

## Cracking a Developmental Constraint: Egg Size and Bird Evolution

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**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).

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