

Endothermy, offspring size and evolution of parental provisioning in vertebrates

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Mammals and birds provide food for their young after birth, but such provisioning is almost absent in other vertebrates. A recent theory suggested that, in addition to thermoregulation, the large discrepancy in size between adult and young ectothermic vertebrates precludes them from providing for their young, whereas the relatively large offspring of endotherms are easier to provision. I show here that reptile neonates and hatchlings are as large as those of mammals and birds. Differences in size between adults and young thus cannot explain the lack of parental provisioning in reptiles. I suggest that the large size at birth is the ancestral condition in amniotes as a whole and that provisioning has thus evolved after endothermy.

ADDITIONAL KEYWORDS: Aves – cleidoic egg – ectotherm – endotherm – Mammalia – Metatheria – offspring size – Reptilia.

INTRODUCTION

In a fascinating recent paper, [Beekman *et al.* \(2019\)](#) try to resolve the puzzle of why parental provisioning of young is nearly ubiquitous in mammals and birds, whereas it is almost entirely absent in other vertebrates. Their solution relies on the following three axes.

Provisioning is less of a cost for mammals and birds. Endotherms need to provide thermal care for their offspring anyway, thus it is a time already spent raising the young, whereas ectotherms benefit more from investing in future reproduction.

Owing to thermal constraints, endotherms have relatively large young in comparison to ectothermic vertebrates. Therefore, endothermic young and adults can share similar foods. Ectothermic young can occupy a greater variety of sizes, enabling the small-sized offspring of ectotherms to specialize on diets different from those of the adults, making parental provisioning unlikely.

These size discrepancies allow ectothermic adults and young to occupy different habitats, again making parental provisioning problematic, whereas the size constraint on endothermic offspring makes them occupy the same habitats as their parents.

[Beekman *et al.* \(2019\)](#) reason that endothermy nearly always necessitates ‘prolonged postnatal care due to thermal constraints’. This might not be such a ubiquitous pattern. Precocial endotherms, which can thermoregulate at birth, are not rare. They range from birds (e.g. Anseriformes, Megapodiidae; [Bennett & Owens, 2002](#)) to mammals (all ungulates, some lagomorphs etc.) and, potentially, to pterosaurs ([Unwin & Deeming, 2019](#)). It might be the case that in warm regions endothermic neonates and hatchlings may also be within their thermoneutral zone for much of the day. Many precocial birds also do not feed their young ([Smiseth, 2019](#)). Nevertheless, I think that [Beekman *et al.* \(2019\)](#) have correctly identified a valid mechanism here, at least for most endotherms, although whether it is retained from the ancestral state or maintained by selection is an open question.

I hypothesize that the size-discrepancy argument, and its subsidiaries of foods and habitats of adults and young, cannot have caused the shift to parental provisioning in endotherms by itself. One major group of vertebrates, the reptiles, have large, direct-developing young, born in the same habitats as their parents, and yet reptiles almost never provision their young. Differences in size between adults and young (often larvae) are probably drastic in most fishes and amphibians, but reptile young are different. In fact,

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reptile young can be very big. The abdomen of female squamates is often much enlarged (Scharf & Meiri, 2013) and full of developing eggs or young, even when only one or two embryos develop (Kratovichil & Kubicka, 2007). Are reptile offspring as large, when hatching or being born, as bird hatchlings and mammalian neonates (in comparison to the size of their mothers)? I hypothesized that the evolution of the cleidoic egg resulted in an ancestral increase in the size of the amniote hatchling, and that large offspring sizes are generally retained in all amniotes, regardless of their thermoregulatory mechanisms. I thus predicted that reptile, bird and mammal sizes, as fractions of the sizes of the adults, will be broadly similar.

MATERIAL AND METHODS

To test whether endotherms have larger offspring, at birth or hatching, than reptiles of comparable sizes, I obtained data on the masses of neonatal and adult mammals from Jones *et al.* (2009; 1069 species) and for hatchling and adult birds of the same species from Myrsvold *et al.* (2015; 782 species). I compared these with my own data (Meiri, 2018, with minor updates, S. Meiri, A. Feldman, R. Schwartz & R. Shine, unpublished observations for mean masses of neonatal and hatchling squamates and adult females (Supporting Information, Appendix S1). The reptile data are based on lengths, transformed to masses based on taxon-specific equations (accounting for the degree of limb loss in relevant lineages; Feldman *et al.*, 2016).

Across species, offspring size varies allometrically with body size (the slope of the log hatchling size/log adult size regression is lower than one in all classes; not shown), whereas the argument by Beekman *et al.* (2019) rests on the discrepancy in size between conspecific young and adults driving differences in habitat use and diet. Thus, the question is not whether endotherms have relatively larger or smaller offspring than ectotherms than expected for their size, but whether they are more or less different from their mother. I therefore compared the ratio of the size of the offspring (at birth or hatching) to the size of the adult across the three amniote classes. Note that I am not regressing these size ratios against their denominator (or anything else; see also discussion by Smith, 1999, 2005), but simply comparing them across classes.

The use of a phylogenetically informed comparison would have been advisable in testing the association between the offspring size to adult size ratio and parental provisioning. However, given the fact that the transition to provisioning happened only twice (in the ancestors of crown groups Mammalia and Aves), a comparison of three monophyletic clades would have

no power to reject the null, making my test overly conservative. Although provisioning is very highly constrained, size ratios are extremely labile, varying by two orders of magnitude in birds and squamates and by five orders of magnitude in mammals (three orders of magnitude in placental mammals; Supporting Information, Appendix S1). I thus run a liberal, non-phylogenetic analysis, reasoning that this could more easily refute my prediction.

RESULTS

The average offspring size to adult size ratio is remarkably similar in all amniote classes (mean \pm SD): $8.2 \pm 5.8\%$ of adult mass in reptiles, similar to mammals ($8.2 \pm 7.6\%$, $t = 0.36$, $P = 0.971$) and slightly more than in birds ($7.0 \pm 4.0\%$, $t = 4.75$, $P < 0.0001$; Fig. 1). The overwhelming pattern is of great overlap (Fig. 1). The only clade showing very different patterns from amniotes as a whole is the Metatheria (marsupials), the neonates of which weigh, on average, a mere 0.04% of their adult mass at birth ($N = 52$ species; vs. 8.6% in placentals). In reptiles, lizards have relatively larger young than snakes (8.6 vs. 5.5%), perhaps because of their generally smaller size (Feldman *et al.*, 2016).

DISCUSSION

I found that the offspring of reptiles are of generally the same size, relative to that of their parents, as those of mammals and birds. Beekman *et al.* (2019: fig. 4) found that the energy content of the eggs of endotherms was higher than that of the eggs of ectothermic vertebrates laid by parents of similar lengths. I assume that this discrepancy derives from Beekman *et al.* (2019) treating all ectotherms together, grouping the large offspring of reptiles with the generally small offspring of fishes and amphibians. Indeed, Beekman *et al.* (2019) acknowledged that the discrepancy between birds and reptiles is orders of magnitude lower than that between birds and amphibians or fishes, and birds have a similar allometric slope to reptiles. More than 30% of their data for reptiles are from turtles. Turtles indeed lay small eggs, but are only ~3% of all reptiles. This might have biased their results more than the exclusion of turtles has biased mine.

At a given length, legged lizard and birds have similar masses (S.M., unpublished observations), whereas snakes and legless lizards of the same length are much lighter (Meiri, 2010; Feldman & Meiri, 2013). Beekman *et al.* (2019) compared the energy contents of eggs with the lengths of adults, rather than with masses as I have done, which might have resulted in a relative overestimation of the sizes

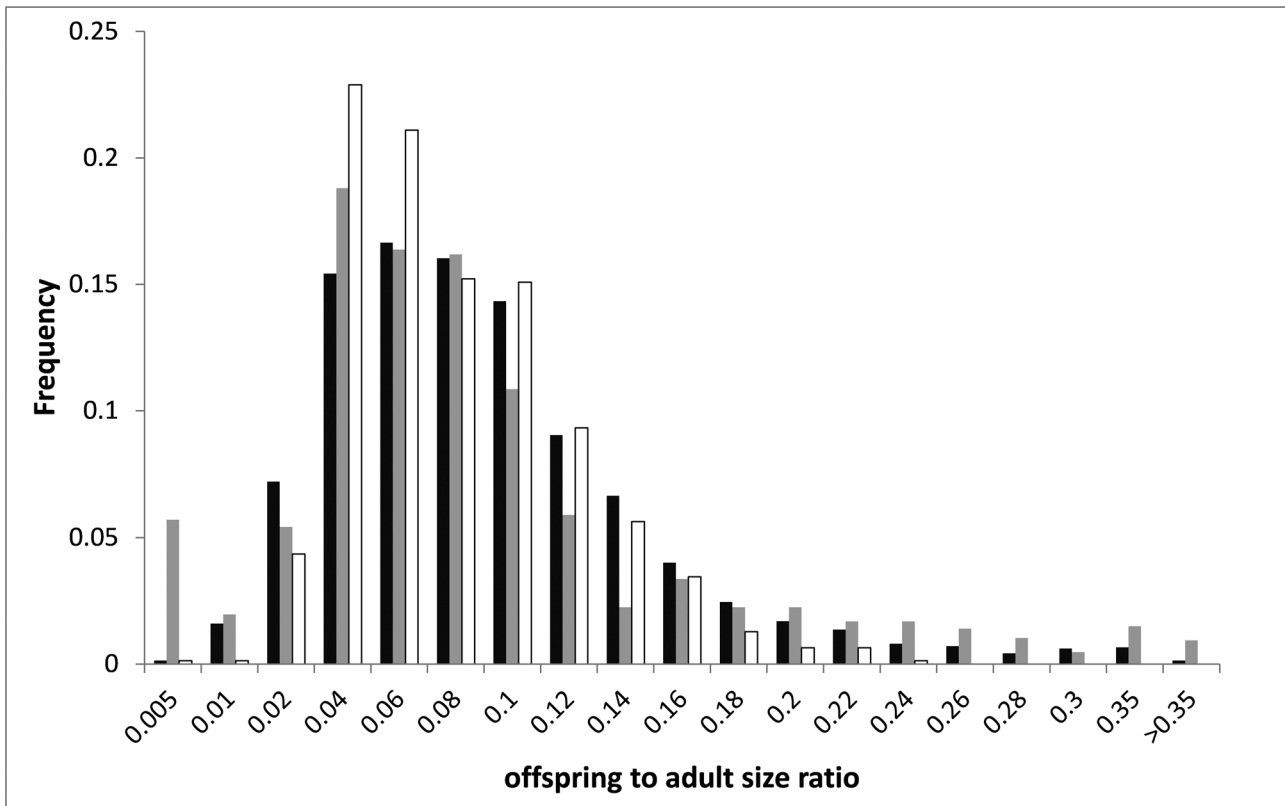


Figure 1. The relative frequencies of the ratio of offspring size to adult size in mammals (grey), squamates (black) and birds (white). The peak at the smallest ratio is almost entirely composed of metatherians, but mammals (mostly bats) also dominate the highest ratio categories. Note that the range of values is narrower in birds than in either squamates or mammals.

of reptiles (i.e. they treated large birds and small reptiles as equivalent).

Most reptiles share with birds and monotremes the ancestral amniotic condition of laying macrolecithal eggs. From these relatively large, yolk-laden eggs emerge relatively large offspring. The evolution of viviparity does not change this condition in either viviparous reptiles (Ramirez-Bautista *et al.*, 2017; S. Meiri, A. Feldman, R. Schwartz & R. Shine, unpublished observations) or placental mammals (Fig. 1). It seems as if the only major transition in the size of amniote neonates occurred in metatherians (marsupials), which give birth to relatively tiny young. Although the sizes of eggs and neonates are labile traits that may vary, even within species and populations, in response to climatic conditions and reproductive strategies (Meiri *et al.*, 2015; Ma *et al.*, 2019), such differences pale relative to the large dichotomy between amniotes and anamniotes. The large offspring of reptiles, birds and placentals differ from the very small ones of most amphibians and fishes. These differences are probably related to the evolution of the cleidoic egg in the ancestor of all amniotes, rather than to the evolution of endothermy in birds and mammals.

Anamniotes also usually have a larval stage, in which, as correctly identified by Beekman *et al.* (2019), they often occupy different habitats and feed on different types of food from adult conspecifics. A minority of taxa develop directly, but the lack of thermal constraints may indeed make the natural history of offspring across ectotherm taxa more flexible than in endotherms (Beekman *et al.*, 2019). Reptile offspring, on the contrary, usually occupy similar habitats to their parents and feed on similar types of food, although they may shift to larger prey as they grow. Although herbivorous squamates often start their lives as insectivores and shift to plant eating as adults (e.g. Greene, 1982; Rocha, 1998; Vidal & Labra, 2008), true herbivory (defined here as feeding mostly on plants) is exceedingly rare in squamates, occurring in ~5% of lizards (e.g. Meiri, 2018) and in no snake.

The different habitats and diets of many anamniote vertebrate young (larvae) and adults may well stem from their different sizes, as suggested by Beekman *et al.* (2019). This may then prevent provisioning in many anamniotes. That said, differences between the food of young and adults need not prevent

provisioning. All mammals, of course, feed on milk when very young, and some birds (e.g. Columbiformes, flamingos; Gill, 1995) and even some caecilian amphibians (Kupfer *et al.*, 2006), likewise provide the young with a special substance ‘manufactured’ by the adults. Furthermore, some nectar-feeding birds provide insects for their growing chicks (Oliver, 1998; Markman *et al.*, 1999). Thus, feeding on different types of food through ontogeny does not automatically prevent provisioning. In mammals, the very different feeding strategies of neonates and adults, the hallmark of the class Mammalia (which pre-dates the wholesale shift to viviparity), virtually guarantees parental provisioning. Provisioning is likely to be irreversible. Thus, even when the conditions in which it may have arisen no longer apply (e.g. thermoregulation in precocial species), parental provisioning persists. Whether provisioning is a consequence or a cause of endothermy is another open question (While, 2019).

I agree with Beekman *et al.* (2019) that if offspring are relatively small and occupy different habitats from adults, this may largely preclude parental provisioning (for a case where different habitat does not prevent provisioning, in dendrobatid frogs, see Summers, 2019). But this is likely to be relevant only for amniotes and thus cannot be the whole story. Reptiles have offspring similar in size to those of endotherms and with similar diets to the adults, but they mostly lack parental provisioning. Large-sized offspring is probably the ancestral state in all amniotes, both ectotherms and endotherms.

In sum, I think that Beekman *et al.* (2019) correctly identified endothermy itself as the driver making parental provisioning beneficial and facilitated its evolution, at least ancestrally. This strong force then resulted in many life-history shifts that are likely to be mostly irreversible (e.g. feeding on milk in mammals), even if offspring are thermally independent at birth. The relatively large size and direct development of reptilian young, however, makes the mechanism of differential diet and habitats seem redundant.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1.