

SHORT COMMUNICATIONS

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VARIABLE RETENTION TIMES FOR RECTRICES AT DIFFERENT LOCI IN A GOLDEN EAGLE

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Perhaps the most obvious feature in the plumage of non-juvenile Golden Eagles (*Aquila chrysaetos*) is the presence of feathers from more than 1 year (Sushkin 1900, Tjernberg 1977, Bloom and Clark 2001). Even captive birds in good health, fed *ad libitum*, do not completely molt each yr (Jollie 1947). It is normal for all (or nearly all) head feathers to be of a single generation (all molted in one season; Ellis unpubl. data). Elsewhere on the body, conspicuously faded feathers lie interspersed with freshly grown feathers even in winter when contour molt has ceased (however, winter molt of a few feathers is not uncommon; Watson 1997, Bloom and Clark 2001, Ellis unpubl. data).

A minor focus in Jollie's (1947) detailed study of molt in the Golden Eagle was rectrix replacement rate. Decades later, Servheen (1976) compared Jollie's data for tail molt of one bird with his own data for two other Golden Eagles. From that treatment, Servheen concluded that center rectrices (loci R1 and L1) never molted less than 35 d apart and R1 is always molted before L1. Unfortunately, both of these studies involved only 1 or 2 yr of data.

Although the scientific literature is awash in articles on avian molt, most of these deal with either the hormone control of molt or they provide data based on one-time examination of many birds. After his extensive treatment of Golden Eagle molt based mostly on captive birds, Jollie (1947) stated: "The tail feathers have lost all semblance to order and irregularities are the rule. . . ." Here, we seek to define order in tail molt by identifying consistent patterns. Our data derive from a continuous 15-yr period for one Golden Eagle and short term observations of two other captive birds.

METHODS

We primarily monitored one adult female Golden Eagle (ca. 22-yr old when obtained from the Red Lodge Zoo, Montana; 45°N, 109°W). This bird was reportedly obtained as a nestling in Montana, was well adjusted to captivity, was received in October 1983, and laid eggs for many years. She was held for 2 yr near Oracle, AZ (32°N, 110°W), then held for 10 yr at two locations (39°N, 77°W and 38°N, 76°W) in the vicinity of Washington, DC. In 1995, she was returned to Oracle, AZ where she remains. The bird was held in outdoor facilities, where she was subject to local light and temperature regimes. During each molt season, the eagle had free range of one of six flight pens (3–7 m wide, 5–12 m long, and 2–3 m high).

Here, we describe her tail molt from 1984–98 inclusively. The value of our study lies in what it suggests about wild eagles and, to a lesser degree, about wild birds of other species. Obviously, this study could not have been performed with wild birds. In wild birds, propensity to molt is governed by body condition, hence by food intake. Whereas in captivity, the variables related to hunger level and body condition can be standardized by feeding *ad libitum*.

Our study then is a description of molt, not influenced by the variable of body condition. Our subject bird was normally fed once a day to satiation. Throughout the study, the bird was in good health as indicated by her well-formed feathers that showed normal coloration, and typically had very few "fault bars" (Grubb 1989). Second, the plumage in this eagle was much less worn and less faded than for wild adult eagles (museum specimens [pers. obs.] and adults observed at nests [Ellis 1979]). Third, the eagle flew well when flown free.

We inscribed on the calamus the date when each feather was dropped. Normally, we collected feathers on the same day they fell. We also refer to the tail molt in two other captive birds. We have five seasons of molt data for a bird taken as a nestling in July 1954 at Kluane Lake, Yukon Territory, Canada. These data were collected by a well-known raptorophile, the late Dr. Walter Spofford. For the second eagle, taken as a nestling in 1973 in Montana, we have three molt-years of data.

DATA ANALYSIS

We recorded feather-retention times in year and in month (to the nearest 0.5 mo). We did not record exact

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Table 1. Rectrix replacement history for an adult female Golden Eagle over a 15-yr period.

LOCUS	YEAR WHEN RECTRIX WAS REPLACED														$\bar{\chi}$ DURATION ^a	
	84	85	86	87	88	89	90	91	92	93	94	95	96	97		98
L6	X		X	X		X		X		X		X		X		1.8
L5	X		X		X		X		X		X		X		X	2.0
L4	X		X		X		X				X		X			2.4
L3	X			X		X		X		X			X		X	2.3
L2	X		X		X		X		X		X			X		2.2
L1	X	X		X	X	X		X		X		X		X		1.6
R1	X		X		X		X		X		X		X		X	2.0
R2	X	X		X		X		X		X		X			X	2.0
R3	X		X		X		X		X		X			X		2.0
R4	X			X		X		X			X		X			2.2
R5	X		X		X		X		X		X		X		X	2.0
R6	X		X	X		X		X		X		X		X		1.9
Total lost	12	2	8	6	7	6	5	7	5	5	7	4	6	5	5	

^a The mean retention time (arithmetic mean) for 14 potential molt seasons (for loci where a rectrix was lost in 1998) or for 12 or 13 potential molt seasons for feathers last replaced in 1996 or 1997.

molt dates for the first-molt year (1984) and for two other feathers, so we were able to measure retention times to the next molt for these 14 feathers only as the number of years. As a result, we have more, but coarser, data (78 retention times) based on yearly records, while for the monthly data, we have a more precise measure but fewer (64) retention times. All analyses were conducted both on yearly and monthly data. Results were similar so we present the statistical analyses only for the monthly data.

We analyzed the effect of side (left-right) and locus (rectrix position 1–6) on the intervals between molt of successive rectrices with a 2-way, fixed-effects, analysis of variance. We partitioned the locus factor into orthogonal-polynomial contrasts to test our hypothesis that feathers at mid-span loci at each side (i.e., loci 3, 4) are retained longer than those of loci 1, 2, 5, or 6. A significant-quadratic locus contrast indicates that a parabola best describes the locus effect (Steel and Torrie 1980). For all analyses, we used the statistical-software package Genstat (Version 5.4.1; Anonymous 1993).

RESULTS

Feather replacement for the 15-yr period is portrayed in Table 1. In 1984, tail molt for this adult was complete (i.e., 12 feathers replaced). Although many species of small raptors go through a complete, annual, tail molt, the maximum number of rectrices Bloom and Clark (2001) observed replaced in wild eagles in 1 yr was nine. This unusual 1984 tail molt may have been due to the change in diet or latitude and was likely due to the heavily-worn nature of the tail (suggesting that eagles have a physiological or behavioral mechanism to detect wear and remove heavily worn feathers). The female did not lay eggs in 1984, and breeding has long been recognized to disrupt, postpone, and otherwise interfere with molt (Ginn and Melville 1983), so this may have been a factor.

The stress of the move to Arizona or being tethered for the first winter may also have been involved (physiological stress as been associated with excessive molt in non-eagles; Payne 1972). After 1984, the eagle never lost more than eight feathers in one molt season (Table 1).

After the eagle replaced all 12 rectrices in one season, 3 yr were required before the eagle was routinely replacing ca. half of its rectrices each year (Table 1). For wild eagles, the number of rectrices dropped in one season ranged from 1–9 (Bloom and Clark 2001). Feathers at some loci were replaced more often than others (Table 1). The L and R central feathers (loci 1) and the outermost feathers or laterals (loci 6) were replaced most often (Fig. 1), whereas the feathers at loci 2–4 were retained longest (>2 yr).

A mean of 6.0 feathers were lost per year for the 15 molting seasons monitored (Table 1). If we exclude the three extreme years (1984–86; 12, 2, and 8 feathers), the mean was similar (5.7 feathers/yr; 1987–98). Overall the mean retention time of individual rectrices (Fig. 1) was 24.4 mo and ranged from 12–36 mo ($N = 63$).

The effect of locus (Table 2) was statistically significant ($F_{5,51} = 4.48, P = 0.002$) due to differences in retention times for feathers at different feather positions as indicated by the highly significant quadratic contrast of locus ($F_{1,51} = 18.99, P < 0.001$). Deviations from this parabolic shape of the locus effects were not significant ($F_{3,51} = 1.03, P = 0.388$).

Rectrix-retention time was symmetric (i.e., there was no significant effect of side), and the interactions between side and locus contrasts were nonsignificant (Table 2), so we pooled data for matched loci L and R and obtained the following least squares averages: 22.0 (± 1.2)

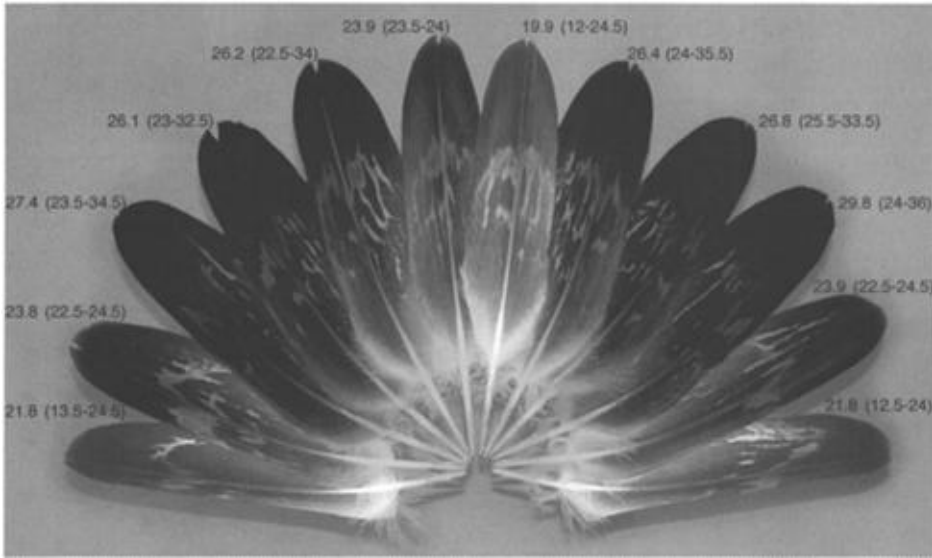


Figure 1. Tail showing mean retention times in months (arithmetic means [minimum and maximum retention times]) at all 12 feather loci. Feathers were digitally altered to reflect mean times. Lightened feathers were replaced more frequently, very dark feathers least frequently. Rectrices are numbered from the center (R1, L1) to R6 at lower left and L6 at lower right.

mo at loci 1; 26.3 (± 1.3) at 2; 26.3 (± 1.4) at 3; 28.5 (± 1.4) at 4; 23.9 (± 1.2) at 5; and 21.8 (± 1.2) at loci 6.

Rectrix molt usually extended from late May (8 of 13 yr) until early August (tail molt ended between the end of July and late August in 10 of 13 yr). At the earliest, the first rectrix fell in mid May; the latest date that the first rectrix fell was in late July. The earliest date of the last rectrix falling was in early July; the latest was early September.

DISCUSSION

The primary function of molt is the replacement of damaged feathers. Feather damage is known or believed to derive from abrasion, mechanical stress during flight, bleaching, fungal and bacterial decomposition, and ectoparasites (Burt 1979, Burt and Ichida 1999, Ginn and Melville 1983, Serra 2001). More heavily pigmented feathers are generally believed to wear better (Voitkevich 1966, Serra 2001). A bird could theoretically strengthen

Table 2. Effects of side and rectrix position (locus) on feather retention time in a female Golden Eagle from 1984–98. The effect of locus and its interactions with side were partitioned into orthogonal polynomial contrasts to test our hypothesis that mid-span feathers on each side (loci 3, 4) are retained longer than are central and marginal feathers (loci 1, 5, and 6).

SOURCE OF VARIATION	df	SS	F	P
Side	1	2.50	0.15	0.698
Locus	5	368.43	4.48	0.002
Linear contrast	1	5.68	0.35	0.559
Quadratic contrast	1	312.02	18.99	<0.001
Deviations	3	50.73	1.03	0.388
Side \times locus	5	58.50	0.71	0.617
Side \times locus (linear)	1	18.72	1.14	0.291
Side \times locus (quadratic)	1	32.04	1.95	0.169
Side \times locus (deviations)	3	7.81	0.16	0.924
Residual	51	838.05		
Total	62	1267.56		

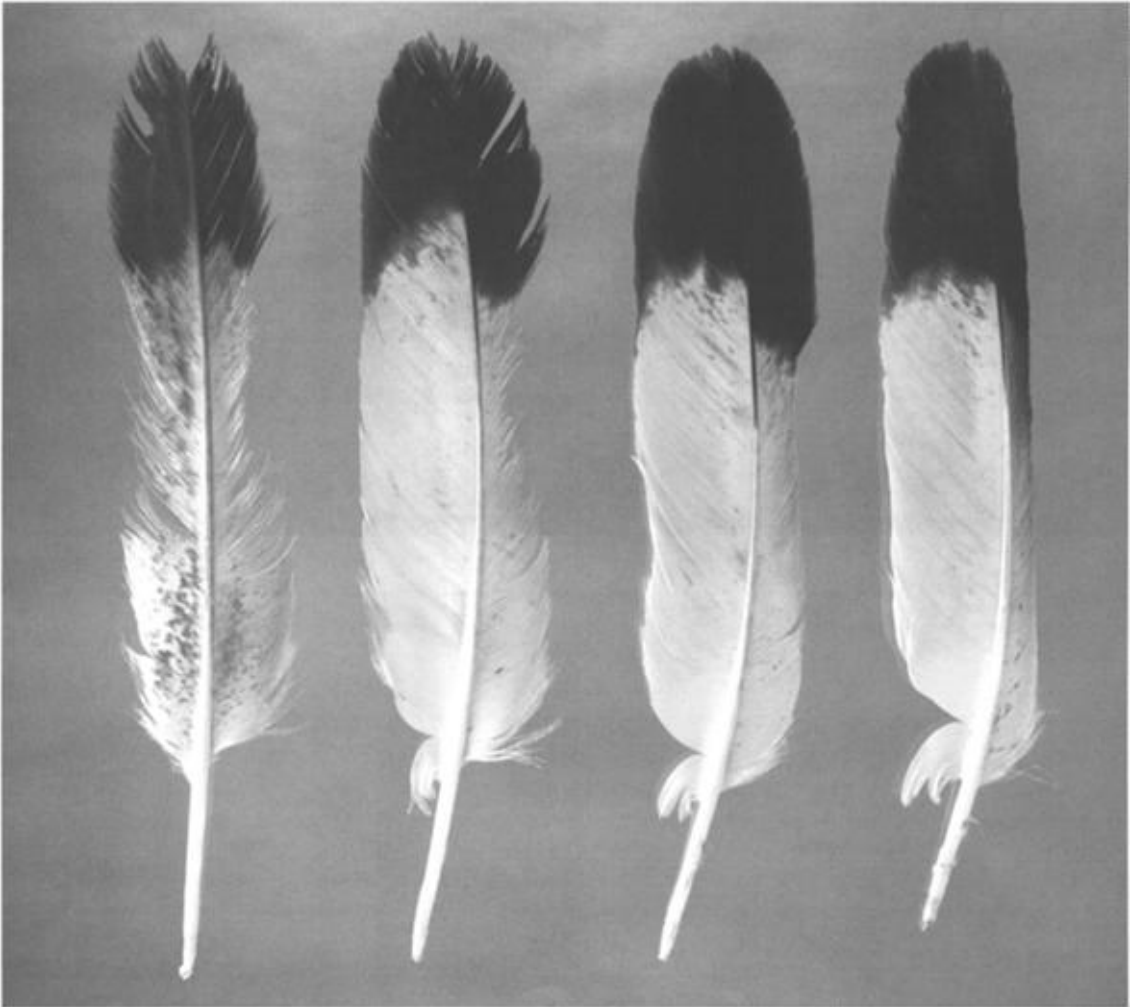


Figure 2. Juvenile rectrices at high-wear and low-wear loci from a second year Golden Eagle after ca. 15 mo of wear. The left-central rectrix (L1, left most feather) shows the greatest breakage and fraying and is shattered on both webs. Moving right (loci L2, L4, and L6 are illustrated), feathers show decreasing wear, and such wear is primarily on the outer (solar-exposed) web. Bird found shot near Flagstaff, AZ, 19 October 2000.

its tail or extend the “life” of its feathers by increasing pigmentation and it could, through natural selection, alter the size, shape, or number of feathers in high-wear/high-stress loci. Another means of compensating for differential wear is to replace feathers at high wear loci more frequently.

The need for different molt rates at various loci is demonstrated by wear patterns in wild eagles. Four feathers, all having been in the tail for the same amount of time, wore at vastly different rates (Fig. 2). The central feathers showed greatest wear and laterals the least. Thus, it is clearly adaptive to replace the most heavily worn central feathers more frequently. It is less easy to explain why the

lateral rectrices were also replaced more frequently in our captive adult (Fig. 1). Bloom and Clark (2001) found that wild yearlings normally replaced rectrices at loci 1 first, then at 6. From the inspection of the tails of museum specimens, direct trauma to the feathers (presumably incurred mostly while capturing prey) may also be somewhat more prevalent at loci 6 than at loci 3–5. However, we feel that a better explanation for the high-replacement rate for lateral feathers derives from their aerodynamic importance in minimizing turbulence, and therefore drag, as the tail cuts through the air stream (Thomas 1993).

We recorded 11 instances of rectrices being retained

longer than 2 yr (Table 1). None of these feathers were at loci 1 or 6. Nine of the 11 were adjacent to growing feathers. Based on these observations we suggest the existence of a physiological mechanism to avoid simultaneously replacing adjacent feathers, a hypothesis consistent with Servheen's (1976) observations. It seems likely that large gaps in the tail are maladaptive by causing aerodynamic instability (Thomas 1993) and by weakening the tail so that growing or unsupported feathers are more likely to be damaged.

For the two other feathers retained longer than 2 yr, two factors may help explain this retention. First, both feathers had grown in late in the season (i.e., their predecessors were molted around 1 August), so a delay in molting 2 yr later resulted in a postponement of molt until the next (third) season. Also, both were at loci where prolonged retention was normal (loci R4, 1993; and L3, 1995; Table 1).

In our captive adult, feathers skipped in one molt were normally (10 of 11 times) replaced early in the following molt. Five (of the 11) were the first rectrices dropped the following season, and one more was lost within a few days of the first rectrix being dropped.

From short-term observations of tail molt in three Golden Eagles, Servheen (1976) concluded that central feathers always molt at least 35 d apart and R1 always precedes L1. For our study eagle, in 1 yr (1988) when both central feathers molted, R1 dropped less than a mo before L1. From our molt data for two other captive Golden Eagles (the Klauane Lake and Montana eagles), left centrals twice fell before the right, so both of Servheen's observations have exceptions.

In conclusion, the general molt pattern is to replace alternate feathers in any one season. Normally, feathers were retained at least 2 yr, with protected feathers (loci 2–4) retained ca. 30% longer. The most consistent circumstance associated with the failure of a feather to molt after two seasons was the presence of a growing feather in an adjacent follicle. Feathers in high-wear positions (loci 1 and 6) consistently molted in alternate years, occasionally more often. This trend is left-right symmetrical. For our well-fed experimental bird, if a feather was retained in the second molt season after replacement, it was nearly always replaced in the first rectrix "molt wave" the following year. The physiological mechanisms controlling these phenomena are at present, unknown. We emphasize that this study was primarily based on data collected from one well-fed captive eagle. How well the patterns described here reflect molt in wild birds that experience periods of food stress and continually stress rectrices during flight and daily hunting activities is unknown. Nor do we know of the prevalence of this mechanism in other species for which the annual tail molt is incomplete.

RESUMEN.—La muda de la cola fue registrada duramente un periodo de 15 años en cautiverio de un águila dorada

(*Aquila chrysaetos*). En promedio solo seis (de 12) rectrices en posiciones mas desgastantes (ejemplo centrales y laterales) fueron remplazadas mas frecuentemente. Las plumas centrales mostraron los niveles mas altos de degradación solar. Las rectrices externas las cuales soportan más estres y son de importancia aerodinámica en el margen de la cola, también fueron remplazadas más frecuentemente. Las plumas en posiciones protegidas fueron retenidas un 30% mas tiempo que las rectrices centrales o laterales. Estas observaciones conllevan a la hipótesis que la muda de rectrices tiene una característica adaptativa en la cual se reemplazan más frecuentemente que las plumas de posiciones de alta importancia. El mecanismo de control de esta muda diferencial es desconocido [Traducción de César Márquez]

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A LOCAL CONCENTRATION OF SNOWY OWLS ON THE YUKON-KUSKOKWIM DELTA IN SUMMER 2000

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KEY WORDS: *Snowy Owl*; *Bubo scandiacus*; *Yukon-Kuskokwim Delta*; *Yukon Delta National Wildlife Refuge, Alaska*.

Snowy Owls (*Bubo scandiacus*) are nomadic and irregular summer visitors in Alaska (Gabrielson and Lincoln 1959, Parmalee 1992), particularly south of their stronghold on the northern arctic-coastal plain (e.g., Barrow). Near Hooper Bay on the Yukon-Kuskokwim Delta (YKD) in southwestern Alaska, Snowy Owls nested commonly (ca. 40 nests) in 1924 (Murie 1929). Despite the extensive activities of biologists in the decades following (particularly since the 1970s), concentrations comparable to those in 1924 have never been reported, and breeding records are virtually nonexistent. The only subsequent report of large numbers of Snowy Owls on the YKD was in 1963, when perhaps as many as several dozen (some nesting) were detected at the eastern end of Nelson Island (Nyctea Hills; J. King pers. comm.).

In summer 2000, Yukon Delta National Wildlife Refuge (YDNWR) personnel flew a series of aerial surveys to document distribution and abundance of fall-staging Bristle-thighed Curlews (*Numenius tahitiensis*). During these surveys, Snowy Owls were recorded regularly. In this paper,

we describe the magnitude of this unusual local summer concentration.

STUDY AREA

The study area was located on the coastal YKD south of Nelson Island (Fig. 1). The roughly triangular area was bounded on the north by the 60°30' parallel, on the southwest by the Bering Sea, on the southeast by the Kinak River, and on the east by Dall Lake (Fig. 1). Elevations ranged from sea level to 135 m above sea level (masl) at the summit of Tern Mountain; however, more than 90% of the study area was <10 masl. This 2545-km² area included four major vegetation associations dominated by a variety of subarctic tundra types. North of Tern Mountain, a 5-km wide band of low wet graminoid meadows was immediately adjacent to the shoreline. Inland of these coastal meadows, there was a wide band of slightly higher tundra, varying in width from 5–30 km. This habitat was characterized by a series of low, ancient beach ridges, a high density of medium-sized lakes, and a slightly more heterogeneous mosaic of plant communities. Although graminoid meadows still dominated, more mesic communities, including graminoid tussock dwarf shrub peatland and lichen dwarf shrub peatland occurred here. Together, these two major habitats comprised the coastal zone of the study area. Farther inland, particularly east of Kegum Kagati Lake, and extending to Dall Lake (Fig. 1), large lakes were prevalent, and the three previously described plant communities were more evenly distributed. Finally, six scattered uplands comprised the only vegetation association in the study area >10 masl. Five of these exceeded 30 masl, and all five supported communities of dwarf shrub heath. These latter two habitats comprised the inland/upland zone of the study area

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