SHORT COMMUNICATION

Body size evolution in Mesozoic birds

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Abstract

The tendency for the mean body size of taxa within a clade to increase through evolution (Cope's Rule) has been demonstrated in a number of terrestrial vertebrate groups. However, because avian body size is strongly constrained by flight, any increase in size during the evolution of this lineage should be limited – there is a maximum size that can be attained by a bird for it to be able to get off the ground. Contrary to previous interpretations of early avian evolution, we demonstrate an overall increase in body size across Jurassic and Cretaceous flying birds: taxon body size increases from the earliest Jurassic through to the end of the Cretaceous, across a time span of 70 Myr. Although evidence is limited that this change is directional, it is certainly nonrandom. Relative size increase occurred presumably as the result of an increase in variance as the avian clade diversified after the origin of flight: a progression towards larger body size is seen clearly within the clades Pygostylia and Ornithothoraces. In contrast, a decrease in body size characterizes the most crownward lineage Ornithuromorpha, the clade that includes all extant taxa, and potentially may explain the survival of these birds across the Cretaceous-Palaeogene boundary. As in all other dinosaurs, counter selection for small size is seen in some clades, whereas body size is increasing overall.

Introduction

The constraint of body size is much more important for flying birds than it is for most other vertebrates, because of the biomechanical limits imposed by powered, flapping flight (Alexander, 1998). We know that the maximum body size of a flying organism is significantly below that for terrestrial or aquatic taxa (Alexander, 1998), and that the requirements of flight have acted to limit or control any body size increase among birds (Vizcaino & Fariña, 1999).

Cope's Rule, named after Edward Drinker Cope (1840–1897), states that during evolution members of a lineage tend to increase in size. Cope (1887) is widely cited as having attributed this trend to an observed

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tendency for clades to originate at small size, but to subsequently evolve towards larger sizes (see also Depéret, 1907). Body size is one of the most important aspects of an organism's biology (Calder, 1984), because it influences development, reproduction, evolution, physiology and ecology (Schmidt-Nielsen, 1984; Jablonski, 1996; Hone & Benton, 2005). In nature 'bigger is (generally) better', or rather, biologically fitter (Kingsolver & Pfennig, 2004; Hone & Benton, 2005) at least in the short term – it has also been demonstrated that larger organisms tend to be more prone to extinction (Webster *et al.*, 2004; Hone & Benton, 2005, 2007). In addition, a large body size has been invoked as an advantage under sexual selection (Benton, 2002), in predator-prey interactions (Benton, 2002), fecundity selection (Blanckenhorn, 2000), and resource competition (Bonner, 1988). Studies have demonstrated Cope's Rule, a clear directed trend towards phyletic size increase [and thus nonrandomness in evolution, in

fossil foraminifera (Arnold *et al.*, 1995), parasitic isopods (Poulin, 1995), North American fossil mammals (Alroy, 1998), extant birds (Maurer, 1998), nonavian dinosaurs (Hone *et al.*, 2005), early amniotes (Laurin, 2004) and pterosaurs (Hone & Benton, 2007)].

Body size evolution, however, must be tested for at appropriate taxonomic levels (Alroy, 2000). For example, rapidly changing sizes that are apparent between species, or over short periods of time will not be observed if size changes are measured between families, or over tens of millions of years. Similarly, slow changes that occur over extended periods will be masked if only sister-species are compared. The solution to this paradox is to test for Cope's Rule at multiple phylogenetic levels, so revealing hidden trends (Hone & Benton, 2007).

Compared with other vertebrate clades, extant birds exhibit a wide range of body sizes: from the 2 g bee hummingbird (*Calypte helenae*) to the 100 kg ostrich (*Struthio camelus*), a more than 50 000-fold weight difference. However, mass distribution across living Aves is severely right-skewed, even on a logarithmic scale – the median extant bird mass is just 37.6 g (Blackburn & Gaston, 1994). Because the dynamics of flapping flight require a certain aerofoil size to weight ratio, there is an upper limit to body mass beyond which it is not feasible for a bird to have a wing large enough to generate sufficient lift (Alexander, 1998; Vizcaino & Fariña, 1999). Because of this constraint, the heaviest extant flying bird is the great bustard (*Otis tarda*), about 1 m long but weighing only 16 kg. It is not known what the upper limit to bird body mass might be: the Miocene *Argentavis* weighed an estimated 75 kg and was still capable of flight (Vizcaino & Fariña, 1999). Flightless birds reach even greater sizes – ostriches (*Struthio*) weigh up to 100 kg, and the

extinct moa reached 300 kg or more (Alexander, 1983; Worthy & Holdaway, 2002).

The earliest bird, *Archaeopteryx* from the Jurassic (ca. 140 Ma), was about the size of a pigeon (Chiappe & Dyke, 2002). The mass of this taxon is debated – only its bones are preserved – estimated to be 0.220–0.330 kg (Yalden, 1984) or 0.135 kg (Henderson, 1999). Little is known about changes in body size over the course of avian evolution, a question that can now be addressed because of recent dramatic improvements in the fossil record of early birds from the Jurassic and Cretaceous (ca. 140–65 Ma; Chiappe, 2002; Chiappe & Dyke, 2002; Zhou, 2004; Fountaine *et al.*, 2005; Feduccia, 2006).

Here we investigate whether birds show evidence for changing body sizes during the first 90 Myr of their history, between *Archaeopteryx* and the base of modern birds (Neornithes) (Fig. 1). Not only do changes in body size have clear implications for the refinement of flapping flight, but variation between clades (a trend towards smaller body size) may provide one possible explanation for the selective survivorship of modern birds across the Cretaceous-Palaeogene (KP) boundary, at the expense of their more basal counterparts.

Materials and methods

Fossil taxa

For this analysis, we culled measurements of fore and hindlimb bones from literature (Table S1) to construct adata set that includes more than 95% of the known diversity of Jurassic and Cretaceous birds (as of late 2006); 117 fossil bird specimens representing 47 distinct species (Table S1). Temporal distributions were
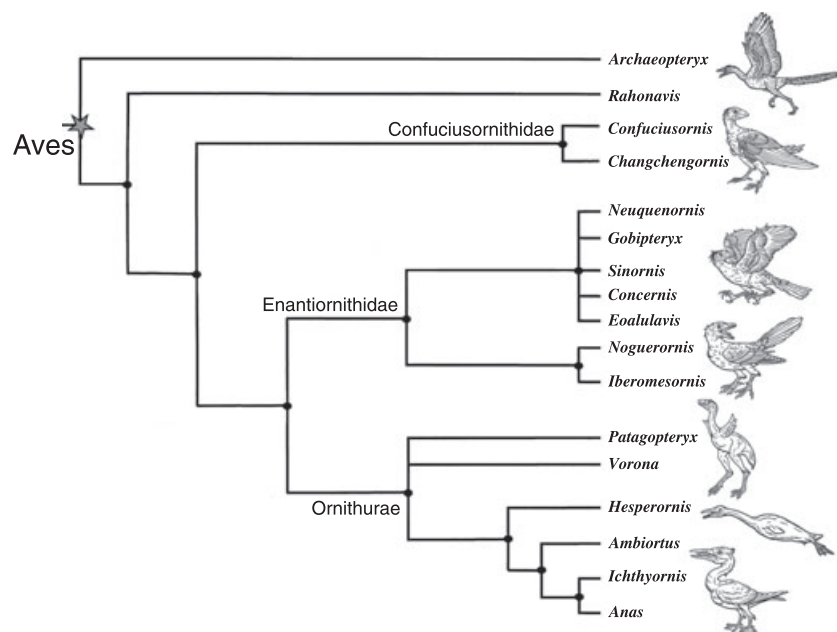
Fig. 1 Summary tree illustrating phylogenetic relationships among Mesozoic birds (modified from Chiappe & Dyke, 2002). Neornithes (modern birds) are represented by a duck (*Anas*). The oldest avian included in our dataset is *Archaeopteryx* (ca. 150 Ma). Other major bird groups in the Mesozoic, with minimum inferred ages, include Confuciusornithidae (ca. 121 Ma); Enantiornithes (ca. 71 Ma); Ornithurae (ca. 70 Ma) and Neornithes (ca. 65 Ma). The latter two lineages together comprise Ornithuromorpha.

also taken from the literature; ranges are expressed by a median time. We use terms such as 'bird', 'Aves', and 'Neornithes' in their traditional, but cladistically-defined meanings (Chiappe & Dyke, 2002); thus 'birds' and 'Aves' refer to the smallest clade comprising *Archaeopteryx*, sparrows, and everything else in between. We then use samples of extant birds to extrapolate body mass in extinct fossil taxa, based on assumptions outlined in Witmer (1995) and Laurin *et al.* (2004).

Mass estimation

We estimate body mass using limb bones and scaling equations. Thus, all calculations were repeated with multiple bone dimensions to obtain a range of estimates; note that although the use of different bones as body mass proxies are subject to variable assumptions and stresses (Table S2), allometric equations based on long bone proportions have nevertheless been shown (Maloiy *et al.*, 1979; Alexander, 1983; Anderson *et al.*, 1985; Anyonge, 1993; Egi, 2001) to be accurate predictors of body mass. Following Maloiy *et al.* (1979), Alexander (1983) and Anderson *et al.* (1985) we performed model II (major axis) regression analyses of log-transformed limb measurements to calculate allometric equations for sub-divisions of our data (Tables S3 and S4). Alexander's (1983) exponents were used in the present analysis, on the assumption that the majority of Jurassic and Cretaceous birds have limb proportions and wing shapes consistent with powered flight (Nudds *et al.*, 2004). Although all relationships reported are best fits to account for individual variation (Frasier, 1984), lengths of the humerus and femur are the most consistent for Mesozoic flying birds (Table S4). These bones are also among the most commonly preserved and show a highly significant relationship to one another ($y = 0.5914x + 10.891$, $R^2 = 0.8896$). Femur length was selected as the ultimate measure of mass because our preliminary analyses showed that this bone gives the most consistent measure of mass for derived allometry (Table S4) and is also most frequently used in the literature. Despite their potential advantages, we did not use volumetric estimates of scale models or 3D slicing approximations to derive body masses (Henderson, 1999), because most fossil birds are preserved only in two dimensions.

Testing for directional changes in body size

We tested for body size increase by plotting estimated body masses against the stratigraphic age of specimens in millions of years, both between and within individual Mesozoic clades. Recovery of a statistically significant positive slope of all points indicates an increase in mean body size, within and between clades at varying levels. Unknown femur lengths were scaled from corresponding humeral lengths and data were log-transformed to normalize distributions. Based on Fig. 1, data were graphed across all taxa and within clades that contain sufficient specimens. Least squares regression lines were calculated for each graph to examine trend variation at differing taxonomic levels (Alroy, 2000; Hone *et al.*, 2005; Hone & Benton, 2007).

Our approach to these data differs from recent analyses of this type (e.g. Hone *et al.*, 2005; Hone & Benton, 2007) because in the case of our Mesozoic bird sample, independent pair-wise comparisons of putative ancestor-descendent pairs of taxa within families were not possible. Such comparisons are usually made based upon either differences in stratigraphy (e.g. Alroy, 1998) or phylogeny (Hone *et al.*, 2005) but they should (of course) take into account higher level taxonomy. Previously, pairs of taxa have been selected from within families as it is assumed that between family comparisons would be invalidated by the differences in morphology and ecology that would separate taxa at this level (Hone *et al.*, 2005; Hone & Benton, 2007).

In the case of Mesozoic flying birds, our knowledge of taxonomy is such that families and similarly ranked clades contain very few genera or species (Table S1). This is further complicated by the stratigraphic distribution of taxa which are limited to just a few geological formations, providing limited separation in time between taxa. As a result, it is not possible to generate meaningful comparisons between taxa, despite the relatively high numbers of species. We are aware that use of simple, nonphylogenetic regression analysis will inflate Type 1 error rate (Martins *et al.*, 2002).

Results

Exponents for body mass in Mesozoic birds

Calculated exponents for Mesozoic flying birds (Table S3) show significant Pearson (1948) *r* values ($P < 0.05$); thus these exponents can be compared directly against one another to investigate change in body size (Fig. 2). Curves are particularly close for femur diameters (Fig. 2b) and relatively close for tibiotarsus diameters (Fig. 2d), an indication, that there may be less variation in bone diameter than in bone length in birds with different modes of life. Curves are also similar for tibiotarsus lengths (Fig. 2c), although they start to diverge at greater body sizes, indicating there is little size difference in tibiotarsus length in smaller birds, but that this element becomes relatively longer in larger running birds. Body size estimates spanning the phylogeny of Mesozoic birds show good agreement – ranges between the highest and lowest estimates for the proxies of *Archaeopteryx*, *Liaoningornis*, *Sinornis* and *Yixianornis* do not exceed 0.206 kg (Fig. 2). However, note that the latter three are among the smallest birds included in the data set; because allometric equations use power functions of linear dimensions, discrepancy between
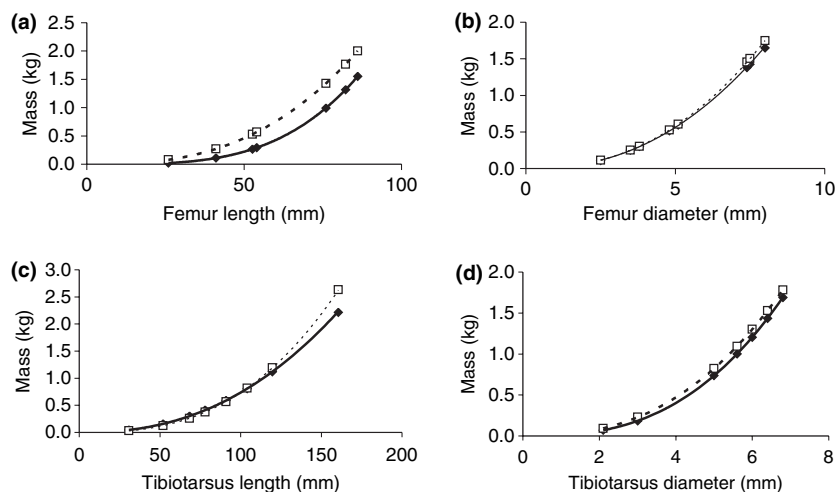
Fig. 2 Variation in mass estimates based on exponents for (a) femur diameter; (b) femur length; (c) tibiotarsus diameter; and (d) tibiotarsus length. The dashed line represents mass estimates based on Maloiy et al.'s (1979) exponent; the solid those based on Alexander's (1983) exponent.

minimum and maximum estimates may be much larger for heavier birds.

Directional changes in body size

Our data show clear evidence for an overall increase in avian body size (Cope's Rule) through the Jurassic and Cretaceous when all birds are treated as a single clade: when the natural log of femoral lengths is plotted against time a significant positive slope is recovered (Fig. 3). However, distribution of sizes within these data is uneven, but is nevertheless very similar to the mass distribution of modern birds (Dunning, 1993); thus despite scatter in the data we show that the mean mass of fossil birds increases through the Jurassic and Cretaceous (Fig. S1). This result is also clade specific: examining trends within different clades reveals different patterns (Fig. 4). The clades Pygostylia (Fig. 4a) and Ornithothoraces (Fig. 4b) both show strong positive trends similar to that of Aves as a whole (Fig. 3). In contrast Enantiornithes (Fig. 4c), although maintaining a positive trend, show much less marked results, and the Ornithuromorpha exhibit a trend towards decreasing size (Fig. 4d).

Discussion

Until the mid-1990s the fossil record of Mesozoic birds was extremely sparse – just a handful of specimens were known across an almost 150 Myr time-span (Chiappe & Dyke, 2002). Such a paucity of fossils meant that even general questions about early avian evolution could not be tested and little was known about size-related trends within basal birds (Feduccia, 1980; Rayner, 1991; Chiappe, 1995). However, because the number of described Jurassic and Cretaceous taxa has more than tripled since 1990 (Chiappe & Dyke, 2002; Zhou, 2004; Fountaine et al., 2005), we are now able to identify specific evolutionary trends within birds through time – such as
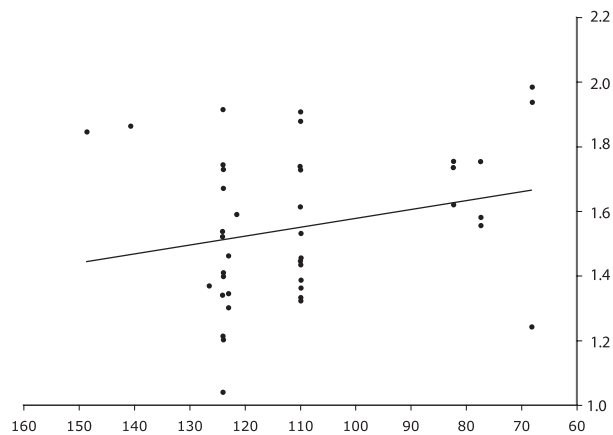
Fig. 3 Scatter plot comparing body mass (y-axis, $\log_{10}$ femur length) of Mesozoic birds against age (x-axis, Ma). Time scale is from late Jurassic (150 Ma) to the end of the Cretaceous (65 Ma). The time of occurrence of each bird species is taken as the mid-point of its total stratigraphic range. Size (mass) is inferred from the length of the femur (see text for details). The best-fitting least-squares regression line is $y = -0.0028x + 1.8525$ ($r^2 = 0.0558$).

changes in size and body mass – and describe how these relate to the refinement of flapping flight and lineages dynamics.

Based on our comprehensive data set of Jurassic and Cretaceous limb proportions (Table S1), we demonstrate an increase in body size with time (Cope's Rule) across the known Mesozoic avian clades. This conclusion is contrary to most previous interpretations of avian evolution and is true overall (all known taxa considered together) and within individual clades, with the exception of Ornithuromorpha – the lineage that ultimately includes extant birds. All identified trends are positive and show a progression towards increasing body size. This is counterintuitive, since many phylogenetically basal birds – *Archaeopteryx,*
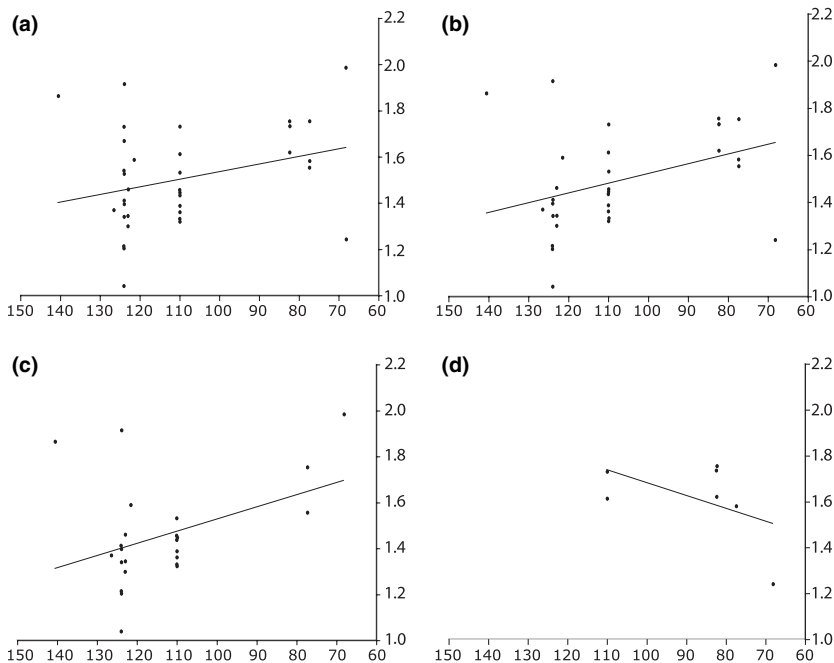
Fig. 4 Scatter plots showing age of records (*y*-axis, Ma) within various clades of Mesozoic flying birds (Fig. 1) with least-squares regression lines for $\log_{10}$ femur length (*x*-axis, body mass): (a) Pygostylia, $y = -0.0033x + 1.8639$ ($r^2 = 0.0887$); (b) Ornithothoraces, $y = -0.0041x + 1.9342$ ($r^2 = 0.1375$); (c) Enantiornithes, $y = -0.0053x + 2.0541$ ($r^2 = 0.1599$); (d) Ornithomorpha, $y = -0.0056x + 1.1233$ ($r^2 = 0.2598$).

Rahonavis and *Shenzhouraptor* – have bony tails and have been considered 'large' in size (Chiappe & Dyke, 2002). Nevertheless, a correlated reduction in variance with the apparent loss of smaller forms (Figs 3 and 4) allow us to term these changes Cope's Rule *sensu stricto* (Hone *et al.*, 2005; Hone & Benton, 2007); however, low numbers of taxa and limiting taphonomic effects temper this conclusion. Effects we have identified are in any case different from the 'small-ancestor problem' of Stanley (1973) – birds did not simply increasing in size from a small ancestor, but diversified into both larger *and* smaller body sizes with respect to their phylogenetically earlier diverging counterparts (Fig. 1).

The higher mean body mass – and narrower size range – seen in Jurassic and Cretaceous birds compared with their extant counterparts (Dunning, 1993) could be a factor of the size of our data sample, or more likely it is real. Previous work has argued for the completeness of the Mesozoic bird fossil record, to the extent that trends reflecting patterns of diversification can be extracted (Fountaine *et al.*, 2005; Dyke *et al.*, 2007). The pattern of increase in mean body mass that we have identified, coupled with an increase in variance, is typical of an expanding and successful clade. It does not require the assumption of a positive driving force that led to increased size, other than the observation that early members of the clade were small (Stanley, 1973). As the avian clade diversified, its members occupied a wider and wider array of niches (Gould, 1988); however, unlike the broadly contemporary volant pterosaurs the entire size distribution of Mesozoic birds does not shift over the course of their temporal range (Hone & Benton, 2007).

This corroborates the presence of different selective pressures influencing the evolution of body size in birds through time when compared with pterosaurs (Dyke *et al.*, 2006; McGowan & Dyke, 2007). A simple explanation for these trends is that perhaps Mesozoic birds had not explored the smallest and largest body sizes seen among extant avians, because the clade was still at an early stage of its diversification. This further suggests that the full range of flight styles available to early birds had also not been fully explored even though we know that Enantiornithes were as aerially diverse as modern perching songbirds (Passeriformes) (Nudds *et al.*, 2004, 2007).

Finally, our analyses have intriguing implications for the survivorship of modern birds (Neornithes) across the KP extinction horizon – unlike the other known clades of Mesozoic birds, this lineage extended across the boundary and diversified rapidly in the Palaeocene and Eocene (Ericson *et al.*, 2006). The clade that includes these taxa, Ornithuromorpha, is the only one of the four Mesozoic lineages that shows a clear trend towards a size decrease through time (Fig. 4d). If smaller organisms really are the more likely survivors of extinction events (Russell, 1977; Stanley, 1990) then this trend has potential to explain the extension of this lineage across the boundary at the expense of their larger counterparts.

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Supplementary material

The following supplementary material is available for this article:

Table S1 Age and measurement data collected for Mesozoic birds.

Table S2 Allometric equations reported by Maloiy *et al.* (1979), Alexander (1983) and Anderson *et al.* (1985) relating bone dimensions to body masses.

Table S3 Correlations of exponents used to estimate body mass.

Table S4 Formulae of the best-fitting least-squares regression line for each of the exponents of body mass plotted against time.

Figure S1 Scatter graph comparing the mass estimates calculated for each proxy, from both Maloiy *et al.* (1979) and Alexander's (1983) exponents.

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