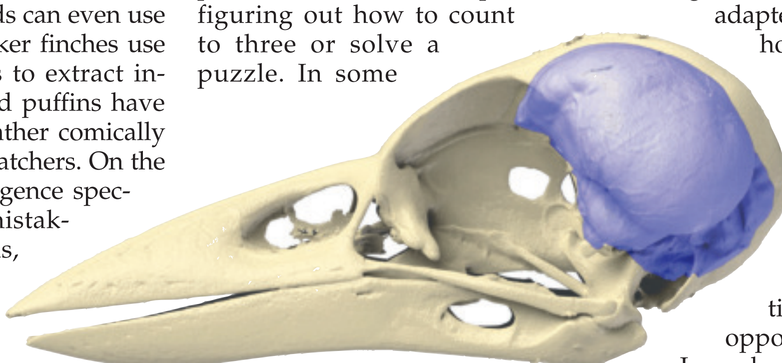
Bird Brain Evolution

Avian smarts run the gamut from ostriches to crows. Why do large brains and high intelligence emerge in some lineages?

Daniel T. Ksepka

Birds are capable of a breathtaking range of behaviors. Alex, the famous gray parrot, learned to count and accumulated a vocabulary of more than 100 words that he combined into phrases and questions. Ravens can solve complex puzzles. In lab experiments, they have figured out that dropping a specific key into a tube will earn them a tasty reward. Some birds can even use simple tools: Woodpecker finches use twigs or cactus spines to extract insects from crevices, and puffins have recently been filmed rather comically using sticks as back scratchers. On the other end of the intelligence spectrum, ostriches will mistakenly swallow golf balls, and while walking the streets of New York City, I have personally seen a pigeon eat a cigarette butt. Although birds confusing artificial objects for potential gizzard grit or food items should not be labeled "stupid," it seems fair to say that the range of avian intelligence is about as wide as that in the mammal world if we exclude humans from the scale. A natural question arises: Why are some birds so intelligent while others remain "simpleminded"?

If surviving and reproducing came down simply to intelligence, the cleverest birds would quickly outcompete their slower-witted counterparts. Things aren't that simple, though, because intelligence isn't "free." Large brains are expensive to maintain, because brain tissue requires much more metabolic energy to sustain at rest than do most other tissues. Our own brains, for example, account for 2 percent of our body weight on average, but consume around 20 percent of our metabolic energy. Having a large brain burning up fuel can be a detriment in environments where the ability to escape predators quickly or overpower rivals is more important than figuring out how to count to three or solve a puzzle. In some cases, intelligence can even become a liability. Carolina parakeets formed social bonds that contributed to their extinction. Humans once hunted these birds for feathers and because they were perceived as crop pests. When one Carolina parakeet was shot, others would rally to the fallen bird and be killed as well, doomed by their own advanced social behavior.



Courtesy of Larry Witmer's Lab, Ohio University

Corvids such as the New Caledonian crow (*Corvus moneduloides*) have larger brains and larger bodies than other songbirds. But their brains are disproportionately large, resulting in some of the largest relative brain sizes among birds. What could be driving their rapid expansion in body size and even more rapid expansion in brain size?

This trade-off has led to a vast range of brain sizes in the vertebrate world. Perhaps the most extreme example is the bony-eared assfish. The bearer of this unfortunate name has a brain about the same size as the brain of a baby trout—despite being 60 times larger. The bony-eared assfish has adapted to life in the slow lane, hovering in the darkness of deep ocean waters where it feeds on small prey such as gastropods. Because only a few simple behaviors are required for this fish to survive, it needs to retain only a minimum amount of brain tissue. Humans occupy the opposite end of the spectrum. Large brains allowed our lineage to develop language, complex tools, art, and agriculture—the things that make us "human." One theory holds that the more efficient bipedal gait of our ancestors allowed them to invest extra energy in larger brains.

In 2014, I joined forces with several colleagues: Amy Balanoff of Johns Hopkins University, one of the foremost experts on dinosaur brains; Adam Smith of Clemson University, a scholar of the fossil record of auks; and Jeroen Smaers of Stony Brook University, a pioneer in new methods for quantifying changes in brain size. Our goal was to put together a task force to map out the big picture of avian brain size evolution. Despite being the only vertebrates with brain expansion

QUICK TAKE

Birds are the only vertebrates whose brains have expanded over the course of evolution at levels that approach those seen in mammals, particularly in primates.

Large brains are metabolically costly. This trade-off has led to a vast range of brain sizes among birds. Corvids and parrots stand out as having remarkably large relative brain sizes.

Mapping relative brain size onto the avian evolutionary tree reveals when brains became smaller or larger, relative to body size and ancestry, and thus how intelligence may arise.

Elsa Loissel

A New Caledonian crow fashions a tool from a twig. This bird, like other corvids, displays many hallmarks of greater intelligence, such as capacity for learning, tool use, and complex social behavior. Their brain evolution stands out as unique among birds.

levels that approach those observed in mammals, birds had long garnered only a fraction of the research effort. So we organized a large gathering of scientists interested in brain evolution, biological imaging techniques, and the fossil record for a Catalysis Meeting at the National Evolutionary Synthesis Center (NESCent).

NESCent was the perfect place for this project. Housed in a converted mill building in Durham, North Carolina, the center served as a supercollider for evolutionary biology, bringing together people with different perspectives to accomplish projects none of them could do alone. On any given day at NESCent, one might find scientists, writers, and artists gathered around tables in cleverly named rooms such as "The Selfish Gene Salon," debating theories. Our team gathered one sunny May morning, arriving one by one from as far away as Scotland and Argentina. After copious amounts of coffee, we started mapping out brain data from dinosaurs, extinct birds, and modern birds. The conversations often stretched late into the evening and sometimes hopped venues to a whiskey bar or Durham Bulls baseball game. By the end of the weeklong meeting, we had laid the groundwork for a suite of analyses pinpointing how brain size shifted along the remarkable evolutionary journey from ferocious theropod dinosaurs to the first birds, and untangling which selective pressures may have led to the startling diversity in relative brain size among the more than 10,000 species of birds alive today.

Scaling Brains

To understand the history of avian brain evolution, it is first necessary to consider the relationship between brain size and body size. Comparing the raw brain size of each species is not very useful because all else being equal, a larger animal will have a larger brain. Nor can we simply divide brain size by body size, because the relationship between the two is not constant. Smaller animals tend to have proportionally larger brains than their larger relatives. A mouse brain weighs less than 0.5 gram but is quite large compared to the overall size of the mouse. A mouse scaled up to the size of an elephant would have an enormous 60-kilogram brain, about 14 times larger than the brain of an actual elephant. Despite the mouse's proportionally larger brain, elephants

Ole Jorgen Liodden/NaturePL/Science Source

A woodpecker finch uses a twig as a tool to extract insects from tree crevices for food.

are considered to be much more intelligent than mice.

Biologists hypothesize that larger vertebrates tend to have proportionally smaller brains, on average, because of their slower metabolism and the physical limits on the size of the brain during growth. Larger animals are not necessarily less intelligent, however, because only a certain amount of brain cells are needed to control basic functions such as breathing and heart rate. Thus, an elephant doesn't need a 60-kilogram brain to achieve higher cognitive abilities than a mouse. On the other hand, the 7-kilogram brain of a blue whale does not convey quadruple the intelligence of the 1.5-kilogram brain of an average human, because the whale has a lot more body to control.

When attempting to estimate "intelligence" from brain size, biologists look not at the raw size of the brain, but rather at how much larger or smaller it is than the expected size for a species of that body mass. By this measure, our brains are about seven times larger than would be expected for a mammal in our size range (50 to 100 kilograms), whereas mouse brains are a bit smaller than expected and elephant brains are just slightly larger than expected.

Accounting for these scaling effects, relative brain size is often used as a proxy for intelligence. Quantifying intelligence in animals is a difficult task, but larger relative brain size is positively correlated with many signs of greater intelligence, such as capacity for learning, tool use, and complex social behavior. For extinct species, relative brain size is often the only variable that can provide insight into intelligence, because fossil evidence of behavior is rare. Scientists have thus devoted much effort to studying the evolution of brain size, especially in primates.

Here's where things get complex, and fascinating: It turns out that not all vertebrates share the same brain-body scaling slope. Each time a new brain-body scaling slope arises, it signifies a major evolutionary or developmental shift. These changes can tell us something about the way adapting to new environments, locomotion strategies, or diets affects the brain-body relationship. In groups with low slopes, the brain size expands slowly as body size increases. In groups with high slopes, brain size scales up more rapidly as body size increases. This relationship means that the long-held practice of treating all vertebrates as if they shared a common slope might cause us to miss out on how the brain is really evolving. For example, the extinct dodo is much maligned as a dim-witted species. However, the dodo was a flightless relative of doves and pigeons, which have a low brain-body scaling slope. Considered in this con-

NOAA Okeanos Explorer's 2016 Deepwater Exploration of the Marianas./CC by Attribution-NonCommercial-ShareAlike

The unfortunately named bony-eared assfish (*Acanthonus armatus*), filmed by a remotely operated underwater vehicle in the Western Indian Ocean, has a brain that is about the same size as that of a baby trout, despite being 60 times larger. Because this fish lives in a deep-sea environment where only a few simple behaviors are required to survive, it needs to retain only a minimal amount of brain tissue.

Stephanie Freese

The relationship between brain size and body size is not constant. Smaller animals tend to have proportionally larger brains than their larger relatives. A mouse brain weighs 0.5 gram but is quite large compared to the overall size of a mouse. A mouse scaled up to the size of an elephant would have an enormous 60-kilogram brain, about 14 times larger than the brain of an actual elephant. Despite the mouse's proportionally larger brain, elephants are considered to be much more intelligent than mice. When attempting to estimate "intelligence" from brain size, biologists look not at the raw size of the brain, but rather at how much larger or smaller the brain is than the expected size for a species of that body mass.

text, the small brain of the dodo can be explained mostly by the fact that it is a scaled-up pigeon, rather than a species that lost its evolutionary marbles.

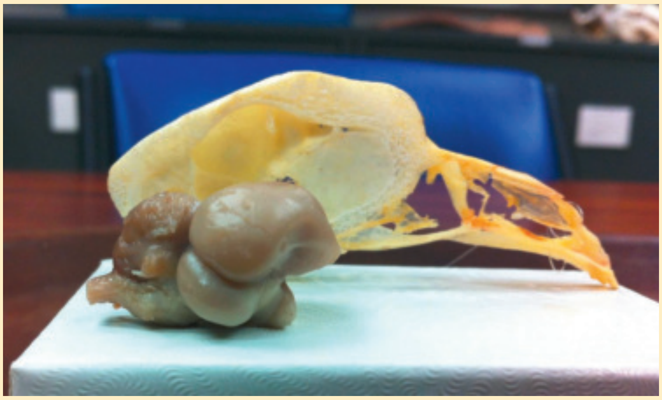
Looking at Ancient Brains

Because birds evolved from theropod dinosaurs, we need to consider theropod brains to truly understand how the avian brain evolved. Doing so meant delving into the fossil record. Brains are fairly gooey and tend to be destroyed by decomposition long before they have a chance to fossilize. However, we can still use fossil evidence to infer brain size in long-extinct species. The brain occupies a bony box within the skull that is aptly named the *braincase*. Determining the volume of a modern bird brain is fairly straightforward: One can simply remove the brain from the braincase, measure it, and plop it in a jar for posterity. For those who prefer to keep their hands clean, a reliable alternative is to fill the empty braincase with tiny lead shot pellets and then measure the amount used. Things get more complicated when we bring fossils into the equation. For about two centuries, our only glimpses into the sizes and forms of the brains of extinct species came from unusual fossils called *natural endocasts* that form when sediments such as silt or mud fill up an empty braincase and then harden into rock. On occasion a fossil skull can break apart (or be broken open by a paleontologist) and reveal a natural endocast, much like a walnut shell cracking open to reveal the nut. Restricted to such fortuitous discoveries, paleontologists learned very little about the brains of extinct species such as dinosaurs for a long time. Natural endocasts are rare, and no curator in their right mind would allow a paleontologist to crack open the skull of an ancient bird such as *Archaeopteryx*.

Since the 1980s, technology has opened a new, nondestructive way to look at ancient brains. *Virtual endocasts* are digital models of the brain created by scanning the fossil skulls with computed tomography (CT) and mapping out the boundaries of the braincase, typically infiltrated with sediment during the fossilization process. I became familiar with this technique about 15 years ago when I was a student. Back then, when paleontologists were interested in the brains of extinct species, we would often ask a friendly hospital technician to slide a few skulls through a medical CT scanner during the slow hours of the night. I fondly recall getting Sharpie-marked DVDs handed to me with fresh new scans of dinosaur or bird skulls at a hospital in New York. In another case, my colleagues and I brought the skull of a remarkable Peruvian spear-billed penguin fossil to a hospital for scanning. We were promptly booted from our seats when a patient from a car accident was rushed into the scanning room. An hour later, with the emergency handled, we sent the penguin skull through the machine.

For extinct species, relative brain size is often the only variable that can provide insight into intelligence.

Medical scanners provided wonderful new images of the braincases of long-extinct species. But the quality of early scans was rough; the low-resolution images made fossil brain scans look blocky, as if they were made of Lego bricks. The fuzzy borders between the bone and rock were due to the low power of the x-ray beam. Medical scanners use weaker beams chicken



Courtesy of Catherine Early

Archaeopteryx

Courtesy of Larry Witmer's Lab, Ohio University

Determining the volume of a modern bird brain, such as the chicken on the left, is fairly straightforward: One can simply remove the brain from the braincase and measure it, or one can fill the empty braincase with tiny lead shot pellets and then measure the amount used. Things get more complicated when measuring fossil braincases. No one wants to crack open precious fossilized skulls. Since the 1980s, technology has opened a new, nondestructive way to look at ancient brains. *Virtual endocasts* are digital models of the brain created by CT-scanning fossil skulls and mapping out the boundaries of the braincase. Early on, medical scanners were used, but their resolution is lower, because they use weaker x-ray beams so as not to harm patients. Today, paleontologists often use industrial micro-CT scanners, which are typically employed for tasks such as testing for cracks in engines. These high-powered scanners would be lethal to humans, but are perfect for producing crisp, high-resolution images of fossil braincases, such as the image on the right of the early bird *Archaeopteryx*.

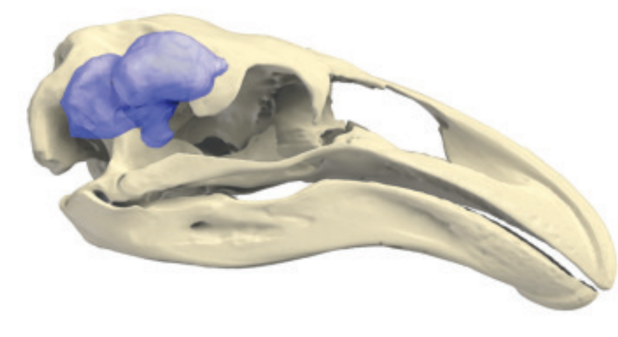
for a reason: so as not to kill patients. Low-power beams can image human bones and organs without causing harmful radiation damage, but they are too weak to fully penetrate solid rock without distortion. Today, paleontologists often use industrial micro-CT scanners, which are typically employed for tasks such as testing for cracks in engines. These high-powered scanners would be lethal to humans, but are perfect for producing crisp, high-resolution images of fossils.

At NESCent, we took advantage of the rapidly growing collection of virtual endocasts from both fossil and modern birds. Our team pooled CT-scan data sets that we had generated for our own individual research projects, and assembled a comprehensive data set of brain scans from dinosaurs, fossil birds, and rare extant species sampled from museum skulls, covering everything from *Tyrannosaurus rex* to the dodo. We added in data from thousands of modern species published in previous papers. Then we were ready to start looking at how bird brains had evolved, from the Jurassic period to the present day.

Mesozoic Origins of the Avian Brain

Reconstructing brain evolution in birds starts with understanding patterns in their dinosaurian ancestors. The gap between dinosaurs and birds once seemed so wide that it was hard

moa (*Dinornis robustus*)



Courtesy of Larry Witmer's lab, Ohio University

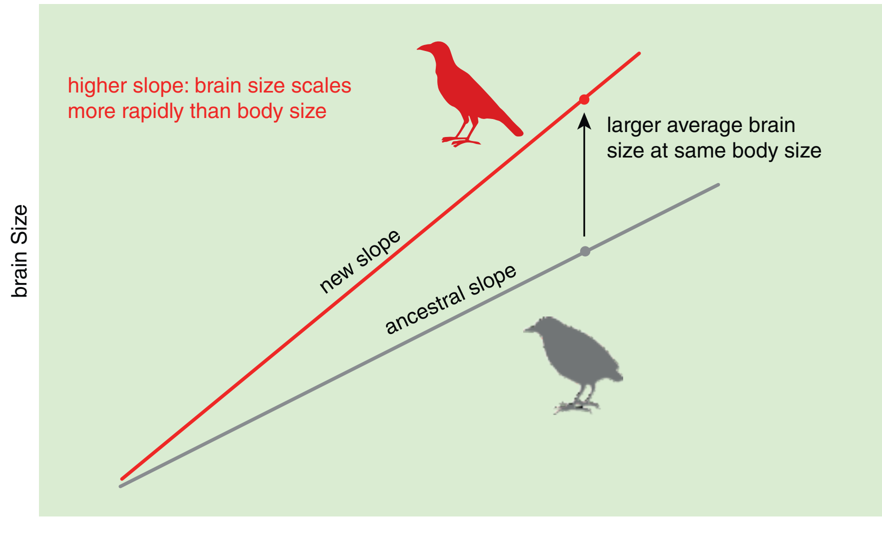
The now-extinct moa evolved tremendous body sizes, with their brains lagging behind until they ended up with the smallest relative brain sizes of all birds. This pattern resulted in moa attaining somewhat comical proportions, with tiny heads perched on the end of long necks that were in turn attached to stout bodies with legs as thick as small tree trunks.

to decipher how sharp-toothed, stiff-tailed theropods could have possibly given rise to beaked, fluffy-winged birds. As feathered dinosaur fossils began to be unearthed at the turn of the century, an ever-growing list of features once considered unique to birds was shown to have evolved in theropod dinosaurs. This list now includes incipient wings, hollow bones pneumatized by an air sac system, a furcula ("wishbone"), a gizzard, pigmented eggs, and even behaviors such as contact incubation. Brain evolution seems to be no exception.

One might expect there would have been a major shift in brain-body ratio coincident with the evolution of flight roughly 150 million years ago, given the dual pressures of expanding the neural circuitry needed for aerial maneuvering and reducing body size to make takeoff easier. Surprisingly, advanced theropod dinosaurs, the early bird *Archaeopteryx*, and early-branching modern birds such as ostriches and pheasants all shared the same brain-body scaling slope in our results. The brain of *Archaeopteryx* is no smaller or larger than expected for a small dinosaur, and indeed earlier work by Balanoff and her colleagues suggests that many theropod dinosaurs had already evolved features previously associated with flight, such as an expanded cerebrum.

Avian brain evolution seems to have been shaken up by one of the worst extinctions of all time, the Cretaceous-Paleogene (K-Pg) mass extinction that took place 66 million years ago. Our team found evidence for only one shift in brain-body scaling during the Cretaceous (a minor change in ducks), but found a rapid burst of brain evolution leading to new brain-body scaling slopes in nine different groups during the Paleocene epoch (the first 10 million years following the mass extinction). A pervasive trend is the shift to higher slopes and decreasing body mass, a pattern observed in groups such as swifts, sandpipers, parrots, and songbirds. Other groups such as birds of prey went in the opposite direction, shifting to lower slopes and larger body sizes. These changes set the stage for the astounding variation in avian ecologies we see today, from the simple lifestyles of doves to the complex social behavior of parrots.

How could a mass extinction trigger such a diversification? One classic explanation for the evolution of large brains is the *cognitive buffer hypothesis*, which posits that large brains provide a buffer against frequent or unexpected environmental changes by allowing more flexible behavioral responses. Studies of modern birds have shown that island-dwelling species tend to evolve larger brains than their mainland relatives to cope with their need to survive in dramatically fluctuating environments. For example, mainland birds might simply migrate out of an area as a hurricane approaches, whereas island species must deal with whatever havoc the storm wreaks on their habitat. One can imagine the aftermath of the K-Pg mass extinction was akin to waking up the morning after a hurricane, a forest fire, and a volcano all hit on the same day. Global ecosystems may have taken hundreds of thousands of years to recover. At the same time, the mass extinction opened new opportunities for modern birds. Many competing groups, including the winged pterosaurs, archaic toothed birds, marine reptiles, and small dinosaurs were wiped out. Surviving bird lineages evolved to take advantage of newly opened niches, and the fossil record documents early adaptors ranging from tiny tree-dwelling mousebirds to diving penguins radiating rapidly in the early Paleocene. (*See "Flights of Fancy in Avian Evolution," January–February 2014.*)



Daniel T. Ksepka

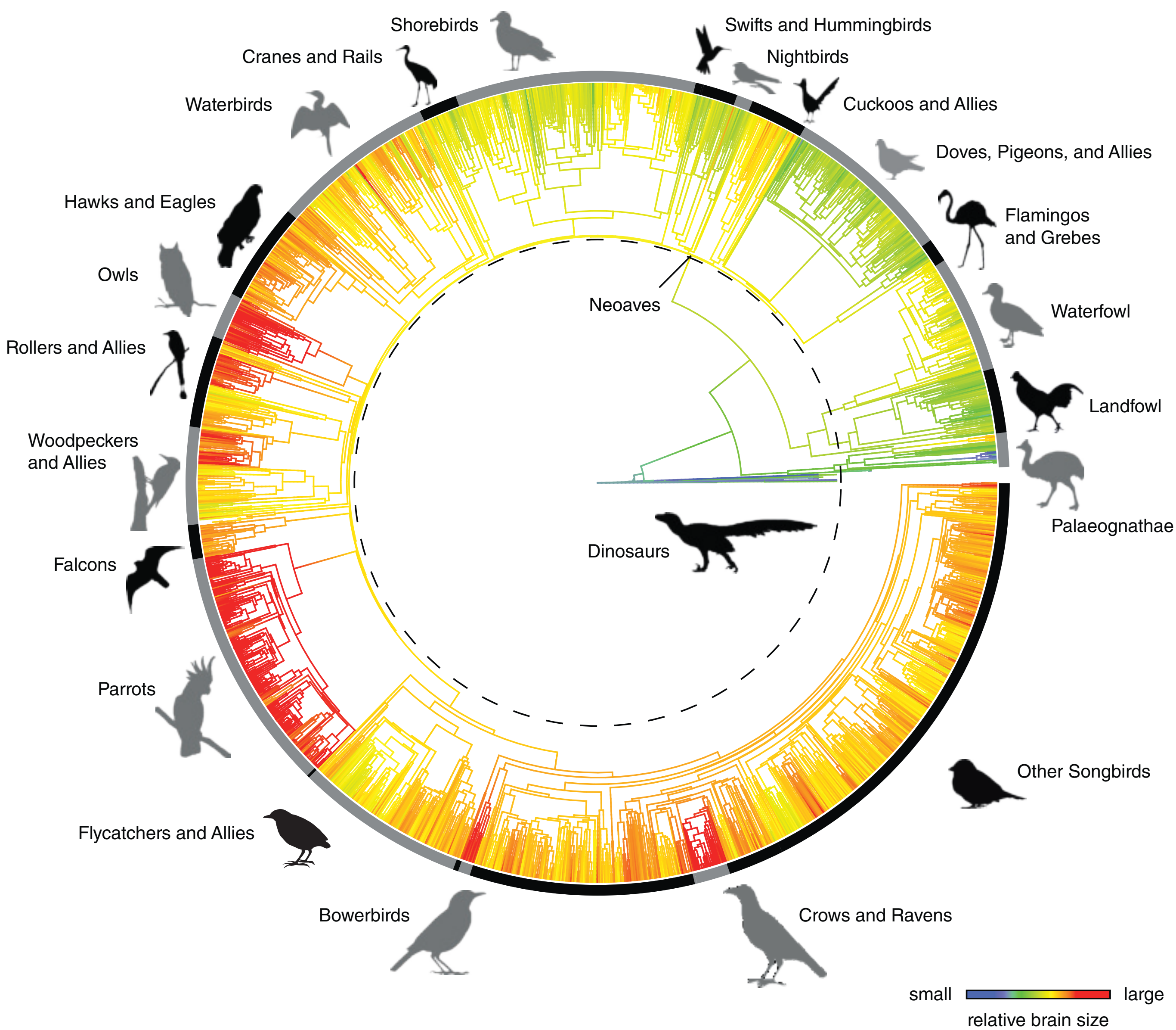
Not all vertebrates share the same brain-body scaling slope. Each time a new brain-body scaling slope arises, it signifies a major evolutionary or developmental shift. Corvids not only have a high brain-body scaling slope, but also the highest rate of brain-body evolution. Much like humans, corvids evolved larger bodies and larger brains at the same time, but their brains expanded even faster than their bodies.

Corvids took the same path that we humans did. They evolved larger bodies and larger brains at the same time.

Scaling Across the Avian Family Tree

Most species of the Palaeognathae—a group that includes large flightless birds such as ostriches and emus, as well as the volant tinamous—inherited the ancestral brain-body slope shared by nonavian theropods and *Archaeopteryx*. However, two palaeognath lineages shifted in new directions. The now-extinct moa evolved tremendous body sizes, with their brains lagging behind until they ended up with the smallest relative brain sizes of all birds—so their brain-body slope was flatter. This pattern resulted in moa attaining somewhat comical proportions,

Relative Brain Size across the Avian Family Tree



Mapping data on the brains of several thousand species of dinosaurs, extinct birds, and modern birds across their evolutionary tree spanning over 125 million years shows the big picture of avian brain evolution. There is a wide range in brain sizes among birds, from relatively small-brained pigeons and turkeys to large-brained parrots and ravens. The picture becomes even more complicated when one considers theropod dinosaurs, the closest extinct relatives of birds. (From D. Ksepka, et al., 2020)

Bird silhouettes from phylopic.org: Lauren Anderson, Nevit Dilmen, Dori (dori@merr.info), Patrick Fisher, Rebecca Groom, T. Michael Keesey, Liftarn, Sharon Wegner-Larsen, Ferran Sayol, L. Shyamal, Emily Willoughby

with tiny heads perched on the end of long necks that were in turn attached to stout bodies with legs as thick as small tree trunks. A nearly opposite pattern occurred in the lovable long-beaked kiwi, in which body size decreased while brain size stayed nearly the same. In other words, the slope between brain size and body size was steeper. This pattern left the nocturnal, soccer ball–sized kiwi at the pinnacle of palaeognath relative brain size.

Although these two cases are intriguing, most of the burst of post-extinction diversification in brain size is concentrated in Neoaves, the most species-rich part of the avian evolutionary tree. In Neoaves, we observed that many different groups evolved higher brain-body scaling slopes not so much because of the brain itself changing size, but because body size decrease outpaced brain size decrease as different groups evolved smaller overall sizes. Swifts and hummingbirds provide one example of this pattern. These birds evolved very small sizes that allowed new specialized flight styles. The hovering flight of hummingbirds, for example, would be impossible for a crow-sized bird. Hummingbirds ended up with a higher brain-body scaling slope, but the driving factor was likely selection for shrinking body size.

Predatory birds, also members of Neoaves, provide another example of stronger selection for body size than brain size. The early evolution of a carnivorous diet in owls, hawks, and falcons is marked by an increase in both brain size and body size. Yet there seems to have been stronger evolutionary selection on body size. Perhaps this result was because of selection pressure related to hunting. Smaller species may have been better able to survive on a diet of rodents, versus larger individuals better able to pick off large prey such as adult ducks, with selection reinforcing these size patterns. Owls themselves turn out to have relatively large brains compared to hawks and falcons. However, it is doubtful whether this large brain size equates to wisdom. Research delving into the finer partitioning of the owl brain shows its size is due in large part to expansion of brain regions dealing with visual acuity rather than higher reasoning.

Crows and Parrots Reach the Peak

Two groups stand out from all the others when it comes to avian brain size: crows and parrots. Parrots are widely considered the most intelligent birds, in large part because of their ability to mimic—or sometimes even learn—human language. Like the flightless kiwi, parrots achieved a higher brain-body slope by decreasing body size rapidly while retaining relatively large brains. They took this pattern to a much greater extreme than kiwis did, resulting in one of the highest brain-body scaling slopes in the bird world. This high slope means larger parrots especially tend to have expanded brains, a trend borne out in remarkably brainy macaws and gray parrots.

As interesting as parrots are, it is Corvidae—the family that includes crows, ravens, and jays—that exhibit the most intriguing pattern of brain size evolution. Corvids belong to the songbird group, but they are much larger than most songbirds. This size disparity is on display every day at backyard bird feeders: Just compare a blue jay to some smaller fellow songbirds such as house sparrows and black-capped chickadees. Corvids are also very intelligent birds. That same backyard blue jay is clever enough to spy on squirrels burying nuts for the winter and then go back and steal their cached supplies after they leave. What makes corvids fascinating is this combination of large brain size and large body size.

Our results indicated that corvids have not only a high brain-body scaling slope, but also the highest rate of brain-body evolution. Corvids are fascinating because they took the same path that we humans did. They evolved larger bodies and larger brains at the same time, but their brains expanded even faster than their bodies. Corvids can rightly be considered the hominids of the bird world.

Parrots and corvids achieved extremely large relative brain size by taking two different evolutionary pathways. Yet there may be at least one factor that propelled them in the same direction. Parrots and corvids are both vocal learners, able to memorize and repeat sounds. The idea that vocal learning might be related to brain expansion is compelling. However, the story is not clean-cut. Corvids account for only about 120 of the roughly 5,000 living species of songbirds, but most other songbirds share a lower brain-body slope. Another complicating observation is that hummingbirds are now also known to be vocal learners, but share the same slope as swifts, which are incapable of vocal learning.

Delving Deeper

Combining fossil and modern data illuminates major patterns in the timing of avian brain evolution. The emerging big picture is that the first birds arose during the Jurassic period and had fairly typical theropod brains. The K-Pg mass extinction set the stage for the explosive radiation of modern birds, both in terms of species diversification and rapid shifts in brain size that helped birds adapt to environments as diverse as tropical rainforests and Antarctic ice shelves. Despite so much of the exciting stuff happening early, it seems that birds reached their pinnacle in brain size evolution relatively recently, because the last common ancestors of modern parrots and modern corvids appeared between 10 million and 20 million years ago. Given that birds have only recently reached this peak, it is possible that even larger-brained birds could evolve over the next 10 million years, provided we give them the opportunity by preventing catastrophic extinctions from climate change and deforestation.

Much remains to be explored. Although the NESCent study sampled 2,020 species, we considered only overall brain size. Future work may gain more insight into the specific neurological adaptations of birds by considering the volumes of different regions of the brain, such as the olfactory bulbs, optic lobes, and cerebellum. It may be possible to go even deeper than that to the cellular level. Corvids and parrots exhibit high neuron densities in the cerebrum (the region of the brain associated with higher cognitive function), and in some species these densities are so high that they approach the raw number observed in primates. As new methods emerge for imaging modern bird brains and inferring brain region boundaries in fossil endocasts, we hope to probe deeper in the minds of birds and nonavian dinosaurs alike.

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