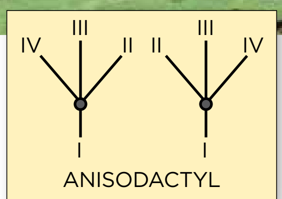
DAVIDE GAGLIO

fancy footwork



The dazzling diversity of avian feet

TEXT **LISA NUPEN**

The many different sizes and shapes of birds' bodies, the astonishing variety of coloration in their plumage and bills and the functional precision of their wings have long intrigued and delighted nature enthusiasts. Perhaps distracted by the bold and beautiful features of avian form, one could be forgiven for overlooking another fascinating aspect of birds' evolution: their feet.

The long toes of African Jacanas represent an anisodactyl arrangement.

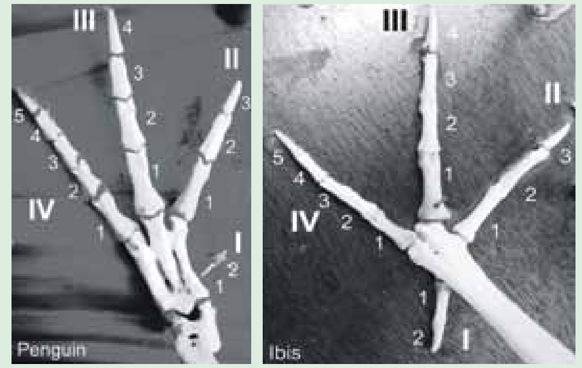
The fact that birds' feet have a dinosaurian jizz is no coincidence, since birds evolved from a group of reptilian ancestors called theropod ('beast-footed') dinosaurs. Like most amphibians and birds today, theropod dinosaurs had four digits on each limb – in other words, were tetradactyl – whereas living reptiles (chameleons, lizards and geckos) most often have five. From this four-toed origin there has been a remarkable diversification in avian hind-limb structure. Although overshadowed perhaps by the evolution of the dinosaurs' forelimbs into wings, this diversification is no less significant. And notably, the structure of birds' feet, especially the orientation and number of digits, or toes, shows great variation at multiple taxonomic levels, providing insight into the birds' different modes of life.

Birds' feet are not only used for locomotion (walking or running, swimming, climbing), but they serve other important functions in perching, foraging, preening, reproduction and thermoregulation. Because of this, the structure of a bird's foot often provides insight into the species' ecology. Often, distantly related species have converged on similar foot types when adapting to particular environments. For example, the four fully webbed, forward-pointing toes – called totipalmate – of pelicans, gannets and cormorants are an adaptation to their marine habitat.

The closely related Shoebill does not have webbed feet, perhaps because of its wetland habitat, but the tropicbirds, which form their own relatively ancient evolutionary lineage, are also totipalmate. Albatrosses, petrels and shearwaters, however, only have three forward-pointing toes (digits II to IV; digit I is vestigial) that are webbed – or palmate – as do penguins, ducks and geese. These species are all adapted to aquatic environments where webbed feet are clearly beneficial for locomotion.

Different foot types can be equally suited to the functional demands of a particular niche or environment. The arrangement of toes in lovebirds, barbets and cuckoos, for example, is different from that in passerines (such as finches, shrikes or starlings) in the same environment. The functional reasons for differences in foot structure can be difficult to explain.

In an attempt to organise and better understand the observed differences among avian feet, biologists have named five general categories that describe the arrangement of birds' toes: anisodactyly, zygodactyly (including semi-zygodactyly), heterodactyly, syndactyly and pamprodactyly. However, like many concepts in biology, there are exceptions, variations and intermediates that violate these 'rules'.



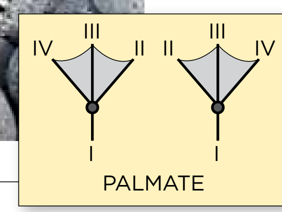
THE BONES IN THE TOES

In almost all birds, the number of bones in each toe is preserved: there are two bones in the first toe (digit I), three bones in the second toe (II), four in the third (III) and five in the fourth (IV). Therefore, the identity of a toe (I to IV) can be determined quite reliably from the number of bones in it. When evolutionary toe-loss occurs, this makes it possible to identify which digit has been lost.

The first, and seemingly ancestral, configuration of birds' toes – called anisodactyly – has three digits (numbered II, III and IV) orientated forwards and digit I (the 'big toe', or hallux) pointing backwards. This arrangement is shared with theropod fossils and is the most common, being found in more than three-quarters of bird species, including the webbed feet of ducks and penguins, most songbirds (such as sparrows and weavers) and pigeons, buzzards, vultures, eagles and gamebirds. The anisodactyl toe orientation is well suited to perching and grasping, especially when the hallux >

The toes of penguins (below left) and gannets (below) are both anisodactyl, but have different webbing patterns (palmate and totipalmate respectively). Both groups are adapted to an aquatic environment.

PETER RYAN



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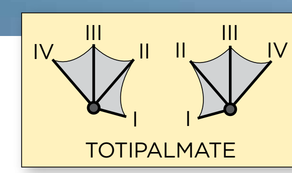
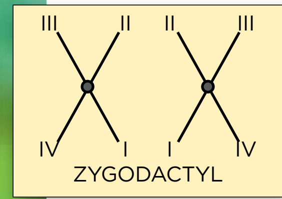
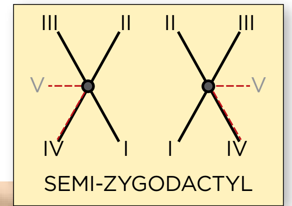
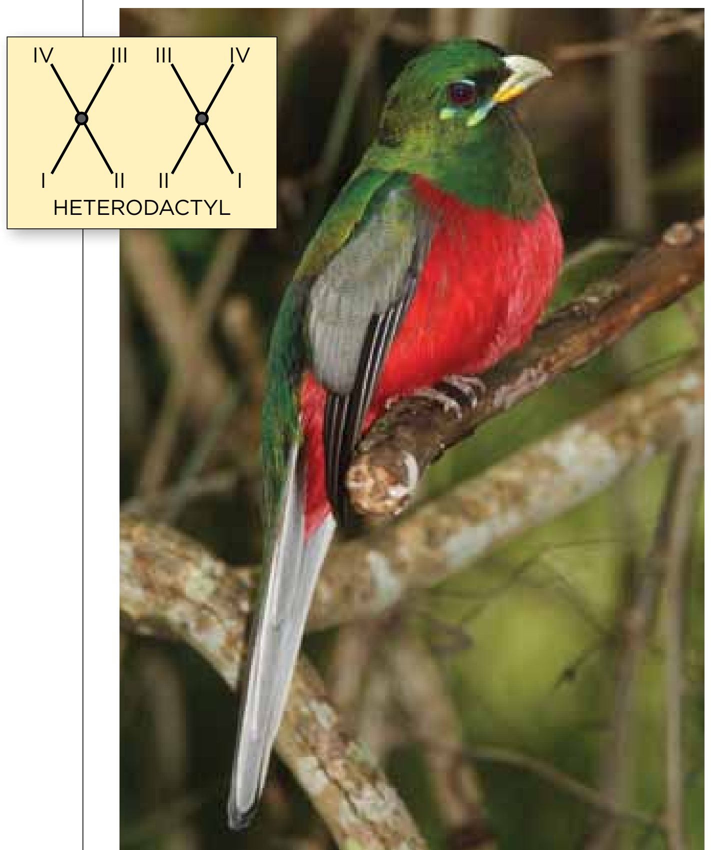




left *Cuckoos exhibit zygodactyly, the second most common toe arrangement among birds.*

below *Semi-zygodactyly – the ability to rotate the outer toe forwards and backwards – occurs in owls.*





ALBERT FRONEMAN (4)

above *Only trogons possess a heterodactyl foot type, which differs from a zygodactyl arrangement in that digits III and IV – not II and III – point forwards.*

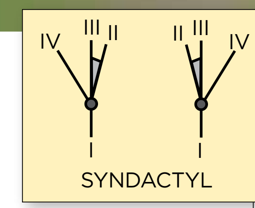
is elongated, but it is not the only evolutionary 'solution' to such activities.

In the second most common foot type among birds – called zygodactyly – digits II and III point forwards and digits I and IV point backwards. Some perching birds, such as cuckoos and turacos, have this arrangement, but it is also well suited to grasping, as in parrots, and climbing, as in woodpeckers. These species are not closely related, which suggests that zygodactyly has evolved multiple times.

Trogons have a unique arrangement of digits – termed heterodactyly – which resembles zygodactyly except that digits III and IV point forwards and I and II backwards. Some advantages to zygodactyly and heterodactyly might include increased grip strength for perching resulting from two pairs of toes opposing each other, and better grasping for similar reasons. Parrots, among other species, routinely manipulate their food using their feet – there are even left-footed and right-footed parrots. Birds such as ospreys, owls, mousebirds and some woodpeckers have the ability to rotate the outer digit (IV) forwards and backwards – described as semi-zygodactyly or ectropodactyly.

There is another configuration – known as syndactyly – in which two or more toes (usually III and IV) are fused to varying degrees. Syndactyly has been well studied in humans as a congenital oddity that arises from specific genetic mutations, and five types of finger or toe fusion have been characterised. In the avian world, the fleshy sheath that unites the anterior digits is thought to increase grip strength when the bird is perching, as it forces the digits to act in concert. Syndactyly is common among kingfishers, hornbills and bee-eaters (Coraciiformes) and there are many intermediate examples of birds with partly fused toes in this group. Extreme syndactyly occurs in the wood-hoopoes and hornbills and diminishes progressively through the kingfishers to only minor fusion in *Upupa* and finally the true anisodactyl feet of rollers. Similarly, among passerines it can sometimes be difficult to distinguish the syndactyl and anisodactyl conditions, as they intergrade closely.

The final arrangement of toes – pamprodactyly – is found among some mousebirds and swifts, >



The fused toes of syndactyl kingfishers may increase grip strength for perching.

CONVERGENT EVOLUTION OF ZYGODACTYLY

The osteological details of foot structure are different in woodpeckers and cuckoos, indicating that these distantly related groups evolved zygodactyl feet in different ways. In fact, zygodactyly seems to have evolved independently in at least four groups of birds: the cuckoos, cuckoo roller, parrots and Piciformes (woodpeckers, barbets, honeyguides and their allies). Whether it evolved due to some adaptive advantage or through random mutation is unknown. It has recently been suggested that anisodactyly evolved from a state of zygodactyly.

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Mousebirds are able to hang, supporting their entire weight on their feet, thanks to the pamprodactyl arrangement of their toes.

and is characterised by all four digits being directed forwards, enabling these species to hang their weight on all four toes and even feed upside-down.

From just this brief look at digit orientation we can see that foot type varies across the avian tree of life. Some early work by Walter Bock in 1959 suggested that the four perching toe configurations seen in modern birds (anisodactyly, syndactyly, heterodactyly and zygodactyly) each evolved in response to selection for a strong set of opposable toes for perching rather than for climbing. Interestingly, several types of foot structure have evolved more than once through convergent evolution; in other words, distantly related birds have evolved similar, but not identical, arrangements of their four toes. Similarly, toe-loss (an evolutionary reduction in the number of toes) is widespread across the avian tree, including in a whole clade of three-toed syndactyl kingfishers.

It is not always clear why evolution produced particular toe arrangements. Nor is it straightforward to identify a common evolutionary driver for any one foot type that explains its origin. In some cases the feet of two species may have almost identical functions but different toe arrangements. Ospreys and owls spread their semi-zygodactyl talons wide when capturing prey, but anisodactyl fish eagles are equally adept at grasping their catch. Zygodactyl and syndactyl birds spend just as much time perching as their similarly sized anisodactyl passerine counterparts (compare bee-eaters, barbets and weavers, for example). It is difficult to explain why some aquatic or marine species are totipalmate and others have lost the hallux (having only three webbed toes). Or why some kingfishers retained four toes while others down-sized to three. Why is the hallux reduced or lost in many cursorial birds, but the roadrunners, as quintessential running ground-birds, retained the same zygodactyl arrangement that is found in other cuckoos? These questions remain to be answered.

The best current understanding is that the different foot types evolved for perching and have been secondarily repurposed for other functions. For example, the zygodactyl foot is used for several different modes of locomotion (such as running and hopping) and, in general, different foot types may be equally suitable for one particular function (perching or grasping). This essentially means that the different arrangements were a kind of evolutionary 'accident' that arose through mutations in various groups of birds – there was no adaptive advantage.

The same goes for toe-loss: it is likely that early on in the evolution of birds, the major selective pressure was for a perching foot, which requires a strong set of opposable toes with which to grasp a branch. Four foot types described here fulfil this need: anisodactyl, zygodactyl, heterodactyl and syndactyl. It doesn't seem to matter how many toes, nor which toes, are involved.

So, when you are next admiring the resplendent plumage or captivating calls of our feathered friends, I hope that you will take note of this diversity and be able to appreciate that some of their splendour and mystery lies in their fascinating feet. ◆

EVOLUTIONARY TOE-LOSS

Several families of birds, including rails, flamingos, grebes, plovers, sandpipers and their allies, show a reduction in the size of the hind toe, and the emu, bustards and quails – known as tridactyls – have lost it entirely. Ostriches are the only two-toed – or didactyl – species, having lost digits I and II. Some examples of zygodactyl birds that show toe-reduction are the Three-toed Jacamar *Jacamaralcyon tridactyla*, the American Three-toed Woodpecker *Picoides dorsalis* and the Spot-throated Flameback *Dinopium everetti*. The ancestrally anisodactyl Three-toed Parrotbill *Paradoxornis paradoxus* from China has lost toe IV, for no clear reason. These examples show that not all toes are evolutionarily necessary. Perhaps if mutations arise that cause toe-loss, they may not be detrimental.

Interestingly, in the Old World alcedinine kingfishers, toe count reflects evolutionary history. The ancestral condition is a classic four-toed syndactyl arrangement, but nested within it are nine species that have three toes (having lost digit IV) and – this is the interesting bit – one species, the Sulawesi Dwarf Kingfisher *Ceyx fallax*, that has three-and-a-half! This intermediate state, essentially a 'missing link' between the two groups, retains the vestiges of a fourth toe.