THE TAIL MOLT OF SMALL OWLS

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VERY little is known, so far, about the tail molt in birds. The most frequent mode is that in which the molt starts with the central pair of tail-feathers, to be followed, successively, by one pair after the other, with the outermost pair completing the molt. The opposite to this "centrifugal" type of molt is the "centripetal" molt in which the outermost pair of feathers is molted first and the molt proceeds inward. An "alternating" type occurs occasionally in which alternate pairs of feathers are molted more or less simultaneously, to be followed by a second "wave" of molt affecting the remaining feathers. In the woodpeckers (Picidae) and tree creepers (Certhiidae) the molt is centrifugal, but begins with the second innermost pair of tail-feathers; the central pair of feathers is molted last, which permits the continuous presence of a functional climbing tail. The tree-climbing woodhewers (Dendrocolaptidae), on the other hand, have a regular centrifugal type of molt. These and various types of irregular molts are discussed in detail by Heinroth (1898) and Friedmann (1930). Wetmore (1914) discovered the remarkable fact that in the Malavsian Helmeted Hornbill (Rhinoplax vigil) only one of the elongated central feathers is molted at a time. In some Passerine birds, in addition to the Certhiidae, the central pair of tail-feathers is molted last, for instance, in the sunbird Aethopyga ignicauda (Mayr, 1941: 480) and in the paradise flycatcher Terpsiphone (Ticehurst, 1938: 408).

Little has been known, so far, about the tail molt of owls. Heinroth (1898: 112) says (translation), "The tail molt appears to be rather irregular among the owls, although the centrifugal type appears to be basic." Friedmann did not examine owls. During a study of south Asiatic *Glaucidium*, we discovered that the tail molt is simultaneous in several species. This is true, for instance, for three adults of *Glaucidium radiatum* in the Koelz Collection: adult male, Bihar, 25 August; two adult males, Bichlia, Central Provinces, 10 and 12 July.

A search through the literature revealed nothing of relevance, but Miss E. F. Chawner (Leckford, Stockbridge, England), who has kept many owls in captivity, wrote us as follows (October 3, 1949): "I have noticed that the small European and African species do as a rule moult their tail-feathers simultaneously, so much that I have sometimes seen them in the morning with full tails and by the evening they will have moulted all the tail-feathers. This was particularly the case with Athene. The large species did not shed their tailfeathers in this way, but did it by degrees."

This still left it desirable to examine in what genera the tail molt is complete, and in what others gradual, also whether there are multiple modes of molt in certain genera or species. Dr. W. Meise (Zoological Museum in Berlin) very kindly supplied us with information on molting specimens of *Glaucidium*, *Athene*, and *Ninox*. These comments (by letter, September 27, 1949) are included in the subsequent accounts.

The results of our investigations indicate that the tail molt appears to be gradual in *Tyto*, *Bubo*, and *Strix*. It is simultaneous in individuals of *Otus*, *Glaucidium*, *Athene*, and *Speotyto*. It is simultaneous in the small species of *Ninox* and gradual in the larger ones. No molting specimens of *Aegolius* or *Micrathene* were examined to permit statements on the tail molt of these genera, although it is presumably simultaneous in both genera.

In addition to the specimens in the Berlin Museum examined by Dr. Meise, this investigation is based on the greater part of the material of the American Museum of Natural History, including the Rothschild Collection. In owls, the sequence of the molt of the primaries appears to be from the innermost (first) out. The state of molt of the wing can therefore be precisely described by the number of the wing-feather most recently molted. The tail-feathers are numbered from the inside out, so that the outermost pair is numbered 6 and the innermost pair 1.

The case histories of a number of molting specimens in the genera Speotyto, Athene, Glaucidium, Otus, and Ninox follow.

Speotyto

1. Speotyto cunicularia hypugaea, A.M.N.H. No. 51,728, adult male, Dr. E. A. Mearns coll., Fort Verde, Arizona, August 28, 1886. Seventh primary molted. All tail-feathers are in sheath and equally long.

Athene

2. Athene noctua ludlowi, Berlin Museum, No. 471,187, Sikkim, adult male, August 15–25, 1938, E. Schäfer. Sixth primary molted. All tail-feathers in sheath, about 40 per cent of their ultimate length.

3. Athene noctua sarda, A.M.N.H. No. 631,192, Sassari, Sardinia, September, 1918. Tail molt nearly completed; all tail-feathers about equally long, with traces of the sheath still adhering.

The beginning of the molt is not always strictly simultaneous, as indicated by a specimen in the Berlin Museum (fide W. Meise):

4. Athene noctua noctua, No. 39.111, Angermuende (Pommerania), female, November 18, 1897. Seven tail-feathers old (4 left, 3 right). The four central tail-feathers of equal length, in sheath and about 75 per cent grown. One tailfeather missing.

April 1954 The late date, as well as the fact that the central feathers are nearly full grown while the outer ones give no indication of molting, suggest that the bird is merely replacing the two central pairs of feathers, which it had lost by accident.

5. Athene noctua bactriana, Gurgan, Mazanderan, Iran, July 11, 1940, W. Koelz, female. Fifth primary molted. A single old tail-feather present; all others in sheath and very short.

6. Athene brama, A.M.N.H. No. 62,882, southern India, no data. Fifth primary molted. All tail-feathers missing.

7. Athene brama, A.M.N.H. No. 62,880, southern India, no data. Sixth primary molted. All tail-feathers in sheath, very short.

Glaucidium

Every *Glaucidium* studied by us that showed tail molt apparently molted all tailfeathers simultaneously. Dr. W. Meise wrote us that among 200 *Glaucidium* in the Berlin Museum there are four adults in molt. The details on these four birds are as follows.

8. Glaucidium brasilianum, Berlin Zoo, September 16, 1918, female. All six pairs of tail-feathers in sheath. There are slight variations in length among them. The longest is 44 mm.; the two central feathers, 24 and 27 mm. Full tail length about 65 mm. Primaries 6 and 7 in molt.

9. Glaucidium perlatum, Berlin Museum, No. 36.1056, Waterberg, South West Africa, W. Hoesch, January 8, 1937, male. Full length of tail normally about 72 mm.; all tail-feathers in sheath, approximately 59 mm., except central pair (37 and 41 mm.). Fifth primary in molt.

10. Glaucidium cuculoides castanonotum, Berlin Museum, No. 36,560, Ceylon, 22.8.1894, female. Full length of tail normally about 62 mm.; all tail-feathers in sheath, 51 to 57 mm. long. Primaries 7 and 6 molted.

11. Glaucidium sjöstedti, Ahonangi, Cameroon, April 14, 1909, G. Tessmann, female. All tail-feathers in sheath, about three-fourth grown, with slight differences in size, central feather 58, outermost 49 mm. Primaries 7 and 6 molted.

In three specimens of G. radiatum and one of G. cuculoides in the Koelz Collection, with either the fifth or the sixth primary molting, all the tail-feathers are short and in sheath.

Otus

12. Otus rufescens rufescens, A.M.N.H. No. 630,182, Benkoker, North Borneo, September 25, 1885. Eighth primary molted, all tail-feathers in sheath, very short.

13. Otus brucei, A.M.N.H. No. 629,983, Baluchistan, June 24, 1898 (Russian calendar). Sixth primary molted. All tail-feathers short and in sheath, except one of the outermost, which is presumably old although it does not appear particularly worn.

14. Otus scops senegalensis, A.M.N.H. No. 630,008, Gassam, W. Senegal, September 2, 1907. Sixth primary molted. All tail-feathers absent, except a single worn outer tail-feather.

15. Otus scops ugandae, A.M.N.H. No. 630,043, White Nile, Uganda, May 1, 1906, male. Fifth primary in molt. Central pair of tail-feathers just beginning to grow (5 mm.); all lateral tail-feathers old.

16. Otus leucotis leucotis, A.M.N.H. No. 630,200, Thies, Senegal, May 10, 1907, female. Sixth primary molted; all tail-feathers in sheath and about equally long.

17. Otus leucotis granti, A.M.N.H. No. 630,230, Transvaal, September 25, 1901, female. Fifth primary molted; central pair of tail-feathers just beginning to grow, all other tail-feathers old.

18. Otus bakkamoena glabripes, A.M.N.H. No. 629,880, Yunnan, July 9, 1910, male. The entire tail is missing; the sheaths of the new feathers not yet visible.

19. Otus bakkamoena umbratilis, A.M.N.H. No. 417,608, Hainan, May 26, 1899, male. The entire tail missing, as in 629,880.

20. Otus bakkamoena lempiji, A.M.N.H. No. 387,998, Buitenzorg, Java, February 19, 1949, male. All, except two central pairs of tail-feathers, in molt.

21. Otus bakkamoena lempiji, A.M.N.H. No. 629,844, Sumatra, February 26, 1917, female. Tail missing.

Ninox

This genus is particularly interesting because it includes small and large species. It can be shown that the simultaneous tail molt is largely a matter of size.

22. Ninox superciliaris, A.M.N.H. No. 411,033, Ambararatabe, Madagascar, April 1, 1931, male. Eighth primary molted. All tail-feathers in sheath, with the central feathers somewhat shorter than the others.

23. Ninox a. affinis, A.M.N.H. No. 630,647, South Andamans, December 1897, female. Wing not molting. Lateral tail-feathers somewhat worn, central pair just completing the molt. This is either a case of irregular molt of the central pair of tail-feathers, or else they lagged far behind the others.

24. Ninox squamipila hypogramma, A.M.N.H. No. 630,676, Batjan, August 1902. A single central tail-feather in molt. Otherwise no signs of molt.

25. Ninox squamipila hypogramma, A.M.N.H. No. 630,678, Batjan, August 1897. No wing molt. All tail-feathers in sheath.

26. Ninox squamipila hantu, A.M.N.H. No. 630,683, Mt. Madang, W. Buru, March 18, 1902, male. Ninth primary molted. All tail-feathers in sheath.

27. Ninox th. theomacha, A.M.N.H. No. 630,700, Mamberano River, North New Guinea. Eighth primary molted. All tail-feathers lost, all but central pair in short sheaths.

28. Ninox odiosa, Berlin Museum, Blanche Bay, New Britain, May 24, 1907. Wing freshly molted. Tail completing its molt, all tail-feathers still in sheath.

29. Ninox jacquinoti eichhorni, A.M.N.H. No. 630,783, Choiseul, Solomon Islands, December 11, 1903, female. Fourth primary molted; all tail-feathers short and in sheath.

30. Ninox jacquinoti jacquinoti, A.M.N.H. No. 630,764, Ysabel, Solomon Islands, June 20, 1901, female. Second primary molted; all tail-feathers short and in sheath.

31. Ninox jacquinoti jacquinoti, A.M.N.H. No. 630,763, Ysabel, Solomon Islands, June 29, 1901, female. Eighth primary molted. Tail molt virtually completed, sheath still adhering to base of central pair of tail-feathers.

32. Ninox jacquinoti jacquinoti, A.M.N.H. No. 219,158, Ysabel, Solomon Islands, August 24, 1927, male. Fourth primary molted. All tail-feathers, except central pair, in sheath.

33. Ninox jacquinoti granti, A.M.N.H. No. 630,791, Guadalcanal, May 18, 1901, male. Sixth primary molted. Tail molt nearly complete, central tail-feathers a little shorter than others and still in sheath.

34. Ninox theomacha rosselliana, A.M.N.H. No. 630,719, Sudest Island, Louisiade Archipelago, March 21, 1898, male. Eighth primary molted; all tail-feathers in sheath and equally long, except central pair which is not yet molting.

35. Ninox theomacha rosselliana, A.M.N.H. No. 630,722, Sudest Island, April 16, 1898, female. Wing not in molt. Outermost tail-feather new, next to outermost in molt, four central pairs of tail-feathers old.

36. Ninox theomacha rosselliana, A.M.N.H. No. 630,720, Sudest Island, March 24, 1898; female. Wing molt completed. Tail-feathers 6 (outermost), 5 and 4 new, 3 and 2 molting, 1 (innermost) old.

37. Ninox theomacha rosselliana, A.M.N.H. No. 630,721, Sudest Island, April 6, female. Ninth primary molted; tail as in 630,720.

38. Ninox punctulata, A.M.N.H. No. 630,730, Makassar, Celebes, September 1895, male. Fifth primary molted; all tail-feathers, except one central one, in sheath.

39. Ninox meeki, A.M.N.H. No. 630,738, Manus, Admiralty Is., September 1913, female. Fifth primary molting; two central pairs in short sheath, all outer ones full grown, without sheath.

40. Ninox meeki, A.M.N.H. No. 630,740, data as 630,738, male. No wing molt; typical centripetal tail molt; 6, 5 completed, 4, 3, 2 progressively shorter, 1 (central pair) not yet molted.

41. Ninox rufa humeralis, A.M.N.H. No. 630,268, Milne Bay, New Guinea, February 1899, female. Strictly centripetal tail molt. Outermost tail-feather (6) fresh, 5–3 almost full grown with base still in sheath, 2 short, 1 (central pair) very short.

42. Ninox rufa rufa, A.M.N.H. No. 630,258, Northern Territory, Australia, November 1909, female. Five outer pairs of tail-feathers fresh, no longer in sheath; central pair, one feather old, the other short and in sheath.

43. Ninox connivens rufostrigata, A.M.N.H. No. 630,356, Morotai, no date. Three outer pairs virtually full grown, but base still in sheath; three central pairs very short and in sheath.

44. Ninox connivens assimilis, A.M.N.H. No. 630,349, New Guinea, December 1913, male. Four outer pairs freshly molted, two central pairs nearly full grown, but still in sheath.

45. Ninox connivens assimilis, A.M.N.H. No. 630,354, New Guinea, December 1913, male. All tail-feathers in sheath; 6, 5, 2, 1 three-quarters grown, 4, 3 full grown.

46. Ninox connivens peninsularis, A.M.N.H. No. 630,305, Dawson River, Queensland, January 31, 1909, female. Strictly centripetal tail molt; all feathers in sheath, 6 full grown, 5-1 progressively shorter.

SIZE, CLASSIFICATION, AND MODE OF TAIL MOLT

There is an obvious correlation between body size and tail molt. It tends to be simultaneous in all small species. For instance, in *Glaucidium* (wing 90–165 mm.), the tail molt is virtually always simultaneous, although the central pair of tail-feathers sometimes has a tendency to be shed later. Since the tail molt in *Glaucidium* is so uniform, no effort was made to record all specimens showing tail molt in our collections.

In the genus Athene (wing 145–170 mm.), the tail molt likewise always seems to be simultaneous. It is true for the only molting specimen of *Speotyto* (wing 165–180 mm.) examined.

In the genus Otus (wing 115–195 mm.) a simultaneous tail molt also prevails. However, in several specimens (13, 14, 15, 17) the molt appears to begin with the central tail-feathers, although in one specimen (20) this pair seems to be lagging behind. The genus *Ninox* is of particular interest because it spans a wide range of size (table 1). The various species with a wing length of less than 210 millimeters have essentially a simultaneous tail molt, although the central pair or two central pairs may lag behind the others. Those with a wing length of 210–230 mm. may have either centripetal,

TABLE 1

Approximate Wing-length in Species of Ninox Studied

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Wing Length	Type of Molt*
157-170	simultaneous (slightly irregular)
160-180	simultaneous
170-180	irregular
175-185	simultaneous (slightly irregular)
180-185	simultaneous (slightly irregular)
180-195	simultaneous (slightly irregular)
186-201	simultaneous
195-208	simultaneous, simultaneous,
	simultaneous (slightly irregular)
190-210	simultaneous
210-220	simultaneous (slightly irregular), centripetal, centripetal, centripetal
220-225	irregular, simultaneous
220-230	centripetal, centripetal (irregular)
255-270	? centripetal, irregular
270-285	centripetal
275-295	centripetal (irregular)
310-330	centripetal
	Length 157-170 160-180 170-180 175-185 180-185 180-195 186-201 195-208 190-210 210-220 220-225 220-230 255-270 270-285 275-295

* Statements separated by a comma refer to different specimens of the same species.

irregular, or simultaneous tail molt, whereas forms with a wing length of more than 230 mm. usually have a centripetal tail molt, although it may be somewhat irregular.

THE SIGNIFICANCE OF SIMULTANEOUS TAIL MOLT

Deviations from a "normal" molt pattern can often be shown to be adaptive, such as the tail molt in woodpeckers, or the simultaneous wing and tail molt in water and marsh birds. But what possible selective significance could a simultaneous tail molt have? No answer to this question can yet be given. The simultaneous loss of all tail-feathers unquestionably reduces the maneuverability of the individual. Normally there will thus be selection pressure for a gradual tail molt. However, a gradual tail molt, involving successively one feather after the other, is presumably based on a more complex physiological mechanism than a simultaneous tail molt. There will thus be a rather intense mutation pressure against it, and this complex mechanism can stay perfect only if maintained by selection. If such selection should relax, a simultaneous tail molt might take its place.

It is thus possible that the simultaneous tail molt in small owls is due to relaxation of selection. The small species may require the tail less in flight than the large ones, also they may feed during the summer on smaller prey (insects) which requires less leverage by the tail. The fact that birds in tail molt nearly always molt the same two or three neighboring primaries indicates that the tail molt of a given individual proceeds with relative rapidity. It is therefore also possible that complete taillessness during a short period is biologically less disadvantageous than is a tail in partial molt for several months.

Summary

The tail molt in owls may be simultaneous, centripetal, or irregular. In the smaller species (wing less than 210 mm.) it is usually simultaneous, in the larger species (wing more than 230 mm.) it is usually

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centripetal.