

Cracking a Developmental Constraint: Egg Size and Bird Evolution

GARETH J. DYKE,*¹ AND GARY W. KAISER²

¹ School of Biology and Environmental Science, University College Dublin, Belfield Dublin 4, Ireland
gareth.dyke@ucd.ie

² Royal British Columbia Museum, Victoria, B.C. Canada V8W 9W2
gansus@shaw.ca

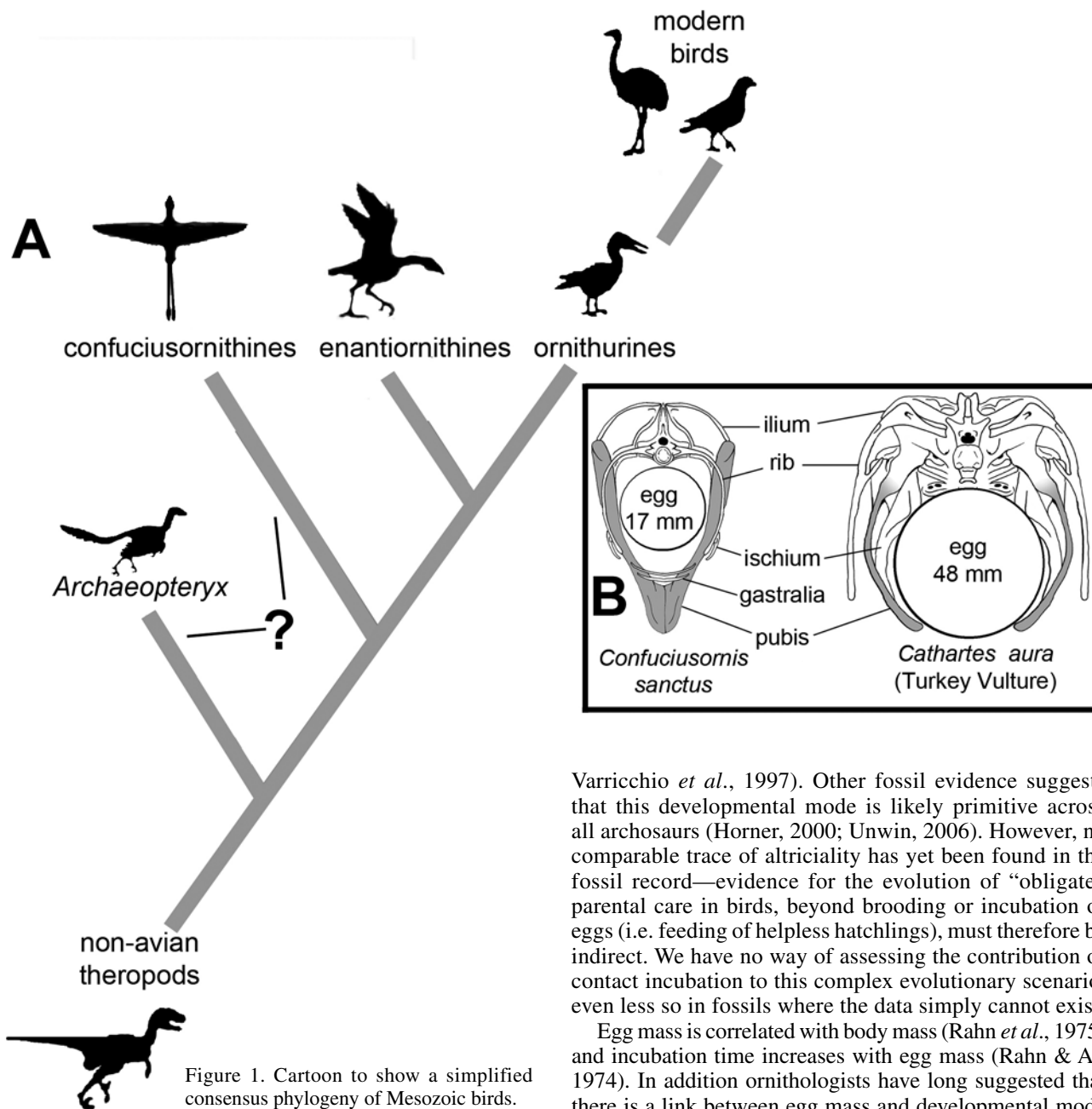
ABSTRACT. It has been suggested that relative egg size in living birds is strongly correlated with the developmental mode of the young; “altricial” (helpless) or “precocial” (independent). Using a data set of extant taxa we show that altricial birds lay relatively larger eggs than their precocial counterparts but that this may be due to the small size of most altricial species. Smaller birds tend to lay relatively small eggs compared to large species. Nonetheless, a predictive egg mass-body mass relationship extends into the avian fossil record. Such a relationship is important to our understanding of avian evolution because relative egg size (and thus available developmental mode) was constrained in many early birds—oviduct diameter was limited by the presence of pubic fusion. Therefore we document the evolution of avian developmental strategies using morphology-based phylogenies for Mesozoic and extant avians and corroborate correlations between developmental strategies, egg weight and female body mass. The sequential loss of precocial features in hatchlings characterises the evolution of birds while altriciality is derived within Neoaves. A set of precocial strategies is seen in earlier lineages, including basal Neornithes (modern birds) and are implied in their Mesozoic counterparts—skeletal constraints on egg size, present in many Jurassic and Early Cretaceous birds (*Archaeopteryx*, *Confuciusornis*, *Enantiornithes*) were lost in later diverging lineages. Attributes of precociality were already present in a number of lineages of non-avian maniraptoran theropods. We propose that the evolution of “unrestricted egg size” may have precipitated subsequent development of the diverse reproductive strategies seen in living birds.

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Birds are unique amongst living vertebrates in the sheer range of developmental strategies and forms of parental care they employ (O’Connor, 1994). This variation, spread across a spectrum that ranges from completely helpless hatchlings (“altricial”) to those that are independent, even immediately flighted (“precocial”), has always proved difficult to classify and understand in a phylogenetic context even when dealing with modern birds (living Neornithes) (Nice, 1962; O’Connor, 1994; Starck & Ricklefs, 1998).

This is because avian developmental strategies are not always consistent within families and are a mixture of behavioural and physiological phenomena (Starck & Ricklefs, 1998). Consequently there has been little evidence of any directional trend when characteristics of this altricial-precocial (A–P) spectrum (effectively degree of “neonate dependence”) have been mapped onto the various phylogenies proposed for birds (Aves) during the 20th century (Cracraft, 1986; Starck & Ricklefs, 1998; Sibley & Ahlquist, 1990; Deeming, 2007a).

* author for correspondence



We also note that the actual characteristics that determine “altriciality” and “precociality” are not absolute: even simple characteristics are subject to observational judgment and are not exactly the same in one lineage of birds as they are in another (Starck & Ricklefs, 1998).

Nevertheless, in spite of a lack of clear phylogenetic association, it has long been suggested that “precociality” is the primitive condition within Aves (Elzanowski, 1981; Starck & Ricklefs, 1998; Zhou & Zhang, 2004). Well-developed feathers in a late-stage embryo of a Cretaceous enantiornithine even suggest “super-precociality” (immediate flight) at hatching in at least one pre-neornithine fossil bird (Zhou & Zhang, 2004). Taken in combination with inferred osteological growth rates for other fossil birds (Chinsamy, 2002; de Ricqlès *et al.*, 2003; Cambra-Moo *et al.*, 2006), and the egg and nest morphologies of some non-avian theropods, evidence clearly points to precociality at the base of Aves (Elzanowski, 1981;

Varricchio *et al.*, 1997). Other fossil evidence suggests that this developmental mode is likely primitive across all archosaurs (Horner, 2000; Unwin, 2006). However, no comparable trace of altriciality has yet been found in the fossil record—evidence for the evolution of “obligate” parental care in birds, beyond brooding or incubation of eggs (i.e. feeding of helpless hatchlings), must therefore be indirect. We have no way of assessing the contribution of contact incubation to this complex evolutionary scenario, even less so in fossils where the data simply cannot exist.

Egg mass is correlated with body mass (Rahn *et al.*, 1975) and incubation time increases with egg mass (Rahn & Ar, 1974). In addition ornithologists have long suggested that there is a link between egg mass and developmental mode (Heinroth, 1922; Amadon, 1943; Tullberg *et al.*, 2002). Although Rahn & Ar (1974) were unable to detect such a relationship, it is supported by other evidence (Nice, 1962; Starck & Ricklefs, 1998; Deeming, 2007ab). If significant, a predictive relationship would be hugely important to interpreting the avian fossil record because of anatomical constraints on egg size (Fig. 1B), exceptional flightless living birds like the kiwi, *Apteryx*, notwithstanding. Here we restrict our discussion to flighted birds where egg size is also constrained by aerodynamic considerations.

In this paper we reconstruct the evolution of the A–P spectrum in living neornithine birds by mapping the distribution of neonate dependence (Nice, 1962; O’Connor, 1994; Starck & Ricklefs, 1998; Deeming, 2007a) onto a recent morphology-based phylogeny (Livezey & Zusi, 2006, 2007) (Fig. 2). Trends were cross-checked against another recent large-scale genomic study that reconstructed the phylogenetic history of birds (Hackett *et al.*, 2008). We then corroborate the presence of previously suggested correlations

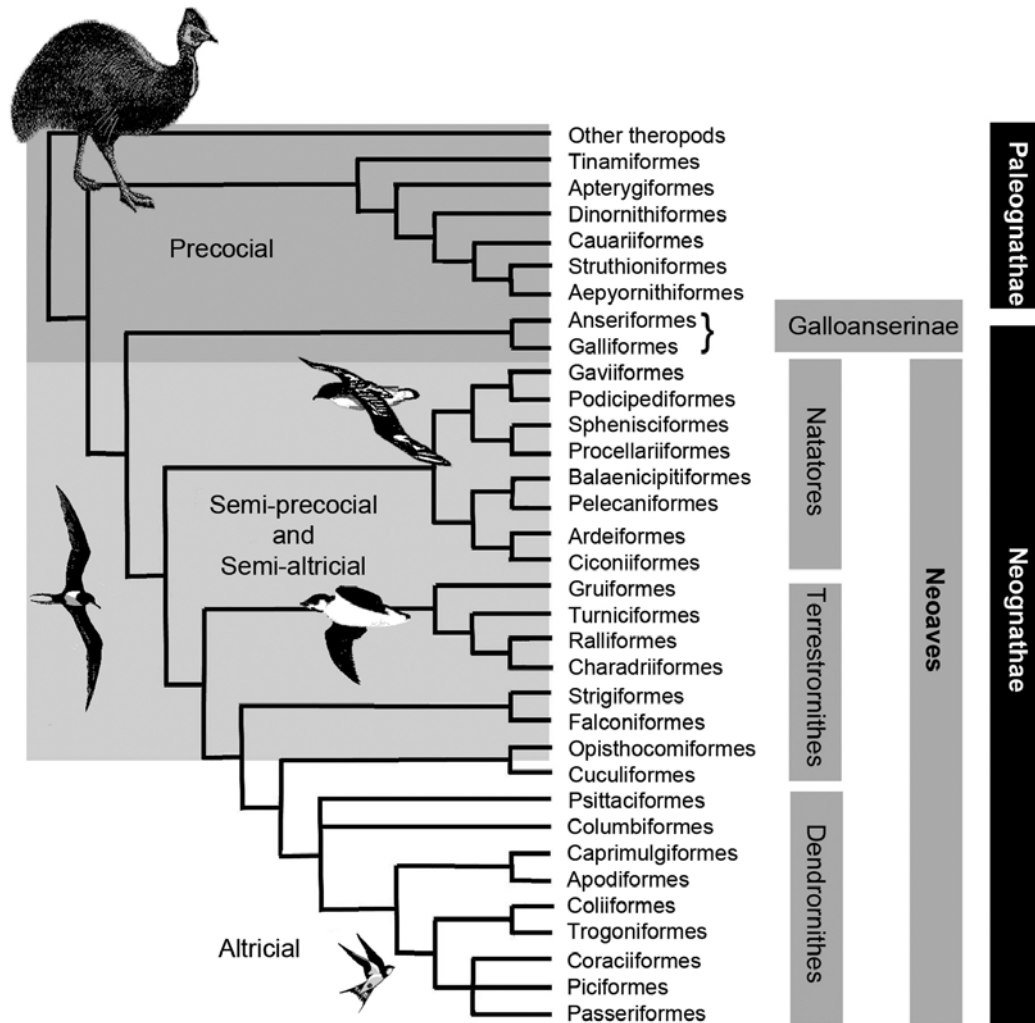


Figure 2. Phylogenetic hypothesis for relationships amongst modern birds (Neornithes) showing altricial and precocial modes of development (Livezey & Zusi, 2006, 2007).

between egg mass and female body mass (Appendix) as proxies for avian parental investment (Deeming, 2007ab). Finally, using femur length to approximate body mass (Hone *et al.*, 2008), we added data for specimens of the abundant and early diverging Cretaceous bird *Confuciusornis* (Appendix) to extend this predictive relationship back into the avian fossil record and to augment our understanding of the theropod origin of birds.

Materials and methods

Our analyses use egg mass and female body mass data for species-level taxa culled from the primary literature and from Dunning (1993; see also Appendix), correlated with the morphology-based phylogeny of Livezey & Zusi (2006, 2007). Data coverage across the major neoavian clades is good, but for this analysis we only have a small (N=2) sample for paleognaths. For the well-represented fossil bird *Confuciusornis*, egg volume was calculated from the measured width of the pelvic canal and extrapolated proportions of modern bird eggs and egg mass from a standard shape/volume equation (Hoyt, 1979). We know (Kaiser, 2007) that the eggs of these Cretaceous birds were more-or-less round, as are those of described enantiornithines (Zhou & Zhang, 2004). Avian femur lengths were extracted from a published compilation (Dyke *et al.*, 2006) and the

RBCM ornithology collection while fossil body mass estimates were calculated using a standard allometric method (Hone *et al.*, 2008). *Confuciusornis* specimen measurements are from Kaiser (2007) and Hone *et al.* (2008), cross-checked with Chiappe *et al.* (1999). Because this paper discusses initial qualitative comparisons, at a very broad phylogenetic scale, a comparative analysis is not presented. This represents an area for future work.

Results and discussion

Extant birds (living Neornithes)

In contrast to earlier studies of avian developmental evolution that require multiple origins of altriciality in birds (Starck & Ricklefs, 1998; Deeming, 2007ab), simple qualitative mapping of neonate dependence onto the phylogenetic hypothesis of Livezey & Zusi (2007) is appropriate because this topology implies a sequential loss of precocial features towards the crown of Neoaves (Fig. 2). Earlier diverging lineages of Neornithes (Paleognathae, Galloanserinae, Gaviiformes, and Podicipediformes) are characterized by a high degree of precociality (del Hoyo *et al.*, 1992–2002; Starck & Ricklefs, 1998). The young of the Pelecaniformes, a later diverging member of the Natatores (Livezey & Zusi, 2007), are the first to exhibit altriciality. The degree of altriciality is highly variable among the Natatores, and often restricted to the early

neonate stages, as in the Sphenisciformes (penguins) and Procellariiformes (petrels). Later stages are typically active and mobile (Dunn, 1975; Simpson, 1976; Warham, 1990; Gaston, 2004). Later diverging groups, such as those clustered in the Terrestrialnithes also exhibit varying degrees of altriciality. In contrast, it does appear to be the case that completely helpless hatchlings—born naked, blind and immobile—characterize the large monophyletic cluster of small, forest-dwelling birds at the crown of Neoaves, Dendromithes (Fig. 2), although more data combined with a phylogenetic comparative analysis will be required to verify this correlation. The most significant incompatibility between our qualitative mapping of neonate dependence (qualitative data from Kaiser, 2007) onto the morphology-based phylogeny of Livezey & Zusi (2007) or the phylogenomic result of Hackett *et al.* (2008), relates to the crownward movement of falconids, which places a group with “semi-altricial” developmental strategies (*sensu* Starck & Ricklefs, 1998) as the closest relative to two other clades (Passeriformes and Psittaciformes) that have fully altricial young. This correlation is intuitive.

The evolutionary transition from precociality to altriciality, correlated with changes in relative egg-size, is not the only aspect of avian reproduction that can be accommodated by phylogeny (Livezey & Zusi, 2006, 2007); broad qualitative trends in duration of incubation and enhanced nestling-care, increasingly sophisticated nest-building and decreases in clutch size are also apparent (Fig. 2). Some of these may be related to an overall decrease in adult size associated with a shift from relatively simple, open environments to the complex three-dimensional structure of tree canopies. As expected from their less-developed hatchlings, the eggs of altricial birds require shorter incubation periods (on average 20.8 days, $n = 18$ non-passerine birds). All Passeriformes produce altricial young and some have extremely short incubation periods, between 10 and 16 days (Skutch, 1945) although this may reflect their small body and eggs (Kaiser, 2007). Birds that produce precocial young incubate their eggs for somewhat longer periods (23.2 days, $n = 5$). Semi-precocial and semi-altricial young appear to be incubated for even longer periods; 24.4 days ($n = 23$) and 32.3 days ($n = 42$) days respectively (del Hoyo *et al.*, 1992–2002). Interestingly, Grellet-Tinner *et al.* (2006) documented a clear egg-size increase within oviraptorid non-avian theropods that they suggested could have occurred to accommodate additional nutrients within the egg.

Small adult body size and intense parental care in altricial taxa may combine to produce shorter periods of nestling dependence (28.5 days) than in semi-precocial (40.3 days) or semi-altricial birds (42.2 days) although this is likely phylogenetically constrained (Deeming *et al.*, 2006). At a very broad level, early diverging precocial birds, and later diverging semi-precocial and semi-altricial taxa, use unsophisticated nests that simply keep their eggs from rolling away. These “nests” tend to be limited to scrapes, cushions of feathers and plant stems, or simple platforms of twigs placed out in the open. At best, they are camouflaged or hidden by adjacent vegetation. A wide range of birds hides its nests in tree cavities, underground burrows, or rock crevices. Some tree cavities boast a thick mattress of feathers but most are bare and many burrow nesters, especially seabirds, place their eggs on the ground, with only a thin pad of vegetation for protection (Warham, 1990; Gaston, 2004). It is only among the most crownward and wholly altricial taxa that we find elaborately constructed woven and moulded nests, an elaboration of the trend noted in non-avian theropod dinosaurs by Grellet-Tinner

et al. (2006). Indeed, this trend, in particular, may prove related again to body size: more complex nests may represent a response to the thermal issues related to small parental size. This represents another area for future work.

Interpreting the avian fossil record

Of clear significance for interpreting the fossil record, our data demonstrate that within the neoavian clade, “fully altricial” birds (*sensu* Nice, 1962; Starck & Ricklefs, 1998; Deeming, 2007a) produce significantly larger eggs (compared to female body mass) (Fig. 3A,B), than those of “precocial” and “super precocial” taxa. However such results likely reflect two distinct evolutionary trends. The first reflects the preponderance of precocial neonates among basal clades and altricial neonates among crown clades. The second reflects trends in body size and a bias in the distribution of body masses among living birds. Members of basal clades tend to be larger than members of crown clades. Both within clades and across class Aves, larger birds have lower egg to body ratios. A sub-sample of birds of comparable weights shows little difference in relative egg size between groups with altricial and precocial strategies. It is more supporting of the conclusions of Faaborg (1988) or Tulberg *et al.* (2002) that larger eggs are necessary for the pre-hatching development of precocial young.

Perhaps of greater evolutionary significance is the tendency of birds (within the subset of birds of comparable weight) that use either semi-altricial or semi-precocial strategies to have relatively large eggs. Some of these groups [e.g., Procellariiformes, Alcidae (Charadriiformes), Phaethontidae (Pelecaniformes)] combine relatively large eggs with minimal clutch sizes (1 or 2).

Combined with the concentration of altricial strategies in smaller birds, our data suggest the possibility of a lower limit on absolute egg size that may preclude precociality in most birds. Final adult body size is also much closer to the mass of the hatchling in small altricial birds than it is in their precocial counterparts (Deeming & Birchard, 2007), suggesting that time-to-independence is also a limiting factor on avian relative egg mass.

Using femur length as a proxy for body mass the predictive relationship between egg mass, body mass and reproductive strategy (Fig. 3) can be extended into the fossil record (Fig. 4). Although this proxy approach does not allow the subdivisions of the A–P spectrum to be distinguished (Appendix), it can be used to extrapolate egg mass relative to body mass across Aves. Corroborated by its pelvic anatomy (Fig. 1B), the relative egg size of the basal Early Cretaceous fossil bird *Confuciusornis*, for example, was small in comparison to that of most living birds (Fig. 4). Constrained by their anatomy, relatively small eggs must characterize most of the early diverging avian lineages (Fig. 1). In *Confuciusornis*'s case, in combination with its inferred growth rate (de Ricqlès *et al.*, 2003; Cambra-Moo *et al.*, 2006) and phylogenetic position (Chiappe *et al.*, 1999; Zhou & Zhang, 2004; Gao *et al.*, 2008) this bird was almost certainly precocial (Fig. 1). Recent studies also determined the growth rate of *Confuciusornis* to have been slower than that of many extant birds (Cambra-Moo *et al.*, 2006): this would also be reflected in extended time-to-independence for its nestlings as is seen in modern precocial birds. *Confuciusornis* appears to have laid an egg comparable in size to that of the extant Buttonquail (genus *Turnix*) even though the adult Buttonquail is a much smaller animal.

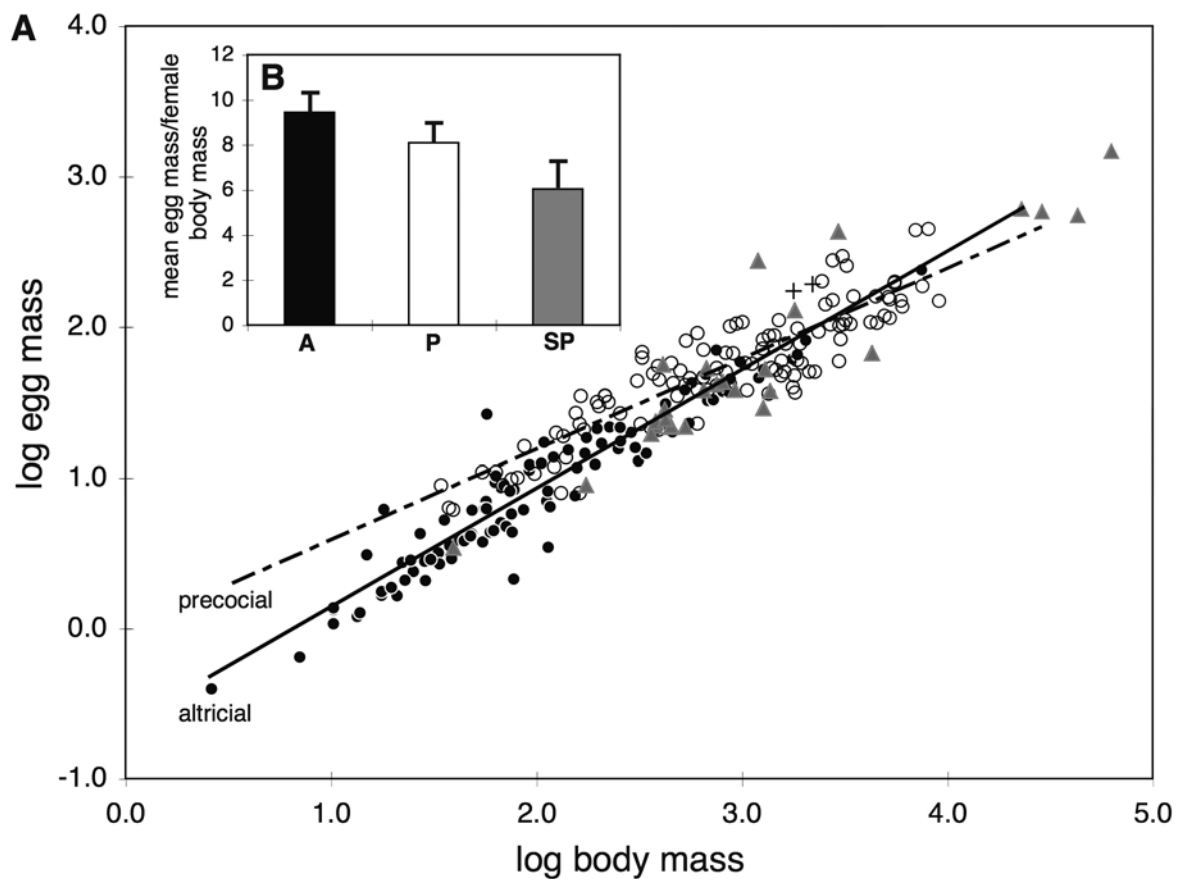


Figure 3. Relationship between egg weight and female body weight in extant birds. (A) Graph to discriminate between altricial [$n = 96$; filled circles; $r^2 = 0.906$, $p < 0.001$; egg mass = $-0.659394 + 0.7889097 \cdot \text{bodymass}$], and precocial [$n = 113$; open circles] (including super precocial [$n = 29$; grey triangles]; $r^2 = 0.801$, $p < 0.001$; egg mass = $-0.164615 + 0.6451872 \cdot \text{bodymass}$) taxa. Both of these results have significantly higher r^2 values than those found for 100 bootstrap replicates that paired body and egg mass at random. (B) Bar chart showing that the three broad developmental modes seen in Neornithes are characterized by significantly different egg/female body mass relationships. Discrimination among all three groups is borne out by averaged data (Kruskal-Wallis test, $p < 0.005$). Abbreviations: A, altricial; P, Precocial; SP, super precocial.

However, the hatchlings of *Confuciusornis* appear to have taken about five times as long to reach their adult size based on an estimate for *Confuciusornis* of 20 weeks (Cambra-Moo *et al.*, 2006) compared to three weeks from hatching to full independence in *Turnix* (Debus, 1996).

Origin of avian neonate adaptations and survivorship

Even in the absence of direct fossil evidence, small relative egg size in basal birds (including *Confuciusornis*) is expected: the eggs of comparably-sized dinosaurs close to the theropod-bird transition were also small (Buffetaut *et al.*, 2005). Indeed, phylogenetic studies predict that in addition to the acquisition and refinement of feathers, retention of a basal small body size was paramount at the “theropod-bird evolutionary transition” (Turner *et al.*, 2007) (Fig. 1). Of course the evolution of feathers would also allow for better heat retention at relatively smaller body sizes while the neonates of many non-avian theropod dinosaurs are known to have been extremely “birdlike”—evidence for precociality in baby theropod dinosaurs comes from osteology and even posture (Xu & Norell, 2004). In addition, just like modern birds, maniraptoran theropods are known to have laid eggs from a single functional oviduct (Varricchio *et al.*, 1997, Grellet-Tinner & Makovicky, 2006; Grellet-Tinner *et al.*, 2006) and in some cases are thought to have cared for their young (Horner,

2000). As far as is known simple nesting structures also characterize both non-avian theropods and basal birds (Grellet-Tinner *et al.*, 2006); there are no known Mesozoic examples of elaborately constructed nest structures comparable to the woven nests of modern Passeriformes (Fig. 3).

Mirroring our “egg size-neonate dependence” hypothesis at the reproductive level, the production of diminutive eggs by early birds is anatomically consistent with the pubic fusion (symphysis) seen in early diverging Jurassic and Cretaceous taxa (i.e. *Archaeopteryx*, *Confuciusornis*, known enantiornithines) and recorded as characters in phylogenetic hypotheses (e.g., Gao *et al.*, 2008): the presence of this rigid pubic structure would have limited the maximum diameter of the egg passing through the oviduct. Some non-avian dinosaurs appear to have attempted to overcome the effects of this constraint by producing elongated eggs that could contain more nutrient than a spherical egg of the same diameter (Grellet-Tinner *et al.*, 2006). Modern avian embryos develop their lightweight skeletons from calcium extracted from the eggshell. The increased surface to volume ratio of elongated dinosaur eggs might have made more calcium available to an embryo developing a long bony tail and the relatively heavy skeleton of a terrestrial animal. Because there is a relationship between egg size and neonate dependence, loss of this structural constraint in the Mid- to Late Cretaceous enabled the production of larger eggs and must have contributed to—even precipitated—the

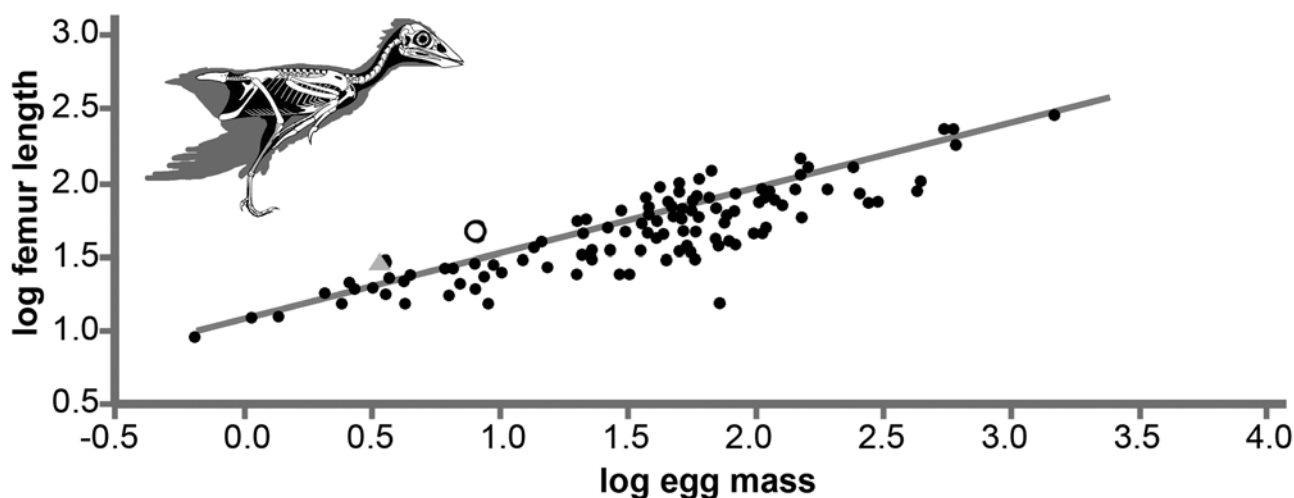


Figure 4. Relationship between femur length (approximates body mass) and egg mass in extant and fossil birds ($n = 117$; $r^2 = 0.758$, $p < 0.001$). These data show that both *Confuciusornis* (cartoon, open circle) and the similarly-sized Buttonquail (*Turnix*) (grey triangle) lay relatively small eggs compared to their body size (Appendix).

subsequent proliferation of avian reproductive strategies. Reduction of constraints on egg size and thus neonate dependence in ornithurine and basal neornithine birds also provides a possible explanation for the “selective survivorship” of modern birds in the aftermath of the end-Cretaceous extinction event.

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Appendix

Data used in the paper. Confuciusornis egg measurement from Kaiser (2007; Kenya Museum number B072). Femur lengths (N=15) from Hone *et al.* (2008), with mean length value verified by Chiappe *et al.* (1999). Abbreviations for development categories are *a*, altricial; *p*, precocial; *sa*, semi-altricial; *sp*, semi-precocial. The last column shows mean femur length and sample size.

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
<i>Accipiter badius</i>	a	21.3	196	2.2923	1.3291	10.9	
<i>Accipiter brevipes</i>	a	21.7	254	2.4048	1.3357	8.5	
<i>Accipiter cooperii</i>	a	43.0	566	2.7528	1.6335	7.6	64.9 (15)
<i>Accipiter gentilis</i>	a	59.0	973	2.9880	1.7709	6.1	82.8 (11)
<i>Accipiter striatus</i>	a	18.5	174	2.2405	1.2672	10.6	48.4 (24)
<i>Alcedo atthis</i>	a	4.3	27	1.4314	0.6340	15.9	15.3 (3)
<i>Alectoris barbara</i>	p	21.9	376	2.5752	1.3407	5.8	
<i>Alectoris chukar</i>	p	22.0	453	2.6556	1.3424	4.9	61.0 (1)
<i>Alectoris graeca</i>	p	21.8	530	2.7243	1.3376	4.1	56.8 (1)
<i>Alectoris rufa</i>	p	21.6	453	2.6556	1.3341	4.8	55.4 (1)
<i>Alectura lathamii</i>	sp	192.0	2210	3.3444	2.2833	8.7	89.5 (1)
<i>Anas acuta</i>	p	41.6	755	2.8779	1.6191	5.5	46.6 (2)
<i>Anas americana</i>	p	52.9	672	2.8274	1.7237	7.9	43.0 (8)
<i>Anas clypeata</i>	p	37.8	653	2.8149	1.5775	5.8	41.4 (5)
<i>Anas discors</i>	p	28.1	422	2.6253	1.4487	6.7	32.9 (3)
<i>Anas platyrhynchos</i>	p	52.2	1301	3.1143	1.7177	4.0	48.1 (7)

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
<i>Anas strepera</i>	p	43.1	808	2.9074	1.6345	5.3	44.1 (4)
<i>Anhinga anhinga</i>	sa	36.3	1338	3.1263	1.5599	2.7	53.8 (6)
<i>Anser albifrons</i>	p	128.5	1809	3.2574	2.1089	7.1	70.9 (1)
<i>Aphelocoma californica</i>	a	6.2	86	1.9337	0.7924	7.2	
<i>Aphelocoma coerulescens</i>	a	5.8	75	1.8749	0.7642	7.7	
<i>Aphelocoma insularis</i>	a	7.1	111	2.0461	0.8507	6.4	
<i>Aphelocoma ultramarina</i>	a	8.2	113	2.0519	0.9149	7.3	
<i>Apteryx australis</i>	p	430.0	2955	3.4706	2.6335	14.6	90.3 (5)
<i>Apteryx owenii</i>	p	275.5	1200	3.0792	2.4401	23.0	76.3 (2)
<i>Apus affinis</i>	a	2.4	25	1.3979	0.3825	9.7	15.4 (1)
<i>Apus apus</i>	a	3.6	38	1.5752	0.5539	9.5	17.5 (3)
<i>Apus caffer</i>	a	2.8	22	1.3444	0.4436	12.6	
<i>Apus melba</i>	a	6.2	18	1.2529	0.7955	34.9	
<i>Apus pallidus</i>	a	3.9	42	1.6222	0.5904	9.3	
<i>Aramus guarana</i>	sa	57.4	1110	3.0453	1.7589	5.2	76.5 (2)
<i>Ardea alba</i>	sa	39.4	812	2.9096	1.5956	4.9	
<i>Ardea cinerea</i>	sa	60.3	1547	3.1893	1.7800	3.9	102.8 (3)
<i>Ardea herodias</i>	sa	50.7	2110	3.3243	1.7053	2.4	99.4 (16)
<i>Ardea purpurea</i>	sa	50.8	830	2.9191	1.7055	6.1	87.3 (3)
<i>Ardeotis arabs</i>	p	107.5	4500	3.6532	2.0314	2.4	
<i>Ardeotis kori</i>	p	151.1	5900	3.7709	2.1793	2.6	145.0 (1)
<i>Balaeniceps rex</i>	sa	159.5	5130	3.7101	2.2028	3.1	127.0 (1)
<i>Bombycilla cedrorum</i>	a	3.2	33	1.5198	0.5051	9.7	19.1 (2)
<i>Bombycilla garrulus</i>	a	3.8	54	1.7340	0.5798	7.0	22.3 (1)
<i>Botaurus lentiginosus</i>	sa	35.1	482	2.6830	1.5452	7.3	
<i>Botaurus stellaris</i>	sa	42.0	867	2.9380	1.6232	4.8	94.6 (4)
<i>Burhinus oedicephalus</i>	p	42.8	459	2.6618	1.6310	9.3	
<i>Cacatua sanguinea</i>	a	23.1	550	2.7404	1.3644	4.2	
<i>Cacatua tenuirostris</i>	a	20.3	455	2.6580	1.3064	4.5	
<i>Calyptorhynchus banksii</i>	a	33.2	720	2.8573	1.5209	4.6	
<i>Calyptorhynchus latirostris</i>	a	32.8	675	2.8293	1.5163	4.9	
<i>Caprimulgus aegyptius</i>	a	8.4	77	1.8882	0.9267	10.9	
<i>Caprimulgus carolinensis</i>	a	17.3	108	2.0330	1.2376	16.0	
<i>Caprimulgus europaeus</i>	a	8.7	67	1.8261	0.9397	13.0	23.4 (2)
<i>Caprimulgus ridgwayi</i>	a	4.3	48	1.6812	0.6311	8.9	21.5 (1)
<i>Caprimulgus ruficollis</i>	a	9.2	69	1.8357	0.9651	13.5	
<i>Caprimulgus vociferus</i>	a	7.0	57	1.7520	0.8481	12.5	21.0 (2)
<i>Casuarius casuarius</i>	p	584.0	29000	4.4624	2.7664	2.0	232.0 (1)
<i>Cathartes aura</i>	a	82.1	2033	3.3081	1.9143	4.0	71.7 (12)
<i>Centropus senegalensis</i>	a	11.7	156	2.1931	1.0700	7.5	
<i>Chlamydotis undulata</i>	p	52.4	1450	3.1614	1.7192	3.6	65.5 (2)
<i>Chlidonias hybrida</i>	p	16.3	87	1.9370	1.2122	8.1	
<i>Chlidonias leucoptera</i>	p	11.0	54	1.7324	1.0414	20.4	
<i>Chlidonias niger</i>	p	11.0	63	1.7987	1.0414	17.5	
<i>Chlorostilbon mellisugus</i>	a	0.4	3	0.4150	-0.3979	15.4	
<i>Ciconia ciconia</i>	sa	105.9	3350	3.5250	2.0248	3.2	94.0 (1)
<i>Ciconia nigra</i>	sa	83.9	3000	3.4771	1.9236	2.8	85.0 (3)
<i>Coccyzus americanus</i>	a	9.4	63	1.7966	0.9731	15.0	27.9 (2)
<i>Coccyzus erythrophthalmus</i>	a	6.3	56	1.7443	0.7993	11.4	26.4 (1)
<i>Coccyzus minor</i>	a	9.0	69	1.8388	0.9518	13.0	
<i>Columba livia</i>	a	14.6	340	2.5315	1.1644	4.3	39.0 (4)
<i>Coracias benghalensis</i>	a	14.6	171	2.2330	1.1643	8.5	
<i>Coracias garrulus</i>	a	15.4	142	2.1523	1.1872	10.8	26.8 (1)
<i>Cuculus canorus</i>	a	3.5	113	2.0531	0.5434	3.1	28.9 (2)
<i>Cuculus saturatus</i>	a	2.1	77	1.8865	0.3313	2.8	
<i>Cursorius cursor</i>	sa	13.7	138	2.1399	1.1379	10.0	
<i>Cypseloides niger</i>	a	5.3	35	1.5490	0.7243	15.0	
<i>Dendragapus obscurus montana</i>	p	28.8	1271	3.1041	1.4594	2.3	68.2 (1)
<i>Diomedea chlororhynchos</i>	sp	202.9	2434	3.3863	2.3073	8.3	
<i>Diomedea epomophora</i>	sp	452.5	8040	3.9053	2.6556	5.6	
<i>Diomedea exulans</i>	sp	445.0	6950	3.8420	2.6484	6.4	103.0 (4)
<i>Diomedea immutabilis</i>	sp	279.0	2750	3.4393	2.4456	10.1	72.7 (19)
<i>Diomedea melanophris</i>	sp	258.0	3206	3.5060	2.4116	8.0	84.0 (1)
<i>Diomedea nigripes</i>	sp	298.0	3069	3.4870	2.4742	9.7	77.6 (18)
<i>Dromaeus novaehollandiae</i>	p	550.0	43080	4.6343	2.7404	1.3	227.9 (11)
<i>Eolophus roseicapillus</i>	a	13.0	311	2.4928	1.1153	4.2	
<i>Falco mexicanus</i>	a	37.6	801	2.9036	1.5752	4.7	73.3 (9)
<i>Falco peregrinus</i>	a	46.4	1201	3.0795	1.6665	3.9	73.0 (10)
<i>Falco rusticolis</i>	a	62.0	1748	3.2425	1.7923	3.5	88.1 (9)
<i>Falco sparverius</i>	a	13.8	120	2.0792	1.1399	11.5	36.6 (15)
<i>Francolinus africanus</i>	p	19.5	362	2.5581	1.2897	5.4	
<i>Francolinus bicalcaratus</i>	p	23.3	381	2.5809	1.3682	6.1	
<i>Francolinus francolinus</i>	p	24.3	424	2.6274	1.3861	5.7	
<i>Fregata magnificens</i>	a	88.2	1344	3.1282	1.9453	6.6	
<i>Fregata minor</i>	a	88.8	1428	3.1546	1.9484	6.2	49.7 (1)

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
<i>Gavia adamsii</i>	p	153.5	5212.5	2.18611	3.71705	2.9	64.1 (1)
<i>Gavia immer</i>	p	152.5	2740	2.18327	3.43775	5.6	58.5 (1)
<i>Gavia pacifica (arctica)</i>	p	98.4	1850	1.993	3.26717	5.3	41.8 (1)
<i>Gavia stellata</i>	p	78.1	1621.5	1.89265	3.20992	4.8	37.8 (1)
<i>Geococcyx californianus</i>	a	20.1	286	2.4568	1.3031	7.0	54.9 (4)
<i>Glareola nordmanni</i>	p	10.7	97	1.9877	1.0310	11.1	
<i>Glareola pratincola</i>	p	10.1	80	1.9036	1.0048	12.6	25.2 (1)
<i>Glaucis hirsuta</i>	a	0.7	7	0.8451	-0.1871	9.3	8.9 (2)
<i>Grus americana</i>	p	188.9	7497	3.8749	2.2762	2.5	
<i>Grus canadensis canadensis</i>	p	161.2	3460	3.5391	2.2074	4.7	
<i>Grus canadensis tabida</i>	p	161.2	4450	3.6484	2.2074	3.6	108.7 (3)
<i>Grus grus</i>	p	202.3	5500	3.7404	2.3060	3.7	
<i>Grus leucogeranus</i>	p	197.2	5475	3.7384	2.2950	3.6	
<i>Gyps fulvus</i>	a	242.0	7436	3.8713	2.3837	3.3	127.7 (2)
<i>Haematopus bachmani</i>	p	46.0	555	2.7442	1.6628	8.3	51.8 (2)
<i>Haematopus ostralegus</i>	p	41.5	526	2.7210	1.6180	7.9	43.7 (1)
<i>Haematopus palliatus</i>	p	46.8	644	2.8089	1.6703	7.3	
<i>Halcyon smyrnensis</i>	a	11.3	91	1.9609	1.0548	12.4	
<i>Heteroscelus incanus</i>	p	19.0	134	2.1274	1.2788	14.2	30.8 (1)
<i>Himantopus himantopus</i>	p	22.8	161	2.2068	1.3578	14.2	33.1 (4)
<i>Himantopus mexicanus</i>	p	21.0	169	2.2271	1.3222	12.4	
<i>Jacana spinosa</i>	p	8.0	161	2.2068	0.9031	5.0	28.4 (4)
<i>Jynx torquilla</i>	a	2.7	34	1.5250	0.4314	8.1	20.1 (1)
<i>Leipoa ocellata</i>	sp	173.0	1785	3.2516	2.2380	9.7	
<i>Lophortyx californicus</i>	p	8.9	175	2.2425	0.9509	5.1	41.8 (3)
<i>Lophotis ruficrista</i>	p	38.5	680	2.8325	1.5857	5.7	
<i>Meleagris gallopavo</i>	p	66.7	4300	3.6335	1.8239	1.6	121.8 (5)
<i>Menura novaehollandiae</i>	a	70.9	746	2.8727	1.8506	9.5	67.0 (2)
<i>Merops apiaster</i>	a	6.3	57	1.7528	0.8007	11.2	
<i>Merops orientalis</i>	a	3.1	15	1.1703	0.4932	21.0	
<i>Merops superciliosus</i>	a	6.2	48	1.6839	0.7902	12.8	
<i>Numida meleagris</i>	p	37.4	1375	3.1383	1.5724	2.7	79.0 (1)
<i>Oceanites oceanites</i>	sp	9.0	34	1.5315	0.9542	26.5	15.3 (2)
<i>Opisthocomus hoazin</i>	p	29.7	793	1.4728	2.8993		65.2 (11)
<i>Ortalis vetula</i>	p	56.0	414	2.6165	1.7482	13.5	65.5 (1)
<i>Otis tarda</i>	p	138.1	6000	3.7782	2.1401	2.3	
<i>Otis tetrax</i>	p	41.4	750	2.8751	1.6165	5.5	55.7 (1)
<i>Otus brucei</i>	a	12.6	105	2.0212	1.0995	12.0	
<i>Otus flammeolus</i>	a	10.4	63	1.7993	1.0179	16.5	26.2 (8)
<i>Otus scops</i>	a	12.3	92	1.9638	1.0899	13.4	29.8 (1)
<i>Pachyptila desolata</i>	sp	30.0	200	2.3010	1.4771	15.0	24.1 (1)
<i>Pachyptila vittata</i>	sp	32.0	196	2.2923	1.5051	16.3	
<i>Pandion haliaetus</i>	a	66.0	1850	3.2672	1.8195	3.6	78.1 (11)
<i>Parus ater</i>	a	1.1	10	1.0086	0.0337	10.6	11.8 (1)
<i>Parus caeruleus</i>	a	1.2	13	1.1239	0.0831	9.1	
<i>Parus cristatus</i>	a	1.4	10	1.0086	0.1403	13.5	12.8 (1)
<i>Parus cyanus</i>	a	1.3	14	1.1367	0.1074	9.3	
<i>Parus lugubris</i>	a	1.7	18	1.2430	0.2227	9.5	
<i>Parus major</i>	a	1.7	21	1.3176	0.2215	8.0	
<i>Parus montanus</i>	a	1.3	10	1.0086	0.1279	13.2	12.9 (1)
<i>Passer domesticus</i>	a	2.8	28	1.4533	0.4502	9.9	18.4 (1)
<i>Passer hispanolensis</i>	a	2.9	24	1.3838	0.4589	11.9	
<i>Passer moabiticus</i>	a	1.8	18	1.2430	0.2492	10.1	
<i>Passer montanus</i>	a	2.1	23	1.3560	0.3243	9.3	17.1 (2)
<i>Passer simplex</i>	a	1.9	20	1.2900	0.2756	9.7	
<i>Pedionomus torquatus</i>	p	9.8	75	1.8751	0.9933	13.1	
<i>Pelecanoides urinatrix</i>	sa	20.0	124	2.0934	1.3010	16.1	24.2 (3)
<i>Pelecanus erythrorhynchus</i>	a	150.0	9050	3.9566	2.1761	1.7	113.7 (2)
<i>Pelecanus occidentalis</i>	a	112.0	3174	3.5016	2.0492	3.5	85.4 (3)
<i>Pelecanus rufescens</i>	a	116.0	5200	3.7160	2.0645	2.2	
<i>Phaethon leturus</i>	sa	45.0	392	2.5933	1.6532	11.5	30.0 (3)
<i>Phaethon aethereus</i>	sa	54.0	750	2.8751	1.7324	7.2	37.1 (1)
<i>Phaethon rubricauda</i>	sa	71.0	645	2.8096	1.8513	11.0	36.9 (2)
<i>Phalacrocorax aristotelis</i>	a	51.0	1598	3.2036	1.7076	3.2	57.5 (1)
<i>Phalacrocorax atriceps</i>	a	60.0	2948	3.4695	1.7782	2.0	58.8 (2)
<i>Phalacrocorax auritus</i>	a	48.0	1540	3.1875	1.6812	3.1	59.3 (5)
<i>Phalacrocorax carbo</i>	a	58.0	1936	3.2869	1.7634	3.0	63.3 (10)
<i>Phalacrocorax olivaceus</i>	a	37.0	1800	3.2553	1.5682	2.1	
<i>Phalacrocorax pelagicus</i>	a	40.0	1759	3.2453	1.6021	2.3	50.1 (2)
<i>Phalacrocorax penicillatus</i>	a	51.0	2252	3.3525	1.7076	2.3	64.8 (3)
<i>Phalacrocorax pygmaeus</i>	a	23.0	603	2.7800	1.3617	3.8	
<i>Phalacrocorax urile</i>	a	48.0	1788	3.2524	1.6812	2.7	61.8 (3)
<i>Phalaropus fulicarius</i>	p	8.0	131	2.1169	0.9031	6.1	19.3 (1)
<i>Phalaropus lobatus (Alaska)</i>	p	6.4	37	1.5705	0.8062	17.2	17.3 (13)
<i>Phalaropus lobatus (Ontario)</i>	p	6.2	39	1.5911	0.7924	15.9	

species	development category	egg mass (g)	female mass (g)	log female mass	log egg mass	egg / female mass %	mm (n) mean femur
<i>Phalaropus tricolor</i>	p	9.0	68	1.8331	0.9542	13.2	21.9 (1)
<i>Pharomachus mocinno</i>	a	17.0	206	2.3139	1.2304	8.3	
<i>Phoenicopterus ruber</i>	p	142.7	2530	3.4031	2.1544	5.6	86.6 (8)
<i>Picooides albolarvatus</i>	a	4.4	59	1.7723	0.6435	7.4	32.5 (2)
<i>Picooides arctica</i>	a	4.8	71	1.8500	0.6812	6.8	24.4 (11)
<i>Picooides arizonae</i>	a	3.9	44	1.6444	0.5868	8.8	
<i>Picooides borealis</i>	a	4.2	48	1.6767	0.6182	8.7	
<i>Picooides dorsalis</i>	a	5.1	67	1.8228	0.7076	7.7	22.6 (11)
<i>Picooides nuttallii</i>	a	2.9	38	1.5832	0.4683	7.7	
<i>Picooides pubescens</i>	a	2.1	29	1.4564	0.3222	7.3	16.7 (9)
<i>Picooides scalaris</i>	a	2.9	30	1.4814	0.4624	9.6	
<i>Picooides villosus</i>	a	4.4	76	1.8791	0.6435	5.8	24.3 (10)
<i>Plegades falcinellus</i>	p	38.5	605	2.7818	1.5858	6.4	
<i>Pluvialis apricaria</i>	p	35.4	214	2.3304	1.5489	16.5	35.7 (2)
<i>Pluvialis dominica</i>	p	27.0	154	2.1875	1.4314	17.5	33.0 (1)
<i>Pluvialis squatarola</i>	p	35.2	214	2.3304	1.5465	16.4	37.4 (3)
<i>Podiceps nigricollis</i>	p	22.8	319	2.5031	1.3579	7.2	31.2 (4)
<i>Podiceps auritus</i>	p	21.0	392	2.5927	1.3222	5.4	32.7 (6)
<i>Podiceps grisegena</i>	p	38.3	1052	3.0222	1.5826	3.6	46.9 (18)
<i>Podiceps podiceps</i>	p	21.6	358	2.5539	1.3336	6.0	
<i>Psophia crepitans</i>	p	72.6	1250	3.0969	1.8612	5.8	15.7 (1)
<i>Psophia leucoptera</i>	p	83.2	1256	3.0990	1.9201	6.6	
<i>Pterocles alchata</i>	a	21.9	225	2.3522	1.3399	9.7	
<i>Pterocles coronatus</i>	a	15.9	300	2.4771	1.2026	5.3	
<i>Pterocles exustus</i>	a	12.4	192	2.2822	1.0919	6.5	
<i>Pterocles lichtensteini</i>	a	15.7	248	2.3945	1.1947	6.3	
<i>Pterocles orientalis</i>	a	21.1	383	2.5832	1.3245	5.5	47.2 (1)
<i>Pterocles senegallus</i>	a	17.6	255	2.4065	1.2460	6.9	
<i>Puffinus assimilis</i>	sp	32.0	222	2.3464	1.5051	14.4	23.7 (1)
<i>Puffinus gravis</i>	sp	102.0	870	2.9395	2.0086	11.7	
<i>Puffinus ilherminieri</i>	sp	35.0	163	2.2122	1.5441	21.5	
<i>Puffinus nativitatus</i>	sp	63.0	324	2.5105	1.7993	19.4	
<i>Puffinus puffinus</i>	sp	58.0	450	2.6532	1.7634	12.9	31.0 (1)
<i>Puffinus tenuirostris</i>	sp	82.0	530	2.7243	1.9138	15.5	36.9 (4)
<i>Rhea americana</i>	p	609.3	23000	4.3617	2.7848	2.6	180.4 (11)
<i>Rhynchotus rufescens</i>	p	38.0	928	2.9673	1.5798	4.1	71.1 (4)
<i>Rhynchotus jubatus</i>	sp	67.5	900	2.9542	1.8293	7.5	
<i>Rissa brevirostris</i>	sp	49.4	367	2.5647	1.6937	13.5	
<i>Rissa tridactyla</i>	sp	55.4	388	2.5883	1.7435	14.3	37.3 (9)
<i>Rostratula benghalensis</i>	sp	12.0	121	2.0828	1.0777	9.9	
<i>Rynchops niger</i>	sp	26.9	254	2.4048	1.4298	10.6	34.8 (2)
<i>Scopus umbretta</i>	a	31.0	423	2.6258	1.4914	7.3	46.8 (1)
<i>Spheniscus demersus</i>	sp	103.0	2960	3.4713	2.0128	3.5	74.0 (2)
<i>Spheniscus humboldti</i>	sp	109.0	4200	3.6232	2.0374	2.6	79.0 (3)
<i>Spheniscus magellanicus</i>	sp	120.0	4900	3.6902	2.0792	2.4	76.3 (2)
<i>Stercorarius longicaudus</i>	sp	44.3	307	2.4874	1.6467	14.4	36.2 (5)
<i>Stercorarius parasiticus</i>	sp	51.6	499	2.6981	1.7130	10.3	38.4 (10)
<i>Stercorarius pomarinus</i>	sp	68.0	829	2.9186	1.8325	8.2	45.8 (1)
<i>Stercorarius skua</i>	sp	91.7	604	2.7810	1.9626	15.2	
<i>Strix aluco</i>	a	38.5	524	2.7193	1.5853	7.3	60.8 (4)
<i>Strix nebulosa</i>	a	52.6	1267	3.1028	1.7211	4.2	88.9 (11)
<i>Strix occidentalis</i>	a	49.0	663	2.8215	1.6899	7.4	67.9 (10)
<i>Strix uralensis</i>	a	37.3	863	2.9360	1.5717	4.3	
<i>Strix varia</i>	a	45.5	873	2.9408	1.6580	5.2	74.6 (15)
<i>Struthio camelus</i>	p	1480.0	63000	4.7993	3.1703	2.3	289.2 (15)
<i>Sula abbotti</i>	sa	112.0	1500	3.1761	2.0492	7.5	
<i>Sula bassana</i>	sa	105.0	3090	3.4900	2.0212	3.4	
<i>Sula capensis</i>	sa	105.0	2670	3.4265	2.0212	3.9	
<i>Sula dactylatra</i>	sa	78.0	1902	3.2791	1.8921	4.1	61.2 (2)
<i>Sula leucogaster</i>	sa	54.0	1382	3.1405	1.7324	3.9	
<i>Sula neboxii</i>	sa	61.0	1840	3.2648	1.7853	3.3	
<i>Sula serrator</i>	sa	94.0	2350	3.3711	1.9731	4.0	
<i>Sula sula</i>	a	58.0	1030	3.0128	1.7634	5.6	47.0 (2)
<i>Sula variegata</i>	sa	76.0	1410	3.1492	1.8808	5.4	54.9 (1)
<i>Trogon elegans</i>	a	8.2	74	1.8681	0.9164	11.2	
<i>Turnix sylvatica</i>	p	3.4	40	1.5966	0.5361	8.7	
<i>Tyto alba</i>	a	26.6	57	1.7551	1.4249	46.7	58.1 (26)
<i>Upupa epops</i>	a	4.5	61	1.7882	0.6532	7.3	22.4 (1)
<i>Uria aalge</i>	s	109.0	1001	3.0004	2.0374	10.9	48.6 (6)
<i>Uria lomvia</i>	sp	106.0	932	2.9694	2.0253	11.4	47.5 (5)
<i>Zenaida asiatica</i>	a	7.7	153	2.1847	0.8865	5.0	
<i>Zenaida macroura</i>	a	6.5	116	2.0626	0.8129	5.6	27.3 (4)
<i>Confuciusornis sanctus</i>	p	8.2					47.0 (15)