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REMIGIAL MOLT PATTERNS IN NORTH AMERICAN FALCONIFORMES AS RELATED TO AGE, SEX, BREEDING STATUS, AND LIFE-HISTORY STRATEGIES

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Abstract. Examination of 1622 specimens indicates that North American Falconiformes show a wide variety of remigial (primary and secondary) replacement strategies, detectable throughout the year by evaluation of replacement patterns in the wings. Most Falconidae undergo complete prebasic molts whereas most Accipitridae display retained secondaries or show stepwise molt replacement patterns (''*Staffelmäuser*''). Among individuals exhibiting *Staffelmäuser,* minimum age can be inferred up to 5 years (fifth-basic plumage) by the number of ''replacement waves'' present among the primaries. It may also be able to infer breeding status during the previous summer by ''suspension limits,'' resulting from the interruption of molt during breeding. Among Accipitridae, *Staffelmäuser* occurred in species with greater mass, higher wing loading, longer migration distance, and more open rather than wooded foraging habitats: species that experience time constraints on molting and incur greater costs from large gaps in the wing. Thus, this study supports both the ''time-constraints hypothesis,'' suggesting that *Staffelmäuser* is a consequence of insufficient time for a complete annual molt, and the ''aerodynamic hypothesis,'' suggesting that *Staffelmäuser* reflects an adaptive need to replace as many feathers as possible without inhibiting flight efficiency. Time constraints may have been a proximate cause of *Staffelmäuser* among Falconiformes, with improvements to flying efficiency being an ultimate adaptive benefit.

Key words: *age, breeding status, Falconiformes, flight efficiency, molt, raptors, Staffelmäuser.*

Patrones de Muda de las Plumas del Vuelo en Falconiformes Norteamericanos en Relación con la Edad, Sexo, Estado Reproductivo y Estrategias de Historia de Vida

Resumen. El examen de 1622 especímenes indica que los Falconiformes norteamericanos muestran una gran variedad de estrategias de reemplazo de plumas del vuelo (primarias y secundarias), que pueden ser detectadas a lo largo de un año, evaluando los patrones de reemplazo en las alas. La mayoría de los Falconidae realizan mudas prebásicas completas, mientras que la mayoría de los Accipitridae retienen las plumas secundarias o muestran un patrón de reemplazo con muda en etapas (''*Staffelmäuser*''). Entre los individuos que exhiben ''*Staffelmäuser*'', la edad mínima se puede inferir hasta 5 años (quinto plumaje básico) por el número de ''ondas de reemplazo'' presentes entre las primarias. También puede ser posible inferir el estado reproductivo durante el verano anterior por los ''límites de suspensión'' que resultan debido a la interrupción de la muda durante la reproducción. Entre los Accipitridae, el *Staffelmäuser* ocurrió en especies con mayor peso, mayor carga alar, con distancias migratorias más largas y de hábitats de forrajeo más abiertos que boscosos: especies que presentan restricciones de tiempo durante la muda y especies que incurren en un mayor costo debido a los grandes huecos en las alas. Así, este estudio apoya tanto la ''hipótesis de restricción de tiempo'', sugiriendo que el *Staffelmäuser* es una consecuencia del tiempo insuficiente para completar una muda anual, y la ''hipótesis aerodinámica'', que sugiere que el *Staffelmäuser* refleja una necesidad adaptativa de reemplazo de la mayor parte posible de las plumas sin inhibir la eficiencia del vuelo. Las restricciones de tiempo pueden haber sido una causa proximal del *Staffelmäuser* en los Falconiformes, con un mejoramiento de la eficiencia del vuelo como un beneficio adaptativo esencial.

INTRODUCTION

Substantial resources are needed to molt large flight feathers in birds (Murphy and King 1991, Lindström et al. 1993), such that constraints of breeding and migration may preclude the ability to replace all remiges within a single molting cycle (Langston and Rohwer 1996, Shugart and Rohwer 1996). In response, large birds have developed various remigial molt strategies to allow replacement of as many feathers as possible

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while minimizing costs to survival and flying efficiency. These strategies include synchronous replacement of all remiges within a short time period (e.g., among loons, grebes, waterfowl, and alcids), replacement of fewer than all remiges during a prebasic molt (e.g., among albatross, owls, and woodpeckers), and stepwise molt or ‘‘*Staffelmäuser*’’ (Stresemann and Stresemann 1966, Ashmole 1968, Snyder et al. 1987, Clark 2004). The last strategy results in multiple ‘‘replacement waves’’ among the remiges and is hypothesized either to allow a greater number of feathers to be replaced while avoiding flight-inhibiting gaps in the wing (Stresemann and Stresemann 1966, Tucker 1991), or as an indirect consequence of individuals not having enough time to replace all feathers within an annual cycle (Shugart and Rohwer 1996). *Staffelmäuser* has been documented in larger taxa, including Pelicaniformes, herons, and condors, that depend on continuous flight throughout the molting period to forage and avoid predation.

The establishment of incomplete molt strategies and *Staffelmäuser* follow predicated sequences of remigial replacement. Among Falconiformes, two different replacement sequences occur during prebasic molts (Bond 1936, Miller 1941, Stresemann 1958, Willoughby 1966; Fig. 1). In Accipitridae (ospreys, kites, hawks, and eagles), primaries are replaced distally from the innermost (p1) to the outermost (p10) and secondaries are replaced proximally from the outermost (s1), proximally from s5, and distally from the tertials (s11–s13 in most species); whereas in Falconidae (caracaras and falcons), remiges are replaced both proximally and distally from nodes at p4–p5 and s4–s5. Although both incomplete replacement of secondaries and *Staffelmäuser* have been reported among some species of Accipitridae (Stresemann and Stresemann 1960, Bierregaard 1974, Prevost 1983, Edelstam 1984, Schmutz 1992, Bloom and Clark 2001), details of these strategies in most species are poorly documented or unknown (*cf.* Poole and Gill 1993–2004, Wheeler 2003).

Breeding Falconiformes are also known to initiate prebasic molt of remiges during the incubation period, suspend this molt during the chick-feeding period, and resume it following the breeding season (Stresemann and Stresemann 1960). This strategy takes advantage of a time period (incubation) when other energy demands have relaxed to complete part of the annual molt (Newton and Marquiss 1982, Walsberg 1983, Pietäinen et al. 1984). Females often initiate this molt earlier than males and are less active during incubation (at which time males feed females), resulting in greater numbers of feathers being replaced. Remex-molt suspensions during the breeding season have been reported for several species of North American Falconiformes (Schmutz and Schmutz 1975, Henny et al. 1985, Espie et al. 1996) but, again, details remain poorly documented and the occurrence of this strategy has not been investigated in most species.

Replacement patterns of remiges can also be used to age Falconiformes through their second or third year of life (Baker 1993, Clark 2004). For example, retained juvenal secondaries among one generation of definitive secondaries indicates an individual in second-basic plumage (see Howell et al. 2003 for molt terminology) whereas two generations of definitive secondaries indicates an individual in at least its third-basic plumage. Likewise, it may be possible to infer age by the number of identifiable replacement waves resulting from *Staffelmäuser*, or to infer breeding status during the previous summer by evidence of molt suspension patterns, but these methods have not been explored.

Through the examination of 1622 specimens, I investigated remigial-replacement strategies in 27 species of North American Falconiformes. My goal was to document which strategies are employed by each species and to attempt inferring age and breeding status of individuals by examining replacement patterns among the remiges. I also compared remigial replacement strategies with age, sex, wing length, mass, breeding and wintering latitudes, migration distance, and habitat, to evaluate hypotheses regarding remigial replacement strategies within Falconiformes and among birds.

METHODS

Specimens of North American Falconiformes were examined at the California Academy of Sciences (CAS), San Francisco, the Museum of Vertebrate Zoology (MVZ), Berkeley, and the Golden Gate Raptor Observatory (GGRO), Sausalito, California. Although approximately 56% of the specimens were from California, the remainder included all subspecies collected throughout North America. Specimens included all individuals collected in at least their second year of life (in second basic plumage), thus excluding those less than a year old. Although limited or partial preformative (first-cycle) molts have recently been documented in most species of falconiformes in North America, only in the White-tailed Kite (see Table 1 for scientific names) can this molt include remiges (Pyle 2005). In all other species, juvenal remiges are retained during the first year of life and age can be determined by their thinner shape and the lack of patterns indicating prior replacement (Fig. 1). First-year raptors can also be distinguished by plumage (Clark and Wheeler 2001, Wheeler 2003).

Birds in their second year were aged by plumage in some species or the retention of juvenal feathers during the second prebasic molt, particularly among the lesser coverts, on the rump, or within the secondaries (Baker 1993, Wheeler 2003). Similarly, birds known to be in at least their third year (in third or definitive basic plumage; hereafter, ‘‘older’’ birds) were aged by plumage in some species and by the retention of definitive feathers from a previous generation. Sex was inferred by plumage in some species, size dimorphism (Snyder and Wiley 1976) in direct comparison with specimens of known sex, and information on the specimen label. Specimens collected during active remigial molt (n = 187) and individuals for which sex was not determined (n = 48) were not included in this study.

On each specimen the primaries and secondaries of the right wing were carefully examined for patterns of fading and wear indicating replacement strategies during the preceding prebasic molt. Birds were scored as showing 1) ‘‘uninterrupted replacement clines’’ without retained feathers, indicating that the previous molt had been a) complete, b) in typical sequence for the family (Accipitridae or Falconidae), and c) not suspended for breeding (Fig. 1); 2) uninterrupted replacement clines except for contrasts in wear (‘‘suspension limits’’) indicating suspension for breeding (Fig. 2); 3) an uninterrupted replacement cline among the primaries but retained feathers of previous generations among the secondaries (Fig. 3); or 4) replacement patterns among primaries indicating *Staffelmäuser* (Fig. 4). Each retained remex was identified as either juvenal or definitive according to its color and shape (Fig. 1 and 3).

Uninterrupted replacement clines were identified by each remex in the molt sequence being successively fresher than the preceding feather, without major contrasts in wear which would result from feather retention or suspension (Fig. 1B, D). Suspension limits were marked by major contrasts between adjacent feathers, the earlier feather in sequence being substantially more worn than the subsequent feather, indicating elapsed time between replacement of the two feathers (Fig. 2). Specimens collected in summer, after molt suspension but not showing active molt (*cf.* Newton and Marquiss 1982), were also included in this sample. Among certain migratory species (e.g., Gyrfalcon, Peregrine Falcon) similar limits may also result from suspension for migration, and this was considered when evaluating breeding-suspension limits in these species. Most individuals that had suspended molt for migration had replaced a greater number of feathers or had also suspended it for breeding, in which case the innermost limit in sequence was inferred to be that of suspension for breeding. Because of irregular sequences of feather replacement, it was not possible to confirm suspension patterns in individuals that also had retained secondaries or had undergone *Staffelmäuser*.

Staffelmäuser usually commences with incomplete replacement of primaries during the second prebasic molt (Ashmole 1968, Shugart and Rohwer 1996); thus, birds in second-basic plumage with retained juvenal outer primaries (Fig. 4A) were classified as showing *Staffelmäuser*. During each subsequent year a new ‘‘wave’’ of replacement commences at p1, while molt in the outer primaries resumes where it had arrested the previous year (Stresemann and Stresemann 1966, Prevost 1983, Bloom and Clark 2001). Depending on subsequent molt extents, multiple replacement waves may be detectable within the primaries (Fig. 4B–D). For each specimen the number of generations among the primaries was recorded, defined by the number of waves, birds with uninterrupted clines defined as showing one generation. Replacement waves were delimited by a substantially fresher feather located proximal to an adjacent, more worn feather (Fig. 4B–D), a result of replacement during a more recent molt. Care was taken not to confuse molt suspensions within the primaries (e.g., for breeding or migration) with replacement waves (Fig. 4B); suspensions were char-

TABLE 1. Sample sizes, remigial molt replacement strategies, and mean number of feathers replaced among 27 species of North American Falconiformes. Primary value includes proportions of individuals showing each strategy.

Species	Sex	*n*	Uninterrupted cline	Suspension limits[a]	Retained secondaries[a]	*Staffelmäuser*[b]
Osprey	F	10	0.00	– (–)	0.00 (0.0)	1.00 (2.5, 2–3)
(*Pandion haliaetus*)	M	13	0.54	– (–)	0.00 (0.0)	0.46 (1.7, 1–3)
Swallow-tailed Kite	F	6	0.83	0.17 (3.0)	0.00 (0.0)	0.00 (0.0, 1–1)
(*Elanoides forficatus*)	M	5	1.00	0.00 (0.0)	0.00 (0.0)	0.00 (0.0, 1–1)
White-tailed Kite	F	21	0.29	0.71 (5.9)	0.00 (0.0)	0.00 (0.0, 1–1)
(*Elanus leucurus*)	M	19	0.37	0.63 (4.7)	0.00 (0.0)	0.00 (0.0, 1–1)
Snail Kite	F	6	0.50	– (–)	0.17 (2.0)	0.33 (1.3, 1–2)
(*Rostrhamus sociabilis*)	M	4	0.25	– (–)	0.00 (0.0)	0.75 (1.8, 1–2)
Bald Eagle	F	7	0.00	– (–)	0.00 (0.0)	1.00 (2.9, 2–3)
(*Haliaeetus lecocephalus*)	M	9	0.00	– (–)	0.00 (0.0)	1.00 (2.8, 2–3)
Northern Harrier	F	37	0.43	0.46 (5.4)	0.11 (3.0)	0.00 (0.0, 1–1)
(*Circus cyaneus*)	M	44	0.70	0.25 (4.5)	0.05 (1.5)	0.00 (0.0, 1–1)
Sharp-shinned Hawk	F	66	0.47	0.28 (4.7)	0.25 (2.4)	0.00 (0.0, 1–1)
(*Accipiter striatus*)	M	80	0.78	0.05 (3.8)	0.17 (1.8)	0.00 (0.0, 1–1)
Cooper's Hawk	F	55	0.22	0.62 (4.8)	0.16 (2.2)	0.00 (0.0, 1–1)
(*A. cooperi*)	M	59	0.37	0.29 (4.3)	0.34 (2.3)	0.00 (0.0, 1–1)
Northern Goshawk	F	28	0.04	0.25 (3.4)	0.71 (2.8)	0.00 (0.0, 1–1)
(*A. gentilis*)	M	43	0.16	0.09 (2.3)	0.70 (2.7)	0.05 (1.1, 1–2)
Gray Hawk	F	16	0.19	– (–)	0.13 (1.5)	0.69 (2.2, 1–3)
(*Asturina nitida*)	M	15	0.20	– (–)	0.07 (1.0)	0.73 (2.0, 1–3)
Common Black-Hawk	F	10	0.10	– (–)	0.10 (2.0)	0.80 (2.3, 1–3)
(*Buteogallus anthracinus*)	M	8	0.13	– (–)	0.00 (0.0)	0.88 (2.5, 1–4)
Harris's Hawk	F	10	0.00	– (–)	0.00 (0.0)	1.00 (2.8, 2–4)
(*Parabuteo unicinctus*)	M	12	0.08	– (–)	0.00 (0.0)	0.92 (3.1, 1–4)
Red-shouldered Hawk	F	31	0.48	0.52 (5.1)	0.00 (0.0)	0.00 (0.0, 1–1)
(*Buteo lineatus*)	M	36	0.78	0.22 (3.6)	0.00 (0.0)	0.00 (0.0, 1–1)
Broad-winged Hawk	F	14	0.14	– (–)	0.07 (1.0)	0.79 (2.6, 1–4)
(*B. playtypterus*)	M	17	0.18	– (–)	0.06 (1.0)	0.76 (2.4, 1–4)
Swainson's Hawk	F	35	0.06	– (–)	0.11 (1.5)	0.83 (2.9, 1–5)
(*B. swainsoni*)	M	39	0.21	– (–)	0.05 (1.5)	0.74 (2.5, 1–4)
White-tailed Hawk	F	7	0.00	– (–)	0.00 (0.0)	1.00 (3.9, 3–5)
(*B. albicaudatus*)	M	8	0.00	– (–)	0.00 (0.0)	1.00 (3.3, 2–5)
Zone-tailed Hawk	F	5	0.00	– (–)	0.00 (0.0)	1.00 (3.4, 2–4)
(*B. albonatatus*)	M	7	0.00	– (–)	0.00 (0.0)	1.00 (3.4, 2–4)
Red-tailed Hawk	F	95	0.02	– (–)	0.02 (1.5)	0.96 (3.3, 1–5)
(*B. jamaicensis*)	M	117	0.05	– (–)	0.02 (2.0)	0.93 (3.4, 1–5)
Ferruginous Hawk	F	15	0.00	– (–)	0.00 (0.0)	0.87 (2.7, 1–4)
(*B. regalis*)	M	17	0.24	– (–)	0.00 (0.0)	0.71 (2.5, 1–5)
Rough-legged Hawk	F	16	0.00	– (–)	0.00 (0.0)	1.00 (3.2, 2–4)
(*B. lagopus*)	M	19	0.00	– (–)	0.00 (0.0)	1.00 (3.4, 2–5)
Golden Eagle	F	12	0.00	– (–)	0.00 (0.0)	1.00 (3.6, 2–5)
(*Aquila chrysaetos*)	M	12	0.00	– (–)	0.00 (0.0)	1.00 (3.6, 3–4)
Crested Caracara	F	6	0.83	0.17 (3.0)	0.00 (0.0)	0.00 (0.0, 1–1)
(*Caracara plancus*)	M	13	0.46	0.53 (3.9)	0.00 (0.0)	0.00 (0.0, 1–1)
American Kestrel	F	170	0.95	0.05 (2.1)	0.01 (1.0)	0.00 (0.0, 1–1)
(*Falco sparverius*)	M	197	1.00	0.00 (0.0)	0.00 (0.0)	0.00 (0.0, 1–1)
Merlin	F	26	0.58	0.42 (4.2)	0.00 (0.0)	0.00 (0.0, 1–1)
(*F. columbarius*)	M	40	0.38	0.60 (2.5)	0.03 (1.0)	0.00 (0.0, 1–1)
Gyrfalcon	F	9	0.22	0.78 (4.4)	0.00 (0.0)	0.00 (0.0, 1–1)
(*F. rusticolus*)	M	3	1.00	0.00 (0.0)	0.00 (0.0)	0.00 (0.0, 1–1)
Peregrine Falcon	F	18	0.39	0.61 (4.1)	0.00 (0.0)	0.00 (0.0, 1–1)
(*F. peregrinus*)	M	13	0.46	0.54 (5.6)	0.00 (0.0)	0.00 (0.0, 1–1)
Prairie Falcon	F	24	0.41	0.58 (5.6)	0.00 (0.0)	0.00 (0.0, 1–1)
(*F. mexicanus*)	M	18	0.44	0.55 (2.7)	0.00 (0.0)	0.00 (0.0, 1–1)

[a] Mean number of feathers replaced before suspension or during incomplete molts shown in parentheses, excluding individuals showing no replacement. Values for suspension limits could not be calculated for individuals showing *Staffelmäuser*.

[b] Mean and range of generations shown in parentheses, as defined by replacement waves, among the primaries of the entire sample.

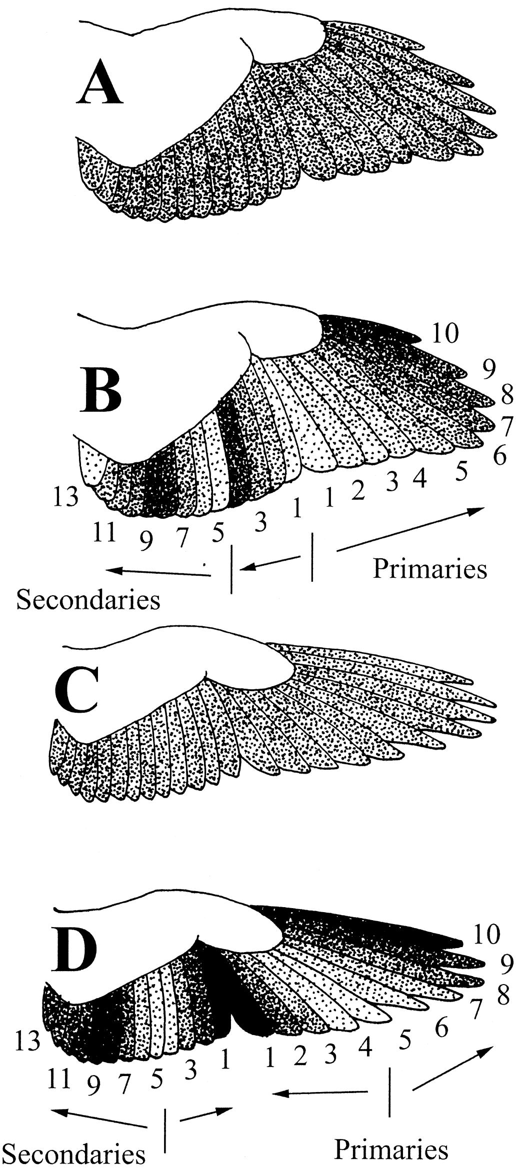

FIGURE 1. Feather shapes of adult and juvenile remiges, remigial replacement sequences, and replacement clines in Accipitridae (A, B) and Falconidae (C, D). Shading indicates age and wear, from older (paler) to newer (darker) feathers. Individuals in their first year (A, C) exhibit uniformly worn remiges whereas those having undergone a complete molt (B, D) show uninterrupted replacement clines, representing a gradient in wear from fresher to more worn feathers, according to the sequence of replacement. Note that the tertials become relatively more worn (and are shown as paler) due to wear rather than replacement strategies.

acterized by a more distal feather being substantially fresher (rather than more worn) than an adjacent proximal feather.

I categorized the 27 species by size, breeding and winter latitudes, migration distance, and habitat. Size variables included mean wing length and mass, by sex, from Snyder and Wiley (1976) and Palmer (1988). Mass was log transformed to normalize this variable. Mean breeding and wintering latitudes were calculated by plotting the midpoint of respective ranges of each species as listed by the American Ornithologists' Union (1998) and through consultation of range maps in Poole and Gill (1993–2004). Mean migration distance was calculated as the difference between mean breeding and mean wintering latitudes. Habitat was scored as either open (11 species that spend all or almost all of their time foraging in open habitats) or wooded (10 species that spend some to most of their time foraging in wooded habitats).

Logistic regression analyses (Hosmer and Lemeshow 1989), using the program STATA (Stata Corporation 1997), were used to infer statistical significance among most comparisons, the dependent variable being molt strategy (whether or not it was employed at the individual or species level). Regression coefficients, standard errors of the coefficient, or *z*-statistics are reported.

RESULTS

The remiges of 1622 specimens of Falconiformes collected in second-basic or subsequent plumages were examined (Table 1). These included 1085 specimens of Accipitridae (502 females and 583 males; 183 birds in second-basic plumage and 543 older birds), and 537 specimens of Falconidae (253 females and 284 males; 21 birds in second-basic plumage and 11 older birds). Because sample sizes were small, age was not considered in further analyses of Falconidae.

UNINTERRUPTED REPLACEMENT CLINES

Uninterrupted replacement clines (Fig. 1B, D), reflecting complete and uninterrupted prebasic molts, were recorded in 22 of the 27 species (Table 1), being absent only in five larger species of Accipitridae that exhibited *Staffelmäuser* patterns in all individuals. Among the other 16 species of Accipitridae, the percentages of individuals (sexes combined) showing uninterrupted clines ranged from 4% in Red-tailed

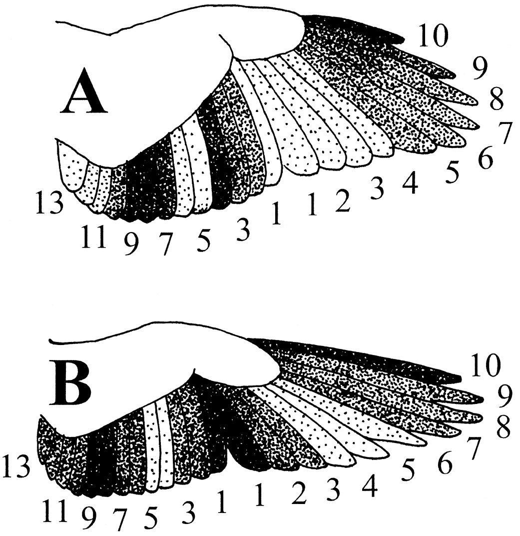

FIGURE 2. Typical examples of suspension limits, indicating interrupted molt during the previous season in breeding Accipitridae (A) and Falconidae (B). Shading indicates age and wear, from older (paler) to newer (darker) feathers. In A, primaries 1–4 and secondaries 1, 5, 6, and 11–13 were replaced in sequence (see Fig. 1) during incubation, followed by suspension of molt and resulting in suspension limits between p4 and p5, s1 and s2, s6 and s7, and s11 and s10. In B, the suspension limits occur between p3 and p4, p6 and p7, s3 and s4, and s5 and s6.

Hawk to 91% in Swallow-tailed Kite. Among the six species of Falconidae, uninterrupted clines ranged from 42% of Gyrfalcons and Peregrine Falcons to 98% of American Kestrels. Individuals of Falconidae were significantly more likely to show uninterrupted replacement clines than those of Accipitridae (logistic regression; $z = 18.9$, $P \leq 0.001$, $n = 1622$). This correlation remained significant after adjusting for wing length and mass ($z = 7.6$, $P \leq 0.001$).

Among Accipitridae, significantly more males than females showed uninterrupted replacement clines (Table 2). This difference was also significant for Osprey, Northern Harrier, Sharp-shinned Hawk, and Red-shouldered Hawk ($z > 2.3$, $P < 0.02$). Among Falconidae, the proportions of females and males showing uninterrupted clines were similar (Table 2), overall and for all six species ($z < 1.3$, $P > 0.20$). Among Accipitridae aged by plumage or retention of wing coverts or body feathers, a significantly higher proportion of birds in second-basic plumage (53 of 183) showed uninterrupted clines than older birds (13 of 543; $z = 8.7$, $P \leq 0.001$).

SUSPENSION LIMITS

Suspension limits (Fig. 2), indicating interrupted molt during the previous breeding season, were recorded in all seven species of Accipitridae that lacked *Staffelmäuser*, and in all six species of Falconidae (Table 1), ranging from 2% of American Kestrels to 67% of White-tailed Kites. Patterns of suspension limits and replacement clines indicated that, within each family, feathers were replaced in typical sequence prior to suspension (Fig. 2). Among the 13 species showing suspension limits (separated by sex), there were no significant effects of physical or environmental variables on the incidence of suspension limits (univariate and multivariate regression; $t < 1.8$, $P > 0.08$, $n = 26$).

Among the seven species of Accipitridae, suspension limits were recorded in a significantly higher proportion of females than males (Table 2), and this pattern was also significant in all three *Accipiter* species, Red-shouldered Hawk, and Northern Harrier (logistic regression; $z \geq 2.0$, $P \leq 0.05$). In addition, significantly more remiges (excluding tertials, which were difficult to assess due to increased exposure and wear) had been replaced during incubation by females (mean 6.0 feathers per female) than by males (4.7 feathers per male; ANOVA, $F_{1,165} = 10.7$, $P = 0.001$), and this difference was also significant in White-tailed Kite, Northern Goshawk, and Red-shouldered Hawk ($F > 4.8$, $P < 0.05$). Among birds that could be aged, suspension limits were found in only 5 birds in second-basic plumage (2 Sharp-shinned Hawks and 3 Cooper's Hawks) and 30 older birds, a significant age-related difference ($z = 3.5$, $P = 0.001$).

Among Falconidae, suspension limits were recorded in similar proportions of females and males (Table 2). Females with suspension limits outnumbered males in all species except Merlin (where 11 females and 24 males showed limits), but in none of these species were proportions significant ($z < 1.4$, $P > 0.15$). Numbers of remiges replaced during incubation were also similar among females (mean 3.6 feathers per female, all 6 species pooled) and males (mean 3.2 feathers per male; ANOVA, $F_{1,98} = 1.9$, $P = 0.17$).

RETAINED SECONDARIES

Retained secondaries with an uninterrupted cline in primaries (Fig. 3) were recorded in 11 species of Accipitridae (Table 1). Most species that

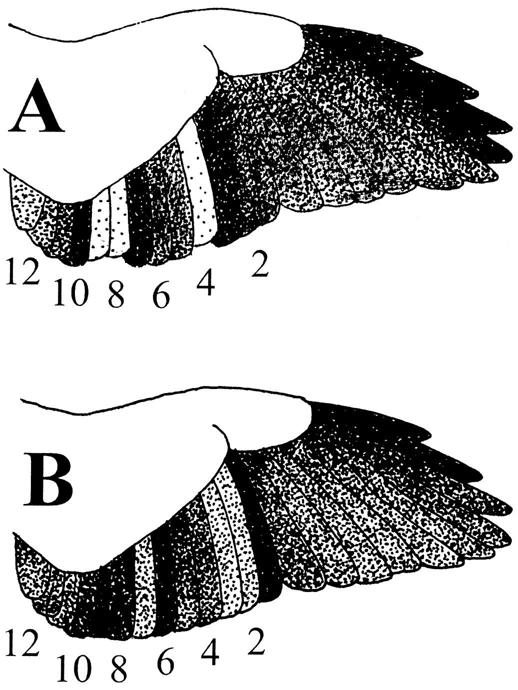

FIGURE 3. Examples of retained juvenal (A) and definitive (B) secondaries in Accipitridae, resulting from incomplete prebasic molts. Shading indicates age and wear, from older (paler) to newer (darker) feathers. Retained juvenal feathers are narrower and become more worn than definitive feathers, resulting in greater contrasts with adjacent replaced feathers than are found with retained definitive feathers. Note that the positions of retained juvenal secondaries (s4, s8 and s9) reflect the last feathers replaced during the normal sequence.

lacked this strategy had high proportions of *Staffelmäuser* patterns, in which both primaries and secondaries were retained. The percentage of specimens showing retained secondaries but replaced primaries ranged from 2% of Red-tailed Hawks to 70% of Northern Goshawks. Only two of 537 specimens of Falconidae were found with retained secondaries, an American Kestrel in second-basic plumage and an older Merlin, each of which had retained s1 on both wings.

Among the 11 species of Accipitridae, the proportions of females and males showing retained secondaries were very similar (Table 2). However, significantly more birds in second-basic plumage (41 of 147 that had retained juvenal secondaries) showed this molt strategy than older birds (101 of 523 that had retained definitive secondaries; logistic regression, $z = 2.3$, $P = 0.02$), although this pattern was not significant in any individual species ($z < 1.4$, $P > 0.15$). In descending order of frequency, retained juvenal secondaries were s8 (31 specimens), s7 (25), s4 (18), s3 and s9 (9 each), and s6 (2) and retained definitive secondaries were s8 (55 specimens), s7 (46), s9 (40), s4 (33), s3 (23), s6 (17), s10 (10), and s2 (3). Thus, the last feathers replaced during the normal sequence of molts are most frequently retained, especially during the second-prebasic molt.

STAFFELMÄUSER

Staffelmäuser (Fig. 4) was recorded in 15 of 21 species of Accipitridae but no species of Fal-

TABLE 2. Sex-specific differences in the occurrence of molt strategies among Falconiformes as inferred by logistic regression analysis. See text for definitions of the four molt strategies.

Molt strategy (*n*)[a]	Sex	*n*	Proportion	Coefficient	SE	*P*
Accipitridae						
Uninterrupted cline (16)	F	455	0.22			
	M	530	0.37	0.75	0.15	0.00
Suspension limits (7)	F	244	0.49			
	M	286	0.20	1.32	0.20	0.00
Retained secondaries (11)	F	377	0.16			
	M	443	0.17	0.00	0.19	0.99
Staffelmäuser (15)	F	283	0.81			
	M	345	0.76	0.31	0.20	0.11
Falconidae						
Suspension limits (6)[b]	F	253	0.21			
	M	282	0.17	0.23	0.22	0.30

[a] Analyses performed only on species showing each molt strategy (see Table 1).

[b] Proportions of individuals with uninterrupted clines among Falconidae are nearly the inverse of these data (see Table 1) and show a similar sex-specific correlation.

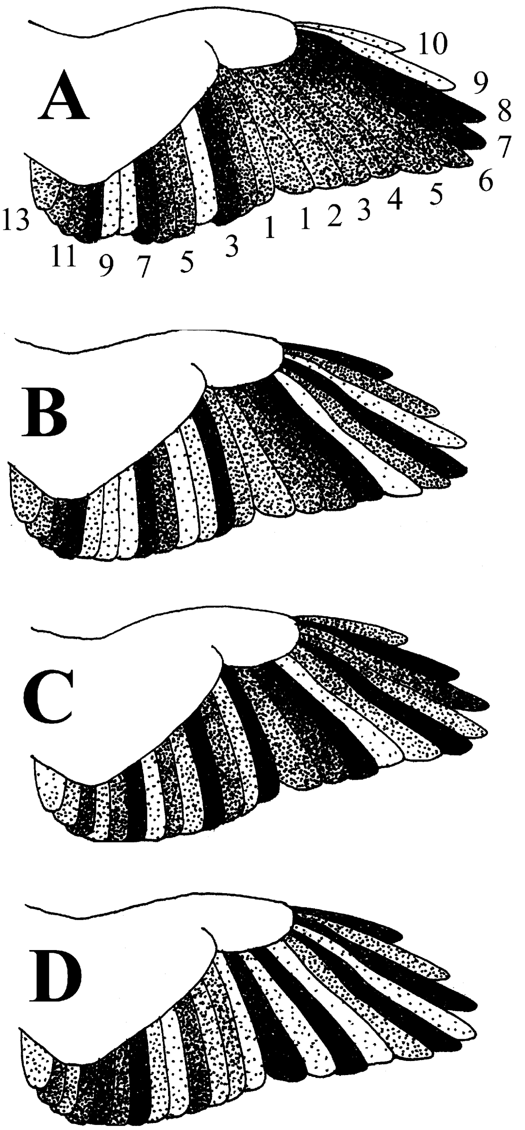

FIGURE 4. Examples of *Staffelmäuser* patterns in Accipitridae. Shading indicates age and wear, from older (paler) to newer (darker) feathers. A) A typical individual in second-basic plumage having retained juvenal outer primaries and medial secondaries during the second prebasic molt, and thus showing one wave and two feather generations. B) An individual in at least its third year showing three waves (terminating at p4, p7, and p10) and including a suspension limit for breeding between p5 and p6. C) An individual in at least its fourth year showing three waves (terminating at p3, p6, and p9) and four generations, p10 being from a previous generation. D) An individual in at least its fifth year showing five waves, terminating at p1, p3, p6, p8, and p10.

conidae (Table 1). The percent of individuals exhibiting *Staffelmäuser* ranged from 3% in Northern Goshawk to 100% in 5 species (Table 1). Similar proportions of females and males showed *Staffelmäuser* (Table 2), and this was also the case among each species (logistic regression; $z < 1.3$, $P > 0.2$). Of the 490 specimens showing *Staffelmäuser*, 77 were in second-basic plumage (having retained 1–7 juvenal outer primaries and 1–12 juvenal secondaries) and 413 were older. Among the 413 older birds, the number of feather generations among the primaries (defined by replacement waves) varied from 2 to 5, and among species the mean number of generations varied from 2.0 in Snail Kite and Northern Goshawk to 3.6 in Golden Eagle (Table 1). Mean number of generations was similar in females (3.3) and males (3.2; ANOVA, $F_{1,409} = 1.9$, $P = 0.17$).

Effects of physical and environmental parameters on the incidence of *Staffelmäuser* in Accipitridae, as determined with logistic regression analysis, are shown in Table 3. Univariate comparisons indicated that species exhibiting *Staffelmäuser* had longer wings, greater masses, longer migration distances, and resided in more open habitats. Mass appeared to have the strongest effect, whereas neither breeding nor wintering latitudes were significant. Multivariate logistic regression provided similar results, except that the correlation with wing length was negative rather than positive. Stepwise procedures indicated that effects of wing length were reversed solely by the addition of the mass term: adjusting for mass, species showing *Staffelmäuser* had shorter rather than longer wings (at the $P \leq 0.1$ level), whereas the reverse was the case when the mass term was omitted.

DISCUSSION

REMIGIAL REPLACEMENT STRATEGIES

Results of this study indicate that Falconiformes show a wide variety of remigial replacement strategies, detectable throughout the year by examination of wear patterns reflecting replacement clines, feather contrasts, and molt limits within the wings. Species of Falconidae typically replace all primaries and secondaries during each prebasic molt, whereas, adjusting for size, a significantly greater proportion of Accipitridae can retain secondaries or show *Staffelmäuser* replacement patterns. This indicates that the re-

TABLE 3. Physical and environmental effects on the incidence of *Staffelmäuser* in 21 species of North American raptors using multivariate logistic regression.[a]

Physical or environmental parameter	Coefficient	SE	z	P
Univariate analysis				
Wing length	0.01	0.01	2.59	0.01
$\text{Mass}_{\text{(Log transformed)}}$	3.40	1.03	3.02	0.00
Breeding latitude	–0.02	0.03	–0.75	0.46
Winter latitude	–0.02	0.02	–0.92	0.36
Migration distance	1.33	0.68	1.94	0.05
Habitat	–1.61	0.72	–2.23	0.03
Multivariate analysis[b]				
Wing length	–8.61	4.95	–1.74	0.08
$\text{Mass}_{\text{(Log transformed)}}$	16.19	7.95	2.04	0.04
Migration distance	0.22	0.11	2.08	0.04
Habitat	–0.41	0.19	–2.15	0.03

[a] For Accipitridae species the dependent variable was separated by sex ($n = 42$).

[b] Independent variables determined by backwards stepwise regression. For the overall model, $x^2 = 39.0$, $P = 0.00$, $R^2 = 0.75$.

placement sequence of Falconidae, with two simultaneous replacement waves proceeding both proximally and distally from centers in each remigial tract, may be a more efficient sequence in terms of replacing all remiges during a molt cycle than that of Accipitridae. This replacement sequence among the primaries is unique in birds and has apparently evolved more recently to enable annual complete molts among falcons.

Intraspecific variation in replacement strategies among Accipitridae suggests that individuals that were afforded enough time or resources to undergo a complete and uninterrupted prebasic molt show uninterrupted replacement clines. These include nonbreeding, one-year old birds and many males and some females, especially of smaller species, that presumably are able to undergo a continuous complete molt during or following breeding. Alternatively, larger birds and those that do not have the resources or time to replace all feathers will either retain secondaries or undergo *Staffelmäuser*. Although there may be a phylogenetic component affecting the occurrence of *Staffelmäuser* in older birds (e.g., it is found in most *Buteo* but few *Accipiter* species), its occurrence also varied at the individual level, from only small proportions of older Northern Goshawks and Black-shouldered Kites (*Elanus caeruleus*, Herremans 2000) to about half of Snail Kites, to most or all individuals of larger *Buteo* hawks and eagles. This suggests that, at least within Falconiformes, *Staffelmäuser* is not simply a consequence of heredity but also reflects time or resource constraints on molting (Shugart and Rohwer 1996; but also see below). The fact that *Staffelmäuser* occurs in such a wide variety of other taxa (e.g., Pelicaniformes, herons, condors), to varying degrees, may support this premise.

Suspension of molt during breeding was shown by all species in which a sizeable proportion of individuals also undergo complete and uninterrupted molts. The lack of a significant correlation between size and molt suspension could reflect a trade-off between the energy required to replace larger feathers and the increased incubation time to do so among larger species. Thus, it is likely that molt suspension during breeding is also shown by larger species that undergo *Staffelmäuser* but its detection is difficult among museum specimens. Studies of live birds at nesting sites may elucidate the frequency with which larger birds suspend molt during breeding.

Otherwise, results of this study on molt suspension for breeding are in accordance with published results: among Accipitridae a higher proportion of females suspend molt after replacing a greater number of feathers (Newton and Marquiss 1982, Henny et al. 1985), whereas among Falconidae results are more varied, with more male than female Merlins suspending molt (Espie et al. 1996). The incidence and extent of molt prior to suspension likely depends on variation in energy constraints according to both sex-specific and species-specific breeding strategies, energetic dynamics, and the physiological or hormonal, molt-related mechanisms involved in this suspension strategy.

DETERMINATION OF AGE AND BREEDING STATUS

Among Accipitridae, a high proportion of individuals can be aged as either in their second year (in second-basic plumage) or older (at least third-basic plumage) through analysis of retention patterns. Among species exhibiting *Staffelmäuser*, the minimum age of individuals can be determined up to their fifth year (fifth-basic plumage) by the number of generations present among the primaries. Complete replacement of primaries within a year is rare in most species that exhibit *Staffelmäuser*; for example, only 4 of 36 Red-tailed Hawks had replaced all primaries during the second prebasic molt and it is less likely that breeding individuals would have the time or resources to replace all feathers. Assuming that no more than 10 primaries are replaced during each cycle, the number of generations therefore indicates an individual's minimum age: those with three are at least in their third-basic plumage, those with four are at least in their fourth-basic plumage, and those with five (certain individuals among many species of *Buteo*) are at least in their fifth-basic plumage. Because of variation in the number of feathers replaced per molt, however, at least a small proportion of adults of most of these species undergo complete molts, presumably during years of early reproductive failure or greater resource availability. In addition, replacement waves may overtake preceding waves when resources allow greater numbers of primaries to be replaced (Prevost 1983). Thus, the specific age of individuals cannot be determined by the number of replacement waves, except when the outermost feathers can be recognized as juvenal, in which case the number of feather generations reflects the age in years (*cf.* Bloom and Clark 2001).

The occurrence and sex-specific findings on suspension limits in this study closely match that of direct nest studies on molt suspension (Newton and Marquiss 1982, Henny et al. 1985, Espie et al. 1996), suggesting that individuals showing these limits reproduced during the previous breeding season. Only five of 183 known-age individuals exhibiting suspension limits were in second-basic plumage and these were in two species (Sharp-shinned and Cooper's Hawks) known to regularly breed in their first year (Henny et al. 1985). Indeed, Rosenfield and Wilde (1982) reported that a breeding one-year-old male Cooper's Hawk had apparently suspended the second prebasic molt after replacing five inner primaries. Thus, it appears that only breeding birds, and possibly only those that reach the chick-rearing stage, suspend molt during the summer; therefore, suspension limits indicate breeding individuals and perhaps only those that were relatively successful.

LIFE-HISTORY IMPLICATIONS

Life-history parameters correlated with *Staffelmäuser* include mass, wing length, migration distance, and habitat preference. The lack of significant effects related to breeding and wintering latitudes indicates that daylight lengths and the timing and duration of breeding do not seem to have consistent effects on molting strategies among North American Falconiformes. Wing length was positively correlated with the occurrence of *Staffelmäuser* according to univariate analysis but became negatively correlated after adjusting for the more significant mass term. This implies an effect of wing loading (Pennycuick 1989) on this molt strategy: the higher the wing load the more likely the species is to exhibit *Staffelmäuser*. Thus, pressure on the wing in flight and bird mass appear to inhibit complete molts more than feather size as determined by the length of the primaries. *Staffelmäuser* was also found in species with longer migration distances and that inhabited more open substrates.

Shugart and Rohwer (1996) speculated that *Staffelmäuser* is a consequence of insufficient time for a complete annual molt (the time-constraints hypothesis) as opposed to an adaptive need to replace as many feathers as possible without inhibiting flight efficiency (the aerodynamic hypothesis). Results of this study support both hypotheses and, indeed, suggest that they are not mutually exclusive. In support of the time-constraints hypothesis is the finding that *Staffelmäuser* or *Staffelmäuser*-like replacement strategies occurred to varying extents in species that typically undergo complete primary molts, such as Northern Goshawk and Black-shouldered Kite. Individuals of these species exhibiting *Staffelmäuser* presumably had experienced years in which resources did not allow enough time to complete the molt (see also Reading 1990), and a *Staffelmäuser*-like molting regime ensued. Species with longer migration distances may also experience greater time constraints on molting.

In support of the aerodynamic hypothesis is the finding that species of high wing load and open habitat preference showed a higher incidence of *Staffelmäuser*, irrespective of bird size or other parameters which presumably constrain time or resources to molt. Birds with higher wing loading would incur a greater cost from large gaps in the wing (Tucker 1991), and those of open habitats are presumably more reliant on sustained flight than those of wooded habitats. The replacement sequence of Falconidae also could be an adaptation for the avoidance of large gaps in the wings during molt. Thus, it appears that time constraints may have been a proximate cause for *Staffelmäuser* but that its effects on flying efficiency has had ultimate adaptive benefits.

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LITERATURE CITED

American Ornithologists' Union. 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, DC.

Ashmole, N. P. 1968. Breeding and molt in the White Tern (*Gygis alba*) on Christmas Island, Pacific Ocean. Condor 70:35–55.

Baker, K. 1993. Identification guide to European non-passerines. BTO Guide 24. British Trust for Ornithology, Thetford, UK.

Bierregaard, R. O., Jr. 1974. Incomplete wing molt and erythrism in Red-tailed Hawks. Auk 91:618–619.

Bond, R. M. 1936. Molting of hawks, with special regard to the Duck Hawk. Condor 38:119–120.

Bloom, P. H., and W. S. Clark. 2001. Molt and sequence of plumages of Golden Eagles and a technique for in-hand ageing. North American Bird Bander 26:97–116.

Clark, W. S. 2004. Wave moult of the primaries in accipitrid raptors, and its use in ageing immatures, p. 795–804. *In* R. D. Chancellor and B.-U. Meyburg [eds.], Raptors worldwide. Proceedings of the 6th World Conference on Birds of Prey and Owls. Budapest, Hungary.

Clark, W. S., and B. K. Wheeler. 2001. A field guide to the hawks of North America. Houghton Mifflin, Boston, MA.

Edelsatm, C. 1984. Patterns of moult in large birds of prey. Annales Zoologici Fennici 21:271–276.

Espie, R. H. M., P. C. James, I. G. Warkentin, and L. W. Oliphant. 1996. Ecological correlates of molt in Merlins. Auk 113:363–369.

Henny, C. J., R. A. Olson, and T. L. Fleming. 1985. Breeding chronology, molt, and measurements of *Accipiter* hawks in northeastern Oregon. Journal of Field Ornithology 56:97–112.

Herremans, M. 2000. Cases of serial descendent primary moult (*Staffelmäuser*) in the Black-shouldered Kite. Ringing & Migration 20:15–18.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York.

Howell, S. N. G., C. Corben, P. Pyle, and D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105:635–653.

Langston, N. E., and S. Rohwer. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. Oikos 76:498–510.

Lindström, A., G. H. Visser, and S. Daan. 1993. The energetic costs of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66: 490–510.

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

Murphy, M. E., and J. R. King. 1991. Ptilochronology: a critical evaluation of assumptions and utility. Auk 108:695–704.

Newton, I., and M. Marquiss. 1982. Moult in the Sparrowhawk. Ardea 70:163–172.

Palmer, R. S. 1988. Handbook of North American birds. Vols. 4 and 5. Diurnal raptors (Parts 1 and 2). Yale University Press, New Haven, CT.

Pennycuick, C. J. 1989. Bird flight performance. Oxford University Press, Oxford, UK.

Pietäinen, H., P. Saurola, and H. Kolunen. 1984. The reproductive constraints on molt in the Ural Owl (*Strix uralensis*). Annales Zoologici Fennici 21:277–281.

Poole, A., and F. Gill [eds.]. 1993–2004. The birds of North America. The Birds of North America, Inc., Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Prevost, Y. 1983. The moult of the Osprey *Pandion haliaetus*. Ardea 71:199–209.

Pyle, P. 2005. Preformative molts in North American Falconiformes. Journal of Raptor Research, in press.

Reading, C. J. 1990. Molt pattern and duration in a female Northern Goshawk (*Accipiter gentilis*). Journal of Raptor Research 24:91–97.

Rosenfield, R. N., and J. Wilde. 1982. Male Cooper's Hawk breeds in juvenal plumage. Wilson Bulletin 94:213.

Schmutz, J. K. 1992. Molt of flight feathers in Ferruginous and Swainson's Hawks. Journal of Raptor Research 26:124–135.

Schmutz, J. K., and S. M. Schmutz. 1975. Primary molt in *Circus cyaneus* in relation to nest brood events. Auk 92:105–110.

Shugart, G. W., and S. Rohwer. 1996. Serial descendant primary molt of *Staffelmäuser* in Black-crowned Night Herons. Condor 98:222–233.

Snyder, N. F. R., and J. W. Wiley. 1976. Sexual size dimorphism in hawks and owls of North America. Ornithological Monographs 20:1–96.

Snyder, N. F. R., E. V. Johnson, and D. A. Clendenen. 1987. Primary molt of California Condors. Condor 89:468–485.

STATA Corporation. 1997. Stata statistical software: release 5.0. Stata Corporation, College Station, TX.

Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vögel. Journal für Ornithologie 107:1–448.

Stresemann, V. 1958. Sind die Falconidae ihrer Mauserweise nach eine einheitliche Gruppe? Journal für Ornithologie 99:81–88.

Stresemann, V., and E. Stresemann. 1960. Die Handschwingenmauser der Tagraubvögel. Journal für Ornithologie 101:373–403.

Tucker, V. A. 1991. The effect of molting on the gliding performance of Harris' Hawk (*Parabuteo unicinctus*). Auk 108:108–113.

Walsberg, G. E. 1983. Ecological energetics: what are the questions?, p. 135–158. *In* A. H. Brush and G. A. Clark Jr. [eds.], Perspectives in ornithology. Cambridge University Press, Cambridge, UK.

Wheeler, B. K. 2003. Raptors of western North America. Princeton University Press, Princeton, NJ.

Willoughby, E. J. 1966. Wing and tail molt in the Sparrow Hawk. Auk 83:201–206.