moult

THE COST OF ANNUAL RENEWAL

TEXT & PHOTOGRAPHS **PETER RYAN**

FEATHERS DEFINE BIRDS, yet they are dead structures that have to be replaced regularly if they are to function efficiently. Moult is thus a necessary evil that all birds face. It requires considerable energy, and birds are at risk while moulting because their flight ability and insulation are impaired. As a result, moult ranks with breeding and migration as one of the key activities in a bird's annual cycle. In the first of two articles on this often overlooked topic, Peter Ryan explores how birds fit moulting into their busy lives.

SOME MAY DEBATE the veracity of Mark Twain's observation that 'Clothes make the man', but there is little doubt that feathers make the bird. Feathers are essential for locomotion, insulation and body protection, as well as determining the appearance of birds.

But once grown, feathers are dead structures, and if they are not replaced regularly, all these functions suffer. Flight capability is perhaps the most obvious cost: if not replaced, the flight feathers deteriorate to the point where they render the bird flightless. However, other impacts should not be underestimated. At high latitudes, adequate insulation is essential to allow birds to survive freezing winter nights, and the insulation and waterproofing provided by feathers also deteriorates with age. And many birds rely on their plumage to attract mates; having a new set of finery is a prerequisite for breeding!

The importance of feathers is indicated by the amount of time and effort birds expend looking after them. Preening and bathing help to ensure that feathers remain in good shape and continue to perform their essential functions for as long as possible. The rate at which feathers wear depends in part on their location. For example, the tips of the outer primaries wear faster than inner primaries because they travel through air faster and are less protected by the secondaries when the wing is folded. Birds can prolong feather life by incorporating pigments such as melanin into their feathers, which explains why >

EDDIE COOMBES

left *Abnormal feather growth, such as this Southern Masked Weaver with elongated thigh feathers, is rarely encountered in wild birds. It appears to be under genetic control because inbreeding and selection among budgerigars has resulted in the so-called 'feather duster' syndrome, a genetic mutation that results in continuous feather growth.*

opposite *Even though almost 20 per cent of their feather growth occurs at sea, King Penguins spend roughly a month ashore each year to replace all their feathers. During this time they rely on stored reserves, losing 44 per cent of their body mass.*

above *Incorporating the black or brown pigment melanin into feathers increases their resistance to wear. As a result, many mostly white birds such as this Sacred Ibis have dark tips to their flight feathers, because the tips are subject to greater wear than other parts of the feathers. Note how the ibis is moulting primary 8 in its left wing but not its right wing. Such asymmetrical wing moult normally results from damage to a particular feather rather than scheduled moult.*

right *The African Penguin is unique among penguins in undergoing some moult at sea. A proportion of juvenile birds undergo a partial head moult, apparently to reduce aggression from adults and allow them access to adult feeding groups.*

many birds have dark trailing edges to their wings and tails. The amount of use also impacts on wear rate: the flight feathers of birds that migrate long distances tend to deteriorate more rapidly than those of resident species.

However, even among sedentary forest birds the combination of physical abrasion, sun damage and attack from bacteria, fungi and feather lice eventually result in the degradation of feathers to the point where they have to be replaced. Indeed, moulting is arguably the most important activity birds undertake in their annual cycle, taking precedence over other activities. It is becoming increasingly apparent that many birds structure their annual cycle around their moults rather than reproduction – after all, individuals may elect not to breed if times are tough, but all birds have to moult.

Unfortunately, just as not moulting incurs costs, so too does >

THE MECHANICS OF **MOULT**

Moult is intimately linked to the process of feather growth, which occurs from specialised follicles in a bird's skin. A new or 'pin' feather emerges from its follicle in a blue-grey waxy sheath, which breaks open to reveal the new feather inside. The actual process of feather formation is conducted by a ring of epidermal collar cells at the base of the follicle, starting with the tip of the feather and progressing along its length until the base is completed.

It seems little short of miraculous that such complex structures as feathers can form from a simple ring of cells. However, there is a convincing series of intermediate steps linking feathers to reptilian scales. The form of keratin used to build feathers is identical to that found in embryonic crocodiles, and the marvellously complex flight and contour feathers are produced by the same process as simple down-feathers. Finally, the recent discoveries of fossils of 'feathered' dinosaurs indicate that feather-like scales were found in numerous lineages of dinosaurs.

Damage to actively growing feathers can result in bleeding, hence they are often called 'blood feathers'. Usually such bleeding stops within a short period, but when large flight feathers are injured it can be persistent and result in significant blood loss. The Sharp-beaked Ground Finch, one of Darwin's Finches, has learned to exploit this as a food resource, pecking at the growing feathers of breeding boobies to obtain a meal of blood. Interestingly, this behaviour only occurs on two remote northern islands in the Galápagos archipelago.

RUMP FEATHERS TEND TO BE MUCH MORE EASILY PULLED OUT THAN FEATHERS ON THE BACK OR CHEST, **PRESUMABLY BECAUSE THIS IS THE REGION MOST OFTEN TARGETED BY PREDATORY BIRDS**

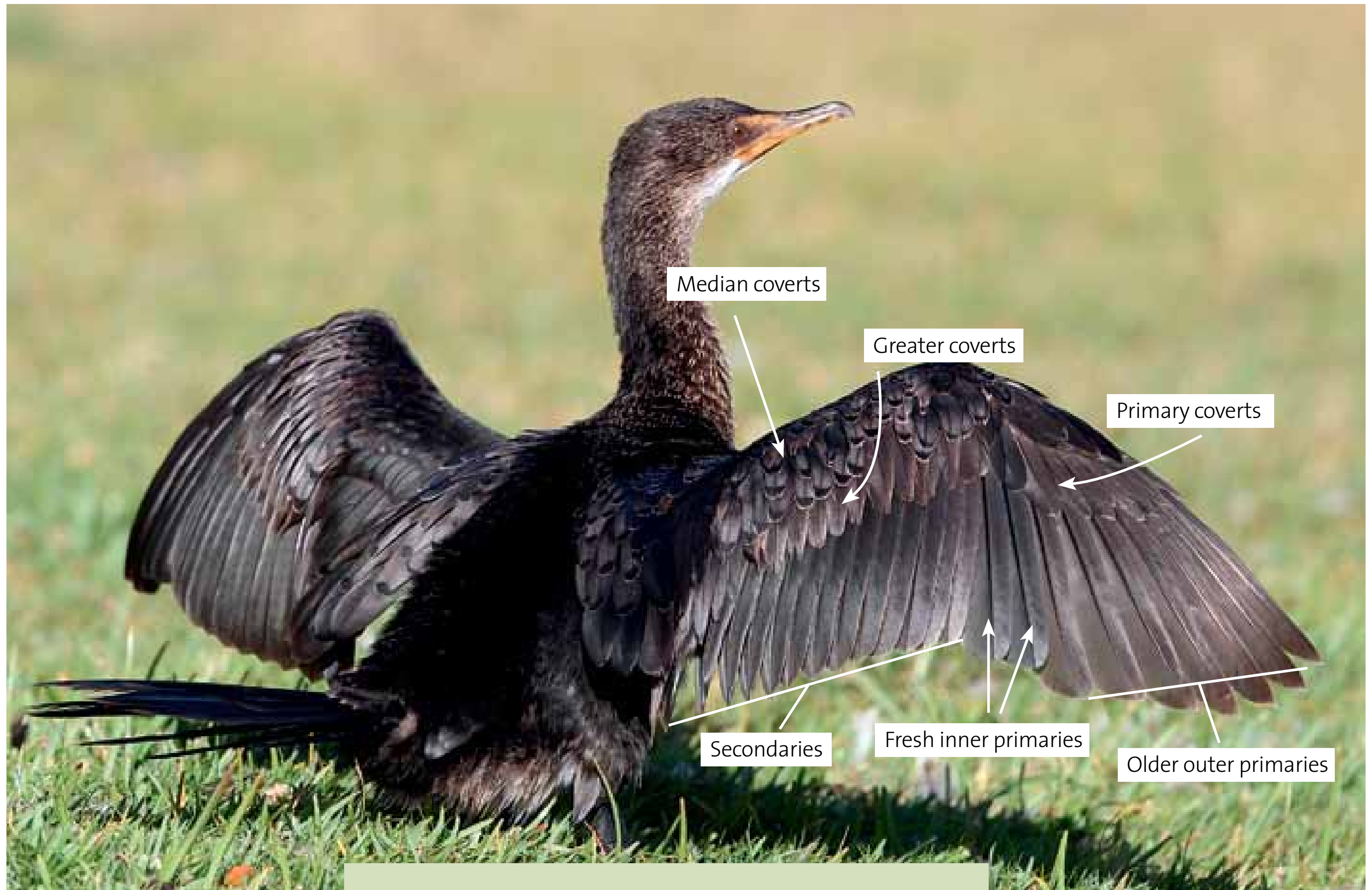
Moult typically occurs when a new feather starts to grow, loosening and eventually pushing the old feather out of its follicle. Such a 'scheduled' moult forms a key part of a bird's annual cycle and typically is triggered by cues such as day length and temperature that result in hormonal changes.

Artificially manipulating a bird's environment or its hormone levels can initiate or suppress moult. In fact, the annual moult is more than just a period of plumage replacement, because it is linked to widespread tissue renovation and results in changes in blood volume, water turnover and bone metabolism. Poultry breeders have known this for years and use this process to stimulate egg production. By depriving hens of food for a few weeks, a so-called 'forced moult' is induced which results in improved laying.

Moult can also be reactive, replacing feathers that are damaged or lost. So-called 'shock moult' or 'schreckmauser' occurs when a bird suffers a fright, such as a near miss from a predator, and usually involves shedding some of the tail and body feathers. This presumably is an adaptive response to reduce the risk of predation. Just as the ease with which lizards shed their tails is linked to their predation risk, a study by Anders Møller and colleagues showed that the force required to remove feathers from a suite of European birds is related to their predation risk by accipiters. Rump feathers tend to be much more easily pulled out than feathers on the back or chest, presumably because this is the region most often targeted by such predatory birds.

You occasionally come across a tailless dove or warbler that presumably has survived a close encounter with a predator. Ringers also are well aware that some birds are much more prone to shed feathers during handling than others; nightjars and trogons are particularly notorious in this regard. Fortunately such feather loss is replaced with relatively little cost to the bird (other than its dignity), because replacement of experimentally plucked feathers does not result in the major metabolic transition associated with the scheduled annual moult.

Feathers become worn if not replaced regularly by moult, and in extreme cases can result in life-threatening consequences for the bird. This Crowned Cormorant has not moulted for several years, resulting in its wing feathers being severely worn and faded, greatly compromising its ability to fly.



As feathers wear they become paler and browner. This young Reed Cormorant has replaced its two inner primaries, which appear blacker and more sharply edged than the remaining seven visible primaries. Most birds have 10 primaries, so there is one feather 'missing', presumably the third primary has been dropped and a new one is growing but is still too small to see. Note how the primary coverts moult in sequence with the primaries, whereas there is little synchrony between the moult of the other coverts and the secondaries. In this individual, the secondaries appear new, the greater coverts are old (apart from the innermost feathers) and most (but not all) of the median and lesser coverts are new.

HOW MANY **FEATHERS**?

Feathers typically make up about five to 10 per cent of a bird's mass (20 to 30 per cent of the lean dry mass). Birds usually have 10 functional primaries (the long flight feathers on a bird's 'hand'), although this varies from nine to 11 among different groups, and 12 tail feathers (sometimes 10 to 16, and up to 28 feathers in snipes, but absent in grebes and some ratites). The number of secondaries (the flight feathers attached to a bird's forearm) is more variable, ranging from six in hummingbirds up to almost 40 in the largest albatrosses. But few researchers have had the patience to count the total number of feathers on a bird.

The number of contour feathers depends on a bird's size and structure. As expected, the smallest number of feathers counted was on a hummingbird, with only 940 feathers. Most passerines have between 1 000 and 3 000 feathers, although the number varies among individuals and with the time of year. For example, tits in the northern hemisphere have up to one-third more feathers in midwinter than immediately following their post-breeding moult, presumably growing more feathers to improve their insulation as winter progresses. Larger birds have more feathers, with the record going to a Tundra Swan, which had more than 25 000 feathers – but 80 per cent of these were tiny feathers on its head and long neck. Including down and other feather types would inflate this number even further.

the process of feather replacement. This is twofold: the actual metabolic cost of producing new feathers, which requires energy and specific nutrients, and the impaired function resulting from having an incomplete set of feathers. Both incur substantial costs. Regular moult involves widespread tissue renovation and the mobilisation of roughly a quarter of a bird's protein reserves. And depending on the extent of their moult, birds suffer reduced flight efficiency, insulation, waterproofing and in some cases diminished camouflage and signalling ability. As a result, birds are under strong selection pressure to structure their moult in such a way as to minimise its impact on their lives.

Birds have adopted two ways of dealing with the rigours of moult. Most have protracted moults, spreading the impact over a long period and minimising the cost per day. Other birds take their lumps and pay the price over a much shorter period – with a resultant higher cost per day. The latter strategy is taken to the extreme by penguins, which replace all their feathers in a single bout. They are unable to forage during the 15–34 days it takes them to complete their moult (the period is related to penguin size, with larger penguins taking longer because their larger feathers take more time to grow). As a result, penguins rely on stored fat reserves during their moult, losing 40 to 45 per cent of their body mass over this period.

Penguins are unique in replacing all their feathers at once, but several other birds (for example, most ducks, geese, grebes, divers, auks and darters, as well as some rails and herons) replace most or all of their flight feathers at once, resulting in a period of enforced flightlessness. A recent study of Common Eiders showed that their metabolic rate increased by around 10 per cent while undergoing their five-week-long flightless moult. As they did not change their foraging effort during this period, they relied on stored reserves to support this greater energetic demand.

Eiders and most other diving birds that undergo a flightless moult use their feet for propulsion under water, so having a flightless moult has little impact on their foraging ability (in fact, the absence of wing feathers should reduce buoyancy and make diving easier). However, for wing-propelled divers such as puffins and auks, it is less clear how their flightless moult affects their diving ability. Recent research by Eli Bridge indicates that Common Guillemots and Tufted Puffins are less efficient divers when their wing area is reduced. As a result they stagger the moult of the primaries and secondaries, apparently to reduce the magnitude of this impact.

FEMALE HORNBILLS ARE AMONG THE FEW TERRESTRIAL SPECIES TO UNDERTAKE A FLIGHTLESS MOULT, **REPLACING ALL THEIR FLIGHT FEATHERS WHILE SEALED INTO THEIR NEST CAVITIES**

A flightless moult requires access to safe moulting areas where the risk of predation is low, which explains the dominance of waterbirds undertaking this option. Some species of cranes and flamingos are able to vary their moult strategy, undergoing a flightless moult in secure locations, and having a slower, progressive moult in areas where the predation risk is greater. Adult female hornbills are among the few terrestrial species to undertake a flightless moult, replacing all their flight feathers while sealed into their nest cavities. In one of the greatest demonstrations of trust among pair members, the female is entirely reliant on the male for support until her feathers have grown.

Most birds replace their flight feathers more gradually, retaining the ability to fly, but not without affecting their aerial agility. The magnitude of their impediment depends on the number of feathers replaced at once and their placement in the wing or tail. The effect of moult on flight performance is intimately linked to body mass, and the resultant wing loading, which is measured as a bird's mass divided by its wing and tail area. Generally birds with high wing loadings face greater constraints than those with lower wing loadings, and having several small gaps tends to be less disruptive than one large gap for these species.

Experimental manipulations simulating moult by reducing wing area confirm a strong effect on flight ability. However, recent experiments have struggled to replicate this effect in birds undergoing a natural moult, suggesting that birds are able to compensate for moult to some extent. For example, hummingbirds manage to fly quite efficiently with as few as three outer primaries because they reduce their body mass while moulting. Other birds become more secretive and move around less when moulting, presumably to reduce the risk of predation during this vulnerable period. >

Some birds make use of the faster rate of wear among pale feathers to change their appearance without resorting to moulting. The black bib of the male House Sparrow becomes more prominent (below, left) once the pale tips (below) wear off, allowing it to appear most intense at the start of the breeding season, several months after the feathers are grown.

This Cape Grassbird looks unusually scruffy because it is undergoing body moult. Note the growing feathers with pale grey waxy bases visible on its crown above its eye. Such birds tend to be silent and undemonstrative, and thus are easily overlooked.

Moult is not the only time in a bird's annual cycle when flight ability is compromised. Pre-migratory fattening and, among adult females, egg production greatly increases body mass, inflating wing loading and reducing aerial agility even without the problem of reduced wing area linked to moult. Similarly, birds tend to want to be in peak condition for breeding and migration, when they face the challenge of provisioning chicks and flying vast distances. As a result, few birds overlap breeding and migration with moult, at least of the flight feathers.

However, there are some exceptions. Many female raptors moult while breeding because they spend most of their time at the nest, relying on the male to undertake most of the hunting. And some seabirds moult while breeding, although they only tend to do so once incubation is under way, so the female doesn't have to compromise her flight performance when she is unusually heavy during the egg-formation stage.

A SMALL PASSERINE MIGHT TAKE 15 DAYS TO GROW ITS LONGEST PRIMARY FEATHER, WHEREAS **IT COULD TAKE A LARGE EAGLE … UP TO 100 DAYS TO GROW ITS LONGEST PRIMARY**

The default position for most birds is to undergo one complete moult each year, typically after breeding, when they replace all their feathers. As discussed, this might occur in a single bout or be suspended to accommodate other key events such as breeding or migration. Some birds have additional moults, usually confined to the head and body feathers, which allow seasonal adjustments to their appearance (for example, the acquisition of breeding plumage) or insulation (more feathers in winter). Male Ruffs and ptarmigans are exceptional in having three or even four partial moults each year, linked to their extravagant neck plumes and need to remain camouflaged year round, respectively. However, seasonal changes in appearance also can result from selective wear, removing paler plumage features such as the pale spots of Common Starlings or exposing the black bib of male House Sparrows.

Only a few species are known to undergo two complete moults a year. It has been recorded from only a handful of passerines, including the Willow Warbler and Black-chested Prinia among southern African birds. Quite why it occurs in some species but is absent from closely related congeners, or even some populations of species and not others, is unclear. Franklin's Gull is the only non-passerine reported to undergo two complete moults a year; one on its breeding grounds after breeding and one on its wintering grounds before returning north (although not all individuals are able to complete the second moult, especially in years when food is scarce).

Moult strategies are related to the size of a bird, because the rate of feather growth (which ranges from two to 11 millimetres a day) increases with bird size much more slowly than does feather size. Thus the time taken to replace a given feather takes appreciably longer in a large bird. For example, a small passerine might take 15 days to grow its longest primary feather, whereas it could take a large eagle, vulture, bustard or crane up to 100 days to grow its longest primary. This makes it impossible for large birds to completely replace all their flight feathers each year without resorting to a flightless moult. Quite how they get around this problem, and a host of other fascinating trade-offs that birds have to make when growing new feathers, is the subject of the second article in this series. ◆