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Ornithology from the Lakeshore

Moult and misfortune

As moulting time – when they change their feathers – is for birds, so adversity or misfortune is the difficult time for us human beings. One can stay in it – in that time of moulting – one can also emerge renewed...

Vincent van Gogh, in a letter to his brother Theo

It is embarrassing to admit that I was never much interested in moult. To me, moult seemed a mouldy subject. Call me Ignoramus.

Feathers are what makes the bird. How otherwise would we be able to identify the species, often also the sex, and sometimes even the age of an individual just by a quick look? Composed of keratin, as are hair and nails, feathers are the most complex integumentary structures found in vertebrates. They enable powered flight and are essential for thermoregulation. They keep the bird warm, even while it is incubating an egg during the Antarctic winter, and they keep it dry, even when it spends most of the year floating on the ocean. Feathers can also play a central role in communication – colourful plumage functions in both love and war – or in avoiding communication – with predators, through camouflage.

Despite their essential functions and despite their remarkable strength (Bonser 1996), feathers are fragile. They can break or bend. They deteriorate over time due to ectoparasites, notably feather lice that chew holes in them, and due to sun exposure and physical wear and tear. Thus, birds must take care of their feathers and they do so in several ways. Individuals often spend a considerable part of their day maintaining their feathers through preening. This activity involves combing the feathers with the beak, putting them back in order, removing lice, and applying a waxy substance from the uropygial gland. The multiple functions of this gland continue to be a matter of debate (Moreno-Rueda 2017). Birds also frequently take a bath, in water, in dust, in the sun (Simmons 1986), or even in ants. The latter has been observed in hundreds of species and is referred to as 'anting'. The most widespread hypothesis to explain this behaviour is that it removes ectoparasites or feather-degrading bacteria and fungi. Sounds plausible, but evidence is still lacking (Revis & Waller 2004). The most peculiar hypothesis is that "ant secretions might cause a peculiarly pleasurable sensation of warmth, possibly with an element of the masturbatory in it" (Whitaker 1957).

In addition to direct feather care, birds have at least two other ways to keep their feathers in good shape. The first one is feather mites. Doña *et al.* (2019) looked through a microscope to examine the diet of 1300 individual mites collected from the feathers of 190 bird species, and what they most often saw in the gut was fungal material. These observations were confirmed by DNA metabarcoding: most diets included fungal DNA, including from genera known to digest keratin, and all diets contained bacterial DNA. But what is perhaps equally important is what the researchers did not find. Neither microscopy nor DNA techniques showed any evidence that the mites feasted on bird bits. The authors concluded that feather mites should no longer be considered ectoparasites, but rather commensalists-mutualists. Birds use feather mites as their dry-cleaning service.

The second, and most important, mechanism, is producing a new jacket, so to speak. Just like our clothes, feathers gradually abrade and need to be replaced. This shedding of old and growing of new feathers is the process of moult. It takes some effort to get into the subject. Even a plumologist might be put off by moult terminology and puzzled by moult scores. However, soon after reading the first chapter of Jenni & Winkler's seminal book 'Moult and ageing of European passerines' on the function and consequences of moult (first published in 1994, but now also 'emerged renewed'), you start to understand how fascinating and multi-faceted this process is.

Moult is a phenotypic trait with extreme and intriguing variation at multiple levels, both within and between species and even within individuals. There is variation in the number of times clothes are changed, with almost every species moulting at least once a year, but many doing it twice and some even three times a year. There is variation in the amount of moult, in the number and type of feathers that are moulted. Although a few species undergo two complete moults per year, most do not always throw out their entire wardrobe. For example, many birds have one complete moult after breeding, but renew only the body feathers before the breeding season. Typically, such partial moult occurs in species where males acquire a garish, ornamental breeding plumage, but females undergo this moult as well.

Moult varies in its onset and duration. Most birds moult in their breeding area in late summer or autumn,

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but many of the long-distance migrants perform or finish their complete moult only after migration in winter. The duration of moult thus varies with life-history traits, and is influenced by environmental factors such as light, temperature and food. Moulting is generally a slow process, simply because an individual cannot get rid of all its feathers at once. Sufficient feathers must be retained to fulfil the essential requirements such as thermoregulation or the ability to fly, although the latter is not always the case. Grebes, ducks, geese and swans shed all their flight feathers at once, and they better think twice about where to hang out when flightless for a few weeks (Gehrold 2014).

Behavioural ecologists are keen to apply a cost-benefit analysis for understanding variation. We consider the selective forces that might have led to different moult strategies in species or populations with different life-histories and inhabiting different environments. As an illustration, I will discuss post-juvenile moult, how it is affected by climate change and how it is linked to sexual selection. My aim is to highlight the magic of studying moult.

Growing up is not easy and young birds face many challenges. One of them is to produce their first set of feathers. And to produce them fast. In particular under high predation risk, selection favours rapid offspring development. However, as with many endeavours – including writing this editorial – speed trades off with quality (Vágási *et al.* 2010). Nestlings that spend less time in the nest produce plumage with less dense barbs relative to adults (Callan *et al.* 2019). They will need therefore a new set of high-quality feathers sooner rather than later, and indeed young birds typically start to renew at least some of their feathers already one to three months after fledging. Replacing your feather jacket is expensive. In fact, moult may well be one of the most energy-demanding activities during the yearly cycle, especially for small birds. Åke Lindström and colleagues (1993) estimated that a bluethroat producing a total of 1.2 g of feathers will need to add 47% to its basal metabolic rate over the entire 54-day moulting period, with a peak of 111% during the most intense moult. For young birds, moult may even be more challenging, given that they are less experienced in obtaining food. A comparative study on birds of the Western Palearctic finds that complete post-juvenile moult is much less common in northern latitudes and in insectivorous species, that is, in species that experience stronger seasonal fluctuations and that exploit more seasonal resources (Kiat & Izhaki 2016). Moult is a matter of favourable times.

Later findings corroborated the hypothesis that under benign environmental conditions young birds replace more of their first-grown feathers. Using data from skin collections of ten natural history museums, from ringing activities in four countries and from published photos, Kiat *et al.* (2019) measured the extent of feather moult in 4012 individuals of 19 passerine species. They found that over the last 212 years, post-juvenile moult became more extensive, correlating with a global increase in temperature. The plumage of yearlings and adults is thus becoming more similar over time.

Of course, moult is not only important to maintain feather functionality. Moult is also a mechanism to adjust the plumage to changing requirements. Perhaps the most obvious is the fluctuating need to signal status or quality. During the breeding season, when competition for resources is at its peak and (extra-pair) mating takes place, selection may favour the development of ornamental plumage, despite the potential trade-off with predation risk. Many species thus show a pre-nuptial moult into gaudy plumage and a post-nuptial moult into a more lacklustre version of themselves. But why do only some species show a pre-nuptial moult? Many questions about how sexual selection influences moult patterns remain unanswered.

One such puzzle comes from Kiat *et al.* (2019). Ten of the 19 species were sexually dichromatic, allowing Kiat and colleagues to estimate sex-specific changes in the extent of post-juvenile moult. Surprisingly, in four species, females showed a stronger response to increased temperatures. Moreover, the magnitude of this sex difference in response was larger in more dichromatic species (see Figure 3 in Kiat *et al.* 2019). Thus, in species where males are more colourful compared to females, females showed a stronger increase in the extent of their post-juvenile moult in response to higher temperatures. In contrast, in monomorphic species, the response did not differ between the sexes. The authors suggest that in dichromatic species, females might benefit more from an extensive moult, because their feathers are often lighter-coloured and less melanin-rich and hence more prone to wear. Perhaps, but let me suggest an alternative explanation.

In several species in which sex-specific moult patterns have been investigated, post-juvenile moult is more extensive in males than in females (e.g. Great Tits *Parus major*, Bojarinova *et al.* 1999; Blue Tits *Cyanistes caeruleus*, Crates *et al.* 2015; Loggerhead Shrikes *Lanius ludovicianus*, Chabot *et al.* 2018), which may relate to timing (males also start moulting earlier than females; Bojarinova *et al.* 1999). Sexual selection might favour a more extensive post-juvenile moult in

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males if plumage-related status or quality signalling has a stronger influence on male mating success. Thus, in species where sexual selection on males is more intense, the cost-benefit trade-off might already be skewed towards more extensive post-juvenile moult in males such that a somewhat more benign environment (higher temperatures) will have less of an effect on this trait in males than in females.

There is much scope for further study here. For example, we need more data from a variety of species on sex differences in the timing and extent of post-juvenile moult (note that Ardea has always welcomed such studies, see Pérez-Granados 2020 in this issue). These data would allow a test of the sexual selection hypothesis, which predicts that sex-differences in the extent of post-juvenile moult correlate positively with sexual plumage colour dimorphism. Following Kiat *et al.* (2019), one can also test the feather strength hypothesis, which predicts that sex differences in the extent of post-juvenile moult are related to sex differences in melanin content of the feathers. We also need a better understanding of the causes and consequences of variation in the extent of post-juvenile moult. For example, a study on Blue Tits showed that breeding males did not differ from non-breeders in the extent of post-juvenile moult, and there was also no significant relationship between moult extent and measures of reproductive success (Crates *et al.* 2015). Thus, the authors suggest that variation in the extent of post-juvenile moult is unrelated to individual quality and has little fitness consequences. On the other hand, experimental work on adult Rock Sparrows *Petronia petronia* provides evidence for a trade-off between moult speed and ornament expression (Serra *et al.* 2007).

In general, variation in post-juvenile moult is an understudied phenomenon that may provide insights into the signalling role of colourful plumage. A key question is how does sexual selection act on the plumage colour of juvenile (yearling) individuals. One hypothesis is that more intense sexual selection favours a more extensive post-juvenile moult, and leads to a higher probability of complete rather than partial post-juvenile moult. However, this hypothesis only makes sense if juveniles benefit from looking like adults, in other words, if they benefit from hiding their inexperience. Some observations clearly speak against this. For example, several species show delayed plumage maturation. Here, juveniles moult into a plumage that is markedly different from the adult plumage. This phenomenon is much more common in males than in females. The evolution of delayed plumage maturation can be explained if signalling lower (juvenile) status is beneficial, for example because dominant adults are less likely to beat you up and kick you out (Lyon & Montgomerie 1986, Hawkins *et al.* 2012). Thus, one can ask whether partial post-juvenile moult is an alternative to delayed plumage maturation – a softer, more flexible version, if you wish – and also a reliable signal of subordinance. At the inter-specific level, one can study the relationship between the intensity of sexual selection, the occurrence of delayed plumage maturation and the extent of post-juvenile moult. At the intra-specific level, I suggest choosing a species with extensive variation in post-juvenile moult, from partial to complete, to study the causes and fitness consequences of variation in plumage colour signals.

As the publisher advertising Jenni & Winkler's upcoming book 'The biology of moult in birds' exclaims: "moult remains a sorely neglected field". Whether you are interested in avian physiology and energetics, in biological timing, in the mechanisms of flight or in sexual selection, studying moult provides many opportunities for discovery. Both the book and the discoveries are something to look forward to in this time of misfortune.

Bart Kempenaers

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