PNAS COMMENTARY

Sexual selection and the evolution of dinosaur flight

Stephen L. Brusatte[a,1]

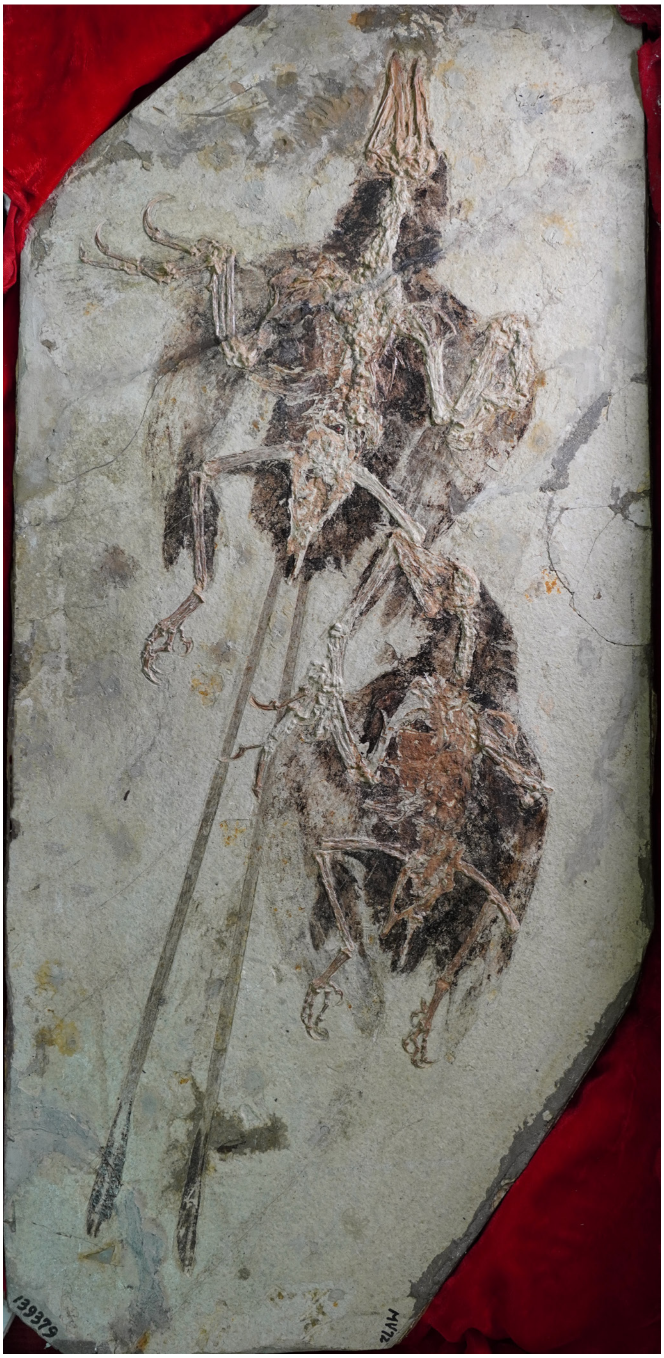

Fig. 1. A *Confuciusornis* couple: a presumed mail with long ribbon tail feathers (*Left*) and putative female without (*Right*). Photo courtesy of Zhonghe Zhou.

"The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!" Charles Darwin wrote to Asa Gray in April 1860 (1), less than 6 mo after he published *On the Origin of Species*. Although Darwin was notoriously prone to stomach pains and countless other ailments, this particular ache was metaphorical. In the flamboyant train of the peacock—its shimmering blue and green tail feathers longer than its body—Darwin saw an outrageous structure that had no obvious advantage in finding food or escaping predators. He could not comprehend how such a thing could evolve through natural selection, the mechanism for change over time that he so thoughtfully articulated in his new book. Perhaps, Darwin surmised, beautiful feathers and other gaudy structures developed because they helped promote reproduction, a process he called "sexual selection" (2). In a new study in PNAS, Zhou et al. identify a fossil analogy to the peacock's tail: a pair of long ribbon-like tail feathers in an extinct bird called *Confuciusornis* (3). In doing so, they show that sexual selection has shaped the evolution of birds for over 120 My (Fig. 1).

Darwin eventually came to admire the peacock's tail, as an emblem of his new idea of sexual selection. In 1871 he published another blockbuster book, usually referred to today by the first part of its title, *The Descent of Man*, because it forcefully argued why humans should be considered as part of the animal kingdom. But the often forgotten second half of the title, *Selection in Relation to Sex*, spoke to the book's other major theme: how sexually selected traits improve an individual's ability to acquire mates, either by making that individual more attractive to potential partners, or better able to compete with its rivals in the mating game. At first, Darwin's ideas were controversial (4), but they became accepted over time. Debate has continued about how sexual selection works: do sexually selected traits—which are often big and bold and colorful—operate by signaling underlying fitness to potential mates, or are those mates simply drawn to the beauty of the ornaments (5, 6)?

Birds are champions of sexual selection. Among the more than 10,000 modern-day species are many examples of extravagant plumage that seem to serve no purpose other than sex. Aside from Darwin's peacocks, consider birds of paradise with pompous feathers streaming off their heads and tails or great argus pheasants whose tail fans are covered with hundreds of pseudo-eyes, or the kaleidoscope of colors in tropical birds (6). That's not to mention the riot of mating dances and rituals and songs, which can also be products of sexual selection (6).

Author affiliations: [a]School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FE, United Kingdom

Author contributions: S.L.B. wrote the paper.

The author declares no competing interest.

See companion article, "Fossil evidence sheds light on sexual selection during the early evolution of birds," 10.1073/pnas.2309825120.

[1]Email: Stephen.Brusatte@ed.ac.uk.

Published January 8, 2024.

How, then, did sexual selection become such a force in avian evolution? To address this question, we must look to the fossil record. Birds evolved from dinosaurs (7, 8), and many dinosaurs had fanciful structures that probably served a role in display and mating, from the horns of *Triceratops* to the head crests of duck-billed hadrosaurs (9). Furthermore, many early birds and their close theropod relatives had a rich variety of feather colors and shapes, which were probably involved in display (10). However, were any of these things actually shaped by sexual selection?

In their new study, Zhou et al. present an impressive attempt to identify both sexual dimorphism and sexual selection in the dinosaur-bird fossil record

Even more fundamentally, how might we identify sexual selection with the fossils we have (11)? One potential signal of sexual selection is sexual dimorphism: when males and females exhibit a marked difference in body size or other anatomical features. Dimorphism is sometimes treated as a necessary condition for inferring sexual selection (12). With dinosaurs, however, it is difficult to even distinguish males and females (13, 14). The biggest problem is low sample size: most dinosaur species are known from a single fossil, and even the best-studied ones like *Tyrannosaurus* and *Triceratops* from usually only a few dozen decently preserved skeletons. This is simply not enough information to rigorously identify differences between males and females.

In their new study, Zhou et al. present an impressive attempt to identify both sexual dimorphism and sexual selection in the dinosaur-bird fossil record. They focus on *Confuciusornis*, a Cretaceous-aged primitive bird from China, known from hundreds of well-preserved skeletons—bones, feathers, and all—entombed in lake sediments choked by the ash of volcanic eruptions, similar to how humans and their dwellings were rapidly buried at Pompeii (15). Previous workers had noticed that many *Confuciusornis* specimens have two long tassel feathers stretching far behind their bodies, whereas others do not, even in cases where the wing and body feathers are exquisitely preserved. One tassel-less fossil was found with medullary bone—a special tissue transiently formed in the bones of females as a calcium reservoir for shelling eggs—which suggests that these less-adorned individuals are females, and by extension, the fancy-tailed ones are males (16). However, this hypothesis remained to be tested with a large statistical analysis of hundreds of *Confuciusornis* specimens.

Zhou et al. compiled an expansive dataset of *Confuciusornis* fossils and measured their skeletal proportions and estimated their body sizes. They find that those individuals with long tail feathers were significantly heavier in mass, on average, than those without the feathers. The ornamented individuals also have a longer hind limb and larger palm of the hand, relative to body mass, which was underpinned by significantly higher growth rates in those bones. The ornamented and un-ornamented individuals began life by looking similar to each other, but then those with the ornate feathers gradually developed longer legs and bigger hands.

Taken together, this is clear evidence for dimorphism in *Confuciusornis*. Around half of the known individuals have long tail feathers, and it's these animals that have heavier bodies and longer legs and hands. The other half lack a lavish tail and have smaller bodies, legs, and hands. Coupled with the prior evidence from medullary bone, these differences in body size and shape between *Confuciusornis* with and without ribbon feathers led Zhou et al. to support the identification of long-tailed individuals as probable males and unornamented ones as putative females. Although this sexual dimorphism doesn't prove sexual selection, the simplest explanation is that those ridiculous tail ribbons in the male *Confuciusornis*—which are so long and skinny that is hard to imagine them serving an aerodynamic benefit—were sexually selected features integral to mating and reproduction.

It is a convincing argument, buttressed by statistical analysis of a large dataset unparalleled for a Mesozoic dinosaur. However, it is not truly surprising. After all, many modern birds—most obviously those peacocks and birds of paradise and pheasants—use their ostentatious tails as display devices, fashioned by the powers of sexual selection (17). In many modern birds—but by no means all—males are substantially larger than females, although the interplay of sex and body size depends on so many things, from mating strategies to investment in egg production and parenting. It's also easy to draw parallels with extant birds to understand why longer limbs in males could impart greater stride length, running speed, and locomotory performance, enhancing their abilities to defend larger territories, gather more food, and outcompete rivals for the affection of their mates (18).

If somebody identified a new species of modern-day bird in which males had prettier tail feathers, larger bodies, and longer legs than females, this wouldn't raise an eyebrow. But that precisely is the point. Zhou et al. have unveiled a 120-My-old bird with the same type of sexual dimorphism and sexually selected features that are familiar in today's birds. Despite its basal position on the bird family tree, its retention of many primitive "dinosaur" holdovers like sharp claws and a small breastbone, and its rudimentary flight ability, *Confuciusornis* was forged by the same processes of sexual selection that operate in birds today.

Some of the earliest birds, therefore, were using their feathers for sexual signaling. The implications of this realization, however, may be even grander. Could sexual selection explain how some dinosaurs started to fly in the first place?

Dinosaurs (or their ancestors) initially acquired feathers for reasons unrelated to flight, as the first feathers were simple fuzz-like bristles, probably helpful in regulating body temperature, but as useless for aerial pursuits as our own heads of hair (10). Many dinosaurs, maybe even most, sported these basic feathers. Some derived theropods, however, elaborated those simple feathers into larger, branching, vaned quill-pens that lined up along the arm (and in some species, the legs and tail). These dinosaurs invented wings. Because birds use their wings to fly, we might assume that wings evolved for flight. The fossils, though, hint at a more subversive story. The wings that appear earliest on the dinosaur family tree, in theropods like ornithomimosaurs and oviraptorosaurs, were small—too small for flying (10, 19, 20). If these sheep-to-horse-sized dinosaurs flapped their incipient wings, any lift or thrust would have been so minimal that their bodies would fail to get airborne.

Why, then, did wings evolve? We must remember that today's birds use their wings for many purposes, not only soaring through the skies. Wings can be used to brood eggs in the nest, to swim, and for display. Might the dinosaur ancestors of birds have also used their wings as sexual signals? It's hard to prove, but there is compelling circumstantial evidence: fossilized pigment-bearing melanosomes reveal that many non-bird theropods had a palette of feather colors and patterns (21). Some, remarkably, had iridescent feathers that glittered in the sun. This has led some researchers to propose that wings first evolved as display structures and were later repurposed as airfoils (20, 22). It is a somewhat anecdotal hypothesis, but Zhou et al.'s identification of sexually selected tail feathers in *Confuciusornis* adds important supporting evidence. Sexual selection was indeed operating on Mesozoic dinosaurs.

When imagining how complicated structures evolve, biologists since Darwin have often agonized about intermediate stages. What adaptive value is half a wing? In the case of dinosaurs, sex may hold the answer. A half-wing may not be any good for flying, but plenty good for attracting mates and intimidating rivals. Sexual selection may have even pushed the development of bigger wings, as ever-larger advertising billboards to woo mates. Then, at some point, the laws of physics would have taken over as these billboards became big enough to provide a bit of lift, a bit of thrust. Flight was born—and if this scenario is correct, it was born inadvertently, a byproduct of sexual selection.

1. C. Darwin, "Letter 2743 of Darwin correspondence project" (Cambridge University, 1860). http://www.darwinproject.ac.uk/entry-2743.
2. C. Darwin, *The Descent of Man, and Selection in Relation to Sex* (John Murray, London, 1871).
3. Y. Zhou *et al.*, Fossil evidence sheds light on sexual selection during the early evolution of birds. *Proc. Natl. Acad. Sci. U.S.A.* **121**, e2309825120 (2024).
4. A. R. Wallace, G. J. Mivart's, Lessons from nature, as manifested in mind and matter. *The Academy* **562** (1876).
5. M. J. Ryan, Darwin, sexual selection, and the brain. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2008194118 (2021).
6. R. O. Prum, *The Evolution of Beauty: How Darwin's Forgotten Theory of Mate Choice Shapes the Animal World–and Us* (Anchor, New York, 2017).
7. S. L. Brusatte, J. K. O'Connor, E. D. Jarvis, The origin and diversification of birds. *Curr. Biol.* **25**, R888–R898 (2015).
8. X. Xu *et al.*, An integrative approach to understanding bird origins. *Science* **346**, 1253293 (2014).
9. S. L. Brusatte, *Dinosaur Paleobiology* (Wiley-Blackwell, Hoboken, 2012).
10. D. T. Ksepka, Feathered dinosaurs. *Curr. Biol.* **30**, R1347–R1353 (2020).
11. R. J. Knell, D. Naish, J. L. Tomkins, D. W. E. Hone, Sexual selection in prehistoric animals: Detection and implications. *Trends Ecol. Evol.* **28**, 38–47 (2013).
12. K. Padian, J. R. Horner, The evolution of 'bizarre structures' in dinosaurs: Biomechanics, sexual selection, social selection or species recognition? *J. Zool.* **283**, 3–17 (2011).
13. D. W. E. Hone, J. C. Mallon, Protracted growth impedes the detection of sexual dimorphism in non-avian dinosaurs. *Palaeontology* **60**, 535–545 (2017).
14. J. C. Mallon, Recognizing sexual dimorphism in the fossil record: Lessons from nonavian dinosaurs. *Paleobiology* **43**, 495–507 (2017).
15. L. M. Chiappe, S.-A. Ji, Q. Ji, M. A. Norell, Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *Bull. Amer. Mus. Nat. Hist.* **242**, 1–89 (1999).
16. A. Chinsamy, L. M. Chiappe, J. Marugán-Lobón, G. Chunling, Z. Fengjiao, Gender identification of the Mesozoic bird *Confuciusornis sanctus*. *Nat. Commun.* **4**, 1381 (2013).
17. M. Andersson, Female choice selects for extreme tail length in a widowbird. *Nature* **299**, 818–820 (1982).
18. J. J. Lees, R. L. Nudds, L. P. Folkow, K.-A. Stokkan, J. R. Codd, Understanding sex differences in the cost of terrestrial locomotion. *Proc. R. Soc. B Biol. Sci.* **279**, 826–832 (2012).
19. D. K. Zelenitsky *et al.*, Feathered non-avian dinosaurs from North America provide insight into wing origins. *Science* **338**, 510–515 (2012).
20. S. L. Brusatte, A Mesozoic aviary. *Science* **335**, 792–794 (2017).
21. Q. Li *et al.*, Melanosome evolution indicates a key physiological shift within feathered dinosaurs. *Nature* **507**, 350–353 (2014).
22. C. Foth, H. Tischlinger, O. W. M. Rauhut, New specimen of *Archaeopteryx* provides insight into the evolution of pennaceous feathers. *Nature* **511**, 79–82 (2014).