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# Patterns of moult in large birds of prey

Carl Edelstam

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The wings and tail of most postjuvenile large birds of prey present a blend of very differently worn quills. By carefully recording the state of wear and fading of every quill in a large number of specimens, whether actively moulting or not, it is possible to reconstruct the details of the underlying moult process. The pattern is serially continuous, with several moult waves proceeding simultaneously but slowly through seven separate moult units in each wing, including the bastard wing; and somewhat irregularly alternating within two moult units in each half of the tail. A key to the determination of age in the immature bird is provided by the periodic generation of new moult waves and by the stepping of wear and fading within each moult wave due to seasonal moult pauses. This, in turn, offers a more reliable guide to the sequence of immature plumages than has hitherto been available for most large raptors.

*Carl Edelstam, Research Department, Swedish Museum of Natural History, S-104 05 Stockholm, Sweden.*

## 1. Introduction

The subject of this contribution is the moult of large birds of prey. My definition of "large" in this context is not strictly by size, but simply covers those species which do not normally replace all flight feathers in one year. These include all species larger than the Old World kites and no species smaller than a buzzard.

## 2. Study methods

Traditionally, the study of moult rests on the examination of actively moulting birds. Large birds of prey in active moult are not too common in collections, and few are trapped and examined alive. Moreover, an analysis becomes complicated by the fact that the wing quills of a large raptor may serve its owner for two years or more; and three or four generations of feathers may be present in the wing at any one time. The result is a blend of heavily worn, moderately worn, and recently grown quills which tends to conceal, to the casual observer, the underlying sequential pattern.

By carefully recording the state of wear and fading of every quill in a large number of postjuvenile specimens, whether actively moulting or not, it is possible to reconstruct the topographical details and time schedule of the moult process.

This, however, is not as simple a task as one might think. Differences in apparent age between adjacent feathers may result from different exposure or toughness and could easily deceive the inexperienced worker. Also, striking differences in the rate of wear and fading of the flight feathers will occur within some species due to individual differences in habits and habitat; and an occasional bird may show significant right/left differences presumably caused by a preference for a particular roosting position.

Skins in active moult may be even more diffucult to handle. Pinpointing the position of a moult gap among the secondaries of a stiff old skin is a tedious task and it may take well over an hour to record in detail the moult of certain museum specimens. Previous workers have, in fact, refrained for this very reason from a detailed study of secondary moult in the larger birds of prey (see Heinroth 1898, and Stresemann & Stresemann 1960). Ideally, one should work with fresh specimens as they arrive in the museum, as I try to do in Stockholm with the many birds that are delivered for research purposes under the "Crown's Game" Act (cf. Edelstam & Delin 1975). Furthermore, on a suggestion by Dr. Urs Glutz von Blotzheim and following the example of the Amsterdam museum, we have made it a rule to prepare most large birds with one wing detached and extended in order to simplify the recording of moult as well as of under-wing patterns.

In the course of the present study, notes were taken of the status of over 70 000 quills in more than twenty species; and I wish to record here my debt of gratitude to the many colleagues in European and American museums who gave me permission to work with the collections in their care. Full details and acknowledgements will be given elsewhere. Only a few examples of the results are presented below.

### 3. The basic accipitrid pattern

Let us start by looking at the moult pattern of a typical accipitrid hawk (Fig. 1, top). As in all birds, moult proceeds in different directions through different parts of the wing. These parts may be termed "moult units". In all accipitrids, the ten primaries constitute one such unit and the outermost four secondaries another one. The remaining secondaries are divided in three different moult units; the bastard-wing in two; and each half of the tail in another two units.

Within each unit, moult starts at one end and proceeds toward the other, as shown in the figure: outward from p1, inward from s1 and s5, and centrifugally from a focus situated somewhere between about s12 (in *Accipiter* and other short-winged hawks) and s22 (in *Terathopius* and *Aegypius*). The four small bastard-wing remiges are moulted centrifugally from number two, counting outwards. The rectrices, finally, are shed in a roughly centripetal order within each half of the tail. This process is completed within one year as a rule in all small accipitrids and some medium-sized ones, such as the Goshawk *A. gentilis* and the *Milvus* kites.

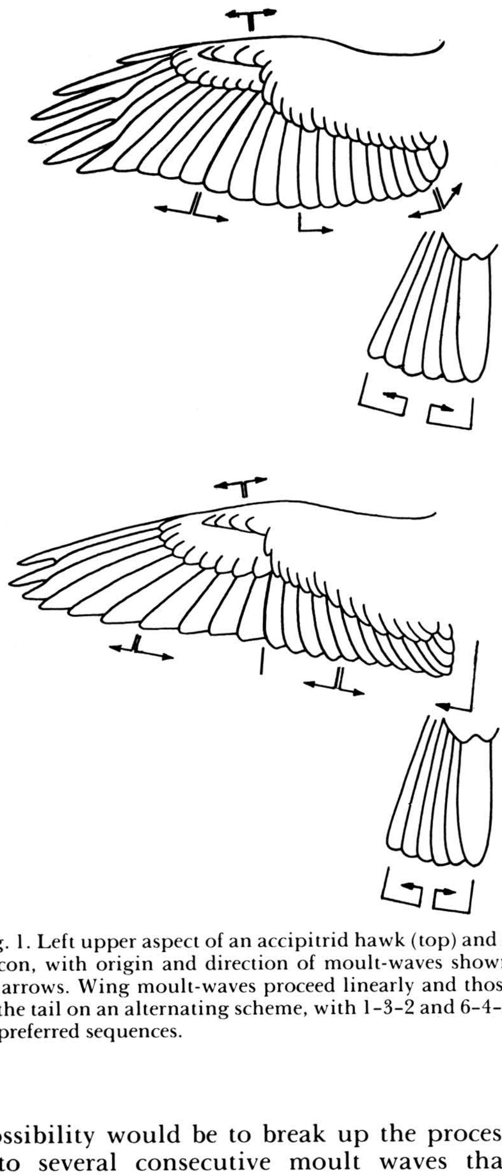

Fig. 1. Left upper aspect of an accipitrid hawk (top) and a falcon, with origin and direction of moult-waves shown by arrows. Wing moult-waves proceed linearly and those of the tail on an alternating scheme, with 1-3-2 and 6-4-5 as preferred sequences.

### 4. Options for large species

In the larger species, a quill takes a long time to grow: 40–60 days or more. Therefore, a single moult wave could not replace the ten primaries within one year, perhaps not even a set of seven or eight secondaries, unless several quills were missing or growing simultaneously which would result in big gaps in the aerofoil. Such gaps would create problems in birds which depend on a first-rate flight performance for securing their prey.

This dilemma could be solved in at least three different ways. The bird may insert an extra focus in the largest moult units. This is the solution chosen by the falcons; it permits even a Gyrfalcon to replace all primaries annually without unduly impeding its flight powers (Fig. 1, bottom). An alternative solution would be to shed every second quill in the first round and then the remaining ones. Most cuckoos moult their primaries in this manner (Stresemann & Stresemann 1961, 1966, Seel 1980), and birds of prey do this in their tail moult, though not too strictly. A third possibility would be to break up the process into several consecutive moult waves that proceed simultaneously through each of the larger moult units. This principle has been called serial moult ("Staffelmauser" in German). Like the centrifugal primary moult of falcons, it serves to scatter the moult fronts along the wing and so creates several small gaps, each of which may be covered by adjusting the adjacent quills.

Serial moult was first discovered by Dorward (1962) in gannets, by Ashmole (1963) in terns and by the Stresemanns (1965, 1966) in gamebirds and in several other groups, including swifts (for swifts, see also De Roo

Fig. 2. Wing of an Osprey aged 22 months. Note at wing tip the two primary moult-waves and the remnants of the outermost (10th) juvenile primary.

1966). The presence of serial moult in raptors was demonstrated by Edelstam (1969) for the Osprey, by Houston (1975) for two African vultures, and by Wattel (1980) for several palearctic raptors and in bustards. Bloesch et al. (1977) found it in the White Stork. The ontogeny of serial moult was discussed by Potts (1971) and its relation to the bird's life cycle by Ashmole (1968) and others.

## 5. Serial moult in birds of prey

My own work shows that, among the birds of prey, serial moult is characteristic not only of all large accipitrids, but also of aberrant groups such as the Osprey *Pandion* (cf. above), the Secretary Bird *Sagittarius*, and the New World vultures, Cathartidae. Serial moult in all these cases is simply overlaid on the particular pattern just described for the accipitrids. The falcons alone have taken a different route. Not only do their primaries moult centrifugally; but their outer secondaries moult in an outward rather than inward direction, and their inner secondaries constitute one rather than two moult units. Only the rectrices and the middle secondaries moult according to the accipitrid mode.

A new moult wave will start at each moult focus at intervals that depend on the rate of renewal of quills characteristic of each species or population. Each wave may be recognized by its stepped sequence of new, intermediate, and worn quills. The periodic emergence of new waves within the larger moult units in particular, and the stepping of wear and fading within each wave due to seasonal moult pauses (if present) permits us to analyze the moult history of the individual bird and so provide a clue to its age. As long as any juvenal quill is still present, we will often be able to assess quite precisely the age of the bird, as illustrated in Fig. 2.

## 6. Moult in the Osprey

Fig. 2 shows the extended wing of an Osprey. This bird was ringed in Sweden as a nestling and recovered not far from its birthplace at an age of 22 months. The presence of two moult fronts among the primaries is evident. A glance at the outermost primary shows this feather to be extremely worn and bleached in spite of its shielded position in the folded wing. Actually, in this case, it is the last remnant of the first, juvenal feather complement and has served for nearly two years. It is just about to be swept away by a wave of more recent quills (p4–9) which is followed in turn by another wave (p1–3), representing the

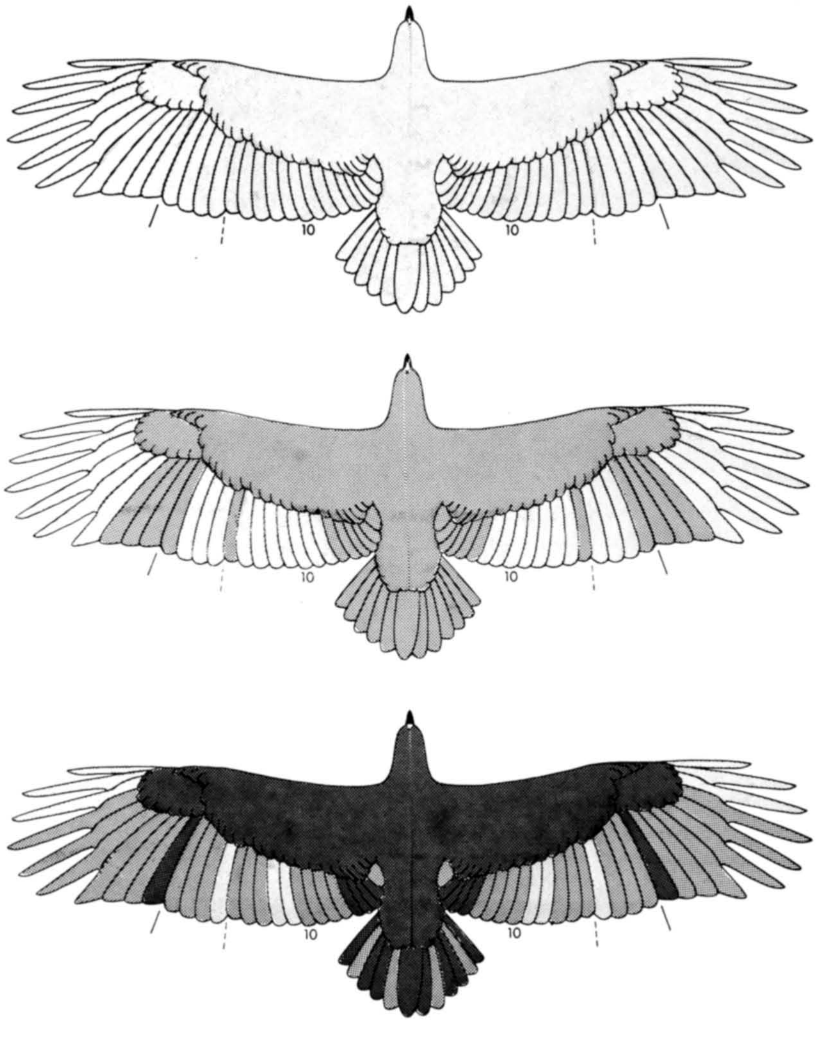


Fig. 3. Upper aspect of a Scandinavian White-tailed Eagle in its first (top), second, and third winter. First generation (juvenal) feathers shown light grey; second generation, medium grey; and third generation, dark grey. The difference in length and shape between juvenal and later quills has not been indicated in this figure.

second and third feather generation, respectively. In other words: p10 has not yet been replaced; p4–9 have been replaced once; and p1–3 have been replaced twice during the bird's life.

The moult of large raptors, like that of other birds, does not proceed at a uniform speed throughout the year. It is suspended as a rule during periods of intense flight activity, such as on migration or, in the male, when he feeds the incubating female. It makes a halt also in times of food shortage, such as at midwinter in high latitudes or during extended droughts. Following such pauses, moult is resumed at the front of each moult wave.

Wing moult in the Osprey begins during the first winter and proceeds relatively rapidly until the first spring migration which does not usually take place until the bird is nearly two years old. In the breeding quarters, females moult from May or June till August and the males mainly in July and August; in the winter quarters, adults of both sexes moult from about October/November through February. Approximately one quarter of all quills is moulted on the breeding grounds and three quarters in the wintering areas. Moult is thus suspended for some three months in spring and slightly less in autumn, presumably for both flight efficiency and energy economy.

The instance of a quill serving for nearly two years in a raptor the size of an Osprey, however, is a rare one. An analysis of the moult of ospreys of known age suggests that the mean life of a primary in the adult bird may be less than 15 months. In large eagles and vultures, wing quills serve for a much longer time.

## 7. Moult in the White-tailed Eagle

Fig. 3 shows schematically the moult status of a Scandinavian White-tailed Eagle *Haliaeetus albicilla* during its first, second, and third winter. Between May/June and October/November of its second calendar year, the young eagle replaces about half the number of flight feathers. Body moult in contrast takes place in a rush mainly from June through August and leaves the bird with a dark, white-mottled plumage quite different from the juvenal one. After a winter pause, moult is resumed about April at approximately the same pace, leaving the third-winter bird with only a few quills of the juvenal generation but also in most cases with some third-generation quills at the inner primary and inner secondary foci. The juvenal quills may be identified in the large eagles and certain vultures by being more pointed and 5–10 percent longer than those of later generations (Fig. 4). The second moult also produces a new, third body-feather coat which is virtually indistinguishable from the previous one.

Following the loss of the last juvenal quills, which usually takes place at the beginning of the third moult when the bird is three years old, moult does not provide a precise guide to the age of the White-tailed Eagle, although the fourth-winter bird is usually recognizeable by a plumage intermediate between the immature and adult one. We may note that the rate of annual renewal of wing-quills remains at about 0.5 throughout life because, although several moult fronts are now present in each moult unit, the progress of each front is correspondingly retarded. In the subadult and adult bird, a new moult wave is initiated at the wing foci approximately every second year. The rectrices are renewed more often on the average.

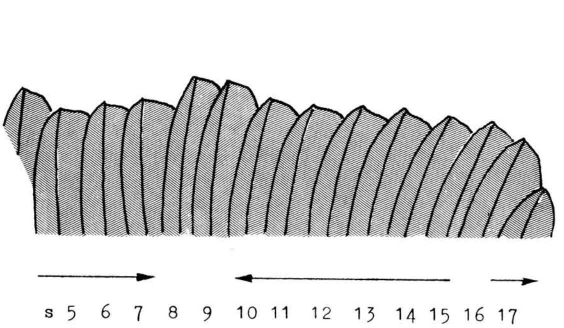


Fig. 4. Tips of juvenal vs. later generation secondaries in the right wing of an immature large eagle.

## 8. Some aspects of variation

Like all biological processes, moult is subject to considerable variation. Greenland White-tailed Eagles moult more slowly than Scandinavian birds which, in turn, moult more slowly than South European and Caspian birds. Moreover, within any area some individuals moult faster than average and some much more slowly, presumably due to differences in nutrition. A captive young eagle with a constant supply of food may renew its entire flight-feather set in one moult period, which adds to the arguments for not using captive raptors in moult studies. On the other hand, one Osprey and one Bald Eagle *Haliaeetus leucocephalus* out of a thousand wild raptors examined by me in the course of this study had obviously postponed their first moult entirely for one year and were in a lamentable plumage condition when collected.

Also, as a bird gets older, inconsistencies will appear that disturb the picture outlined here. Such inconsistencies are more common in captives, and apparently also in the largest (or non-hunting?) species; in an adult large vulture, it may be difficult occasionally to trace any organized moulting pattern at all. This, in addition to the short moult waves, explains why the Stresemanns (1960, 1966) considered the moult pattern of adult large birds of prey to be basically irregular, and why Houston (1975) did not recognize the basic pattern of secondary moult in *Gyps*.

## 9. Concluding remarks

Moult studies have an intrinsic interest by disclosing details of a major cyclical event in the bird's life. They may also throw new light on the relation between different systematic groups (see E. Stresemann 1967); although nothing really new has come out of the present work in the latter respect, for the aberrant moulting mode of falcons was demonstrated in part already by Heinroth in 1898, and the isolated position of the New World vultures seems so firmly established (Jollie 1976-77; Feduccia 1980) that little weight can be attached to the fact that they moult like accipitrids.

Finally, a thorough knowledge of moult is essential for the assessment of age in many birds and certainly so in large raptors, whether in the museum or in the field. This in turn opens the door to some challenging questions — for instance, why the immature plumages of certain closely related species have evolved along quite different paths. These aspects of moult study are likely to appeal also to the general ornithologist.

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