EVOLUTION

Who's Your Daddy?

The male-only nest care system of some birds may have its evolutionary origins in theropod dinosaur behavior.

Richard O. Prum

The recognition that birds are theropod dinosaurs has redefined the science of ornithology as extant dinosaur biology (*1*). The placement of birds in a detailed evolutionary context has led to exciting discoveries about the commonalities birds share with their dinosaur ancestors, including feathers (*2*) and possibly flight (*3*). Insights have been gained into both the origins of avian biology and the natural history of some of the most charismatic dinosaurs—the meat-eating, bipedal theropods. The dividends continue with the report by Varricchio *et al.* on page 1826 of this issue (*4*), in which the authors show that fatherhood in theropods was about more than just looking macho and gnashing teeth.

Parental care in theropod dinosaurs. Fossil evidence has shown that theropod dinosaurs such as *Oviraptor* cared for their young (**left**) (*6*). Based on a new analysis, Varricchio *et al.* (*4*) hypothesize that it was male theropods who provided the care, similar to living birds at the base of the avian phylogeny, including ostriches (*Struthio camelus*) (**middle**) and highland tinamous (*Nothocercus bonapartei*) (**right**).

Biological views of dinosaur parenting have evolved a lot over the past century. In 1924, Osborn named a Cretaceous theropod *Oviraptor*, or "egg seizer," because it had been fossilized "in the very act of robbing [a] dinosaur egg nest" (*5*). In 1995, new specimens showed that *Oviraptor* was not stealing those eggs, but caring for them and possibly even brooding them (see the figure, left panel) (*6*). Now, Varricchio *et al.* (*4*) present compelling evidence from three theropods closely related to birds—*Troodon*, *Oviraptor*, and *Citipati*—that the individuals caring for those clutches of eggs were males. Because the basal lineage of living birds, or the earliest branch in the avian phylogenetic tree, also has predominantly male-only nest care, their discovery may have uncovered the dinosaurian origins of the breeding biology of living birds.

Varricchio *et al.* use two lines of evidence to support their revolutionary conclusion. First, they compared clutch volumes to adult body sizes for a sample of living archosaurs—the group of reptiles that includes crocodilians, birds, and other dinosaurs. They found that *Troodon*, *Oviraptor*, and *Citipati* have larger clutch volumes for their body sizes than most of the more than 400 extant species of birds and crocodilians examined, but that their clutch volumes closely match the expected values for birds with exclusively male parental care. Clutch volumes can evolve to be larger in species without maternal care, because females may have more resources to devote to eggs if they provide no care and because a "clutch" may be composed of eggs from multiple females. Second, Varricchio *et al.* took advantage of a distinctive feature of avian reproductive physiology to determine the sex of the dinosaurs from their bones. Many female birds lay down a distinctive layer of spongy, medullary bone inside their long bones during reproduction (*7*). Recent observations of medullary bone in the theropod *Tyrannosaurus rex* as well as in basal birds (*7*) indicate that female *Troodon*, *Oviraptor*, and *Citipati* should also exhibit medullary bone. Varricchio *et al.* show that the *Troodon*, *Oviraptor*, and *Citipati* individuals fossilized at nests lacked medullary bone, independently supporting the conclusion that they were males.

Over 90% of living birds have biparental care. A small group of species have exclusively female care, but less than 100 species of living birds have exclusively male parental care (*8*). In these species, males build the nest, incubate the eggs, and raise the young, whereas females mate with multiple males and lay their eggs in multiple nests, which may or may not be within a defended territory. The birds with the most consistent pattern of male nest care are the basal lineage of living birds, called Paleognathes, which include the flightless ostrich, emu, cassowary, kiwi, and rhea, and the flying neotropical tinamous (*9*) (see the figure, right panel).

Some behavioral ecologists have hypothesized that male-only parental care was the original breeding system of living birds (*8*), and the basal phylogenetic position of Paleognathes has been used to support this hypothesis (*10*). In the absence of any data on parental care in extinct dinosaurs, however, phylogenetic systematists have argued that female-only parental care, found both in birds and crocodilians, was the primitive breeding system of birds (*11*). Most recently, Wesołowski (*12*) argued against the theropod origin of avian breeding behavior while reiterating the male-care-first hypothesis. In a result that is sure to surprise both

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camps, Varricchio *et al.* show that the theropod origin of avian breeding behavior is consistent with male parental care as the primitive breeding system of birds, thus resolving the conflict between ecological and phylogenetic ornithologists.

These researchers have an excellent track record of establishing details of extinct theropod biology that have changed our views of the origins of avian biology. In 1997, Varricchio *et al*. (*13*) proposed that *Troodon* laid their eggs two at a time and that the uniquely avian behavior of laying the clutch of eggs over a series of days evolved in theropods before the origin of birds or flight. This bold idea was dramatically confirmed in 2005 with a discovery of an oviraptoran fossil with a pair of shelled eggs inside her pelvis (*14*).

According to the new hypothesis (*4*), the parental behaviors of living Paleognathes (like the cassowary) and extinct theropods (like *Oviraptor*) are homologous, and their breeding systems remained unchanged since their common ancestry. But could male parental care have evolved independently in Paleognathes and Cretaceous dinosaurs? There are many lineages between the Paleognathes and the oviraptorans and troodontids (including the huge, flightless, colonial diver *Hesperornis*, the pigeon-sized *Confuciusornis* with elongate ornamental tail feathers, and the archetypal *Archaeopteryx*). Many of these creatures seem so similar in ecology to various modern birds with biparental care that it is tempting to think that their breeding biology should also be similar. However, Varricchio *et al*.'s hypothesis may be supported by the observation that the male-only parental care system has resisted evolutionary change. Most Paleognathes have retained this breeding system, despite substantial ecological radiation, since before the K/T boundary over 65 million years ago (*15*, *16*). Thus, there may be substantial constraints to evolving female incubation if her female ancestors have not done so for tens of millions of years before her.

In the absence of a coherent hypothesis for the origin of birds during the greater part of the 20th century, most evolutionary explanations of avian biology focused on how unique birds are (*1*). Scientists are now identifying the dinosaurian origins of many of the formerly unique features of birds. Are there limits to ornithological revelations that the theropod origin of birds will yield? It seems not. Focused research and lucky paleontological discoveries may someday uncover the theropod origin of bird song, avian respiration, and more.

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10.1126/science.1168808

COMPUTER SCIENCE

The Ethical Frontiers of Robotics

The use of robots to care for the young and the old, and as autonomous agents on the battlefield, raises ethical issues.

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Robots have been used in laboratories and factories for many years, but their uses are changing fast. Since the turn of the century, sales of professional and personal service robots have risen sharply and are estimated to total ~5.5 million in 2008. This number, which far outstrips the 1 million operational industrial robots on the planet, is estimated to reach 11.5 million by 2011 (*1*). Service robots are good at dull, dangerous, and dirty work, such as cleaning sewers or windows and performing domestic duties in the home. They harvest fruit, pump gasoline, assist doctors and surgeons, dispose of bombs, and even entertain us. Yet the use of service robots poses unanticipated risks and ethical problems. Two main areas of potential ethical risk are considered here: the care of children and the elderly, and the development of autonomous robot weapons by the military.

The widespread availability of service robots has resulted from several developments that allowed robots to become mobile, interactive machines. Artificial intelligence has not met its early promise of truly intelligent machines, but researchers in the emerging field of human-robot interaction have implemented artificial intelligence techniques for the expression of emotion, language interaction, speech perception, and face recognition (*2*, *3*).

Sophisticated control algorithms have been developed (*4*) and have been combined with advances in sensor technology, nanotechnology, materials science, mechanical engineering, and high-speed miniaturized computing. With the prices of robot manufacture falling—robots were 80% cheaper in 2006 than they were in 1990—service robots are set to enter our lives in unprecedented numbers.

In the area of personal-care robots, Japanese and South Korean companies have developed child-minding robots that have facilities for video-game playing, conducting verbal quiz games, speech recognition, face recognition, and conversation. Mobility and semiautonomous function are ideal for visual and auditory monitoring; radio-frequency identification tags provide alerts when children move out of range. The robots can be controlled by mobile phone or from a window on a PC that allows input from camera "eyes" and remote talking from caregivers.

Research on child-minding robots in the United States (*5*) using the Sony Qurio and large-scale testing by NEC in Japan with their PaPeRo have demonstrated close bonding and attachment by children, who, in most cases, prefer a robot to a teddy bear. Short-term exposure can provide an enjoyable and entertaining experience that creates interest and curiosity. In the same way, television and computer games may be used by parents as an entertainment or distraction for short periods. They do not provide care and the children still need human attention. However, because of the physical safety that robot minders provide, children could be left without human contact for many hours a day or perhaps for several days, and the possible psychological impact of the varying degrees of social isolation on development is unknown.

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