Evolving Ideas on the Origins of Parental Care

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As little as 30 years ago, ornithologists did not accept that birds could be considered feathered reptiles. Although it was logical to herpetologists, who saw characteristics linking the two classes of vertebrates—scales on birds' legs and feet, skeletons of flying reptiles, birdlike nest structure of some reptiles, and a fluid-filled amniote egg—ornithologists often were appalled, considering birds more evolutionarily advanced. But modern taxonomy now classifies birds within the Dinosauria, or true dinosaurs, a clade of archosaurs, or "ruling reptiles."

Furthermore, the unearthing of more dinosaur fossils, some of which have impressions of feathers; better identification of fossilized dinosaur eggs to species; and more sophisticated research techniques all support the close dinosaur–avian relationship. Finding dinosaur eggs with identifiable embryos "provides a better basis for understanding the reproductive biology because we better understand their phylogenetic relationships," notes paleontologist Frankie Jackson, of Montana State University in Bozeman. She refers to recent research on dinosaur eggs, embryos, and fossils found at nests as "a surprise."

One of the surprises, published in an elegant study by David Varricchio (Montana State University, Bozeman), Jackson, and four others, is that three maniraptoran theropods, *Troodon, Citipati*, and *Oviraptor*, had male parental care of the nests (19 December 2008 issue of *Science*). The findings are noteworthy because the theropod dinosaurs are direct ancestors of birds. "I think the results were a surprise to us; and from my own maternal biases, I assumed maternal care arose first," says Jackson.

"I think the most compelling implication of these results is that...to understand avian biology, we have to understand the roots of avian biology, dinosaur biology, particularly theropod biology," notes evolutionary biologist and ornithologist Richard Prum, of Yale University.

Roy Chapman Andrews, the explorer and director of the American Museum of Natural History, found the first fossilized dinosaur nest in 1922 in the Gobi Desert of Mongolia. The nest, displayed at the museum and misidentified as that of *Protoceratops*, a quadrupedal dinosaur with a shield-like head, was actually that of *Oviraptor*. This type of misidentification of egg parentage is not uncommon because, notes Jackson, eggs may be classified by means other than direct identification of the embryo, such as identifying bones found in close association with the nest. "Both *Troodon* and *Oviraptor* eggs were originally assigned to the wrong dinosaur," Jackson says.

Prum, in his commentary published in the same issue of *Science*, notes that the name *Oviraptor* is a misnomer, as it indicates that a fossil specimen found on a nest was thought to be robbing eggs from it. Other specimens have now revealed that the animals probably died while "caring for...and possibly even brooding" the eggs. The current study details evidence showing that the brooding or guarding animal was most likely a male.

Varricchio and colleagues analyzed data for 433 extant species of birds and crocodilians on parental care behavior (paternal, maternal, or biparental), average body mass of adults, and total clutch volume. They then divided their results into four care and taxonomy groups to determine which model best fit the data they had on *Troodon, Citipati*, and *Oviraptor*. The care groups broke down as follows: birds with paternal care, birds with biparental care, birds with maternal care, and crocodilians, which have maternal care at the nest (biparental posthatching). According to the analysis, the maniraptoran data best fit the bird paternal care model. Jackson explains that *Troodon*, "an approximately 'person-size' carnivorous dinosaur," produced eggs that were "unusually large compared to the body size of the animal." Clutch sizes also were large. This, Prum points out in his commentary, may be comparable to what occurs in the palaeognaths, the basal group of birds, which produce large clutch volumes and have paternal nest care. The Palaeognathae include ostriches, emus, kiwis, cassowaries, rheas, and tinamous.

To support their hypothesis, the researchers microscopically studied thin sections of the leg bones of adult *Citipati* and *Troodon* found on nests. Bones from females that had recently ovulated would show evidence of resorption, as the animals needed large amounts of calcium and potassium for eggshell deposition. The sectioned bones showed no evidence of resorption, indicating these animals were most likely males.

This study provides evidence that paternal care, as seen in the basal Palaeognathae, probably evolved initially in theropod dinosaurs. This clarifies what Prum sees as a debate among ornithologists, who "have been trying to use a lot of different ecological arguments to argue why paternal care likely came first." Yet most birds, members of the more advanced Neognathae, have biparental care, and some have maternal care. Prum asks, "If male care came first, when did female care come, and why?"

"We...are currently gathering data on reptiles with no [parental care] and maternal care," Varricchio says. "We hope to make a broader comparison with dinosaurs later this year." Dinosaurs, he explains, "show greater variety in their eggs...than either modern birds or crocodilians," which may indicate they had a "wide variety of reproductive styles and behaviors."

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