Chancellor, R. D. & B.-U. Meyburg eds. 2004
Raptors Worldwide
WWGBP/MME

Wave Moult of the Primaries in Accipitrid raptors, and its use in ageing immatures

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ABSTRACT

Stresemann & Stresemann (1966) described wave moult in the primary remiges ('Staffelmauser' in German; also translated as 'step-wise moult') for some families of birds but not for Acccipitrid raptors, even though many of the species in this family (especially the larger ones) show it. Primaries of Accipitrid raptors are replaced from P1 (inner) sequentially outward. Waves are formed when not all of the ten primaries are replaced in any annual moult cycle. In the next annual cycle, moult begins anew at P1 as well as continuing with the next feather from where it left off in the last cycle. Two or three, occasionally four, wave fronts of new primaries can be seen in the primaries of some raptors, especially larger ones, e.g., eagles. Knowledge and understanding of wave moult can ascertain the ages of immature raptors in those species that take three or four years to attain adult plumage, as these species typically do not replace all of the primaries in any moult cycle. Juvenile eagles show all primaries the same age. Second plumage eagles show two ages of primaries, newer inner ones and older retained juvenile outer ones. Third plumage eagles show two waves, with the first wave proceeding to P8, P9, or P10, and the second to P3, P4, P5, or P6. Fourth plumage eagles usually show new outer P10 from the first wave, new P5 to P7 from the second wave, and new P1 to P3 from the most recent wave. Fifth plumage eagles are essentially in adult plumage. I have verified wave moult in more than 70 species, mostly eagles, but also in snake eagles, chanting goshawks, one kite, one large hawk, and many of the larger buzzards.

INTRODUCTION

Accipitrid raptors replace their primaries in sequence from the inner (P1) to the outer (P10)(Stressemann & Stressemann 1960, 1966). This has been

reported for many species, e.g., Golden Eagle *Aquila chrysaetos* (Bloom & Clark 2001, Jollie 1947), Sharp-shinned Hawk *Accipiter striatus* (Miller 1941), Eurasian Sparrowhawk *Accipiter nisus* (Newton & Marquiss 1982), White-tailed Eagle *Haliaaetus albicilla* (Edelstam 1984), African Fish Eagle *H. africanus* (Prout-Jones & Milstein 1986), Osprey *Pandion haliaetus* (Prevost 1983), Little Eagle *Hieraaetus morphnoides* (Debus 1989), and Common Buzzard *Buteo b. buteo* (Piechocki 1963). Some individuals of more than seventy species replace fewer than ten primaries during the annual moult period. Moult in these species is suspended or dramatically reduced during periods when food resources are reduced, i.e., for migration or in winter. Moult is resumed anew when food resources increase, e.g., in spring or when migration is completed. The inner primary, P1, is replaced at the start of every annual moult cycle, regardless of whether or not all primaries had been replaced during the last cycle (Bloom & Clark 2001, Edelstam 1984, Heeremans 2000, Prout-Jones & Milstein 1986, Piechocki 1963). In those species with incomplete primary moult, moult continues sequentially where it left off in the last cycle and as well as again at P1, thus forming 'waves' of moult. This phenomenon was described as 'Stauffelmauser' or 'wave moult' (This can also be translated as 'step-wise moult' or 'relay moult') by Stressemann and Steressemann (1966), although they did not mention it for the family Accipitridae. From two to four waves of primary moult can occur, with each wave proceeding sequentially from P1 to P10 over the period of two to four years. Large raptors that have three or four immature plumages can be aged by the primary moult: Juveniles show no moult, second plumage birds show one 'wave' moult in the inner primaries, third plumage birds show two waves of moult, and fourth plumage birds show three waves of moult.

METHODS

For more than 20 years I have been examining the moult of the primaries of raptors captured for banding and ringing on four continents, from photographs of their spread wings, and from museum specimens. I have inspected hundreds of raptors in hand or as museum specimens for primary moult and examined at least one individual of more than 130 of the more than 230 Accipitrid species and looked at more than a hundred photos of the underwings of Accipitrid raptors. I have read and studied the literature on primary moult.

The ten primaries are numbered sequentially from the inner as P1 to the outer as P10.

RESULTS

I have observed primary moult in at least one individual of more than 130 of the 230 plus species in Accipitridae. All moulting Accipitrid raptors began their primary moult at the same moult center, P1. This is the first primary to be replaced in the first (post-juvenile) moult, followed in ascendant sequence by the replacement of P2, P3, and so on up to P10. For smaller species that replace all ten primaries annually, this sequence is followed every year, regardless of the age of the raptor. However, some individuals of more than seventy species of Accipitrid raptors, especially larger ones, do not replace all ten primaries in

any annual moult cycle, beginning with their first annual moult (Table 1). In these species, primary moult continues sequentially in the next moult cycle where it left off in the last cycle, and, importantly, also *a new wave begins at P1.* As a result, primary moult now occurs in two or more locations in the primaries of each wing; this was described by Stresemann & Stressemann (1966) as 'Staffelmauser', or 'wave moult' (also translated as 'step-wise moult') in English. They list many families that show this type of primary moult but do not include Accipitridae

If a raptor moults fewer than ten primaries in its post-juvenile moult, *e.g.*, only P1 to P6, it will replace P7 at the beginning of its second annual moult cycle and will also again replace P1. The first feather to be replaced can be either the next in sequence or P1. See Figures. 1-3 for examples of P1 being replaced before P10. Thus feathers are now being replaced at two locations. This fact tells us that the raptor has initiated at least two moults, and, as a consequence, is more than two years old. At the initiation of the third annual moult, if the first 'wave', i.e. that initiated at the post-juvenile moult, had progressed to the outer primaries (true for most eagles), moult will continue there, e.g., at P9 or P10. It will also continue at the location where the second annual moult left off, e.g., P4- P6, and also initiate a new wave moult at P1; it will show three waves of moult. Larger raptors, eagles and vultures, other than juveniles and second plumage immatures, usually show two or three (sometimes four) wave moults in the primaries, each led by a newly replaced feather. This indicates, for immatures, that this individual has initiated two or three annual moults and is more than two or three years old.

Primary moult, especially that of adults, is sometimes not symmetric.

Figure 1. Primary moult in an adult Common Buzzard (*Buteo buteo*). Note that P7 and P1 are both growing and that P10 is fresh. (Slovakia, June)

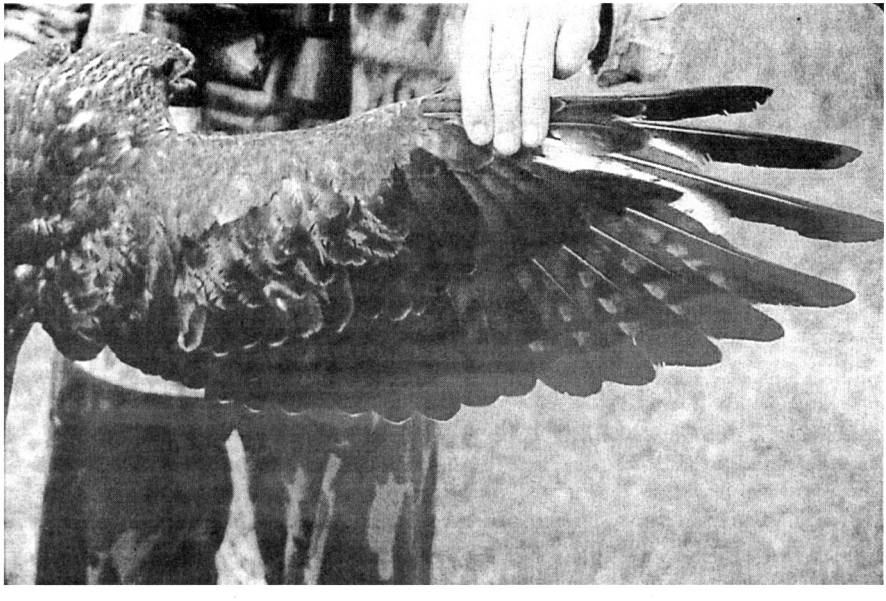


Table 1. Species that have shown wave moult in the primaries.

Osprey	*Pandion haliaetus*	Harris's Hawk	*Parabuteo unicinctus*
W. Honey-Buzzard	*Pernis apivorus*	Black-collared Hawk	*Bursarellus nigricollis*
O. Honey-Buzzard	*Pernis ptilorhynchus*	Gray Hawk	*Buteo nitudus*
Black-shouldered Kite	*Elanus caeruleus*	Swainson's Hawk	*B. swainsoni*
Snail Kite	*Rostramus socialabilis*	Galagapos Hawk	*B. galagopaensis*
Red Kite	*Milvus milvus*	White-tailed Hawk	*B. albicaudatus*
Black Kite	*M. migrans*	Red-backed Hawk	*B. polysoma*
African Fish Eagle	*Haliaaetus vocifer*	Zone-tailed Hawk	*B. albonatatus*
White-bel. Sea Eagle	*H. leucogastor*	Red-tailed Hawk	*B. jamaicensis*
White-tailed Eagle	*H. albicilla*	Common Buzzard	*B. b. buteo*
Bald Eagle	*H. leucocephalus*	Steppe Buzzard	*B. (buteo) vulpinus*
Steller's Sea Eagle	*H. peligacus*	Mountain Buzzard	*B. oreophilus*
Cinereous Vulture	*Aegypius monachus*	Forest Buzzard	*B.(oreophilus)trizonatus*
Lappet-faced Vulture	*Torgos tracheliotos*	Long-legged Buzzard	*B. rufinus*
Red-headed Vulture	*Sarcogyps calvus*	Upland Buzzard	*B. hemilasius*
Hooded Vulture	*Necrosyrtes monachus*	Ferruginous Hawk	*B. regalis*
Griffon Vulture	*Gyps fulvus*	Rough-legged Hawk	*B. lagopus*
Slender-billed Vulture	*G. tenurostris*	Augur Buzzard	*B. augur*
Indian Vulture	*G. indicus*	Jackal Buzzard	*B. rufofuscous*
Himalayan Vulture	*G. himalayensis*	Harpy Eagle	*Harpia harpyja*
Cape Vulture	*G. coprotheres*	Lesser Spotted Eagle	*Aquila pomarina*
White-rumped Vulture	*G. bengalensis*	Indian Spotted Eagle	*A. hastata*
White-backed Vulture	*G. africanus*	Greater Spotted Eagle	*A. clanga*
Egyptian Vulture	*Neophron percnopterus*	Tawny Eagle	*A. rapax*
Bearded Vulture	*Gypaetus barbatus*	Steppe Eagle	*A. nipalensis*
Short-toed Snake Eagle	*Circaetus gallicus*	East. Imperial Eagle	*A. heliaca*
Beauduoin's Snake Eagle	*C. beaudouini*	Golden Eagle	*A. chrysaetos*
Black-breasted Snake	*C. pectoralis*	Wedge-tailed Eagle	*A. audux*
Brown Snake Eagle	*C. cinereus*	Verreaux's Eagle	*A. verreauxi*
West. Banded Snake Eagle	*C. cinerascens*	Wahlberg's Eagle	*Hieraaetus wahlbergi*
So. Banded Snake Eagle	*C. fasciolatus*	Bonellis's Eagle	*H. africanus*
Bateleur	*Terathopius ecaudatus*	African Hawk Eagle	*H. spilogaster*
Gymnogene	*Polyboroides typus*	Booted Eagle	*H. pennatus*
Pale Chanting Goshawk	*Melierax canorus*	Ayres's Eagle	*H. ayresii*
North. Goshawk	*Accipiter gentilus*	Changeable Hawk	*Spizaetus cirrhatus*
White Hawk	*Leucopternis albicollis*	Mountain Hawk	*S. nipalensis*
Gray-backed Hawk	*L. occidentalis*	Martial Eagle	*Polemaetus bellicosus*
Common Black-Hawk	*Buteogallus anthricina*	Crowned Eagle	*Stephanoeatus coronatus*
Great Black Hawk	*B. urubitinga*		

Figure 2. Primary moult in an adult Red-tailed Hawk (*Buteo jamaicensis*). Note that P1 is growing and the P10 is juvenile. (PA-USA, May)

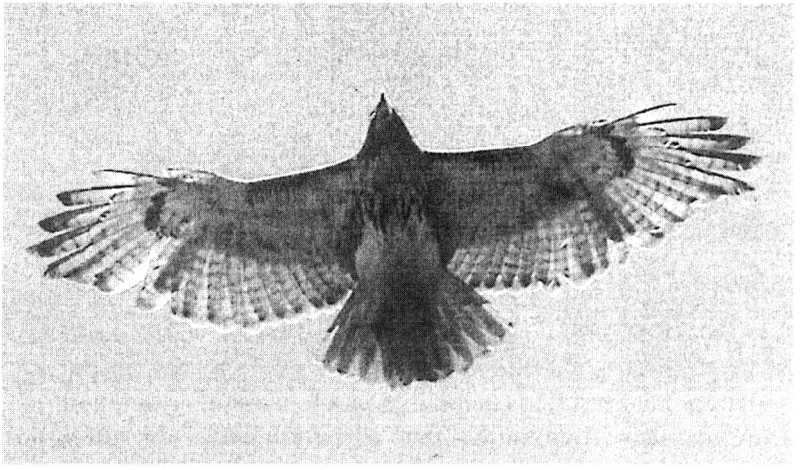
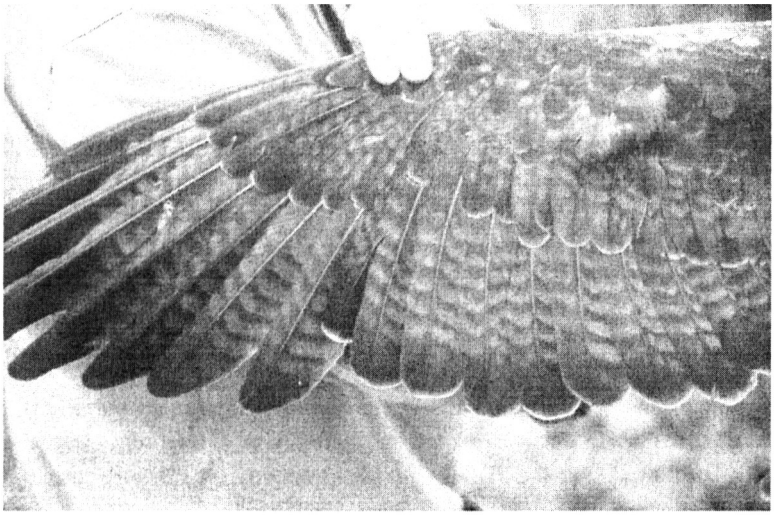


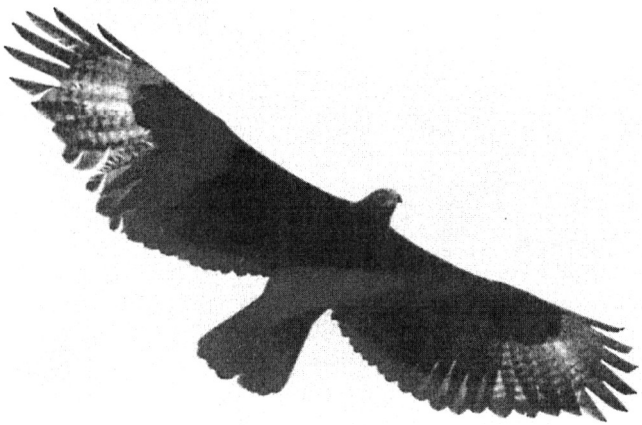
Figure 3. Primary moult in a second plumage White-tailed Hawk (*Buteo albicaudatus*). Note that P1 is growing (Beginning its second annual moult) and that P10 is retained juvenile. (TX-USA, March)



How waves of moult are formed

Figure 4 is a photograph of an adult Verreaux's Eagle *Aquila verreauxi,* in flight. Wave moult in the primaries of both wings is clearly evident, with P10, P7, and P4 appearing darker, thus fresher, than the others, as they were the most recently replaced and are the heads of the three waves; this is more visible on the upper wing. Note the contrast between P7 and P8 and P4 and P5, with P7 and P4 much darker, thus fresher. Note also that P9 is paler than P10, and that P8 is yet paler, and that P6 and P5 are progressively paler than P7. The color gradations are because P8 was replaced before P9, which was replaced before P10, as older feathers show more fading from weather. Same with P5-7 and P1-4, which are more visible on the lower wing.

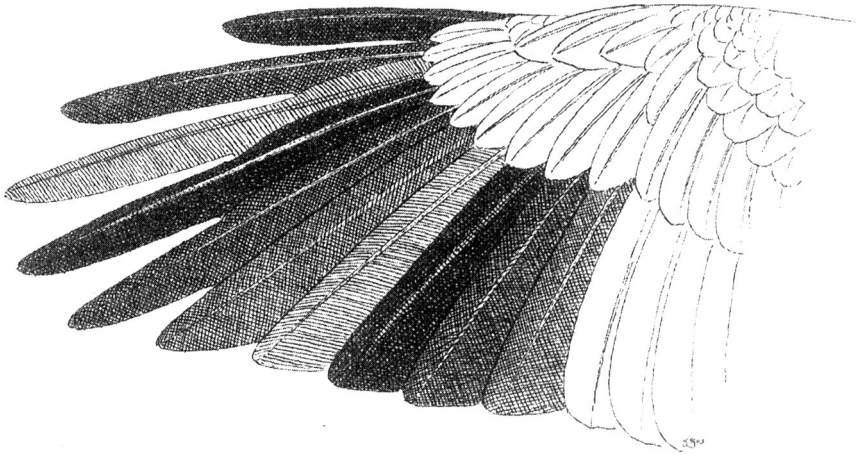
Figure 4. Primary wave moult in an adult Verreaux's Eagle (*Aquila verreauxi*) showing three waves: one at P10, another at P7, and a third at P4. (Kenya, August)



The wave with P10 at its head most likely began with P1 more than two years ago and progressed sequentially to P10. We can only see P8-P10 of this wave, as the next wave, with P7 at its head, has replaced P1 to P6. P7 is the head of the second wave, which most likely began over a year ago. P1-6 had been replaced earlier in this wave, however, only P5 and P6 are visible, as P1-4 were replaced again in the third wave. P4 is the head of the third wave, with P1-4 having been replaced during the most recent moult.

Figure 5 is a representation of primary wave moult in an adult eagle and shows three waves, with P10, P7, and P3 appearing darker, thus fresher, than the others, as they were the most recently replaced and are the heads of the three waves. Note the contrast between P7 and P8 and P3 and P4, with P7 and P3 much darker, thus fresher. Note also that P9 is paler than P10, and that P8 is yet paler, and that P6, P5, and P4 are progressively paler than P7. The color gradations are because P8 was replaced before P9, which was replaced before P10, as older feathers show more fading from weather. Same with P4-7 and P1-3.

Figure 5. Primary wave moult of an eagle showing three waves: the oldest at P10, another at P7, and a third, the most recent, at P3. See text.



Ageing by primary moult

Immatures of large Accipitrid raptors are distinguished from adults by plumage and can be aged as to year class by the moult of the primaries. Other characters, such as plumage and secondary and tail moult, are also useful in ageing. Those other characters are outside the scope of this article.

Juveniles. Juveniles are usually easy to determine. They have not replaced any flight feathers (Except possibly a replacement feather in a random location). They also have different plumage and tail pattern from the adults in most species. See Figure 6.

Second plumage. They show two ages of primaries: newly moulted inner primaries, usually from three to eight or nine, and old faded outer ones. See Figure 7.

Third plumage. They show two waves of primary moult. The outer primary, P10, is usually retained juvenile. See Figure 8.

Fourth plumage. They show three waves of primary moult. See Figure 9.

Figure 6. Juvenile primaries. All are the same age, with no moult. Note that all of the secondaries are also the same age.

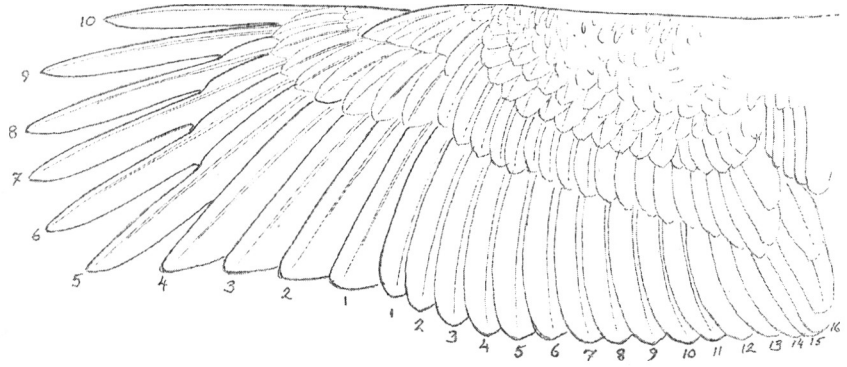


Figure 7. Second plumage primaries. New inner primaries with retained juvenile outer ones.

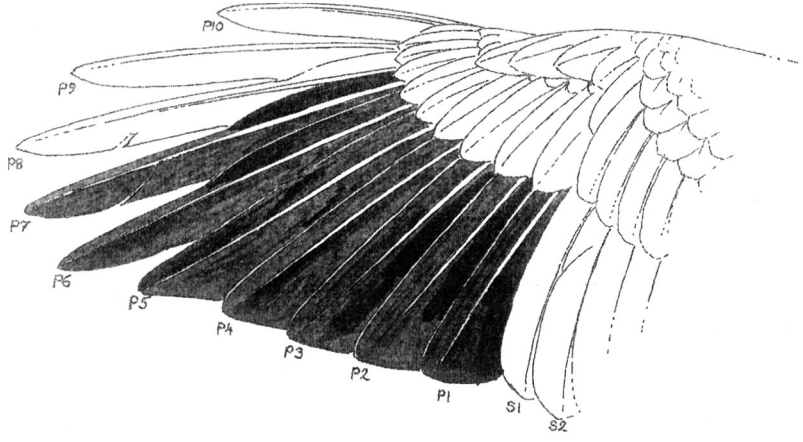


Figure 8. Third plumage primaries. Two waves of primary moult, with the first wave reaching P9 and the second wave P3. Useful in ageing only with immatures, as adults can show this pattern

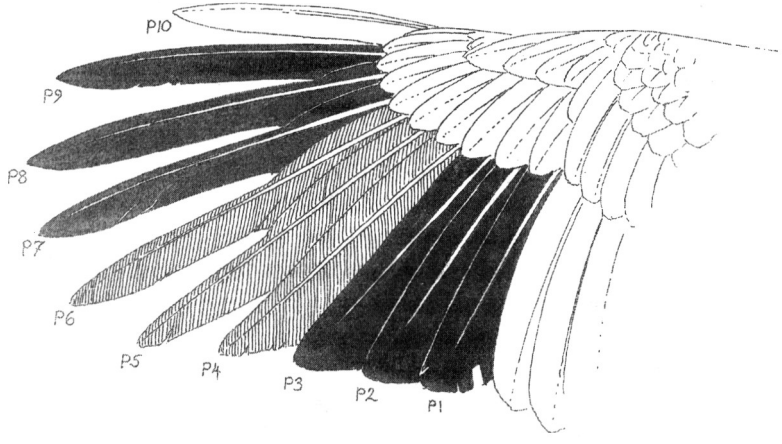
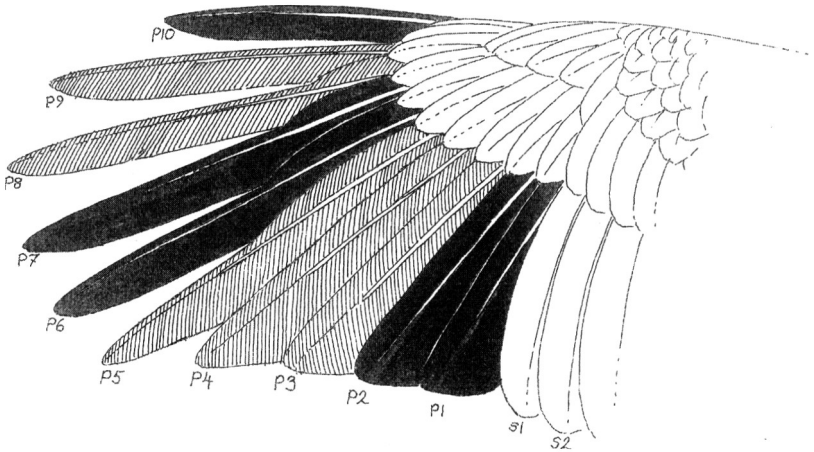


Figure 9. Fourth plumage primaries. Three waves of primary moult, with wave 1 at P10, wave 2 at P7, and wave 3 at P2. Useful in ageing only with immatures, as adults can show this pattern.



DISCUSSION

The fact that moult begins anew at P1 at the beginning of each annual moult cycle, regardless of whether or not it had completed all ten primaries in the previous cycle, is key in ageing immature raptors, as the number of waves of primary moult gives a minimum age. It is the 'carbon dating' for ageing immature raptors. Raptors with no primary moult are juveniles, and those with one wave of primary moult in the inner primaries have been through at least one annual moult season. Likewise, those exhibiting two waves of moult have been through two moult cycles and are more than two years old, and so on with three waves.

The advantage of moulting primaries in waves for large raptors is that large gaps in the primaries are avoided, as a primary can be dropped in one location as the head of one wave and its replacement begun and then another feather can be dropped in another location corresponding to another wave. The dropping of the next feather in each wave then can be delayed until the preceding primary is completely or nearly completely grown in, avoiding large gaps in the wings.

It is interesting that Stresemann & Stresemann (1960, 1966) did not recognize that some Accipitrid raptors exhibited wave moult. Even though they describe this phenomenon in the latter work (1966) for several other families. They incorrectly characterized the primary moult of the larger Accipitrid raptors as being somewhat random (their modes 3a and 3b), with two or three moult centers that vary in location. They do describe that the moult sequence is from P1 to P10 in the smaller raptors (their mode 2) that complete their primary moult annually. But they call it as descendent rather than ascendant. This is most likely because the primaries had been numbered in Europe (but not in North America) from outer to inner until recently (See Stresemann and Stresemann (1966) or the English translation of it by Kalma (1966) for a discussion of why ascendant numbering is better.).

The use of moult scoring for numerically determining the extent of primary moult (e.g., in Ginn & Melville 1983) is useful only for those species that replace all ten primaries annually. It makes no sense for those species that show wave moult.

Tjernberg (1988) and Tjernberg & Landgren (1999) do not use primary wave moult for ageing immature Golden Eagles. They began with the assumption that adult plumage was attained after six moults. I believe that all large eagles attain adult plumage or essentially adult plumage after four annual moults or when they are 4 ½ years old and all are completely adult after 5 moults (5 ½ years old). This is true for Bald Eagles *Haliaaetus leucophelus* (McCullough 1989, Clark 2001, Gerard & Bortolotti 1988), White-tailed Eagles *H.* albicilla (Helander et al 1989), African Fish Eagles (Prout-Jones & Milstein 1986), Steppe Eagles *Aquila nipalensis* (Clark 1996), and Golden Eagles (Bloom & Clark 2001, Jollie 1947). Tjernberg's claim that Scandinavian Golden Eagles take six moults (6 ½ years) to attain adult plumage needs verification. I have looked at specimens of immature Golden Eagles from northern Europe and found that their the moult is the same as that of North American eagles, with the caveat that more white is retained on the tail feathers in the first four immature plumages of the former.

The immature Golden Eagle in-hand shown on plates 493-494 of Forsman (1999) shows one wave of primary moult, with P1-5 fresh, P 6 growing, and P7-10 old. This is a classic second plumage eagle, but the caption states that this is a third plumage eagle. The moult pattern of this eagle is the same as that of many second plumage Golden Eagles in North America (Bloom & Clark 2001). If it were a third plumage eagle, then it should show new inner primaries and two waves of primary moult.

Richter (1974) described the primary moult of an immature White-tailed Eagle and showed it in photographs and diagrams. Primaries P4 and P9 were growing, and P3 and P8 were the most recently replaced. This eagle is in its third plumage and shows two waves of primary moult. It was around two years old when the photographs were taken.

Primaries of all Accipitrid raptors are replaced sequentially ascendant from P1 to P10. A new 'wave' of moult is initiated at P1 at the start of every annual moult cycle, regardless of whether or not all ten primaries were replaced in the last cycle. In species that replace fewer than 10 primaries annually, this forms waves of moult in the primaries; it is this fact that permits one to age immature eagles in their first four years.

ACKNOWLEDGEMENTS

I thank my colleagues Pete Bloom and John Schmitt for sharing their vast knowledge of raptors, photographs, and data on moulting. John drew all of the illustrations used herein.

A. Barkhuesen, Z. & H. Bernitz, P. Bloom, M. Britten, O. Curtis, S. Danko, K. Duffy, E. Gorney, O. Hatzofe, A. Hinde, C. Jackson, A. Jenkins, M. McGrady, C. McIntyre, K. Meyrom, A. Moritz, V. Prakash, C. Schultz, T. Talliards, S. Thomseth, M. Virani, and R. Yosef were companions in capturing raptors.

P. Bloom, J. Bouton, L. Fink, G. Jacobs, A. Hinde, and others provided photographs of captured raptors showing wave moult in the primaries.

I thank the curators of numerous museums throughout the world for permission to look at raptor specimens.

REFERENCES

BLOOM, P. AND W. S, CLARK. 2001. Molt and sequence of plumages of Golden Eagles, and a technique for in-hand ageing. *North American Bird Bander* 26(3): 97-116.

CLARK, W.S. 1996. Ageing Steppe Eagles. *Birding World* 9:269-274.

CLARK, W. S. 2001. Aging Bald Eagles. *Birding* 33:18-28.

DEBUS, S. J. S. 1989. Plumages and moult of the Little Eagle *Hieraaetus morphnoides*. *Australian Bird Watcher* 13:103-113.

EDELSTAM, C. 1984. Patterns of moult in large birds of prey. *Ann. Zool. Fennici* 21:271-276.

FORSMAN, D. 1999. *The raptors of Europe and the Middle East*. T & AD Poyser, London.

GERRARD, J. M, AND G. R. BORTOLOTTI. 1988. *The Bald Eagle, Haunts and Habits of a Wilderness Monarch*. Smithsonian Inst. Press, Washington, D. C.

GINN, H. B., & D. S. MELVILLE. 1983. *Moult in birds*. BTO guide 19. British Trust for Ornithology. Tring, Herts, UK.

HERREMANS, M. 2000. Cases of serial descendant primary moult (Staffelmauser) in the Black-shouldered Kite *Elanus caeruleus*. *Ringing & Migration* 20:15-20.

HELLANDER, B., B. EKMAN, J. E. HAGERROTH, P. A. HAGERROTH, AND J. ISRAELSSON. 1989. [Age-specific field characteristics of the White-tailed Sea Eagle, *Haliaaetus albicilla* L.] **In** Swedish with an English summary. *Var Fagelvarld* 48:319-334.

JOLLIE, M. 1947. Plumage changes in the Golden Eagle. *Auk* 64:549-576.

KALMA, S. 1966. Translation into English of STRESEMANN, E., AND V. STRESEMANN. 1966. *J. fur Ornith*. 107:332-333. Peabody Museum of Nat. Hist., New Haven, CT.

MCCOLLOUGH, M. A. 1989. Molting sequence and aging of Bald Eagles. *Wilson Bull.* 101:1-10.

MILLER, A. H. 1941. The significance of molt centers among the secondary remiges in the Falconiformes. *Condor* 43:113-115.

NEWTON, I, AND M. MARQUISS. 1982. Moult in the Sparrowhawk. *Ardea* 70:163-170.

PIECHOCKI, R. 1963. Vorlaufiges uber die Mauser der Hansschwingen beim Mausebussard (*Buteo buteo*). *J. fur Ornith*. 104:182-184.

PREVOST, Y. 1983. Moult in the Osprey *Pandion haliaetus Ardea* 71;199-209.

PROUT-JONES, D. V. AND P. L. MILSTEIN 1986. Sequential moult with age class establishment in the African Fish Eagle *Haliaaetus vocifer*. *S.-Afr. Tydskr. Natuurnav.* 16:17-26.

RICHTER, H. 1974. Zur Schwingenmauser des Seeadlers (*Haliaaetus albicilla* L.) *Beitr. Vogelkd. Leipzig* 20:310-315.

STRESEMANN, E., AND V. STRESEMANN 1960. Die Handschwingen der Tagraubvogel. [English summary] *J. fur Ornith*. 101:373-403.

STRESEMANN, E., AND V. STRESEMANN 1966. [The molt of birds.] In German. *J. fur Ornith*. 107:332-333.

TJERNBERG, M. 1988 [Age determination of Golden Eagles *Aquila chrysaetos*.] In Swedish with brief English summary. *Var Fagelvarld* 47:321-334.

TJERNBERG, M., AND T. LANDGREN 1999. [Age determination of Golden Eagles *Aquila chrysaetos*.] In Swedish with brief English summary. Kungsorned 1999:16-23.

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