

striking ^A balance

MOULTING FLIGHT FEATHERS

TEXT & PHOTOGRAPHS **PETER RYAN**

In the March/April and May/June 2014 issues of *African Bird-life*, Peter Ryan described how moult plays a key role in the annual cycles of birds. In the final article in this series, he explores how birds replace their flight feathers to minimise the impact on flight, and how large birds cope with the challenges of moulting, given limits on the rate at which feathers grow.

FLIGHT FEATHERS are the largest feathers on most birds and, because of their importance for flight, much attention is focused on their replacement. The first article in this series (March/April 2014) discussed the extreme case of simultaneous wing moult, when so many feathers are grown at once that the bird endures a period of enforced flightlessness. Most birds adopt a more gradual approach, replacing a few feathers at a time, which allows them to go about their daily activities more or less as normal.

Flight feather growth is often the most visible form of moult, because it results in gaps in the wings or tail that are obvious in flight, especially in large, soaring birds. It can also change a bird's jizz, causing you to question its identity. For example, Fork-tailed Drongos and Yellow-billed Kites lose their characteristic forked tails when moulting their outer-tail feathers, and birds with pointed wings can have rounded wing tips when growing their outer primaries.

The gaps in the wings and tail during moult do affect flight performance, but birds have evolved strategies to minimise these costs. One of the simplest of these is to limit the number of feathers moulted at the same time, depending on the importance of flight to the bird in question. For example, flycatchers generally moult fewer primaries at once than warblers, because they are more reliant on aerial agility. The number of feathers grown at the same time also depends on their position on the bird's body and perhaps the size of the feathers. Many petrels moult up to five of their short, inner primaries together, whereas they seldom grow more than three outer primaries at the same time.

The pattern of moult is best known in the primaries, the main flight feathers attached to a bird's 'hand'. The sequence in which the primaries are replaced depends on the type of bird. In most species, moult starts with the innermost primary (P1) and progresses sequentially to the outermost >

Southern albatrosses tend to replace their primaries every two years. Immature birds moult P8–10 (and sometimes a few inner primaries) sequentially in one year, and P1–7 the following year, gradually replacing more feathers each year as they get older. Once they start to breed, the number of feathers replaced each year depends on the time available between breeding attempts. However, smaller species, such as this Indian Yellow-nosed Albatross, can have more eccentric moults. This individual appears to have three generations of primaries: from the outside of the wing, P10–8 are old, P7 is new, P6–2 very old, and P1 new. By comparison, the remainder of the wing is mostly new.



MARIETJIE FRONEMAN

above *Lesser Jacanas* are one of only a handful of birds reported to replace their primaries 'backwards', starting with the outermost feather (P10) and working inwards towards the body. It is not known why this pattern is so rare; it has the advantage of replacing the most important flight feathers first.

opposite, left Many migrant terns replace all their inner primaries and outer secondaries twice a year. When the two moults are well segregated there is a marked contrast between the pale inner primaries and blackish outer primaries, as is the case with this *Sandwich Tern*. However, when the two moults overlap, the contrast is more subtle.

primary. There are exceptions to this rule, however. Falcons typically start with P4, with waves of replacement moving inwards and outwards, finishing with the inner and outer primaries at roughly the same time. And although they tend to start with P5 or P6, parrots share a similar pattern, providing yet another character in common between these two groups which are now thought to be closely related. (But some owls and kingfishers also share this unusual moult pattern, so one has to be careful not to read too much into these similarities.)

Not all primary moult follows the same sequence within bird families. Indeed, even within a species the pattern can vary depending on age, sex and location. However, the jacanas exhibit an unusually diverse set of moult patterns for a small, structurally uniform group of birds. Most species show the typical in-to-out gradual sequence of primary replacement, but African Jacanas usually have a flightless moult and the Lesser Jacana starts with P10 and works inwards to P1. It shares this peculiar reverse moult with only a handful of other bird species, including the Limpkin and trumpeters. Quite why this might be is unknown, but replacing the

outermost primaries first seems to make a lot of sense. If you only have limited time and energy, why not first replace the feathers that experience the most wear, which in general are the outer primaries?

Two mechanisms have been proposed to regulate moult sequence: the stimulation of adjacent follicles in a sort of chain reaction, or differential sensitivity to hormonal stimuli among feather follicles. Neither mechanism has been demonstrated, but the notion that feathers trigger moult in their neighbours is refuted by the eccentric primary moult shown by cuckoos. They replace feathers in a seemingly haphazard sequence, but when studied carefully there appears to be a systematic pattern. For example, the Common Cuckoo typically replaces its primaries in the order P7-9-4-1-2-5-10-8-3-6. Such a jumbled sequence has the advantage of spreading the aerodynamic cost of growing feathers across the wing, reducing the overall impact.

THE PROBLEM OF BEING LARGE

Large birds face the greatest challenge when it comes to scheduling the moult of their flight feathers, because the rate at which feathers

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grow does not keep pace with the increase in feather length necessitated by increasing body size. Feather growth rates range from around two to 11 millimetres per day, whereas primaries range from 30 to 700 millimetres. A male Kori Bustard has to grow almost six metres of primaries on each wing, and when you add in the secondaries, the total balloons to more than 16 metres of flight feathers on each wing! Even if it grew these feathers at the maximum rate and replaced three feathers at the same time, it would take more than a year to replace all its flight feathers. To make matters worse, the gaps in the wing and tail formed during moult have a greater impact on flight performance in large birds,



so they are not able to compensate by increasing the number of feathers grown at once.

Quite simply, large birds don't have enough time to replace all their primaries, let alone all their flight feathers, in one year, without seriously compromising their ability to fly. If they can't resort to a synchronous, flightless moult, their only recourse is to replace a subset of their flight feathers each year. They also don't want to have several feathers growing next to each other, because this increases the aerodynamic costs, so most species engage in stepwise moult or *staffelmauser* (wave moult). In young birds this usually starts with a standard moult sequence, starting from P1 and working slowly outwards. Before this cycle has reached the outer primaries, however, a second wave of moult starts, and then a third, and so on. In some raptors you can see up to five moult centres each slowly working their way across the primaries alone.

Albatrosses use a slightly different strategy, moulting different sets of primaries each year. The details vary depending on the genus, but among the *Thalassarche* albatrosses with which southern African birders are most familiar, the usual pattern

is to replace the outer three primaries (P8-10) in their second year, then the inner seven primaries in their third year, etc. Together with changes in bill and plumage colour, this allows us to age immature mollymawks up to at least five years old. As they get older, progressively more feathers are replaced, and the pattern starts to break down.

Once albatrosses start to breed, the number of feathers moulted each year depends to a large extent on whether or not the breeding attempt is successful, and indeed whether they attempt to breed at all. Failed breeders have more time to moult than those that are tied to the colony (and not moulting) until their chick fledges. There is some evidence that inability to moult sufficient feathers ultimately forces some birds to skip a year's breeding attempt, and that in at least one species we know that birds which attempt to breed while retaining a large number of old feathers in their wings are more likely to fail their breeding attempt than are birds with newer wing feathers.

Before leaving the subject of large birds, it's worth noting that some birds exhibit multiple waves of primary moult for reasons other than the inability to replace all their



feathers in a single cycle. Many terns moult some inner primaries twice or even three times a year. This is best developed in smaller, migrant species, and has been attributed to their post-breeding (pre-basic) moult being so protracted (lasting up to seven months) that the first feathers replaced (often grown on the breeding grounds before the bird migrates) need renewing before the return migration. However, recent evidence from Common Terns suggests that the number of feathers replaced a second time also serves as a signal of mate quality, because it is greater in males and increases with age. >

above *Woodpeckers* have stiffened tail feathers that help to support them while feeding on vertical trunks. The constant abrasion results in heavy wear, especially of the longest, central pair of feathers, clearly visible in this *Bennett's Woodpecker*. They have an unusual pattern of tail moult, replacing the central pair of feathers last, once the adjacent feathers have grown.



Giant petrels are among the largest birds that undergo a complete primary moult each year without losing the ability to fly. They do this in part by overlapping moulting with breeding, and in part by moulting several primaries at once. This Southern Giant Petrel has lost the three inner primaries, showing the 'stepped wing' shape characteristic of many giant petrels.

OTHER FEATHER TRACTS

Moult of the secondaries and tail feathers tends to start once primary moult is well advanced. Secondary moult typically commences in the innermost feathers (tertials) and works outwards, while a second wave starts with the outermost secondary and works inwards. However, there are numerous exceptions to this pattern. Many long-winged birds that have lots of secondaries replace large numbers of them at once. They offset the loss of wing area this incurs at least in part by first replacing their greater coverts before starting their secondary moult. By comparison, primary coverts tend to moult in tandem with their associated primary (with the exception of juveniles of several disparate groups, where the primaries are moulted without replacing their coverts).

Tail moult usually is symmetrical, starting with the central pair of feathers and moving outwards. However, woodpeckers and tree creepers, which have particularly stiff tail feathers adapted to support them while climbing trees, replace the central pair last, once the rest of the tail is fully grown and can help to brace the bird while the central pair grows. The number of tail feathers grown at once also varies greatly, even among closely-related species. For example, Cory's Shearwaters replace their tails very slowly, growing only one feather at a time, whereas many White-chinned Petrels produce all their tail feathers at once. The reason, if any, for this difference is unknown.

The timing and sequence of body moult tends to be poorly documented – in part because it is harder

to quantify than flight-feather moult. During the complete pre-basic moult, replacement of body contour feathers generally overlaps with wing moult, but contour feathers on different parts of the body moult at slightly different times. In general, the showiest feathers are replaced last so that they are in the best possible condition at the start of the breeding season. The importance of the timing of moult of different feather tracts has taken on additional importance in the past few decades thanks to the increasing use of stable isotopes in feathers as natural tracers (see box).

Much remains to be learned about the basics of bird moult. And the more we learn, the more exceptions we find to the patterns described here. It is clear that the extent of moult varies among individuals, depending on the bird's resources and the time available for moult. Hopefully this series of articles has instilled a new respect for birds and the pressures they face to renew their feathers.

If you want further information on moult, Steve Howell's Peterson Reference Guide *Molt in North American Birds* (2010) provides a very readable account of moult in general as well as a family-by-family description of moult patterns in North American birds. Unfortunately there is no equivalent summary for African birds. ♦

FEATHER TRACTS, MOULT AND STABLE ISOTOPES

Although birds appear to be covered in feathers, in most birds the follicles are restricted to specific feather tracts or pterylae, with bare patches in between (apteria). Exceptions to this pattern include ostriches, mousebirds and penguins. It is assumed that the ancestral condition was to have a uniform covering of feathers, but at least in the penguins this feature probably evolved more recently to ensure an even covering of feathers for insulation. The presence of apteria improves the ability of birds to thermoregulate on hot days: by exposing these bare patches, they can radiate body heat passively – provided the air is cooler than their skin.

The timing of moult varies among and within feather tracts. Until recently, almost all attention on moult phenology centred on the flight feathers, and especially the primary feathers. However, the increasing use of stable isotopes as natural tracers has focused

attention on the need to understand the timing of moult in other feather tracts.

Stable isotopes occur in several elements commonly found in living organisms, such as hydrogen, carbon, nitrogen, oxygen and sulphur. The rare heavy isotopes of these elements tend to accumulate in biological tissues because they are less easily metabolised. Stable isotopes thus give an indication of the trophic level of an animal (that is, where it sits in a food web) and, given consistent regional differences in some elements, can reflect where an animal has been feeding. Because feathers are dead structures, they 'trap' the stable isotope signature of the animal at the time they are formed. By sampling a range of feathers grown at different times, we can infer seasonal changes in diet and location. However, this presupposes we know when each feather is grown.