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FEATHER GROWTH AND REPLACEMENT STRATEGIES

TEXT & PHOTOGRAPHS **PETER RYAN**

In the March/April 2014 issue of *African Birdlife* Peter Ryan described how feathers grow, and how moult plays a key role in the annual cycle of birds. In the second article on this fascinating topic, he expands on how birds have evolved different strategies to cope with the numerous constraints they face when replacing their feathers, and explores how moult changes the way birds look.

FEATHERS have allowed birds to flourish across the globe, but they need to be replaced regularly if they are to function effectively. Feathers grow from follicles in a bird's skin and, with the exception of the powder down, feather growth is episodic, resulting in discrete generations of feathers.

The type of feather produced changes during the life of a bird. Precocial chicks hatch with a layer of down to help them keep warm. Flamingo and penguin chicks moult into a second downy plumage before the first contour feathers develop. However, passerine chicks have only a few wisps of down because they rely on their parents to keep them warm when they first hatch, and chicks of some hole-nesting species such as kingfishers and woodpeckers lack any down – their juvenile contour feathers are the first feathers they grow.

Contour feathers provide waterproofing and protection, and improve insulation by shielding the down layer. In many passerines and at least some other orders of birds, the juvenile contour feathers are poor facsimiles of adult feathers, weighing less and having fewer barbs. Juveniles of these species look 'soft' as a result. Their first set of body feathers is replaced within a few months of fledging, which might seem to be a waste of resources. However, these birds typically face a high risk of predation as nestlings, so evolution has favoured strategies that allow them to leave the nest as soon as possible – at the expense of feather quality. In general, juvenile feather quality increases with the duration of the nestling period.

The trade-off between feather growth rate and quality persists throughout a bird's life. For example, in Grey Plovers feather wear rate increases in relation to the speed of moult, probably because slower growth allows more melanin (which enables a feather to better withstand wear) to be deposited in each feather. However, the duration of moult is determined more by moult intensity (the number of feathers growing at once) than >

Chicks of precocial birds, such as this Black-winged Stilt, have a first plumage of down feathers. Such chicks only start to grow contour feathers midway through the nestling period.

Many birds use a second body moult to vary their appearance for breeding. This male Southern Red Bishop is completing moult into its distinctive, brightly coloured breeding (alternate) plumage, but many old, drab, non-breeding (basic) feathers still have to be shed. Male bishops have to replace all their body feathers in order to acquire a full set of breeding finery. Female bishops may also replace some body feathers at this time, but lose fewer than adult males. The flight feathers are not moulted until after breeding, but male widows with extravagant tail streamers replace their tail feathers in both the pre- and post-breeding moults.

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Juvenile passerines such as this Cape Robin-chat typically fledge with soft, lax contour feathers, which are replaced within a few months of the birds leaving the nest.

by the rate of individual feather growth. Interestingly, there is little evidence that moult intensity affects feather growth rates. However, a bird's nutritional and health status does affect the duration and extent of moult. Albatrosses with large numbers of stomach nematodes moult fewer feathers per year than birds with few parasites.

In one of the most compelling demonstrations of the costs imposed by rushing moult, Jan-Åke Nilsson and Erik Svensson delayed the onset of moult in adult Blue Tits by prolonging the birds' breeding season. Although the tits completed their post-breeding moult on time, the quality of their plumage was compromised, increasing their cost of thermoregulation by 15 per cent during winter. This reduced their survival, and those birds that endured to the following year bred later and produced smaller clutches. Similarly, when moult by Common Starlings was delayed experimentally, the birds increased moult intensity, resulting in reduced feather mass, strength and durability.

The rate of moult depends in part on the time constraints imposed by other activities in a bird's annual cycle. In general, birds don't moult while breeding or migrating. As a result, immature birds can afford to take longer to moult than adults, and migrant species tend to moult faster than resident species because they have the added constraint of a migration. Some birds complete their moult before leaving their breeding grounds; others wait until they reach their non-breeding grounds before moulting; and still others start to moult while on their breeding grounds, suspend moult while travelling, and complete it after arriving at their non-breeding grounds.

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There are interesting geographic differences in the prevalence of these three strategies. Among North American migrant passerines, barely 10 per cent of species breeding in the eastern half of the continent migrate before moulting, whereas at least half of the western species do so. The difference appears to be linked to the paucity of food in the more arid west of the continent in late summer. Many of the western species that migrate before moulting only travel as far as the Mexican monsoon belt, moult there, then continue further south to their main wintering areas.

By comparison, in Eurasia there is no obvious effect of climate on when and where passerines migrating into Africa moult; more than 40 per cent of species delay the onset of moult until they reach Africa, irrespective of the location of their breeding grounds. Migrant passerines also tend to moult later in Africa than their New World counterparts. This is thought to be related to the greater rate of feather wear in Africa, where most migrants winter in savanna habitats, compared to the extensive use of forest and woodland in the Neotropics. It seems that birds delay their moult in Africa because they need fresh feathers for the northward migration and subsequent breeding season. Further support for this hypothesis comes from *Phylloscopus* warblers; those migrating to the forests of South-East Asia moult earlier than their African counterparts.

Less is known about patterns of moult duration among tropical and southern temperate birds. In general, moult is more protracted in the south, and in some cases can occur at a low level year round. In one interesting study, Red-billed Quelea primary moult duration was estimated to increase from 75 days in Namibia through 83 days in Botswana to 101 days in Gauteng and 124 days in the Eastern Cape. This discrepancy apparently resulted from differences in feather growth rates rather than in the intensity of moult, and reflected regional differences in when moult started, as birds from all four regions completed their moult in August.

All birds have to moult, but the number and pattern of moults varies among and within species. Some birds moult once a year, usually after breeding, and so the only change to their feathers' appearance during the year is due to wear. Other species moult twice or even more frequently, allowing them to refresh their plumage and potentially change their appearance seasonally. These changes are often linked to breeding activity, with the complete post-breeding moult generating the non-breeding or winter plumage, and the pre-breeding moult (usually incomplete because it doesn't involve the flight feathers) generating the breeding plumage.

The nature of the feathers grown is determined by the bird's hormonal condition, however, not the timing of moult. By manipulating hormone levels, researchers can induce juveniles to develop adult plumage and adults to retain their breeding plumage during the post-breeding moult. Photoperiod also can affect the type of plumage grown. Southern Red Bishop males kept under artificially long day lengths retain their breeding plumage in the post-breeding moult, even though their testes regress. And even in nature one sees variations in the intensity of expression of breeding plumage, linked to individual differences in hormone levels and the degree to which feather growth coincides with periods of peak hormone levels. The bewildering diversity of immature gull plumages, which are a pastiche of juvenile and adult body feathers, results from individual differences in hormonal status and the timing of moult.

Confusion between moult sequence and function led Phil Humphrey and Ken Parkes to propose a new terminology for moults and the resultant plumages. Their concept has been adopted with more enthusiasm in the Americas than in the Old World, but it's worth learning the basics, if only to be able to interpret American field guides.

The simplest strategy involves only one moult per year, which usually takes place after breeding. This post-breeding moult gives rise to what the Humphrey–Parkes system calls the 'basic' plumage and so is known as the pre-basic moult. This so-called 'basic strategy' is found in albatrosses, petrels, raptors, swifts and a few gulls.

Large gulls show a dizzying array of 'immature' plumages because they undergo two moults per year, and the colour of their back feathers depends on the timing of moult as well as on the bird's age. This Kelp Gull, about 16 months old, mostly exhibits a mix of older feathers from its first alternate plumage and fresh feathers from its second basic plumage, but still retains a few very old juvenile coverts.

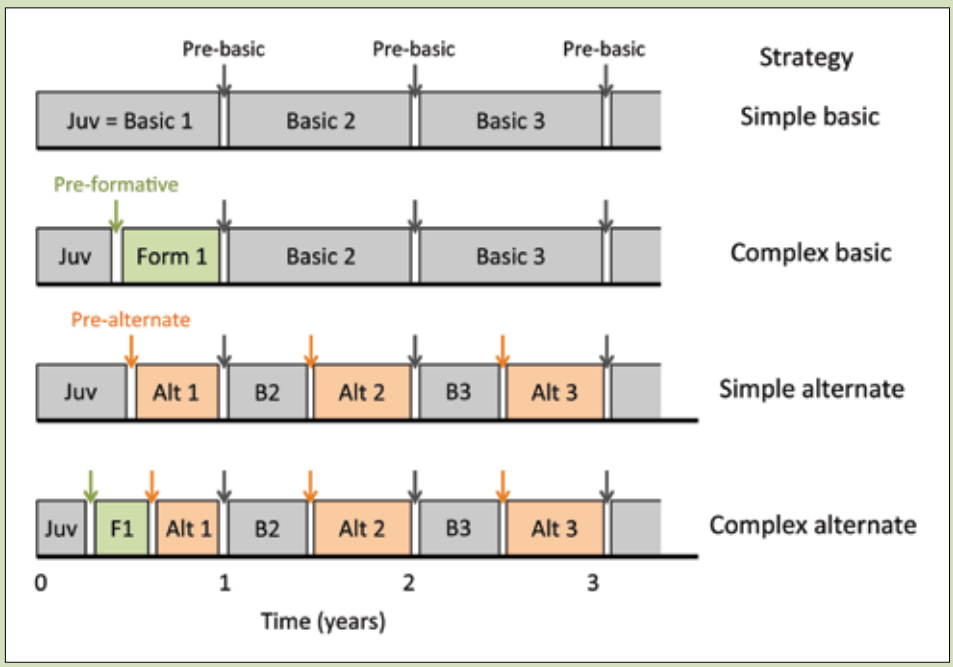
Some birds have an additional post-juvenile moult in their first year, replacing the hastily-grown feathers with a 'formative' plumage (grown during the pre-formative moult). This 'complex basic strategy' is exhibited by gamebirds, ducks, rails, cranes, several seabird groups, and many terrestrial birds. It is widespread especially in temperate systems where breeding is strongly seasonal, because juvenile plumage is grown before the annual pre-basic (post-breeding) moult.

If the juveniles were to wait until the following year to moult, their feathers would be more than one year old, yet juvenile feathers tend to be of lower quality than adult feathers, so many of these birds have an >

In February, this young Barn Swallow is midway through its pre-formative (post-juvenile) moult, roughly six months after fledging. Its head feathers, outer primaries and central secondaries all clearly need replacing and wouldn't last another eight months until the swallow's first basic moult.

additional moult. This may or may not include the flight feathers, and may or may not resemble subsequent plumages. Some species have more than one formative moult, especially if they continue to grow in size after leaving the nest (for example, many gamebirds).

Then there are the birds that have two or more moults per year. As well as the post-breeding or pre-basic moult, a second moult before the breeding season gives rise to the breeding or 'alternate' plumage – hence the moult is known as the pre-alternate or pre-breeding moult. In some species, this moult simply replaces badly worn feathers with new feathers resembling the old ones. However, in many species the new feathers appear quite different, generating a distinctive breeding plumage. Birds undertaking this moult strategy are said to follow the 'alternate strategy', which might be simple (only two feather generations in the first year: juvenile and first alternate) or complex (three generations: juvenile, formative and first alternate). Such moults may be confined to just one sex or occur in both sexes, and are found in grebes, most waders, gulls and terns, some ducks and many passerine families. Finally, some birds such as ptarmigans have additional moults, termed supplemental moults.



The four main moult strategies described by the Humphrey–Parkes moult scheme, where basic = non-breeding plumage, and alternate = breeding plumage. Arrows show moult events.

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The Humphrey–Parkes system also recognises 'definitive' plumages – those that don't change with age (that is, adult plumages). Most birds attain their definitive plumage(s) within one to two years of fledging, but it can take up to four years in gulls, seven years in large raptors, and plumage continues to change virtually throughout the long life-spans of the great albatrosses.

We have run out of space, and haven't got to the patterns of flight-feather moult, which are interesting in their own right and can be crucial in enabling us to age birds. We also haven't discussed how large birds manage to replace all their feathers each year. These topics will have to be deferred to the final article in this series. ◆