THE SIGNIFICANCE OF MOLT CENTERS AMONG THE SECONDARY REMIGES IN THE FALCONIFORMES

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The sequence of replacement of the secondary feathers of the wing is fairly constant in any one species of bird and often it is similar throughout larger taxonomic units. The pattern of replacement in the quail and grouse, for example, adheres to a fixed and peculiar pattern (see Salomonsen, Moults and Sequence of Plumages in the Rock Ptarmigan, 1939:35-36). Heinroth (Sitzungsber Gesell. Naturforsch. Freunde Berlin, 1898: 95-118) has illustrated several different types of sequence. The most prevalent manner among birds generally is that in which molt begins at two separate centers, one at the outer end of the series, the other at or near the inner end, the replacement progressing toward the middle of the forearm. In long-winged species additional centers may occur, but these are found also in some short-winged types. Such is true of the moderately short-winged accipitrine hawks.

A survey of molting hawks reveals that a center in the middle of the forearm is normal in the Falconiformes. This center is shown in Heinroth's diagram of *Aquila* (fig. 7, p. 101) at secondary number 5. The matter that now needs to be emphasized is that either secondary 4 or 5, and no other, initiates the molt in this part of the wing.

In the small and middle-sized members of the Accipitridae, molt begins at three points: secondary 1, 5 (less commonly 4), and 10, 11 or 12. From secondary 1 molt progresses inward toward 4; from 5 it progresses inward toward 10; and from the inner center it spreads to adjacent numbers as far outward as 9. A specimen (Mus. Vert. Zool. no. 61344) of Sharp-shinned Hawk (*Accipiter velox*), taken July 19, 1932, is especially suitable for indicating the process. This bird was molting from the brown immature plumage to the blue-gray adult plumage and therefore was a bird in its second summer. The diagram (fig. 29) shows the condition of the major wing feathers; new feathers are shaded and those that are in process of growth are represented by shorter quills. Points to be noted are (a) the usual orderly replacement of the primaries and their corresponding greater primary coverts, (b) the three centers in the secondary series at 1, 5, and 12, (c) the early replacement of the greater secondary coverts, and (d) the outward progression in the four principal feathers of the tertiary series. The carpal remex apparently had not yet been replaced, but the carpal covert was just growing in. The latter feather of course belongs to the series of greater secondary coverts.

Supporting evidence for the order of replacement which I have described was derived from the following birds that were in critical stages of molt: 2 *Astur atricapillus*; 7 *Accipiter velox*; 1 *Accipiter nisus*; 4 *Accipiter cooperii*; 3 *Buteo swainsoni*; 1 *Buteo solitarius*; and 2 *Circus hudsonius*.

In the eagles and larger hawks the replacement of secondaries is comparatively irregular, as also in the Cathartidae. Apparently it is not uncommon for individuals to fail to molt all the secondaries in a single year. However, when there is replacement, almost invariably there is activity beginning at secondary 4 or 5, and if the process is carried far, it usually follows the pattern found in *Accipiter*. The chief irregularities consist of the molt spreading outward from 4 and 5 as well as inward, and of occasional extra centers toward the inner end of the series at 8 or 9. Among molting Red-tailed Hawks (*Buteo borealis*), fifteen showed a center at secondary 5, and seven at secondary 4.

In the falcons and caracaras (Falconidae) the molt program differs from that in the Accipitridae in that activity centering at secondary 1 is retarded and may in effect be suppressed. The molt beginning at secondary 4 or 5 regularly spreads outward as well as inward, and secondaries 1 and 2 fall after 3. In this connection it is noteworthy that the primary molt in falcons does not begin with 1, but at a point farther out in the series. The following molting falconids were examined: 12 *Falco sparverius*; 1 *Falco columbarius*; 1 *Falco albigularis*; 1 *Falco peregrinus*; 1 *Falco mexicanus*; 2 *Polyborus cheriway*.

As a result of Steiner's (Jenaische Zeitsch. Naturwiss., 55, 1918:221-496) exhaustive investigation of the subject of diastataxy, it is known that the series of secondary remiges is a composite of two embryonic groups of feathers in both eutaxic and diastataxic birds. The four outer secondaries belong to the same longitudinal row of embryonic feathers as the greater under coverts of the proximal part of the forearm, and accordingly the inner secondaries correspond to the greater upper coverts of the distal forearm. In the embryo the distal parts of the longitudinal feather rows shift around the angle of the posterior margin of the wing, moving toward the dorsal surface. Continuous longitudinal rows are reformed by the joining of nonidentical rows at the point where differential movement has taken place. At this point of junction in diastataxic birds, namely, between the fourth and fifth secondaries, an extra greater covert is retained, without a secondary feather to match it. The Falconiformes are diastataxic and this extra covert is always to be found (see fig. 29).

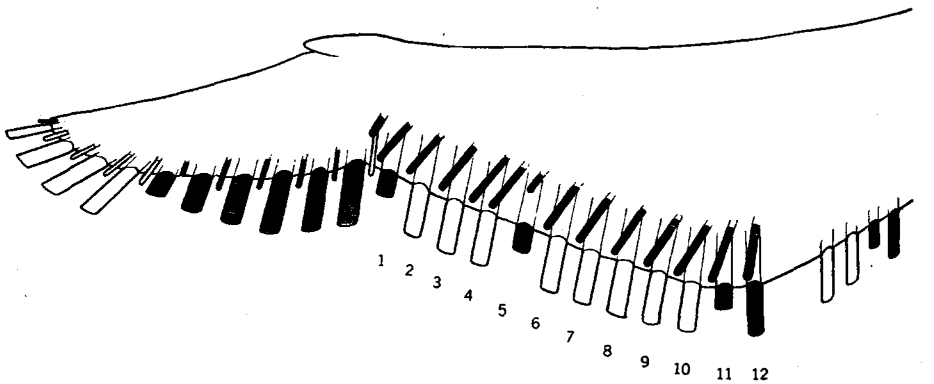

Fig. 29. Dorsal surface of left wing of Sharp-shinned Hawk (Mus. Vert. Zool., no. 61344), showing molt of remiges and greater coverts. Secondaries are numbered. Shaded quills represent new feathers, white quills old feathers, and short quills those which are growing.

In the author's study of secondary molt in shrikes (Univ. Calif. Publ. Zool., 30, 1928:410-415) it was found that the two molt centers, inner and outer, frequently spread to meet in the region of secondary 5. It was noted that this was suggestive of the two separate embryonic rows that joined at this point to make the definitive series of secondaries. The special significance of a constant molt center in Falconiformes at secondary 4 or 5 lies in its localization exactly at the diastataxic break. It may be supposed that there is some regulating device within each of the series of major flight feathers that induces molt to proceed, one or two feathers at a time, beginning at one or both ends of the series. It is entirely to be expected that the disturbance at the diastataxic point would supply, so to speak, a broken end of a chain of feathers, and as such it would be susceptible to whatever internal stimulus initiates molt in series of flight feathers.

The occurrence of more than two molt centers in the secondary remiges has been regarded as an adjustment accompanying great elongation of the middle segment of the wing. Whether elongation in the Falconiformes was in some way the cause of a new center which became focused at the diastataxic break, or whether the center merely occurs as a reflection of an embryonic situation cannot be determined. There is evidence in the true falcons that a shorter wing, with more crowded secondaries, leads to reduction in centers. But in these birds the diastataxic center persists and the center at the wrist is suppressed.

The wrist region, for both primaries and secondaries, is especially crowded in shortened wings. It appears likely that crowding tends to retard molt just as pressure of structures beneath the skin tends to reduce or eliminate feather growth (see Burt, Univ. Calif. Publ. Zool., 30, 1929:434). In the short wings of quail, secondaries 1 and 2 always molt after the remainder of the series. Further support for this generalization is seen in the delay in replacement of the crowded, vestigial carpal remex in the angle of the wrist joint (fig. 29) in *Accipiter*, and the lag in growth of the carpal covert and of one of the greater secondary coverts which occurs at the crowded point in this series of feathers in the diastataxic region. The comparative freedom of terminal members of series of remiges, perhaps resulting in better blood supply, may conversely be the reason for the molt starting with these members. Secondaries 4 and 5, which are slightly farther apart and less crowded than the other secondaries may enjoy a similar advantage.

Once a remex has started to grow, the greatly increased vascularization of growth should somewhat increase the blood supply of adjacent feathers in the row. By this means the next feather germ may be stimulated. If the threshold of reaction of feather germs to a general internal stimulus is prevailingly high, and assuming that the stimulating agent (possibly thyroxin; see review by Salomonsen, *op. cit.*, 388-393) is received through the blood stream, only certain feather germs that are well vascularized to begin with would respond. They would constitute molt centers. From them, by means of increased local vascularization, a wave of induction would pass along the series of feather germs.

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