds (Neornithes).

The relationships of the different paleognath families remains unclear. Traditionally (Brodkorb, 1971) the Tinamidae have been considered the sister group to all other extant paleognaths, though recent unpublished nuclear DNA analyses suggest they are in fact nested inside the ratites (J. Harshman, pers. comm.). The relationships of the ratites also remain controversial, with morphological and molecular analyses disagreeing, and they will be discussed further in Chapter 5. The most recent survey of this group considers the single order Struthioniformes to contain both ratites and tinamous (Davies, 2002), and thus it should strictly be considered the equivalent of the crown-group Paleognathae. Various other taxonomic groupings (Dinornithiformes, encompassing Dinornithidae and Anomalopterygidae, Casuariformes, and Rheiformes) have been recognized as ratite orders by previous authors, but their validity is questionable until agreement has been reached on the higher-level relationships of the ratites; nevertheless, they are useful labels for various ratite clades and will be used as such in the following text. For the purposes of this study, a working phylogeny (Figure 1.1) has been compiled from the mtDNA trees of Haddrath and Baker (2001), Cooper et al (2001), Burbidge et al (2003), and Baker et al (2005). This may well change with the publication of further nuclear DNA analysis.

The most distinctive feature of the ratites is their size, and many questions to do with the ratites hinge on size and scaling. The Elephant Bird *Aepyornis*, despite being the largest bird known, is only one-twentieth the size of an actual elephant, even though the mean body size of flightless birds is larger than that of non-flying mammals (Chapter 2).

Because most ratite species are extinct, any study of scaling in this order requires us to estimate their body mass from bone measurements, which often involves extrapolating beyond the masses of living birds. Extinct ratites in addition show a different morphology from most extant species, so allometric changes in body proportions have to be distinguished from adaptations to different locomotory modes (Chapter 3).

As well as exhibiting a variety of different body shapes, ratites vary enormously in their clutch size. Kiwi (*Apteryx*) lay a single enormous egg, supposedly a relict of their giant ancestor. To test the assumption that kiwi eggs are oversized, we need to examine the scaling of ratite egg size and clutch mass (Chapter 4).
If kiwi do not descend from a giant ancestor, they could have dispersed to New Zealand in the Tertiary and later become flightless, as molecular phylogenies suggest. This is not consistent with the traditional model of ratite evolution, which relies on a Gondwanan radiation from a single flightless ancestor (Chapter 5).

All these questions rely on different ways of understanding body size, that most obvious and most profound animal property without which nothing in evolutionary biology makes sense.
Order Struthioniformes sensu stricto
Family Tinamidae
  47 species in 9 genera
  South America
Family Rheidae
  *Rhea americana*  Greater rhea  South America
  *Pterocnemia pennata*  Lesser (Darwin’s) rhea  South America
Family Dromaiidae
  *Dromaius novaehollandiae*  Emu  Australia
  † *Dromaius ater*  King Island emu  Australia
  † *Dromaius baudinianus*  Kangaroo Island emu  Australia
Family Casuariidae
  *Casuarius casuarius*  Southern cassowary  Australia, New Guinea
  *Casuarius bennetti*  Bennett’s (dwarf) cassowary  New Guinea
  *Casuarius papuanus*  Westerman’s cassowary  New Guinea
  *Casuarius unappendiculatus*  One-wattled cassowary  New Guinea
Family Anomalopterygidae
  † *Megalapteryx didinus*  Upland moa  New Zealand
  † *Anomalopteryx didiformis*  Little bush moa  New Zealand
  † *Emeus crassus*  Eastern moa  New Zealand
  † *Euryapteryx curtus*  Coastal moa  New Zealand
  † *Euryapteryx geranoides*  Stout-legged moa  New Zealand
  † *Pachyornis elephantopus*  Heavy-footed moa  New Zealand
  † *Pachyornis mappini*  Mappin’s moa  New Zealand
  † *Pachyornis australis*  Crested moa  New Zealand
Family Dinornithidae
  † *Dinornis novaezealandiae*  North Island giant moa  New Zealand
  † *Dinornis robustus*  South Island giant moa  New Zealand
Family Apterygidae
  *Apteryx mantelli*  North Island brown kiwi  New Zealand
  *Apteryx australis*  Tokoeka  New Zealand
  *Apteryx owenii*  Little spotted kiwi  New Zealand
  *Apteryx haastii*  Great spotted kiwi  New Zealand
  *Apteryx rowii*  Rowi  New Zealand
  † *Apteryx sp.*  undescribed Eastern kiwi  New Zealand
Family Struthionidae
  *Struthio camelus*  Ostrich  Africa, † Asia
Family Aepyornithidae
  † *Mullerornis agilis*  Elephant bird  Madagascar
  † *Aepyornis maximus*  Elephant bird  Madagascar
  † *Aepyornis hildebrandti*  Elephant bird  Madagascar

Table 1.1: The Recent paleognaths. Extinct species denoted †.
References


Worth, C. Brook. 1940. Egg volumes and incubation period. *Auk* 57, 44–60.