J Raptor Res. 39(4):378–385

FIRST-CYCLE MOLTS IN NORTH AMERICAN FALCONIFORMES

PETER PYLE[1]
The Institute for Bird Populations, P.O. Box 1436, Point Reyes Station, CA 94956 U.S.A.

ABSTRACT.—I examined 1849 specimens of 20 North American Falconiform species to elucidate the occurrence and nomenclature of partial first-cycle molts. As reported in the literature, American Kestrel (*Falco sparverius*) and White-tailed Kite (*Elanus leucurus*) have relatively complete body-feather molts that occur during the first fall; in the kite, this molt can also include up to all rectrices and 2–6 secondaries, but no primaries—an unusual pattern for such partial molts in first-year birds. Evidence of partial first-cycle molts was found in 16 of 18 other species (among *Pandion, Haliaeetus, Circus, Accipiter, Asturina, Buteo, Aquila,* and *Falco*) for which such molts have not been previously elucidated. Maximum extent of body-feather replacement among individuals of these 16 species varied from 5–50%. On the other hand, most species showed evidence that this molt could be absent (11–100% of birds remaining in juvenile plumage until commencement of the complete or near-complete prebasic molt that occurs during the first summer). I argue that these partial molts are best considered *preformative molts* (following Howell et al. 2003) rather than "first prebasic" molts, as defined by Humphrey and Parkes (1959). Variation in the extent and timing of preformative molts may reflect various constraints according to species-specific breeding, migrating, and foraging strategies. The apparent lack of function for this molt suggests that ancestral Falconiformes exhibited a more extensive preformative molt, as found in related orders of birds, but that this molt has since become vestigial, at least in the larger species.

KEY WORDS: *American Kestrel;* Falco sparverius; *White-tailed Kite;* Elanus leucurus; *preformative molt; hawks; falcons.*

MUDAS DEL PRIMER CICLO EN FALCONIFORMES NORTEAMERICANOS

RESUMEN.—Examiné 1849 especímenes de 20 especies norteamericanas de Falconiformes para establecer la ocurrencia y la nomenclatura de mudas parciales del primer ciclo. Como había sido informado en la literatura, *Falco sparverius* y *Elanus leucurus* presentan mudas relativamente completas de las plumas corporales que tienen lugar durante el primer otoño, aunque en *E. leucurus* esta muda puede también incluir algunas o todas las rectrices y 2–6 secundarias pero ninguna primaria. Esto constituye un patrón poco usual de mudas parciales durante el primer año de vida. Encontré evidencia de mudas parciales en el primer ciclo en 16 de las 18 especies adicionales (en los géneros *Pandion, Haliaeetus, Circus, Accipiter, Asturina, Buteo, Aquila* y *Falco*) para las cuales no se había determinado previamente la ocurrencia de mudas de este tipo. El máximo grado de reemplazo de las plumas del cuerpo en los individuos de esas 16 especies varió entre el 5% y el 50%. Por otra parte, la mayoría de las especies mostraron evidencia de que esta muda podría estar ausente, pues entre el 11% y el 100% de los individuos mantuvieron el plumaje juvenil hasta comenzar la muda prebásica completa, o casi completa, que tiene lugar durante el primer verano. Sugiero que estas mudas prebásicas deben considerase mudas preformativas (siguiendo la terminología de Howell et al. 2003) en lugar de "primeras mudas prebásicas", como fueron definidas por Humphrey y Parkes (1959). La variación en la extensión y en el momento de ocurrencia de las mudas preformativas podría reflejar distintos limitantes de acuerdo a las estrategias reproductivas, de migración y de forrajeo específicas de cada especie. La falta aparente de funcionalidad de esta muda sugiere que los Falconiformes ancestrales exhibían una muda preformativa más extensiva, como se ha documentado en órdenes de aves relacionados, pero que esta muda se ha vuelto vestigial, al menos en las especies de mayor tamaño.

[Traducción del equipo editorial]

North American Falconiformes exhibit various molt strategies during their first year of life. In most species, juvenal plumage is reportedly retained until the first spring or summer (when a year old), at which point a complete or near-complete prebasic molt commences, usually with the shedding of the innermost primaries in Accipitri-

[1] Email address: ppyle@birdpop.org

dae or the medial primaries in Falconidae (e.g., Miller 1941, Palmer 1988, Forsman 1999, Wheeler 2003). In American Kestrel (*Falco sparverius*) and certain kites, by contrast, most to all juvenal body feathers are replaced during the first fall, well before molt of the primaries commences during the following summer (Bent 1937, 1938, Parkes 1955, Palmer 1988, Miller and Smallwood 1997).

For some species of Falconiformes, a limited number of body feathers are reported to be replaced during the first fall, winter, or spring, prior to the shedding of primaries during the first spring or summer. For example, Wheeler (2003) reported that in the Red-shouldered Hawk (see Table 1 for scientific names), "the first prebasic molt begins on the breast, then is noticeable on the back and scapulars" before molt of primaries begins, and Forsman (1999) reported that in the Northern Harrier, "single body-feathers and tail-feathers may be replaced from late winter" prior to the complete molt the following May to October. Similar limited molts in fall, winter, or spring have been reported for Osprey (Bent 1937), Northern Goshawk (Bent 1937, Dement'ev and Gladkov 1951, Forsman 1999), Gray Hawk (Dickey and van Rossem 1938, Wheeler 2003), and several species of Falconidae (Cramp and Simmons 1980, Forsman 1999, Wheeler 2003).

Most authors consider this limited body-feather replacement to be the initiation of the prebasic molt at a year of age (hereafter, "first complete molt") rather than a separate molt; indeed, Wheeler (2003) even interprets the fall molts in first-year American Kestrel and kites as part of the first complete molt, terminating with the flight feathers the following summer. This interpretation appears to disregard the additional body molt that occurs in one-year-old birds concurrent with flight-feather molt in these species (Parkes 1955, Palmer 1988). Herremans and Louette (2000), on the other hand, document that such molts in certain Old-World species of *Accipiter* are distinct from the first complete molt.

Thus, there remains confusion about both the occurrence of partial first-cycle molts in Falconiformes and whether or not body-feather replacement in the first fall, winter, or spring should be considered part of a separate partial molt or as the initiation of the first complete molt. To investigate the occurrence and extent of partial first-cycle molts in Falconiformes, I examined 1227 specimens of 20 North American species collected during their first year (age = 0–12 mo), prior to initiation of primary molt, and 622 specimens collected in their second year (12–24 mo old) or later.

METHODS

Specimens of Falconiformes were examined at the California Academy of Sciences (CAS), San Francisco, the Museum of Vertebrate Zoology (MVZ), Berkeley, and the National Museum of Natural History (USNM), Washington, DC. Specimens were collected throughout North, Central, and South America, but all specimens represented species or subspecies exhibiting boreal breeding cycles. Data are presented for 20 species with $N \geq 16$ first-year individuals examined (Table 1).

Specimens examined included birds collected during their first year of life, prior to the shedding of primaries during the first complete molt, and birds determined to be in their second year of life. Age of first-year birds was determined by plumage features (Palmer 1988, Wheeler 2003), the presence of indicative fault bars (Hammerstrom 1967), tapered and relatively worn outer primaries and rectrices, and absence of wear and color patterns among flight feathers indicating previous molts. Birds in their second year were aged by the presence of predefinitive plumage in some species or the retention of juvenal feathers during the first "complete" molt, particularly among the lesser coverts, on the rump, or within the secondaries (Wheeler 2003).

Each first-year specimen was examined carefully for replaced body feathers in patterns indicating molt. Body molt in Falconiformes typically begins on the head and throat and proceeds caudally (Palmer 1988, Wheeler 2003). Thus, feathers showing wear patterns suggesting replacement in a caudal direction were assumed to have resulted from molt rather than adventitious replacement (e.g., after accidental loss). Replaced feathers were often intermediate in color or patterning between those of first-year and second-year birds (Fig. 1), facilitating their identification. The proportion of newly-replaced body feathers, to the nearest 5%, was estimated for each specimen. Those showing <2.5% replacement were scored as 0%, further ensuring that birds with adventitiously replaced feathers were not included in the sample evincing molt. All primaries, secondaries, and rectrices were also examined for evidence of symmetrical replacement indicating molt. Secondaries were numbered proximally from the outermost (s1) to the innermost (s13 in most species) feather.

Second-year birds were examined for uniformity of feather generations, particularly in tracts for which partial molts were detected in first-year birds. The goal of this examination was to assess whether or not feathers replaced during the first year, prior to initiation of primary molt, had been replaced for a second time during the first complete molt.

RESULTS

Partial First-year Molts in White-tailed Kite and American Kestrel. I examined 22 specimens of

Table 1. Proportion of individuals showing evidence of molt and maximum percent of body feathers replaced, among specimens of 18 species of North American Falconiformes, during three time periods within the first year Values represent sample size of specimens examined, proportion of individuals showing evidence of molt, and maximum proportion of body feathers replaced among individuals sampled.

	September–November			December–February			March–May		
Species	*N*	Proportion Molting	Maximum Percent Feathers Replaced	*N*	Proportion Molting	Maximum Percent Feathers Replaced	*N*	Proportion Molting	Maximum Percent Feathers Replaced
Osprey (*Pandion haliaetus*)	10	0.40	10%	3	1.00	20%	2	1.00	35%
Bald Eagle (*Haliaeetus leucocephalus*)	8	0.12	5%	5	0.60	30%	3	1.00	40%
Northern Harrier (*Circus cyaneus*)	35	0.00	0%	18	0.33	15%	16	0.44	50%
Sharp-shinned Hawk (*Accipiter striatus*)	80	0.00	0%	43	0.12	10%	48	0.31	45%
Cooper's Hawk (*Accipiter cooperii*)	59	0.08	10%	26	0.31	10%	14	0.64	10%
Northern Goshawk (*Accipiter gentilis*)	30	0.00	0%	6	0.00	0%	10	0.00	0%
Gray Hawk (*Asturina nitida*)	12	0.00	0%	7	0.14	5%	6	0.33	10%
Red-shouldered Hawk (*Buteo lineatus*)	11	0.45	10%	11	0.45	10%	2	0.00	0%
Broad-winged Hawk (*Buteo platypterus*)	10	0.00	0%	9	0.00	0%	7	0.00	0%
Swainson's Hawk (*Buteo swainsoni*)	7	0.57	10%	5	1.00	25%	15	0.86	40%
Red-tailed Hawk (*Buteo jamaicensis*)	48	0.21	5%	54	0.26	10%	27	0.37	20%
Ferruginous Hawk (*Buteo regalis*)	23	0.13	5%	10	0.50	5%	5	0.60	10%
Rough-legged Hawk (*Buteo lagopus*)	16	0.31	5%	10	0.50	15%	4	1.00	10%
Golden Eagle (*Aquila chrysaetos*)	6	0.17	5%	9	0.22	5%	3	1.00	5%
Merlin (*Falco columbarius*)	51	0.04	5%	33	0.33	15%	18	0.50	50%
Gyrfalcon (*Falco rusticolus*)	15	0.07	10%	12	0.42	30%	5	0.20	25%
Peregrine Falcon (*Falco peregrinus*)	27	0.19	10%	13	0.46	25%	13	0.85	20%
Prairie Falcon (*Falco mexicanus*)	24	0.29	15%	12	0.50	15%	9	0.89	20%

White-tailed Kite and 183 specimens of American Kestrel collected between September and May of their first year. A partial to complete body-feather molt during the first fall was confirmed for all individuals of both of these species. Proportions of replaced feathers indicated that, in both species, this molt had completed or nearly completed by December, with little or no additional molt taking place during January–May, until initiation of the first complete molt. Examination of six White-tailed Kites and 15 American Kestrels undergoing their first complete molt and 73 kites and 274 kestrels in definitive plumage (showing uniform body plumage) confirmed that another complete body

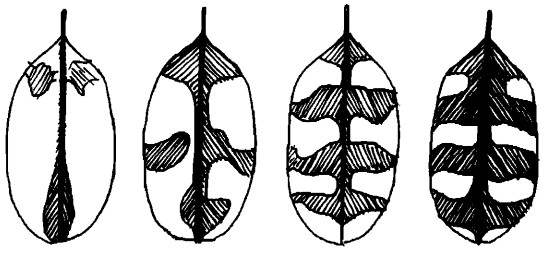

Figure 1. Pigment patterns on underpart feathers of Cooper's Hawks. A—Typical juvenal feather; B—Formative feather replaced in September (CAS62145); C—Formative feather replaced in January (CAS33560); D—Typical definitive feather.

molt occurs in these species concurrent with the flight-feather molt at a year of age.

In White-tailed Kite, 13 first-year individuals collected between January and the initiation of the first complete molt (with shedding of the innermost primaries) had replaced a mean 97.7% of body feathers. All 13 kites had replaced at least some lesser coverts (but no median coverts) and the central two to all 12 rectrices ($\bar{x}$ = 6.9 feathers). In addition, five individuals were found that had replaced 2–6 secondaries during the partial molt, symmetrically on both wings and apparently in the same sequence as observed in complete molts, as determined from clines in wear. The two specimens with the most extensive partial first-year molts were collected in California: MVZ24493 (10 January) and CAS73280 (22 February), each with 100% of the body feathers, all 12 rectrices, and s1–s2, s5, and s11–s13 replaced. No primaries had been replaced during this molt in any individual.

In American Kestrel, 92 individuals collected between their first January and the initiation of the first complete molt had replaced a mean of 90.8% of body feathers. The amount of feathers replaced ranged from 40% of the body and no wing coverts (CAS 73504 collected 26 April) to 100% of the body feathers, all lesser coverts, and up to three proximal median coverts, but no flight feathers (several specimens).

First-year Molts in other North American Falconiformes. Evidence of body-feather replacement prior to initiation of primary molt was recorded in 16 North American Falconiformes (all but Northern Goshawk and Broad-winged Hawk; Table 1). Replaced feathers were observed primarily on the back and breast (Fig. 2). Specimens collected in fall and early winter had replaced some feathers on the crown, throat, and upper back; whereas many spring specimens had replaced larger scapulars and some breast feathers, but had retained most to all feathers of the crown, upper back, and throat. Newly-replaced feathers on the underparts tended to show patterns resembling juvenal feathers when molted in fall and definitive feathers when molted in spring, with a clinal rate of pattern change with time (Fig. 1). The seasonal timing at which definitive characteristics in these feathers were acquired appeared to vary, occurring during the late fall and winter in some species (e.g., Sharp-shinned Hawk, Red-shouldered Hawk, and Peregrine Falcon) and during the spring or later in others (e.g., Swainson's and Rough-legged hawks).

Extent of this molt showed substantial intraspecific and interspecific variation (Table 1). Among the 16 species showing these molts, the mean maximum recorded extent for all species combined was 25.6%, varying from 5% in Golden Eagle to 50% in Northern Harrier and Merlin (Table 1). Examples of specimens showing extensive body-feather replacement included Northern Harrier MVZ144731 (collected in March with 35% replacement), Sharp-shinned Hawk MVZ99723 (May, 45%), Swainson's Hawk CAS13889 (April, 40%), Red-tailed Hawk CAS27181 (April, 20%), Rough-legged Hawk MVZ173433 (December, 20%), and Peregrine Falcon CAS73587 (December, 25%; Fig. 2). On the other hand, at least some individuals (11–80%) of 12 species (or 11–100% of 14 species when Northern Goshawk and Broad-winged Hawk are included) collected in March–May showed no feather replacement (Table 1), and six specimens were recorded that had begun shedding primaries during the first complete molt, but remained in complete juvenal body plumage. No first-year birds of these 22 species showed symmetrical replacement of any flight feathers prior to initiation of the first complete molt.

Two replacement patterns according to season were observed among these 16 species (Table 1, Fig. 3). In Northern Harrier, Sharp-shinned, Cooper's, Gray, and Ferruginous hawks, Merlin, and Peregrine and Prairie falcons, molt had commenced in few birds in fall, some birds in winter, and most birds in spring. In Osprey and Red-shouldered, Red-tailed, and Rough-legged hawks, molt had occurred in some birds in fall, appeared to be suspended in many birds over winter, and was re-

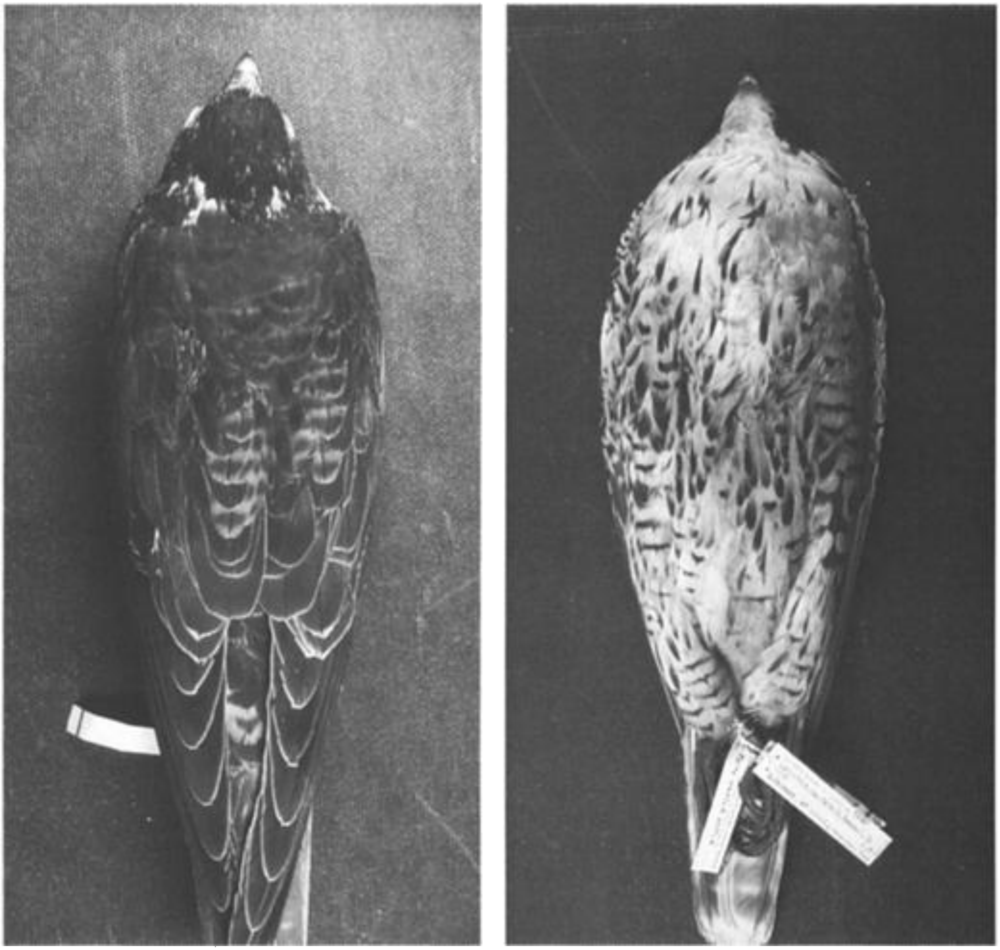

Figure 2. Dorsal and ventral aspects of a first-year Peregrine Falcon (*F. p. anatum*) collected 15 December in California (CAS73587) showing evidence of 25% body-feather replacement during a preformative molt (see Discussion). Formative feathers on the dorsum are bluish and barred, and formative feathers on the underparts are unstreaked (breast) and barred (belly and flanks), resembling definitive feathers in these regions.

sumed or initiated in some birds in spring. The patterns for Bald and Golden eagles, Swainson's Hawk, and Gyrfalcon appeared to be intermediate, with molt occurring throughout the first year (Table 1).

Feather-replacement Patterns in Second-year Birds. Totals of 27 birds collected while undergoing the first complete molt and 146 second-year (12–24 mo-old) birds following completion of this molt were examined, including at least six individuals of all species in Table 1, except for Gray Hawk, Red-shouldered Hawk, and Merlin, for which second-year and older individuals could not be distinguished. For the smaller species (including all falcons), there was no evidence that feathers replaced during the first fall, winter, or spring had been retained during the first complete molt. All 27 birds undergoing this complete molt appeared to be replacing all body feathers (or most feathers in the case of the larger species; see below). On second-year birds that had completed body molt, all scapulars as well as crown, back, and underpart feathers were uniform in wear, reflecting a complete molt within a relatively short time period. For the three species mentioned above, examination of 75 birds in definitive plumage (likely including second-year birds) also showed no variation in feather wear. For five of the larger species, Osprey, Bald and Golden

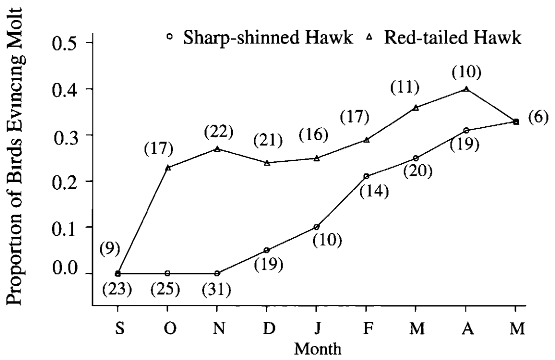

Figure 3. Proportion of individuals evincing body molt, by month, in two species of North American Falconiformes showing differing seasonal-replacement strategies.

eagles, and Red-tailed and Ferruginous hawks, variation in wear among the body feathers precluded confirmation that feathers replaced during the first year were replaced again during the first complete molt. In the two species of eagle, up to many juvenal body feathers could be retained during the first "complete" molt, so it is possible that feathers replaced during the first year may also have been retained during this molt.

DISCUSSION

Traditionally, both the partial first-fall molts of North American Kestrels and kites and the complete molts of other 1-yr-old Falconiformes have been considered the "first prebasic molts," according to the molt terminology of Humphrey and Parkes (1959). However, Howell and Corben (2000) suggested that the complete first prebasic molts of most Falconiformes may be homologous with the second prebasic molts of kestrels, kites, and most other birds. Accordingly, Howell et al. (2003) proposed a revised molt terminology for the first cycle, redefining the *prejuvenal molt* as synonymous with the *first prebasic molt,* the complete molt at the end of the first molt cycle as the *second prebasic molt,* and any inserted molts during the first cycle as *preformative molts.*

Evidence of body-feather replacement during the first year was found in 18 of 20 species examined and, for at least 15 species, the "first complete molt" appeared to include those feathers replaced during the first cycle. By definition (Humphrey and Parkes 1959, Howell et al. 2003), the additional body-feather replacement during the first year should be considered separate, inserted molts; using the terminology of Howell et al. (2003), they should be considered preformative molts followed by the complete or near-complete second prebasic molt at a year of age. Under the terminology of Humphrey and Parkes (1959), the "first prebasic molt" referred to the limited body-feather molt during the first fall, winter, or spring of some individuals or species and to the complete molt at a year of age in other individuals, even within species (*cf. Elanus caeruleus* in Marchant and Higgins 1993), and presumed homology between individuals and species was lost.

In the remaining two species, Northern Goshawk and Broad-winged Hawk, evidence of preformative molts may have been missed in this study due to low sample sizes, especially in spring. Indeed, body-feather replacement during the first year has been reported for Northern Goshawk (Bent 1937, Dement'ev and Gladkov 1951, Forsman 1999). A first-year Broad-winged Hawk (Slater Museum of Natural History No. 2367) collected 1 June reportedly had replaced some breast feathers (Clark and Anderson 1984), although this individual had initiated the second prebasic molt (D. Paulson pers. comm.). It is possible that the constraints of migration may preclude the occurrence of a preformative molt in Broad-winged Hawk; however, substantial evidence of this molt was found in the migratory Swainson's Hawk. In general, birds that migrate to the tropics or Southern Hemisphere often display more extensive first-winter molts, possibly due to more abundant and stable food resources and greater day-lengths with which to forage (Myers et al. 1985, Pyle 1998). Thus, preformative molts should be expected in some Broad-winged Hawks. The evidence, therefore, suggests that preformative molts likely occur in at least some individuals of all North American Falconiformes.

Including the pattern of White-tailed Kite and American Kestrel, three seasonal strategies of preformative molt were identified. Consideration of the ecology and life history of the species comprising each group revealed no evident explanations for conditions or constraints leading to each molt pattern. There appeared to be a slight phylogenetic component, with a majority of species among *Accipiter* and *Falco* delaying preformative molts until winter or spring (see Herremans and Louette 2000), whereas more species among *Buteo* initiated preformative molts in fall. Northerly breeding and wintering species also tended to show a greater amount of preformative molt in fall; perhaps first-year birds of these species can take advantage of abundant food resources in the fall, but suspend molting during winter when food becomes scarce. Such variation might also be expected within species that show a wide latitudinal breeding range. Within genera, smaller species (including White-tailed Kite and American Kestrel) generally showed higher proportions of birds molting a greater amount of feathers. This correlation is expected based on the added energy required to replace larger feathers (Lindström et al. 1993), and may also be part of a signaling mechanism for species more likely to undergo breeding in their first year (Kemp 1999, Herremans and Louette 2000). Finally, species inhabiting open areas exposed to higher amounts of UV radiation appeared to undergo more extensive preformative molts. However, there were exceptions to all of these patterns, and it is likely that the extent and timing of preformative molts in Falconiformes reflect various constraints according to a complex combination of species-specific, breeding, migrating, and foraging strategies.

Replacement patterns by season indicate that breast feathers and scapulars can be molted later in winter or spring during preformative molts, while juvenal crown, throat, and upper back feathers had been retained, an unusual sequence of feather replacement for Falconiformes (Palmer 1988, Wheeler 2003). This suggests a triggering mechanism for the preformative molt, by which body molt of some feathers is bypassed, resulting in spring birds initiating molt at a later point in the sequence. Thus, sequence as well as extent may vary individually, depending on initiation date. Similarly, hormonal processes controlling feather pattern appear to develop clinally throughout the first year (and sometimes beyond), resulting in delayed acquisition of definitive plumage that varies in timing by species. In Swainson's Hawk and Crested Caracara (*Caracara cheriway*), acquisition of definitive plumage is delayed until the following summer or later, resulting in identifiable second-basic plumages, intermediate in pattern between juvenal and definitive plumages (Wheeler 2003). For the two eagle species, acquisition of definitive plumage requires up to 4 or 5 yr to complete.

Within many species, the preformative molt appears to occur in only a proportion of individuals, with some birds retaining full juvenal plumage until the second prebasic molt. Similar variation in the preformative molt was found among Eurasian *Accipiters* (Herremans and Louette 2000). Thus, some individuals exhibit a "Simple Basic Strategy" (lacking a preformative molt) whereas others exhibit a "Complex Basic Strategy" (including a preformative molt, but lacking prealternate molts) according to Howell et al. (2003). However, at the species level, Falconiformes are best described as exhibiting the Complex Basic Strategy, with the preformative molt ranging in extent from absent to partial.

Evolutionarily, the existence of these variable and at times ephemeral preformative molts may suggest that ancestral Falconiformes exhibited more extensive preformative molts that have become vestigial in most (larger) species that do not breed at age one and can commence the second prebasic molt at an earlier age (Wheeler 2003). Phylogenetic evidence suggests that ancestral Falconiformes branched from a common ancestor that also included Podicipediformes, Pelecaniformes, and Ciconiformes (Sibley and Ahlquist 1990), orders which currently display extensive preformative molts (Palmer 1962, Howell et al. 2003). Alternatively, it is possible that these preformative molts in Falconiformes have become inserted over time, from an ancestral species that lacked such molts; however, the apparent lack of functionality for these molts may argue against this alternative hypothesis. A better understanding of molt and plumage homologies in Falconiformes awaits further study of both molts and phylogenetic relationships.

ACKNOWLEDGMENTS

I thank Jack Dumbacher and Douglas J. Long (CAS), Carla Cicero (MVZ), and James Dean (USNM) for access to collections under their care and Dennis Paulson of the Slater Museum of Natural History, Puget Sound, WA, for examining a specimen of Broad-winged Hawk for me. The manuscript benefited from comments by Steve N.G. Howell, Christopher W. Thompson, William S. Clark, Josef K. Schmutz, and Marc Herremans. Funding for the study of molts and plumages was provided by the Neotropical Migratory Bird Conservation Act (grant No 2601) administered by the U.S. Fish and Wildlife Service. This is Contribution No. 232 of The Institute for Bird Populations.

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Received 12 February 2004; accepted 6 June 2005
Associate Editor: Ian G. Warkentin