

*All birds
have
them...*

TEXT BY PHIL HOCKEY

feathers

*T*he feather is one structural characteristic that birds do not share with any other living creature. Feathers range in size from the miniscule to the very large, in colour from the drab to the extravagant and in shape from the long and thin to the short and rounded. All birds have them, all birds need them and all birds spend a great deal of time looking after them. In this article, Phil Hockey answers some fundamental questions about the origins, structure and functions of feathers. ▶



Form

Where did feathers come from?

There is little doubt that modern birds are derived from theropod dinosaurs – indeed, birds are the only dinosaurs that escaped the mass extinctions of 65 million years ago. And yet there is an anachronism in that all fossil birds discovered to date have feathers, but there are no feathered dinosaur fossils, although seemingly plume-like structures have been found on the forelimbs of two dinosaurs, *Masitisaurus* and *Ralikhomopus*, that roamed Lesotho some 200 million years ago.

One essential precursor to the evolution of feathers is the evolution of at least partial warm-bloodedness (endothermy). Feathers would be a disadvantage for cold-blooded (ectothermic) animals because they would slow down the rate at which such animals could gain body heat from the sun. Structural and distributional evidence indicates that some dinosaurs had achieved at least partial endothermy before the cretaceous apocalypse consigned them to the history books – but by this time, birds with modern-type feathers had been around for at least 80 million years or so!

Despite the lack of any conclusive evidence, the relatedness of birds and dinosaurs opens the possibility that the origins of modern feathers lie in reptilian scales. Some reptiles that predate

birds by about 70 million years did have elaborate scales, such as those along the back of Europe's *Longisquama*. The problem facing scientists in their search for this 'missing link' is that there is no fossil evidence for the intermediate stages – even the oldest bird fossils have 'modern' feathers, and there are no modern birds that have primitive feathers (whatever 'primitive feathers' might have looked like). Even today, there is no consensus on how the transition occurred, if indeed it did: whilst scale and feather development share some features, other facets, such as the nature of the proteins involved, are quite different.

How does a feather develop?

The first signs of feathers appear on the embryo inside the egg only a few days after the start of incubation. Disc-like thickenings of the outer layer of the skin (the epidermis) soon develop as backward-pointing cone-shaped structures (the follicles). At the base of the follicle lies the dermal papilla, a small lump of cells covered by an epidermal cap. This cap produces a circle of cells, called the epidermal collar, and it is from this that the feather arises. Initially, the growing feather has an outer sheath surrounding the feather proper, and an inner layer of nutrient-providing pulp. The first part of the growing feather to develop is the tip – all growth occurs from the base. ▷

Because feathers comprise dead tissue – which therefore cannot regenerate and has to be replaced during moult – birds have to devote much time to keeping their primary asset in as good a condition as possible.

YOU'RE SO VANE: The importance of preening

Because feathers are essential for flight, insulation and display, birds spend much time caring for their plumage. If feathers are ignored and become damaged they cannot be repaired, because they are made of dead tissue. In the case of some very small-winged species, such as diving-petrels, the loss of even a small number of primaries may be enough to render them flightless, thereby condemning them to starve to death. Preening often follows bathing: it is thought that one of the functions of bathing – apart from that of cleaning – may be to make the feathers more pliable and easier to preen.

A bird preens either by running feathers through its bill, or by wiping its bill across the feather surface. The former technique is probably most important for restoring individual feather structure (that is, rearranging the barbs and barbules), removing dust and old preening oils and applying new oils. The latter is more important for rearranging clusters of feathers and for drying them. Most birds have a preen gland, located close to the base of the tail. This gland secretes the oils that birds need to waterproof their feathers. Birds that lack a preen gland compensate

for this in various ways, including having very loosely structured feathers that do not need oiling (for example, Common Ostrich *Struthio camelus*) or by having powder-down feathers (for example, herons).

The preen-gland oils are also thought to have antibiotic properties effective against pathogens such as feather-degrading bacteria. A recent discovery suggests that the roles of these oils may be even more far reaching. The preen gland of the Green Wood-Hoopoe *Phoeniculus purpureus* contains a bacterium (a species known only from this bird) that produces a complex cocktail of noxious chemicals which acts as a predator deterrent. This is the first demonstration of chemical defence among birds in which the repelling compounds are derived from microbes.

Some birds also seem to derive a feather-care benefit from ants, either squatting down so that ants can run over their feathers, or actively picking up ants and rubbing them over the plumage. The precise benefits of this are still debated, but the formic acid and other secretions produced by the ants may have insecticidal or fungicidal properties, helping to protect the feathers.



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Once the tip is pushed from the skin, final development is complete and the living cells die. At the same time, the protein within the cells is changed into hard beta-keratin, such that the fully developed feather comprises only dead tissue.

Feathers are not randomly arranged across the bird's body, but grow in tracts, called pterylae. Nor are feathers uniform in structure: feather types fall into six different categories: contour (or body), flight, filoplume, semiplume, down and bristle.

A typical contour feather comprises a shaft, oval in cross section, from which barbs protrude to form the feather vane. Small, hooked barbules project sideways from the barbs, forming a mesh which binds the barbs together, rather like a zip fastener – should this mesh become separated or tangled, the bird can repair it by preening. Towards the base of the feather there is usually a downy region, where the barbules are smooth and non-interlocking. Contour feathers provide both streamlining and protection for the skin, while their downy lower sections also provide insulation.

Flight feathers are longer and stiffer than contour feathers, have little down at the base and, because of the tremendous pressure they are placed under when the bird is flying, are anchored to the bones by connective tissue. Filoplumes are thin, hair-like feathers with tufts of barbs only at the tip. They grow adjacent to the contour feathers, but unlike the latter have no muscles at their bases, although their follicles are well supplied with nerve endings. The main function of filoplumes seems to be to provide sensory information that the bird needs in order to keep its contour feathers in the best position, for example when bathing, flying or preening.

Semiplumes have a well-developed shaft and wholly downy vanes; they grow mostly along the edges of feather tracts. Their main function is insulation, but in swimming birds they also aid in increasing buoyancy. Down feathers are similar to semiplumes, but either lack a shaft completely or have only a poorly developed one. They are soft and fluffy and serve as insulation. In many birds they comprise 'powder down' – a highly specialised type of down that breaks into a fine powder when the bird preens. The powdered down is preened



CHRISTIAN BOIX-HINZEN

COLOUR ABNORMALITIES

Because of the complicated ways in which feather colouring is determined, there is always the chance that something can go wrong as a result of a genetic glitch, disease or inadequate diet. The most common causes of plumage abnormalities are genetic, and usually involve a shortage or excess of one or more pigments. The total absence of pigment is called albinism, in which all feathers are white and the soft parts are pinkish. A reduction in the level of all pigments is termed leucism (and is much more common than true albinism) and the absence of a subset of pigments is termed schizochroism.

Sometimes, one pigment replaces others – in the case of erythrisms, all melanins are replaced with a single chestnut-red pigment. An excess of brown or black pigment results in melanism, and an excess of yellow pigment causes xanthochroism. In nature, birds with plumage abnormalities are seen fairly regularly, but these are almost invariably pigment abnormalities rather than structural ones, because birds with the latter rarely survive.

onto the contour feathers and serves as a water repellent.

Finally, bristles are spiky feathers, usually with very few barbs, and are mostly concentrated on the head and neck. They have a diversity of functions, including protective (around the eyes and ears), sensory (like cat's whiskers) and also (in insectivorous birds such as nightjars and swifts) acting as a net around the gape, helping in prey capture. In some instances, such as the head tuft of a Grey Crowned Crane *Balearica regulorum*, they also serve an ornamental function.

What gives feathers their colour?

Feather coloration can be produced in two ways – either by pigments within the feather itself, or by adaptations in feather structure. There are two types of feather pigments: melanins produce colours in the black-brown-yellow spectrum and lipochromes in the yellow-red-blue-green range. Melanins are derived from amino acids in the bird's diet, whereas lipochromes are chemically similar to blood pigments.

Colours produced by feather structure can be classified as either iridescent (reflective) or non-iridescent. Iridescent

colours, such as on the throats of several sunbirds, are only visible at certain angles, non-iridescent colours can be seen at all angles. Iridescent colours are formed from the interference of light by different layers of melanin in the feathers' barbules. The surface from which these colours are reflected is either the interface between melanin and the air, or between melanin and keratin. ▷

Above Most colour abnormalities are genetic, such as in this Northern Black Korhaan.

Opposite Iridescent colours are caused by light interference and are only visible from certain angles.

Below The bristles around the gape of nightjars assist in prey capture.



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function

Flight

Feathers are not essential for flight; for example, bats are highly aerially agile, but have no feathers. And similarly, not all feathers are used directly in flight. Feathers are, however, among the supreme adaptations for flight and have the added advantage over bats' wings that they can be replaced on a regular basis, by moulting. They are not the only adaptation birds have for flight – they also have highly modified lungs and very light, hollow bones. In fact, the feathers of many birds weigh more than their skeletons – in some large eagles, up to almost three times as much.

Although individual feathers are masterpieces of evolutionary design, they have the advantage that the design is highly flexible and a bewildering array of feather shapes and sizes have resulted. Whilst all birds have fundamentally the same bone structure in their wings, it is the feathers that are responsible for the array of wing shapes displayed by modern birds, from the long, narrow wings of albatrosses used for dynamic soaring to the long broad wings of vultures, used for thermal soaring, and the tiny, rounded wings of many passerines, whose lifestyle demands great aerial agility.

Why the fancy coloration?

The diversity of bird coloration and ornamentation has fascinated scientists for a long time, and numerous explanations have been put forward, not all of which are mutually exclusive. These explanations cluster into four groups. The 'physiology hypotheses' suggest that the distribution of and amount of melanin is linked to protection of the feathers. Birds living in abrasive environments are predicted to have ▽

The mathematics needed to describe the dynamics of flight are formidable. Whilst they form the basis for the design of modern aeroplanes, no aeroplane could mimic the aerodynamic perfection and flexibility of this Black-headed Heron.

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GERALD CUBITT

GOING TO EXTREMES

Some birds have exploited the adaptability of feather design to the extremes. Many birds have tails that are extremely long relative to their bodies. In Central and South America, the Fork-tailed Flycatcher *Muscivora tyrannus* has a tail that accounts for 77 per cent of its total length. The largest feathers of all are the central tail feathers of the Great Argus *Argusianus argus* (above) of the Malay Peninsula, Sumatra and Borneo. These are up to 1.73 metres long and 130 millimetres wide, longer than the ornate tail coverts of a male peacock. The longest tail feathers belong to Reeves's Pheasant *Syrnaticus reevesii* of north-central China – these occasionally reach 2.4 metres in length.

These, however, are by no means the limits to the sizes that feathers can grow. In Japan, selective breeding over more than 300 years of the Onagadori strain of the Red Junglefowl *Gallus gallus* has resulted in birds with tail coverts several metres long – one even reached an impressive 10.59 metres! These birds are kept as ornaments and are exhibited at shows, to which they have to be taken in custom-built boxes in which their tails can be curled round and round.

Tail feathers and tail coverts are often among the most ornamental of feathers, but a few species have ornamented wings. An African example of such ornamentation is the Pennant-winged Nightjar *Macrodipteryx vexillarius*. During the breeding season, the second primaries of males grow up to 600 millimetres long and are used in display flights to attract females. Once this task is successfully completed, the feathers are shed and replaced with ones of normal length.

more melanin because melanin serves to toughen the feathers. Additionally, some researchers have proposed a thermoregulatory role for coloration, but this remains open to debate. The 'foraging hypotheses' propose, *inter alia*, that dark facial masks coupled with dark bills reduce glare and that the flashes of colour in some birds' wings (or the black-and-white striped coloration of some diving seabirds, such as African Penguins *Spheniscus demersus*) serve to either flush or disorientate prey.

Two groups of hypotheses relate to signalling, to either other species or members of the same species. Signals to others include camouflage (for predator avoidance, such as in nightjars), aposematism (bright colours signalling that you are distasteful) and mimicry. The last is probably rare, but it has been suggested that African black flycatchers (*Melaenornis* spp.) mimic aggressive and distasteful drongos (*Dicrurus* spp.).

Undoubtedly, however, the hypotheses for which the best supporting evidence exists are those related to intraspecific signalling. Many birds use patches of colour to enhance behavioural displays. African examples of such would include the sunbirds with bright pectoral tufts that are visible only during displays, and the elongated and startlingly white back and rump feathers of the Black-backed Puffback *Dryoscopus cubla*, raised in display. Colour can also be used to warn conspecifics of danger; although this is well known among mammals, such as deer, evidence for warning coloration among birds is slim as most birds signal danger vocally.

In species where there is considerable variation in plumage, this variability may aid in individual recognition. Although probably not common, this effect has been demonstrated experimentally in Ruddy Turnstones *Arenaria interpres*, which are less aggressive to neighbours they 'know' than to unknown intruders. In species whose plumage varies with age and sex, this type of variability can be used to signal dominance status. Interestingly, young African Penguins have evolved a means of 'cheating the system'. Adult penguins generally are intolerant of juveniles in foraging groups and, given that even foraging birds spend much time on the surface, it is probably the juveniles' plain rather than



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patterned face that gives away their status. After juveniles leave the colony, they spend 12 to 22 months at sea before returning to land for their first moult. This is a long time to be excluded from cooperative hunting groups. Some juveniles, however, are crafty and undergo a head moult at sea, emerging from this with heads (above water) resembling adults, and bodies (below water) retaining their juvenile plumage.

Many birds – primarily during the breeding season – are brightly coloured and many, such as whydahs, develop elaborate ornamented feathers. Charles Darwin recognised that these were features that probably contributed little to survival and in many cases, such as the long-tailed widowbirds, they were probably even a threat because the birds become far less manoeuvrable. Darwin concluded that the key to this ornamentation was the acquisition of a mate (or mates) – a type of selection known as sexual selection. It can operate either through competition among males (as is the case in the House Sparrow *Passer domesticus* and the Red-tufted Sunbird *Nectarinia johnstoni*

of East Africa, which signal dominance with bibs and pectoral tufts respectively) or through female choice (as in Long-tailed Widowbird *Euplectes progne* and Jackson's Widowbird *E. jacksoni* of Kenya and northern Tanzania, where females select males with the longest tails).

Because plumage coloration somehow pervades almost every element of a bird's life, from survival to mating and feeding, to consider for any one species that it plays only one role would be naive. Some experiments have conclusively shown links between coloration and behaviour, but it seems intuitively likely, rather like mating systems themselves, that if combinations of colour are adaptive and have evolved through processes of selection, they represent a compromise. In some cases, this compromise may be driven by extremes, such as the need to be seen by potential mates, but not by potential predators. The answers to the question 'why the fancy coloration?' are probably very much more complex than is realised at present and doubtless will keep students of bird coloration busy for many years to come. □

The male Long-tailed Widowbird in breeding plumage has a very eye-catching tail, but it must be lost as soon as its mate-attracting role is completed.