

ORNITHOLOGICAL MASTERCLASS

2 Bird Evolution

Chris Cooney and **Gavin Thomas** take us on a whistle-stop tour through the last 165 million years to explain just where today's birds come from.

▲ Fossils like *Archaeopteryx* have revolutionised our understanding of avian evolution.

How did birds evolve?

Over the course of 150 million years, birds have evolved from a single common ancestor to the 10,000 species alive today. But what is the evolutionary origin of this diversity? This remained one of the most fiercely debated questions in evolutionary biology for decades and only reached a scientific consensus in the 1990's – not all dinosaurs were wiped out during the mass extinction at the end of the Cretaceous period, 65 million years ago. Some survived, and these are birds.

The discovery of *Archaeopteryx* in Germany in 1861 provided the first major clue. *Archaeopteryx* had bird-like features, such as wings and feathers, alongside other distinctly non-avian features; a bony tail, forelimb claws (seen today only in juvenile *Hoatzin*) and teeth. In the late-1990s thousands of fossils from the early Cretaceous (130–120 million years ago) were discovered in north-eastern China, providing compelling evidence of the transition from dinosaurs to birds. These remarkably complete fossils have wings

and vaned feathers – with a stiff central shaft and hooked hair-like barbules – just like modern birds.

We now know that birds belong to a group of dinosaurs called the theropods, which includes the giant *Tyrannosaurus* and the diminutive *Velociraptor* (famous for their oversized appearance in the first *Jurassic Park* film). Vaned feathers appear in the theropod group Maniraptora and wings in the Paraves (Fig 1). Exactly which fossil represents the earliest bird is still debated but current evidence suggests that *Archaeopteryx* was a true bird and the earliest known representative of the taxonomic class Aves, dating the origin of birds to the mid-late Jurassic period (165–150 million years ago).

Numerous bird groups appeared and went extinct in the Jurassic and Cretaceous periods. Two groups, the toothed, flying Enantiornithines and the large, mostly flightless, diving Hesperornithiformes, lived throughout the Cretaceous. Modern birds (the

Neornithes) did not become diverse and widespread until after the end-Cretaceous (K-Pg) mass extinction. Recent work using genomic data has revealed two remarkable (and controversial) insights. First, the majority of bird orders originated after the K-Pg mass extinction. Second, the early branches of the Neornithe tree of life may not have followed a 'bifurcating' pattern where each branch splits into two. Instead, the early expansion of non-passerine bird orders was an explosion of evolution, with up to eight major groups emerging in the geological blink of an eye. The reasons for this explosive expansion are uncertain but their emergence in a rapidly changing world following widespread extinction may have allowed birds to exploit and adapt to previously inaccessible resources. Over the next 65 million years, birds became the most successful group of terrestrial vertebrates, spreading across the globe and becoming more species rich than mammals, amphibians and reptiles.

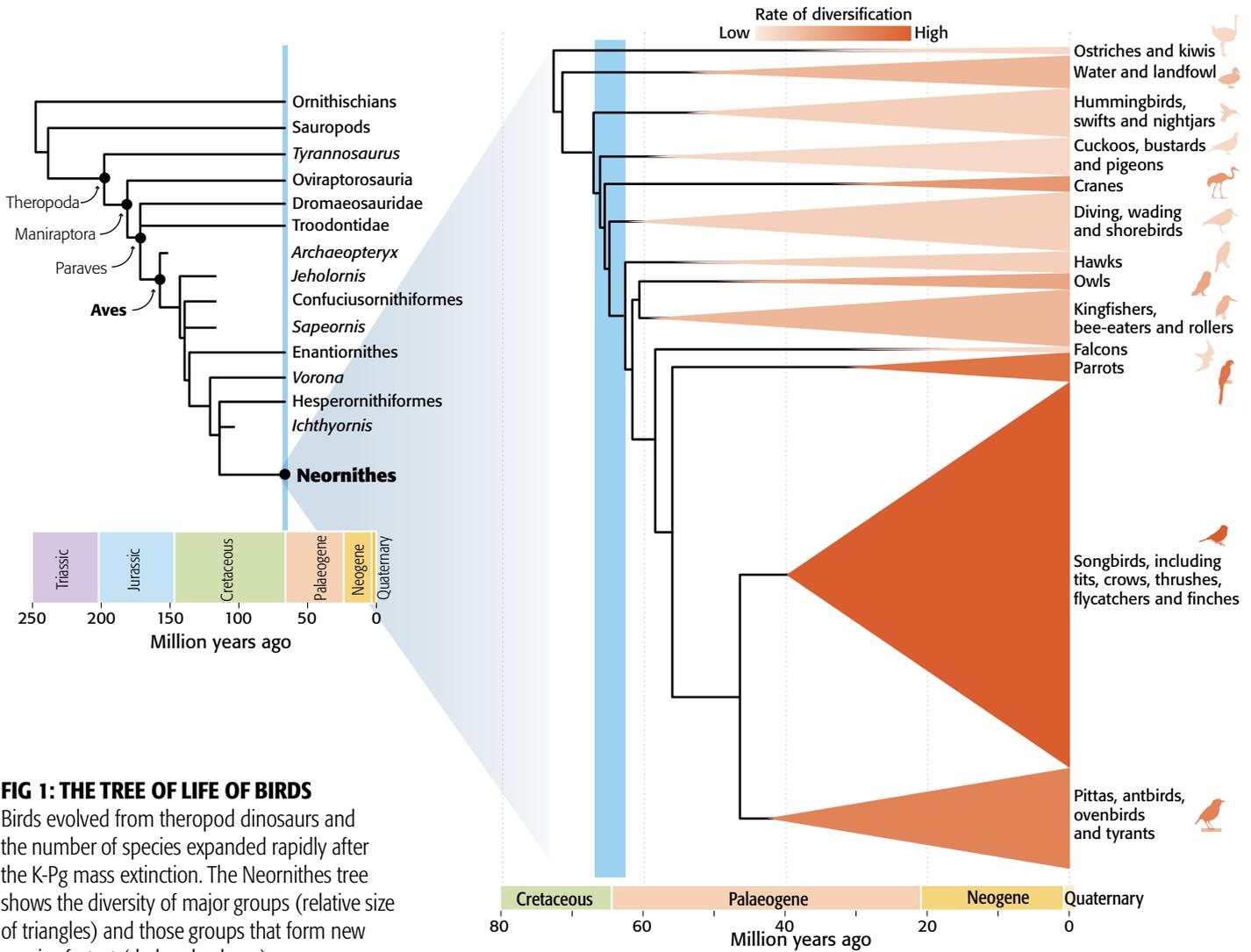


FIG 1: THE TREE OF LIFE OF BIRDS
 Birds evolved from theropod dinosaurs and the number of species expanded rapidly after the K-Pg mass extinction. The Neornithes tree shows the diversity of major groups (relative size of triangles) and those groups that form new species fastest (dark red colours).



▲ New Zealand's critically endangered Kakapo had a known adult population of 123 individuals in June 2016.

Conserving bird evolutionary diversity

The evolutionary tree of life contains a wealth of information beyond the relationships among species. For instance, we can identify which species have few close relatives and evolved long ago. If these species became extinct, we would lose a disproportionately large amount of evolutionary history that can never be recovered. Some researchers have suggested that preserving species that represent unique parts of the tree is critical. Sadly, with limited funding it is often necessary to make pragmatic decisions about which species to prioritise for conservation action. By putting the most at-risk species first, and then ranking species according to the amount of evolutionary history that they represent, we can identify species that are on the 'EDGE' (Evolutionary Distinct, Globally Endangered). The top five ranked species are as diverse as they are unique: Giant Ibis, New Caledonian Owllet-nightjar, California Condor, Kakapo and Kagu. Until recently, the idea of combining evolutionary history with threat status was largely confined to the pages of academic journals, but we are finally seeing real-world applications, most notably through the Zoological Society of London's EDGE of Existence initiative.

The global diversity of birds

Today, the diversity of birds is far from equally distributed. Some groups have expanded spectacularly, like the passerines with almost 6,000 species, whereas others, like the Hoatzin and Oilbird are evolutionary oddities with few close relatives. A long-standing question is whether species rich groups are older than groups that are species poor. The underlying idea is simple: all else being equal, a group that arose 100 million years ago should contain more species than one that arose only 10 million years ago. However, the evidence points to an alternative explanation – some groups are predisposed to give rise to new species at faster rates than others. The diversity of different major bird groups is closely related to the rate at which new species originate. In some groups, new species form at remarkably high rates – like songbirds – whereas in others the rates are slow. Much current research is focused on measuring how fast species arise (the speciation rate) in an effort to tease apart why this varies so much.

Just as the distribution of species in major bird groups is uneven, so too is

the distribution of birds globally. Around 250 species breed in Britain, an area of 244,000 km². This compares to roughly 1,500 species in Ecuador (284,000 km²). Species numbers peak in the Tropics, but what causes this variation? Since birds first evolved, the Earth's tectonic plates have moved and continental landmasses have shifted, but the regions that form the Tropics today have been climatically stable, while temperate and Polar regions have experienced many changes. This has led to the suggestion that species have steadily accumulated in the Tropics over millions of years – species originate and themselves give rise to new species with little impact of climate-driven extinctions, whereas similar species accumulation in temperate and Polar regions could be tempered by extinction due to climatic volatility. It has also been suggested that speciation rates are higher in the Tropics, but for birds there is little evidence of this. In fact, speciation rates seem to be highest on average across much of the New World (North and South America) and on many islands, but lower in the Old World (Europe, Africa, Asia).

Wrens: adaptation in action

Data from ringing and the Breeding Bird Survey show how tiny Wrens are locally adapted to the differences in the Great British climate. Wrens in Scotland are larger and can store more body fat than those further south, making them better able to withstand cold weather. Whether Wrens' rate of evolutionary adaptation is able to keep pace with the rate of climate change remains to be seen.

www.bto.org/wrens-adapt

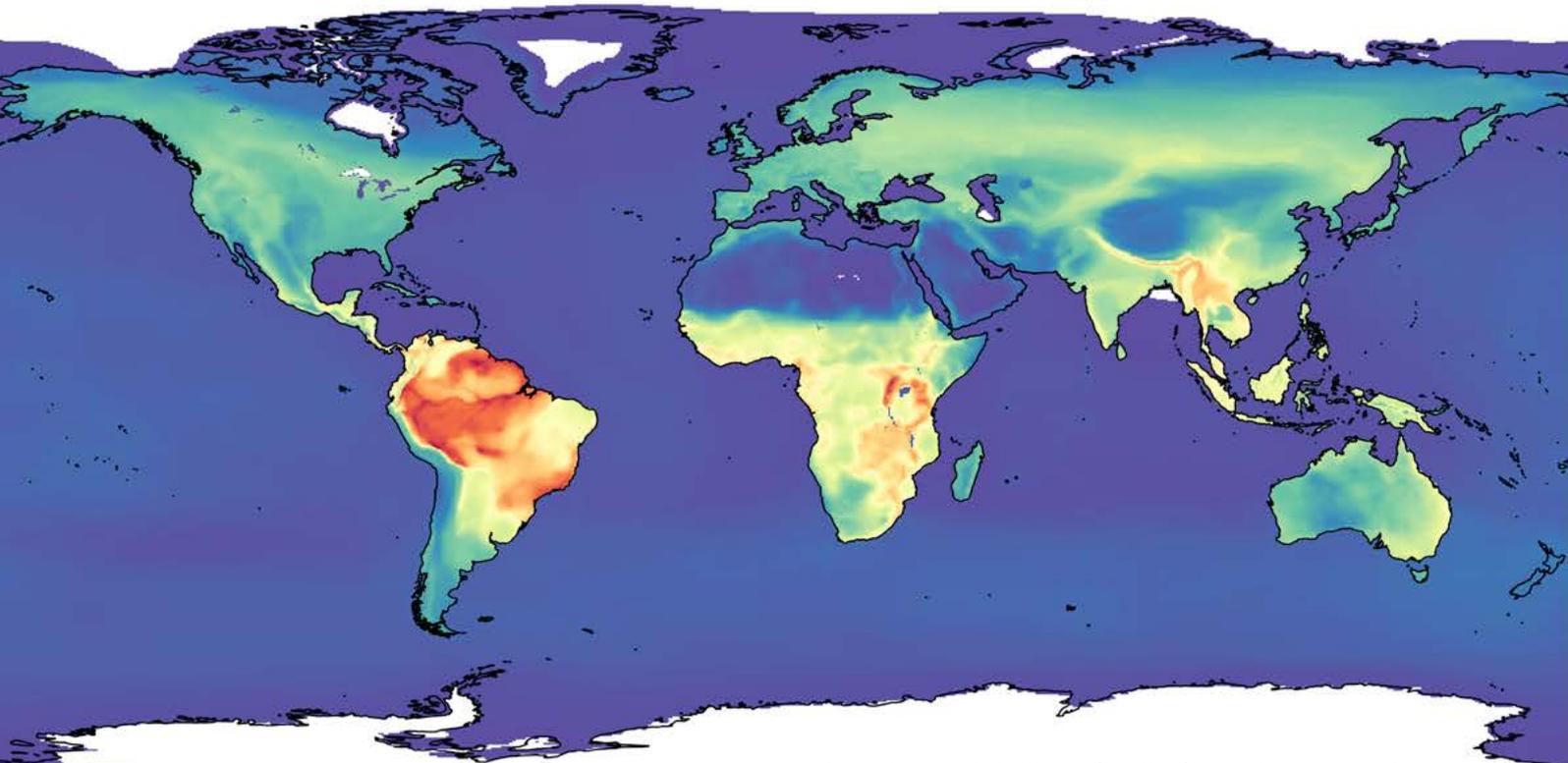
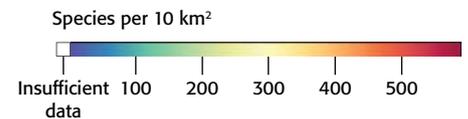


► Wren body mass varied by around 5% between the warmest and coldest regions.

PHOTOGRAPHS: ALLAN DREWITT/BTO

FIG 2: GLOBAL MAP OF THE DIVERSITY OF THE WORLD'S BIRDS

Species richness peaks in the Amazon forest of South America and in tropical mountain ranges.



Source: Based on distribution data from BirdLife International and NatureServe 2015.

How do bird species multiply?

A species is defined as populations whose members can interbreed with one another. So how does one species split into two? Islands provide natural experiments – ‘laboratories of evolution’ – that offer valuable insights into the origins of bird species. One of the most important examples is that of Darwin’s Galapagos finches – an iconic case of ‘adaptive radiation’, where a group diversifies rapidly to fill different ecological roles. Scientists have painstakingly documented the evolution of these famous finches, each of which has a highly specialised beak shape to extract food and survive in this complex archipelago. This long-term study has not only revealed how natural selection generates different beaks, but also given clues as to how 13 finch species arose from a single ancestral population that migrated to the islands 2–3 million years ago. A typical scenario sees two populations becoming separated geographically

and adapting to their respective habitats. Over time, changes in behaviour and appearance accumulate to the point where individuals from each population do not mate if they come back into contact. The two populations no longer mix, so can be considered distinct species. Both geography and ecology are key to understanding the origin of Darwin’s finches, as isolated populations adapt to variable environmental conditions, setting the stage for the formation of new species. By observing evolutionary changes to their beaks in real time, Darwin’s finches continue to provide clues as to how the great diversity of birds arose and continues to evolve. Bill size and shape is an important feature of other famous island radiations, such as the Hawaiian honeycreepers and Madagascan vangas, and this highly adaptable tool may ultimately prove to be key to understanding the expansion of birds on a global scale.

The authors

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FIG 3: THE DIVERSITY OF BIRD BEAKS

Top left to bottom right by row: Crossbill, Avocet, Keel-billed Toucan, Southern Cassowary, Rhinoceros Hornbill, Scarlet Macaw, Sickle-billed Vanga, Sword-billed Hummingbird, Shoebill, American Flamingo, Jabiru, Helmeted Curassow.

How to measure a bird's beak

The length, width and depth of a bird's beak can be measured with calipers, but this approach tells us little about shape. Characteristics such as curvature, hooks, casques (most strikingly found in hornbills) and ceres are missed, but are important for understanding how birds use their beaks. A complementary approach is to measure beak shape using 3D scans. Using museum specimens, it is possible to generate digital replicas of beak shape for almost all 10,000 bird species. Each beak model is ‘landmarked’ to compare the shape across species, involving placing points

at key locations on each 3D beak, which are then assessed mathematically. The bird with the most ‘average’ beak measured so far is the Rusty-fronted Barwing. Among British birds, the bill of the Carrion Crow is remarkably unremarkable – generalist feeders tend to have average bills that can be turned to many purposes. The oddities are more specialised. Fig 3 shows some unusual bill shapes in the Mark My Bird online database. Databases like this provide an avian natural history digital archive that enthusiasts can analyse, explore and enjoy.

Evolutionary change in our gardens

We now know from BTO Garden BirdWatch data that bird feeding has driven evolutionary change in Blackcaps. Many Blackcaps breeding in central Europe now winter in Britain instead of southern Europe, and this new migration route has become genetically encoded thanks to winter feeding in gardens. Blackcaps wintering in Britain also have narrower and longer beaks than those wintering in Spain, suggesting that British migrants have adapted to a more generalist diet.

www.bto.org/blackcap-change

Get involved

Explore the diversity of bird beaks:
www.markmybird.org

Search the bird tree of life:
www.onezoom.org/OneZoom/static/OZLegacy/EDGE_birds.htm

Find out more about conserving the evolutionary history of birds:
www.edgeofexistence.org