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Letter to the editor Open Access

Smarter birds, smaller eggs, and less parental care time

DEAR EDITOR,

Natural selection favors encephalization (i.e., enlargement of relative brain size) not only because it ultimately enhances the survival of organisms but also because it does not impair reproductive success. However, little is known regarding how encephalization does not impact the reproductive success of organisms. Here, by analyzing a dataset of more than 1 000 modern bird species, we found that female birds with increased relative brain size show a significant reduction in total prehatching maternal investment (TPMI, i.e., offspring investment before hatching, proxied by egg mass×clutch size) in reproduction activities, notably by laying smaller eggs rather than reducing clutch size. Interestingly, female birds that lay small eggs also show a significant decrease in the time cost of parental care (hatching and fledging). Given that the cumulative probability of brood mortality is time-dependent, reduced parental care time potentially enhances reproductive success by decreasing the probability of predation-associated brood mortality. Notably, reduced TPMI coevolved with encephalization in land birds, which may explain their rapid adaptive radiation following the Cretaceous-Paleogene (K-Pg boundary) mass extinction.

Encephalization has been strongly favored by natural selection. For example, multiple successive encephalization events have occurred during the evolution of different animal classes (Ksepka et al., 2020). A primary tenet of natural selection theory suggests that traits that ensure better survival are not selected unless they also ensure (or at least do not affect) long-term reproductive success (Nur & Sydeman, 1999). Therefore, encephalization should not impact reproductive success. However, an increase in brain size is accompanied by an increase in energy costs, thereby reducing the availability of energy for other functions such as reproduction. Under such circumstances, species may reduce their metabolic energy investment in reproduction if they coevolve a compensatory strategy to maintain reproductive success.

Measuring changes in reproductive energy investment that accompany encephalization should help elucidate the compensatory strategies used by species. Although both parents invest in reproduction, females typically spend more time and energy in such activities (Dawkins & Carlisle, 1976). Hence, researchers often use maternal energy investment in reproduction as a proxy for parental energy investment.

Egg production represents one of the most significant energy costs for birds. Egg mass reflects the energy females have invested in an offspring prior to hatching. Thus, egg mass is usually used as a proxy for prehatching maternal investment (PMI, i.e., female investment per offspring before hatching). In this study, we investigated how females reallocate reproductive energy investment during evolutionary encephalization and which concurrent selection strategies help reduce adverse effects on reproductive success.

We first collected raw relative brain size (referred to as brain size hereafter), egg mass, clutch size, and life history data (hatching time and fledging time) of birds from previous studies (Supplementary Materials and Methods) and generated a dataset of 1 214 extant species in Neognathae (Neoaves and Galloanseres, covering 42 orders and 186 families). We used brain size of a species as a proxy for female brain size of that species. Using phylogenetic generalized least squares (pGLS) analysis to test the relationship between brain size and TPMI (clutch size×egg mass), we found a significant negative correlation between the two parameters (R^2=0.75, P<0.001, slope=–0.49 with 95% CI (–0.50, –0.41)). This suggests that birds with greater brain size tend to allocate less TPMI to reproduction (Figure 1A). Subsequent analyses revealed that brain size was strongly

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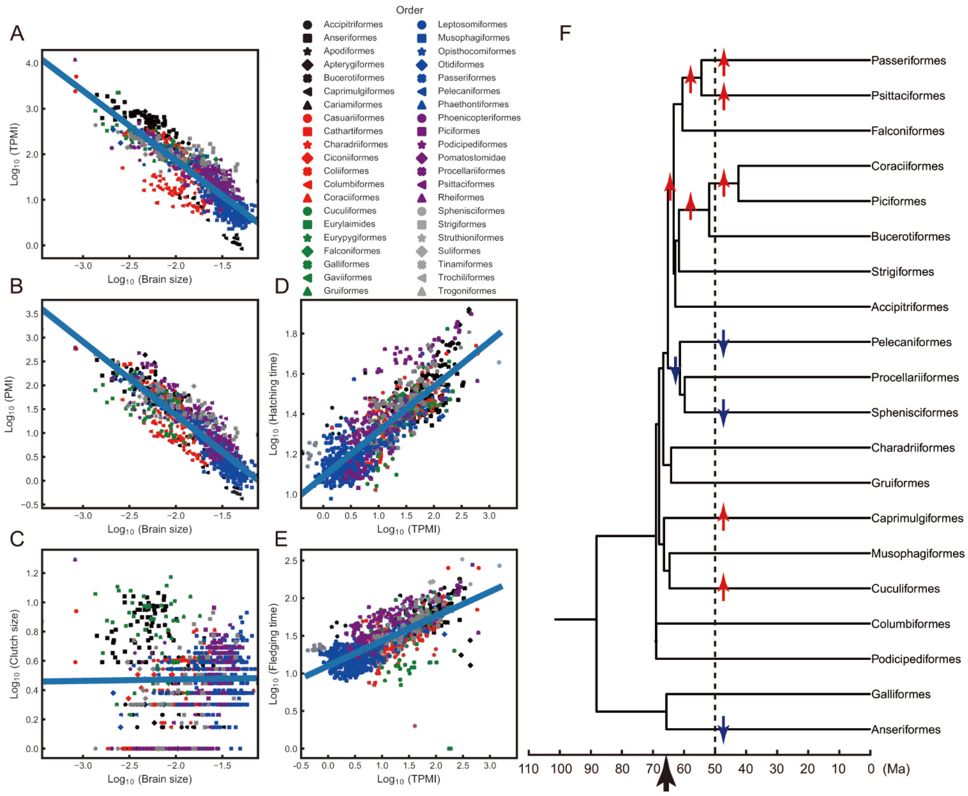

Figure 1 Correlation analyses among parameters (A–E) and significant evolutionary shifts in brain-TPMI slopes across avian phylogeny (F)

A–C: Brain size is plotted against TPMI (*n*=1 142), PMI (*n*=1 142), and clutch size (*n*=1 142). D, E: TPMI is plotted against hatching time (*n*=1 214) and fledging time (*n*=1 214), respectively. F: Significant shifts in brain size-TPMI slopes in bird phylogeny. Red and blue arrows denote higher and lower shifts, respectively. Black arrow indicates K-Pg boundary 66 million years ago. Gray dashed line represents approximate ending time. Bird phylogeny is derived from previous studies (Supplementary Materials and Methods). Different shapes or colors in A–E denote different avian orders. Brain size, TPMI, PMI, clutch size, hatching time, and fledging time were log-transformed before correlation testing.

and negatively correlated with egg mass (R^2=0.78, P<0.001, slope=–0.51 with 95% CI (–0.52, –0.50)) but not clutch size (R^2=2.40e–4, P=0.60). This implies that the reduction in TPMI, co-occurring with increased brain size, is achieved by laying smaller eggs (i.e., decreased PMI) rather than reducing clutch size (Figure 1B, C). Furthermore, we found the same pattern when performing the same analysis within each order (*n*=22). We next determined the extent to which females reduce TPMI in reproduction by examining the slopes derived from linear regression of brain size and TPMI. Overall, a female that increases brain size by one unit will reduce prehatching investment by 0.49 units (slope=–0.49). Taken together, we conclude that birds with greater brain size reduce prehatching investment in reproduction by laying smaller eggs.

To determine whether changes in TPMI among female birds with different brain sizes affect parental time costs, we measured the correlations between TPMI and parenting time (i.e., correlations between prehatching and post-hatching investment). As parental care mainly involves the hatching and fledging periods (Cooney et al., 2020), we analyzed the effect of parental time costs on reproduction during these two stages. We first estimated the correlation between TPMI and hatching time by controlling for phylogeny and found that TPMI was positively correlated with hatching time (Figure 1D, R^2=0.53, P<0.001), suggesting a reduction in hatching time for birds with greater brain size. Since predation of eggs is a major cause of reproductive failure during hatching (Ricklefs, 1969), a shortened hatching time is expected to reduce predator exposure and the probability of egg predation.

We next explored the relationship between TPMI and fledging time and found a positive correlation (Figure 1E, R^2=0.53, P<0.001), suggesting a reduction in fledging time in females with greater brain size. Given that the cumulative probability of brood mortality is time-dependent (Martin, 2014), earlier fledging tends to reduce brood mortality. Similar to hatching, a shortened fledging time is expected to reduce predator exposure (Martin, 2014; Ricklefs, 1969). Furthermore, as fledglings always disperse in space, the probability of brood mortality will be further decreased (Martin, 2014). Thus, species with reduced TPMI, followed by shorter hatching and fledging times, may potentially increase the probability of reproductive success.

Given that species with reduced TPMI exhibit lower offspring investment, how are such hatchlings capable of fledging earlier? To address this question, we compared the hatchlings of altricial and precocial birds. Altricial birds have larger brains than precocial birds (Martin, 1981), but, unlike precocial hatchlings, are blind, helpless, and entirely dependent upon parental care. Thus, to fledge earlier, altricial hatchlings need to grow faster than precocial hatchlings. Three processes may explain why the growth rate of altricial hatchlings outpaces that of precocial hatchlings. First, altricial hatchlings usually receive higher quality food than precocial hatchlings (Bennett & Harvey, 1985). Second, altricial hatchlings tend to develop a more robust digestive system (e.g., larger intestines) compared to precocial hatchlings, thus enhancing nutrient absorption and consumption (Starck & Ricklefs, 1998). Third, movement to find food, an energy-intensive process, is unnecessary for altricial hatchlings.

As noted above, birds with reduced TPMI and shortened hatching and fledging periods may display an increase in reproductive success. We therefore explored how the brain size-TPMI strategy evolved in avian history. We compared the slopes of brain size-TPMI (n=22 orders) with ancestral slopes and identified 12 orders with significant evolutionary shifts (Supplementary Materials and Methods). Among them, eight orders of land birds exhibited more negative slopes than their ancestral slopes (i.e., higher shifts, Figure 1F), suggesting that land birds show a greater reduction in TPMI than their ancestors. Indeed, encephalization is thought to be associated with the rapid adaptive radiation of land birds (Ksepka et al., 2020). One explanation is that encephalization enables organisms to better survive unexpected environmental changes (Ksepka et al., 2020). However, natural selection favors traits that allow organisms to better survive while maintaining (or even increasing) reproductive success (Nur & Sydeman, 1999). If so, other intrinsic factors should maintain reproductive success in coevolution with encephalization. Our findings suggest that reduced TPMI in land birds serves as one such intrinsic factor.

We also identified four waterbird orders with smaller brain size-TPMI shifts (Figure 1F) in bird phylogeny. These four orders exhibited higher TPMI relative to their ancestors (Figure 1F), an evolutionary trend opposite to that of land birds. Nonetheless, the abovementioned patterns are consistent with the observation that most waterbird species lay relatively large eggs and their offspring are precocial. As waterbird species tend to nest in open areas and face a much higher predation risk than land birds (Martin, 2014), their precocial chicks can walk soon after hatching, thus reducing predation pressure. In addition, thermal protection is critical for hatchlings living in aquatic environments, which may explain the more developed natal down of waterbird precocial chicks (Pap et al., 2020). To this end, females need to allocate sufficient resources to the egg, enabling the young to develop natal down well before hatching.

SUPPLEMENTARY DATA

Supplementary data to this article can be found online.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

X.J.Z. conceived and supervised the study. S.K.P. and D.P.W. wrote the manuscript. S.K.P. and X.H.Z. analyzed the data. All authors read and approved the final version of the manuscript.

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