MOLT OF FLIGHT FEATHERS IN FERRUGINOUS AND SWAINSON'S HAWKS

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ABSTRACT.—Based on 137 breeding Ferruginous and 316 breeding Swainson's hawks, the sequencing and timing of flight feather molt showed great variability. Primary molt preceded secondary and rectrix molt. Different molt centers were discernable among the primaries, in which feather loss proceeded from proximal to distal remiges. Among the secondaries and tertiaries, molt centers were less distinct and direction of feather loss alternated. The hawks differed in the location and number of primary molt centers by species and sex. There was considerable variation both in pattern and timing of molt between wings of the same individuals, between individuals caught in different years, and between parents and offspring. The timing of molt was later in years when reproduction was also later. However, within years the stage of molt was poorly correlated with time of hatch.

Muda de las plumas de vuelo en la raptora de la especie *Buteo regalis* y en la de la especie *Buteo swainsoni*

EXTRACTO.—Basadas en 137 aguilillas de la especie *Buteo regalis* y 316 individuos de *Buteo swainsoni*, ambas especies en su ciclo reproductivo, la secuencia y la época de muda de las plumas de vuelo mostraron gran variabilidad. La muda de plumas primarias precedieron a la de las secundarias y a la de las rectrices. Diferentes centros de muda fueron discernibles dentro de las primarias; en ellos la caída de plumas ocurrió en dirección de adentro hacia afuera del cuerpo. Entre las secundarias y las terciarias los centros de muda fueron menos distinguibles, y la caída de plumas alternó en dirección con respecto al cuerpo. Según la especie y el sexo, estas aves difirieron en cuanto a la ubicación y el número de centros de plumas primarias en muda. Hubo considerable variación tanto en la norma como en la época de muda entre las alas de los mismos individuos; entre individuos cogidos en diferentes años; y entre los padres y sus crías. La época de muda fue retardada en los años en que la reproducción también fue retardada. Sin embargo, dentro de cualquier año, el progreso de la muda de plumas ha sido pobremente correlacionada con la época de empollar.

[Traducción de Eudoxio Paredes-Ruiz]

After fledging from gabboonship (Hamerstrom 1984), my wife Sheila and I attempted to emulate the Hamerstrom approach to field studies of raptors. We equipped ourselves with an 18-column spiral-bound banding book and molt cards (Hamerstrom and Hamerstrom 1971), and began to study competition (Schmutz et al. 1980) and predation (Schmutz et al. 1979) by prairie buteos in Alberta in 1975–77. The Hamerstroms believed in capturing and marking birds (Hamerstrom and Hamerstrom 1973, Hamerstrom 1986) when studying behavior and its interaction with survival and population dynamics. Once a bird was in the hand, it only made sense to them to record as much about it as possible in order to test, in a post hoc *manner, questions posed later. Without being exposed to this philosophy, I probably would not have collected the data described below.*

I compare the molt of flight feathers of Ferruginous (*Buteo regalis*) and Swainson's hawks (*B. swain-* soni). These two species of hawks may differ in their pattern of molt because they exhibit different migration and breeding schedules (Schmutz et al. 1980). These differences may dictate different rates of overlap in breeding and molt (e.g., Foster 1974) since Swainson's Hawks arrive on their breeding grounds and breed later than Ferruginous Hawks do (Schmutz et al. 1980). Each molt record obtained in this study represented a single point in time. The pattern of molt was deduced from molt records obtained at different times. To my knowledge, molt in Ferruginous Hawks has not been described previously whereas in Swainson's Hawks it has been described only for some captive individuals (Cameron 1913) and for two free-ranging adults (Palmer 1988). Molt data are from breeding adults (≥2 years old) and hence the various postulated selective factors important in plumage maturation (e.g., Thompson 1991) probably do not apply here. Since this study represents a comparison of the complex life-history

traits molt and reproduction, where presumed causal links between these traits are evaluated, a number of potential methodological biases discussed by Clutton-Brock and Harvey (1984) are relevant.

STUDY AREA AND METHODS

I recorded the molt of flight feathers (remiges and rectrices) of Ferruginous and Swainson's hawks livetrapped (Hamerstrom 1963) near Hanna, Alberta, between 1975–78 and 1982–91. Primary feathers were numbered 1–10 from the proximal to distal end of the wing, rectrices 1–6 from inner to outer portion of the tail. Secondaries and tertiaries were not differentiated but simply called secondaries from 1–13, distal to proximal. The molt records were taken from Ferruginous Hawks caught during the nestling period of their young between 29 May and 26 July and Swainson's Hawks between 30 June and 25 August. Two Ferruginous and four Swainson's hawks that were caught during laying or incubation were not included in the data sets. Because a large sample of molt records was available for Swainson's Hawks captured in 1983 and thereafter, I used the earlier records only when an individual Swainson's Hawk was captured both before and after 1983. In these analyses, I rejected the null hypothesis when $P < 0.05$.

I analyzed molt of the right wing on a total of 137 Ferruginous and 316 Swainson's hawks. The actual number of molt records used in these analyses varies because in 1984–85 I recorded molt for primaries and rectrices only, and in some cases I could not decide whether a feather was old or new. A feather was recorded: as "old" if it was faded and the edges of the vane worn; as "missing"; as "new" if the distal end of the feather bore a small tip, the edges of the vane were smooth and the rachis contained no blood; as "recent" if the tip of the feather showed only slight fading and wear; or as "growing." For growing feathers, the estimated length was recorded in tenths of the length of adjacent feathers (Hamerstrom et al. 1971). For subsequent analyses the categories new and recent were combined. It is possible that not all feathers were equally readily detected as new. It was difficult to discern replaced from old primaries among the seventh to the tenth because these feathers are most densely pigmented and stiff, the tenth also being shorter. As a consequence, these most distal feathers are less likely to fade or to show wear. However, since missing or growing feathers are identified easily and since their pattern of loss was similar to the pattern of total molt (see Fig. 1 below), this source of error was probably minor.

In addition to presenting data on the molt of individual feathers, I calculated a "molt sum" and recorded "molt centers." Molt sum represents the combined sum of missing feathers (recorded as 0.01), growing feathers (0.1–0.9) and new feathers (1). This sum was calculated for primaries and rectrices separately. Molt centers are groups of missing, growing, new or recent remiges separated by old feathers. The location of a molt center along the wing was identified by the feather with the lowest number. This feather therefore also identifies where molt began within a particular group of molting feathers, since molt in primaries proceeded distally (see below).

The sex of the hawks was determined by body weight. In the case of Ferruginous Hawks, there was no overlap in weight of the sexes. I categorized adults heavier than 1550 g as females (J.K. Schmutz unpubl.). Four Swainson's Hawks fell in the overlap region between 900–950 g and were not categorized to sex. I determined the hatching date of the first nestling by backdating, using a growth curve for primary no. 4 (Schmutz 1977) as the Hamerstroms had done.

RESULTS AND DISCUSSION

One of the functions that a repeated and energetically costly molt may serve is to replace broken feathers that otherwise seriously impede flight (Tucker 1991). Since completed feathers are without a regenerative capacity, a regularly occurring molt seems adaptive. Between 1984–91, 9 (0.5%) of 1952 individual remiges and rectrices on 122 Ferruginous Hawks were broken, 5 of these on the same individual. Seven (0.2%) rectrices and no remiges were broken on 4 of 277 Swainson's Hawks. It is possible that broken feathers are more common than these data suggest, as individuals with broken feathers may be unable either to complete the migration or to join the breeding cohort, and consequently may not appear in the sample analyzed.

Molt Pattern. Both species, but especially Ferruginous Hawks, were molting more of their primaries than either secondaries or rectrices (Fig. 1) at the time of capture. As might be expected, the later nesting and hence later caught Swainson's Hawks were further along in their molt than were Ferruginous Hawks. Apart from a single peak for primary no. 1 (Fig. 1), molt was not simply ascendant or descendant in either of the three groups of flight feathers. Also, the molt pattern is much more complex than data from a few individual Swainson's Hawks (Palmer 1988) imply. Molt often involved more than one molt center and occurred in "waves" termed "serial molt" (e.g., Edelstam 1984) or "Staffelmauser" (Stresemann and Stresemann 1966). Such a wave-like molt was also exhibited by the Common Buzzard (*Buteo buteo*; Bloesch et al. 1977).

Primary no. 1 represented the most important molt center in both species (Table 1). Among some male Ferruginous Hawks, a second molt center was located in the primary 6–8 region (Fig. 1). Among male Swainson's Hawks, two additional molt centers were located in the primary 5–6 and 8–9 regions (Fig. 1). Molt centers were less distinct in the secondaries, but male Swainson's Hawks did show molt centers in the secondary 1, 5 and 11 region, as suggested by Miller (1941).
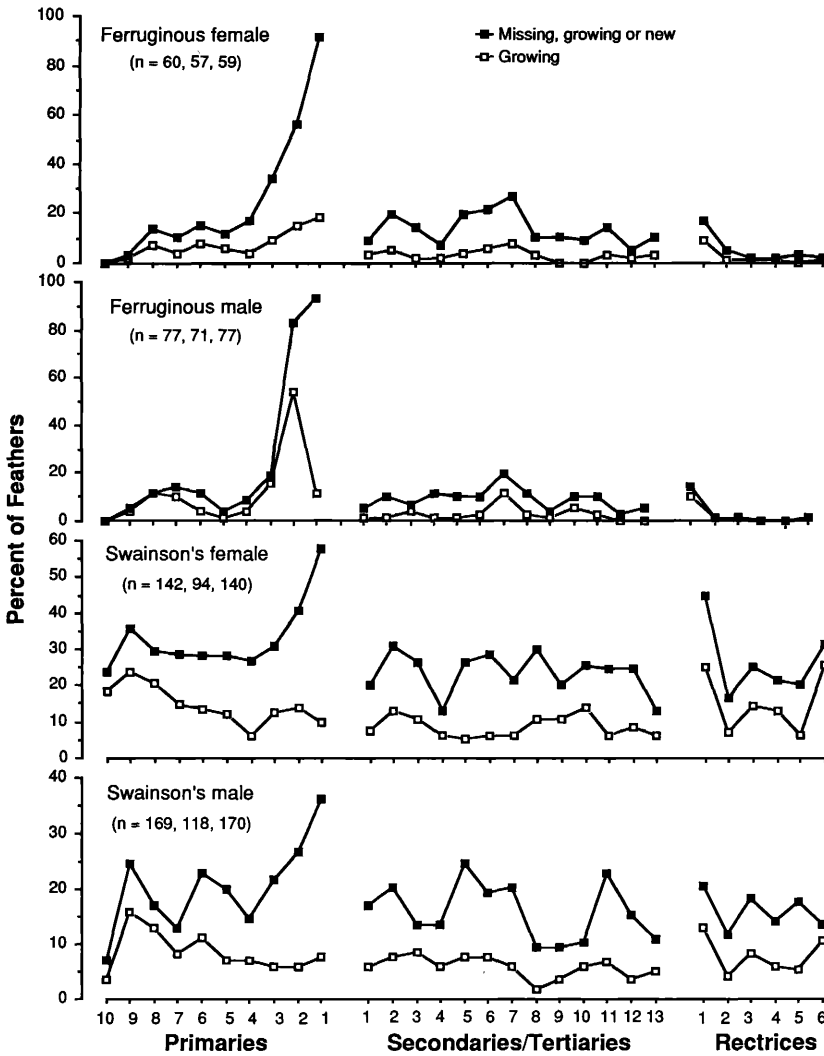
Figure 1.   The percent of feathers of Ferruginous and Swainson's hawks in Alberta in various stages of replacement during the nestling period.

Considering all molt centers, the molt pattern differed between species (G = 18.23, df = 2, P < 0.001). Ferruginous Hawks had always replaced primary no. 1, and on 77% of individuals also feathers in other molt centers, for a maximum of three centers in total. Swainson's Hawks, in contrast, replaced feathers in as many as five molt centers which did not always involve primary no. 1.

Female and male Ferruginous Hawks used the same molt centers, whereas Swainson's Hawks did not. Female and male Ferruginous Hawks showed

molt centers in similar positions (G = 0.57, df = 2, P = 0.753) and of similar number (G = 1.34, df = 2, P = 0.531). More female (74%) than male (34%) Swainson's Hawks involved primary no. 1 (G = 26.06, df = 3, P < 0.001). More female than male Swainson's Hawks also showed more molt centers at the same time (G = 9.11, df = 2, P = 0.018). In another large-bodied bird, the Wandering Albatross (*Diomedea exulans*), breeding females and males also differed in the number of molt centers used, but nonbreeders did not differ (Weimerskirch 1991). The

Table 1. Molt centers in the primary feathers of Ferruginous and Swainson's hawks, arranged first by primary number and then by the number of molt centers. Because the stage of molt could influence the number of molt centers, only those records with a primary molt sum of 2 or higher were included. The resulting average molt sum for Ferruginous Hawks was 2.7 for females, and 2.5 for males, and for Swainson's Hawks 3.2 for females and 2.6 for males.

MOLT CENTER	FERRUGINOUS HAWK FEMALE	MALE	SWAINSON'S HAWK FEMALE	MALE
1	4	12	4	
1, 3	5		1	2
1, 3, 4		1		
1, 3, 5		1		
1, 3, 5, 7, 9				1
1, 3, 5, 8			1	
1, 3, 5, 8, 10			1	
1, 3, 5, 10			1	
1, 3, 6	1			1
1, 3, 6, 8			1	
1, 3, 6, 9			2	
1, 3, 7	1		3	1
1, 3, 7, 10			2	
1, 3, 9			1	1
1, 4	1	2		1
1, 4, 6, 9			1	
1, 4, 7		2	1	
1, 4, 7, 9			1	
1, 4, 8			7	1
1, 4, 9			5	2
1, 4, 10			1	
1, 5	1		2	3
1, 5, 7		1	2	
1, 5, 8	1		2	1
1, 5, 9		1	6	3
1, 6	3	4	7	2
1, 6, 8		2		
1, 6, 9			8	2
1, 6, 10			4	1
1, 7	3	6	5	
1, 7, 9		1	2	2
1, 7, 10			1	
1, 8	5	7	6	2
1, 9	2	3	1	2
1, 10			1	
2		1		
2, 4				1
2, 4, 9			1	
2, 5			1	
2, 5, 7			2	1

Table 1. Continued.

MOLT CENTER	FERRUGINOUS HAWK FEMALE	MALE	SWAINSON'S HAWK FEMALE	MALE
2, 5, 7, 9			1	
2, 5, 8			1	
2, 5, 9				2
2, 6, 8			1	
2, 6, 9			2	3
2, 6, 10				1
2, 7				1
2, 7, 9			1	
2, 8				2
2, 9				2
3, 5			1	2
3, 5, 10			1	
3, 6, 8				1
3, 6, 9			1	2
3, 6, 10			1	
3, 7			1	
3, 7, 9				1
3, 7, 10			1	2
3, 8			1	3
3, 8, 10			1	1
3, 9			1	
4, 7			1	1
4, 7, 10				1
4, 8				1
4, 8, 10			1	
5, 7, 9				1
5, 8				1
5, 9				1
5, 10			1	
6, 9				3
6, 10				1
8, 10				1
9				1
Total	28	43	102	65

patterns in the hawks studied are consistent with the hypothesis that the later arriving Swainson's Hawks (Schmutz et al. 1980) molt their feathers more rapidly by involving more molt centers than do Ferruginous Hawks. The use of more molt centers may permit a more rapid molt while reducing the size of gaps between feathers.

I deduced the direction of feather loss for each molting group of feathers by recording on which side of a new feather a growing feather was located. For primaries of Ferruginous Hawks, 70 (93%) of 75

growing feathers were on the distal side of a new feather. For Swainson's Hawks the proportion was 69 (92%) of 75. Thus, although not ascendant across all primaries, molt within groups of primaries progressed distally regardless of the location of the molt center. Molting secondaries and tertiaries were more often interspersed with old feathers and hence fewer molting feathers could be found adjacent to new feathers. For both species' secondaries and rectrices combined, 24 (52%) molted inward and 22 outward. This two-directional molt was significantly different from the prevailing outward progression in primaries ($G = 41.60$, $P < 0.001$). Secondary and rectrix molt were also not centrifugal as would be indicated by an alternating ascendant and descendant feather loss away from a molt center. Secondary and rectrix molt is perhaps best described as highly variable with molting feathers interspersed with old feathers. Primary molt may be more precisely controlled than either secondary or rectrix molt because the primaries are more important for propulsion (e.g., Welty 1962).

The Timing of Molt. Molt appeared to start during laying or early in incubation. Two Ferruginous Hawks caught during laying or very early in incubation (24–25 April) were replacing primary no. 1 and one was also replacing secondary no. 5. Of three Swainson's Hawks caught 14–24 May, only one was molting, replacing secondary no. 6. A fourth Swainson's Hawk caught during incubation on 17 June, was replacing two primaries, no. 4 and no. 8.

The hawks were highly variable in their progress of primary and rectrix molt as evident from the wide scatter of molt sums during the nestling period (Fig. 2A, 3A). Dolnik and Gavrilov (1980) found that some individual Chaffinches (*Fringilla coelebs*) started their molt up to 4 wk before others. In their study the end of the molt was more synchronous than the beginning, suggesting that molt proceeded at different rates.

To examine whether females and males molted at different rates, I counted the number of data points of male molt sums that were above and below the least-square regression line that best fitted the data points for females. This method is useful because it takes into account the small increase in molt sum over time and because males and females were not always caught on the same dates. Male Ferruginous Hawks had progressed further in their molt, as evident from 46 male sums that were above and 27 below the female's line. This was significantly different from an expected distribution of 50:50 (binomial test, $P = 0.012$). In contrast, male Swainson's Hawks (16 above and 152 below) molted more slowly than females ($P < 0.001$), as do harriers (*Circus cyaneus*; Schmutz and Schmutz 1975).

Judging from the slope of the line fitting the molt sum of primaries and rectrices during the nestling period, Ferruginous females and males replaced 0.016 and 0.011 feathers, respectively, in one day. Similarly, Swainson's females and males replaced 0.073 and 0.017, respectively. Extrapolating from these slopes, Ferruginous and Swainson's hawk females and males would require an estimated 1403, 1006, 219 and 941 days, respectively, to replace their primaries and rectrices. Cameron (1913) found that flight feather molt in captive Swainson's Hawks lasted about 6 mo. The unlikely length of time estimated in my study could be explained by 1) a different rate of molt at different times of the year, 2) molt spread over more than 1 yr or 3) a bias in recording new feathers. I was conservative in my judgement of what constituted a new feather. Old feathers often seemed to be of different ages, but it was impossible to distinguish with confidence a feather replaced early in the same or late in the previous year (cf., Edelstam 1984). It is possible that some feathers replaced during incubation faded and wore sufficiently quickly for me to record them as old during the nestling period.

On the study area, Ferruginous Hawks hatched over approximately 2–3 wk and Swainson's Hawks over 4–5 wk (Schmutz et al. 1980). Attempting to explain the great variability in the progress of molt in both species, I plotted molt sum in relation to hatching of the oldest young. This slightly improved the amount of variation explained among female Ferruginous and male Swainson's hawks, but decreased it among male Ferruginous Hawks and female Swainson's Hawks (Fig. 2B, 3B).

Another possible reason for the great spread in molt sums may have been the inclusion of molt data from different years. A comparison of the stage of molt between years is complicated by the different molt sums between the sexes and because the hawks were caught on different dates. To overcome these differences, I expressed the stage of a hawk's molt in terms of deviation, the number of primary and rectrix feather units away from the mean for the particular date (Fig. 2A, 3A). I then compared this deviation between years. The results suggested that, over 4 yr when sample sizes ranged from 17–35,
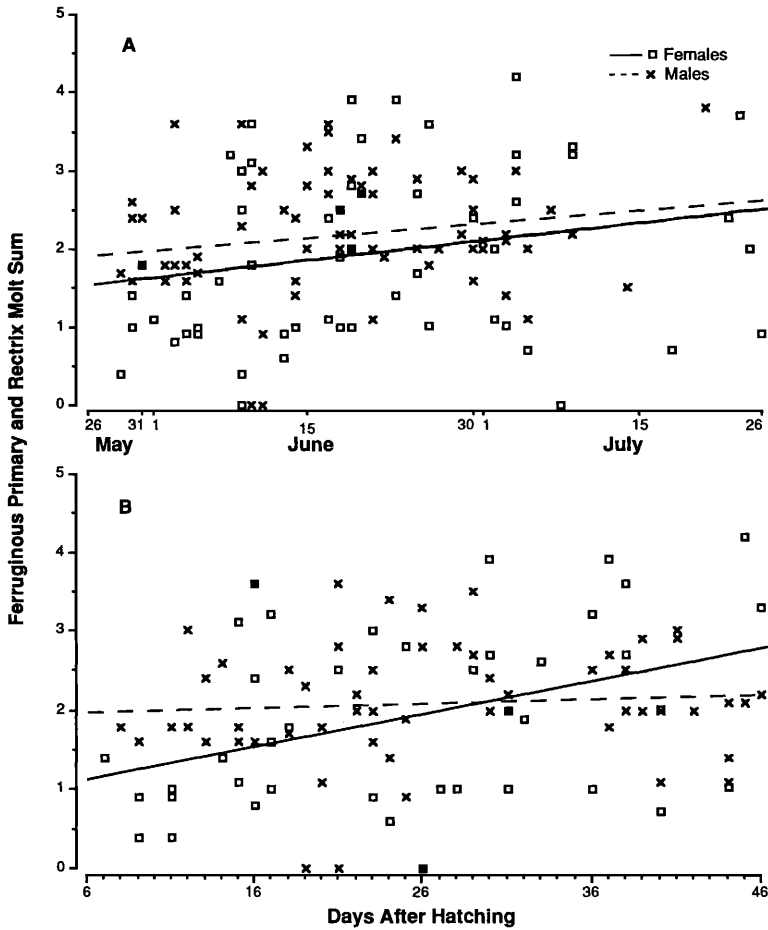
Figure 2.   The sum of primary and rectrix molt of Ferruginous Hawks caught during the nestling period in Alberta, in relation to calender date (A; female r = 0.207, N = 589, P = 0.120 and male r = 0.174, N = 73, P = 0.001) and hatching of the first young (B; female r = 0.400, N = 42, P = 0.008 and male r = 0.073, N = 57, P = 0.590).

Ferruginous Hawks did not differ in their progression of molt (ANOVA F = 1.07, P = 0.365). However, their hatching dates also did not differ (ANOVA F = 1.51, P = 0.217). Swainson's Hawks did differ in their stage of molt (ANOVA F = 4.51, P < 0.001) over 6 yr when sample sizes ranged from 15–94. The Swainson's Hawks' mean hatching dates differed also during those years (ANOVA F = 8.11, P < 0.001). In years when hatching occurred later, molt was delayed (r = 0.828, N = 6, P = 0.042). Thus, while the progress of molt was poorly synchronized with an individual's timing of reproduction within any one year (Fig. 2B, 3B), as a group Swainson's Hawks tended to molt as much as a week later when reproduction was also delayed.

Individual Variability. Although the hawks when considered as a group were highly variable in both the pattern and timing of molt, this could be due to variation between but not necessarily within individuals. I compared differences in molt centers between wings within individuals and between records of the same individual caught in different years. I used only primary molt here since molt in these feathers was most consistent. Intra-individual variation has been considered important by others, and has been used to evaluate heritability of some morphological characters (Falconer 1960). The observation that even within wings of the same hawk there was considerably variability in the sequence in which feathers were lost suggests that feather replacement
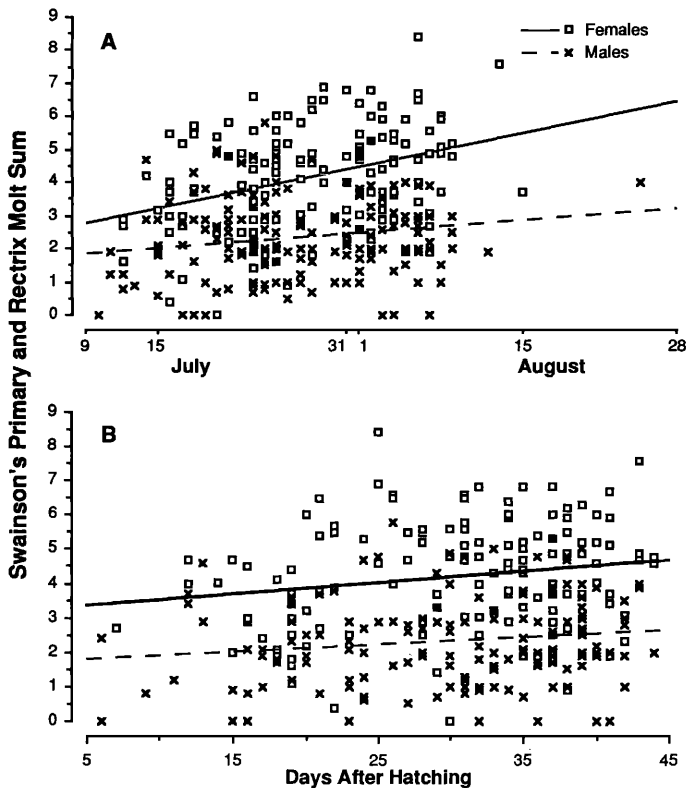
Figure 3.   The sum of primary and rectrix molt of Swainson's Hawks caught during the nestling period in Alberta, in relation to calender date (A; female r = 0.345, N = 141, P < 0.001 and male r = 0.110, N = 164, P = 0.161) and hatching of the first young (B; female r = 0.148, N = 137, P = 0.032 and male r = 0.175, N = 155, P = 0.030).

need not be a precisely regulated biological event. Of 25 individuals of each species selected at random, 11 (44%) Ferruginous (Fig. 4) and 11 (44%) Swainson's hawks (Fig. 5) showed either a different number or location of molt centers between right and left wings.

When comparing molt pattern of the same individual between years, the number of molt centers used could have been confounded by the stage of molt. Since primary no. 1 frequently molted first and other molt centers began later (see Fig. 1), an individual caught early in the season in one year and late in the season in a subsequent year could have shown a different pattern due to differences in time of capture alone. To minimize this potential bias I included molt records of the same individual in successive years only if the molt sum of primaries was within the equivalent of one feather. Using this

restriction, a sample of 9 Ferruginous Hawks and 29 Swainson's Hawks was left for analysis. Both species had either a different number and/or location of molt centers. By scoring the data for both species combined, as having molt pattern the same (molt centers identical in number and position) or different, I found that there was more variation within individuals between years than within individuals between wings (G = 22.49, P < 0.001).

Part of the variation in molt pattern within individuals between years may be due to the hawks completing their molt cycle in a given feather group only in the second year, at which time they may also be initiating a new cycle. Piechocki (1963) found that a 1 yr old, captive Common Buzzard molted primaries 1–8 and retained primaries 9–10. During the following summer, this hawk replaced primaries 1–6 and 9–10, retaining primaries 7–8. In two sub-
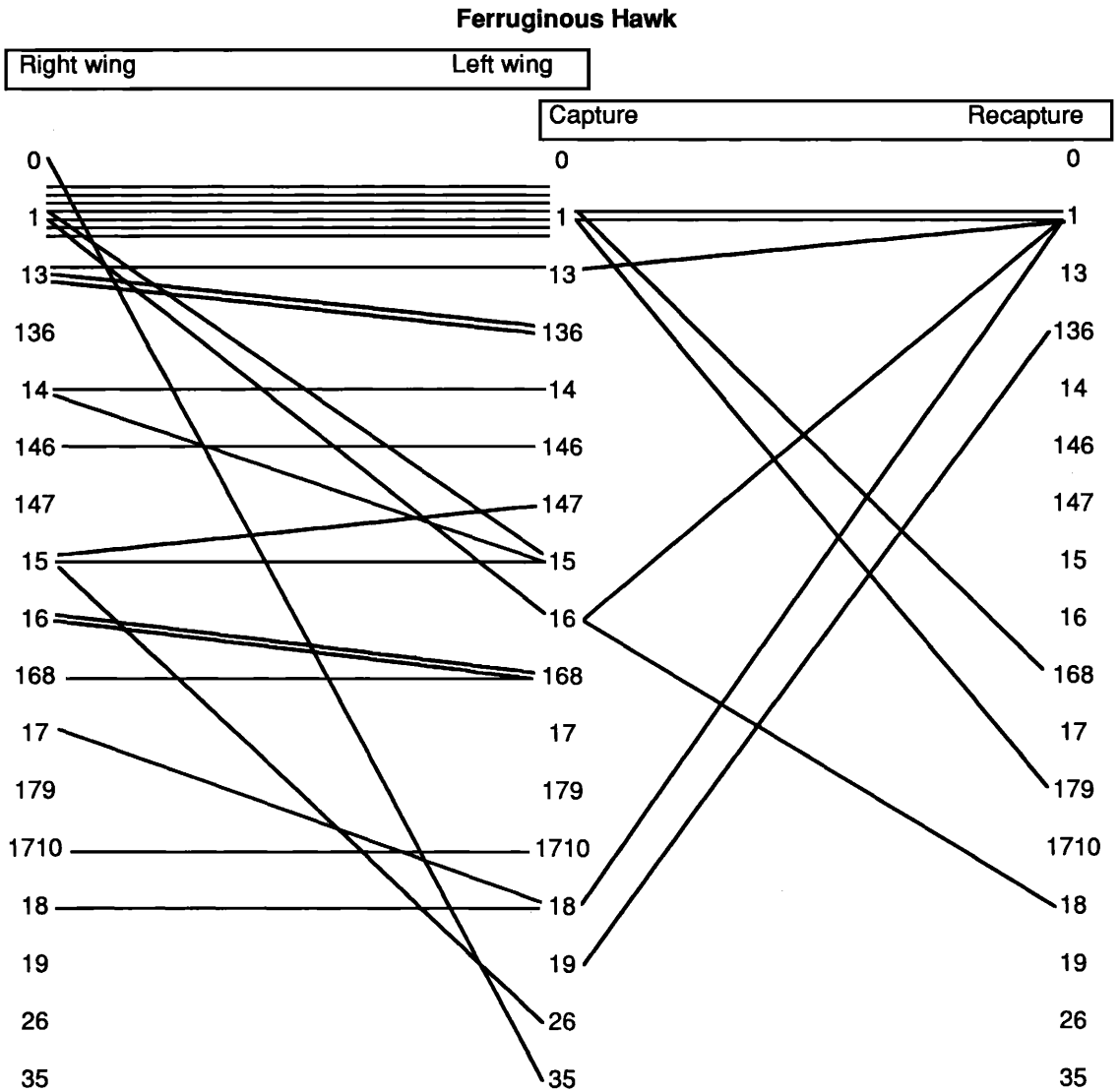
Ferruginous Hawk

Figure 4. Differences in molt centers (see text) between right and left wings of 25 randomly selected Ferruginous Hawks and between records of 9 breeders caught 1–2 years later.

sequent molt cycles, four and then five different primaries were retained, giving rise to different molt centers and a greater complexity in molt.

Not only did the hawks in this study show different molt centers in different years, but also there was no evidence that timing of their molt was consistent among years. For ten recaptured Ferruginous Hawks, there was no significant correlation between the degree of deviation in molt sums among years (r = 0.560, P = 0.092). Similarly, the stage of molt measured in molt sum was also not correlated for 52 recaptured Swainson's Hawks among years (r = 0.010, P = 0.943).

The data presented are based on breeding hawks and hence do not permit a comparison of molt between breeding adults and younger nonbreeders. On
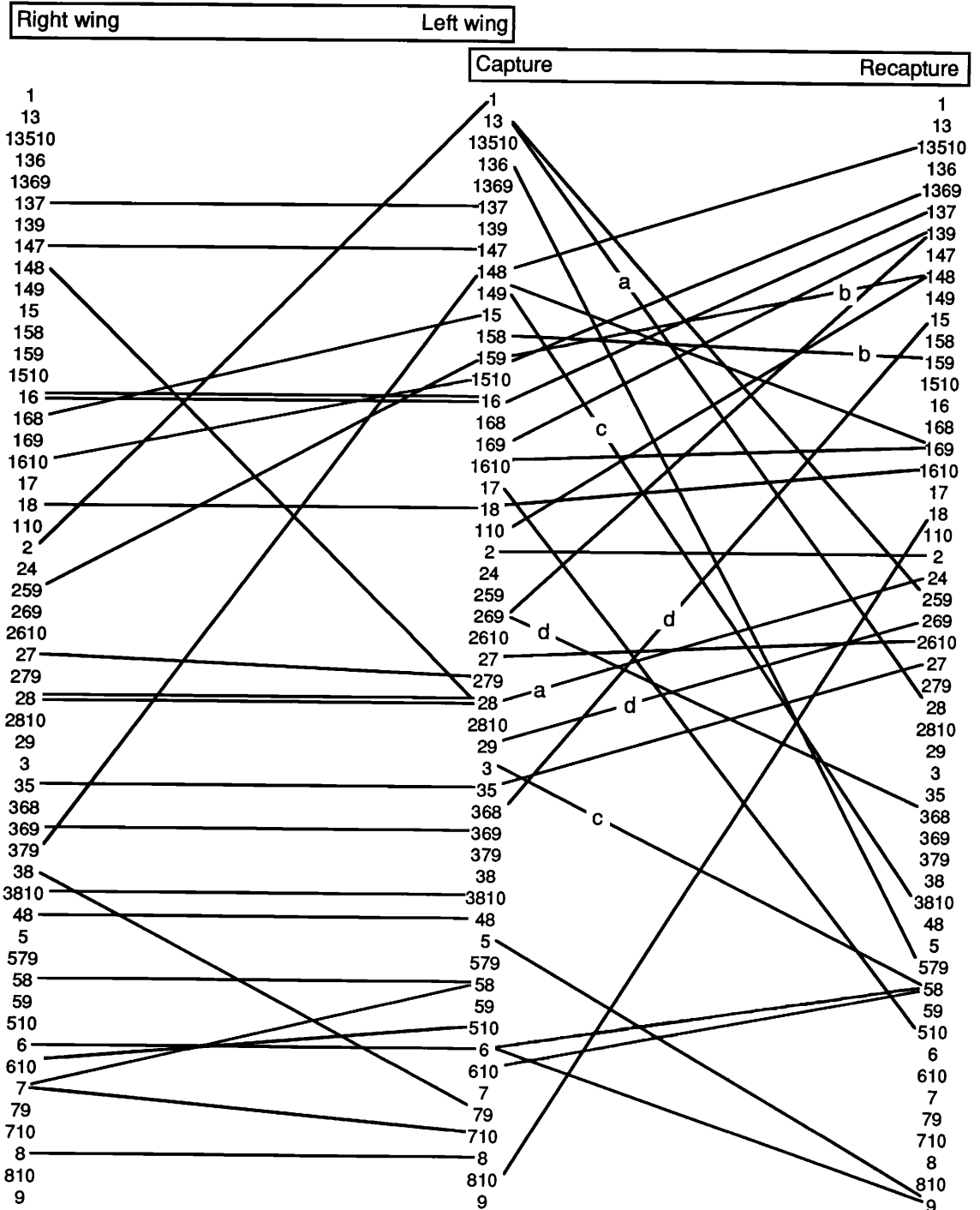
Swainson's Hawk

Figure 5.   Differences in molt centers (see text) between right and left wings of 25 randomly selected Swainson's Hawks and between records of 29 breeders caught 1–12 years later. Letters that interrupt lines signify individuals recaptured more than once.

occasion, individual Ferruginous, Swainson's and Red-tailed hawks (*B. jamaicensis*) that frequented the study area showed unusually large gaps in their flight feathers. Such individuals also molted so many body feathers at once that their heads appeared white. I believed that these individuals were young non-breeders, because they did not seem to be associated with a nest and behaved subtly non-territorial and inconspicuous (e.g., Weir and Picozzi 1975). The youngest breeders caught were one male Ferruginous Hawk and one female Swainson's Hawk at the age of 2 yr. The Ferruginous Hawk had a molt sum of 3.2 and a molt center at primary no. 1 and no. 4. The female Swainson's Hawk was perhaps unusual in having only one molt center at primary no. 1 despite a high molt sum of 4.6. Only three other captured females of unknown age had a single molt center at primary no. 1 with a molt sum of 2.0 or higher. It is possible that hawks molting their flight feathers for the first and possibly second time can be distinguished by their molt pattern from older adults, as is the case in the White Stork (*Ciconia ciconia*; Bloesch et al. 1977) and the Barn Owl (*Tyto alba*; P.H. Bloom pers. comm.).

Because each record provided insight into a hawk's molt only at a single point in time, the question of whether these hawks took 2 yr to replace all their flight feathers was not possible to answer unless birds were caught in successive years. Selecting individuals which differed by no more than one feather in their primary molt sum (see above) and were caught in successive years, each of eight Ferruginous Hawks had replaced their primary no. 1 in a successive year. However, none of 11 other molt centers located in more distal positions on the wing in the first year had showed any molt in the second year. Of 42 molt centers in the wings of 17 Swainson's Hawks recaptured 19 times in successive years, 12 (29%) of the molt centers were again molting and 30 were not. These data are sufficient to conclude only that at least some feathers are replaced in successive years. Other feathers not yet replaced at the time of recapture may have been replaced later. Reading (1990) found that a Northern Goshawk (*Accipiter gentilis*) retained one primary for 2 yr in a seven-year study. This hawk retained 45 of 96 secondaries and tertiaries for 2 yr in a six-year period.

Given the degree of variability in the molt of individual hawks between years, it was not surprising to find great variability also between parents and offspring. Among five parents and their four off-

spring for each of Ferruginous and Swainson's hawks, there was no indication that similar molt centers were used. Also, parental deviation from the mean molt sum was not correlated with offspring deviation ($r = -0.514$, $N = 10$, $P = 0.129$ for both species combined).

Relationships to Ecological Variables. Pietiäinen et al. (1984) found that Ural Owls (*Strix uralensis*) with an above average number of young molted on average fewer feathers at a time. They postulate that the owls balanced energy demands for molting against energy required for reproduction.

There was no evidence of a relationship between molt sum and brood size for Ferruginous or Swainson's hawks. Since brood sizes differed among years (Schmutz and Hungle 1989), I expressed reproductive success in terms of deviation from the yearly mean brood size for the species. I used the number of young raised to near fledging (banding age) making the assumption that this measure reflected the combined territory and individual quality. The correlation between deviation in molt sum and deviation in brood size was $r = 0.010$ ($N = 41$, $P = 0.950$) for Ferruginous Hawk females, $r = 0.173$ ($N = 58$, $P = 0.194$) for Ferruginous Hawk males, $r = 0.059$ ($N = 137$, $P = 0.492$) for Swainson's Hawk females and $r = 0.150$ ($N = 155$, $P = 0.062$) for Swainson's Hawk males. For all but Swainson's Hawk females the sign of the correlation was positive not negative as might be expected. These results are inconsistent with an explanation involving a balancing of energy. Molt sum in harriers was also not correlated with number of young (Schmutz and Schmutz 1975). Morton and Morton (1990) concluded that the control of postnuptial molt in a passerine was independent of reproduction.

The search for a simple negative relationship between molting intensity and reproductive success clearly ignores many subtle constraints that affect energy assimilation and its subsequent expenditure (e.g., Morton and Morton 1990). Even if such a relationship did exist, one could probably construct several plausible scenarios to explain this relationship (cf., Lewontin 1978).

While some molt patterns were apparently repeated with some consistency (e.g., primary molt preceding secondary and rectrix molt, the prevailing use of some molt centers over others, and differences between species and the sexes), the overwhelming conclusion that arises from this study is one of considerable variability in the molt of flight feathers.

There is little doubt that a proper set of feathers is important, first for survival and second for successful reproduction. However, apart from a few basic constraints (e.g., staggering growing feathers to maintain flight capabilities, molting when food is abundant) the pattern by which feathers are replaced may matter little. This may be the case, even if the annual replacement of feathers itself is energetically costly (e.g., King and Murphy 1985).

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