POSTNUPTIAL MOLT IN HARRIS' SPARROWS[1]

WILLIAM A. DEGRAW

Department of Biology, University of Nebraska at Omaha, Omaha, NE 68182-0040

MICHAEL D. KERN

Department of Biology, College of Wooster, Wooster, OH 44691

Abstract. We studied the postnuptial molt of captive male and female Harris' Sparrows (*Zonotrichia querula*) exposed to photoperiods simulating those on the breeding grounds and ambient temperatures of 22–25°C. Postnuptial molt was completed in about 82 days in individual birds. It began with the loss of P_1 and concluded with replacement of contour feathers in the dorsal and ventral body tracts. Peaks of molt intensity essentially coincided in all of the major feather tracts. Intensity was highest between days 28 and 59 of molt. Primaries were replaced in the sequence normal for other passerines, but secondaries exhibited considerable deviation from the typical passerine pattern. Rectrices were often molted centrifugally, from R_1 through R_6, but several were dropped and replaced simultaneously. Body molt, which is described in all tracts separately, began shortly after P_1 was shed and continued until the end of the molt period.

Postnuptial molt is protracted and lasts considerably longer in captive Harris' Sparrows than in other North American *Zonotrichia* which summer either at high northern latitudes or high altitudes. The time-course of molt in Harris' Sparrows suggests that (1) periods of breeding and postnuptial molt may overlap, and (2) postnuptial molt is completed during the fall migration.

Key words: Postnuptial molt; Harris' Sparrows; Zonotrichia querula; intensity of molt; rate of molt.

INTRODUCTION

Crowned sparrows (*Zonotrichia*) are perhaps the best studied group of passerines in the Western Hemisphere (Chapman 1940, Blanchard 1941, Wolfson 1954, Banks 1964, Cortopassi and Mewaldt 1965, King 1973, Lewis 1975; and many others). Representatives of the group occur throughout the Americas. Some are sedentary (e.g., *Z. leucophrys nuttalli* in North America and *Z. capensis costaricensis* in Central America), while others are latitudinal migrants of short (*Z. l. pugetensis*), medium (*Z. l. oriantha*), or long (*Z. l. gambelii*) distances.

In North America, western members of the group have received considerable attention, but midwestern and eastern forms, including the Harris' Sparrow (*Z. querula*), have been largely neglected. In this paper, we attempt to rectify that situation somewhat for *Z. querula*, a medium-distance migrant which overwinters in the midwest as far south as Texas and summers in northern Canada.

Several years ago we examined thyroid activity, and blood volume and composition in Harris' Sparrows undergoing postnuptial molt (deGraw and Kern 1985, Kern and deGraw 1986), but we did not present a detailed description of the molt on which those studies were based. Aside from a passing mention in Baumgartner (1968) and a brief description in an unpublished master's thesis (Sheffield 1975), almost nothing is known about the postnuptial molt of *Z. querula*. Here we describe the stages, timing, and intensity of molt in Harris' Sparrows and compare it to work on other crowned sparrows (Miller 1961, Mewaldt et al. 1968, Morton et al. 1969, Wolf 1969, Davis 1971, King 1972, Morton and Welton 1973, Lewis 1975, Mewaldt and King 1978).

Our study was done on a captive population under simulated natural conditions. We assume that the postnuptial molt, which captive sparrows experience under simulated natural conditions, is a faithful replica of this molt in free-living birds. A substantial number of studies on several *Zonotrichia* have demonstrated that the molt of captives, with minor effects on molt duration (Mewaldt and King 1978) and sex differences in onset (Morton and Welton 1973), is indistinguishable from that of free-living birds.
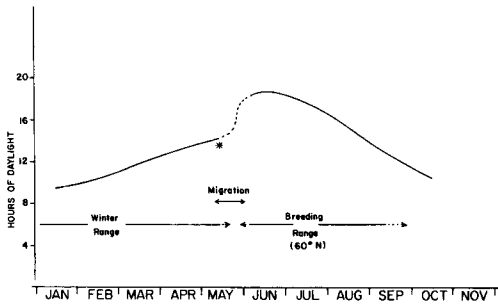
FIGURE 1. Photoperiods to which captive Harris' Sparrows were exposed: natural photoperiods at Omaha, Nebraska in an outdoor aviary before 19 May (*), simulated natural photoperiods indoors thereafter. Photoperiod was changed every 3 days between 19–27 May (dashed line) to simulate changes experienced during migration, then once each week during the remainder of the study (solid line) to match day lengths at 60°N latitude.

MATERIALS AND METHODS

Harris' Sparrows were captured with mist nets from migrating flocks near Omaha, Douglas County, Nebraska, in the autumn and from populations near Syracuse, Johnson County, Nebraska, in the winter. Prior to this study (about 6 months) they were housed in large, outdoor flight cages and exposed to natural photoperiods and ambient temperatures but protected from wind and snow. They were moved indoors in mid-May, caged individually, and exposed to increasingly long daily photoperiods simulating those experienced by free-living birds migrating northward to the southern third of their breeding range (60°N latitude) in North America (Fig. 1). The temperature to which the caged birds were exposed was 22–25°C. Such treatment induced a complete postnuptial molt. Birds always had access to Purina Game Bird Starter Mash mixed with white millet (1:1 by volume) and fresh water.

Fourteen birds (eight males and six females) were examined every other day until molt began and every 2–4 days thereafter to document the onset, sequence, and intensity of molt. We quantified molt using a "standard molt index" which has been adopted by several investigators in previous studies of molt in *Zonotrichia*. Each molting primary or secondary wing feather (pin or brush) was assigned a score of one point, as was each molting rectricial feather. Body and crown molt were scored separately on a scale of one to

three points, depending on whether the molt was light (one point), medium (two points), or heavy (three points). Using this system, the maximum possible molt score for an individual bird is 54 points.

We also measured the rate of growth of each primary and secondary remigial feather in the left wing and of the innermost pair of rectricial feathers with a metric ruler notched to fit easily against the skin at the base of the feather. The feather was straightened out against the ruler when measured. In addition, we noted such things as shedding interval between individual feathers in remigial tracts on both wings, the symmetry of the molt on the two sides, and adventitial molt. To best evaluate body molt, we kept detailed records of the progress of molt in all of the body tracts.

Data were examined by Student's t-test, regression analysis, one-way analysis of variance, and Student-Newman-Keuls and Scheffe's multiple range tests (Zar 1974). Values in this paper are means ± one standard deviation.

RESULTS AND DISCUSSION

GENERAL CHRONOLOGY OF POSTNUPTIAL MOLT

Postnuptial molt began on 28 June–15 July (average for all birds = 5 July) and ended on 10 September–30 October (average = 8 October) in our group of Harris' Sparrows. These dates are somewhat later than Sheffield's (1975) 11 June–9 July and 24 August–7 September, respectively, for another group of captive *Z. querula* from the Omaha area. The overall duration of molt in individual birds (81.9 ± 13.4 days; range = 64–108 days) was also considerably longer than his mean of 63.1 days. We suspect that these differences are due to the simulated conditions under which the birds were studied: whereas we exposed sparrows to conditions they would experience while migrating north, i.e., to several abrupt increases of equal length in day length between 15:9 and 18:6 (L:D) at 3- to 5-day intervals between 19–27 May followed by smaller changes at weekly intervals, Sheffield exposed birds to photoperiods that simulated ambient conditions in the Omaha area (i.e., conditions on the northern edge of *Z. querula*'s wintering area).

Peaks of molt intensity essentially coincided in all of the major tracts (Figs. 2, 3), as they do in other crowned sparrows undergoing postnup-
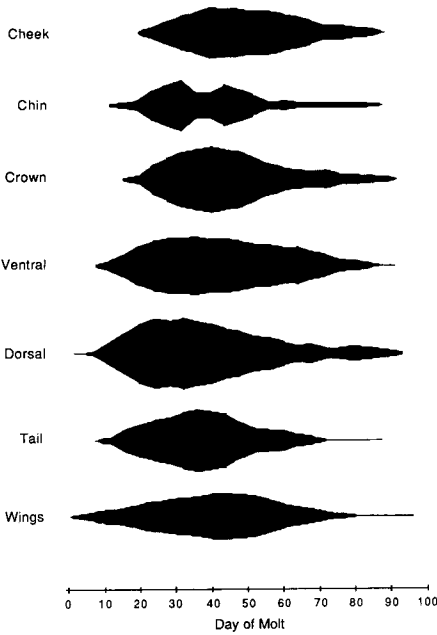
FIGURE 2. Timing and intensity of molt in major feather tracts of captive Harris' Sparrows exposed to simulated natural photoperiods. The height of each polygon represents molt intensity in each feather tract, expressed as a percentage of maximum molt index observed in each feather tract. Day 0 = shedding of P1.
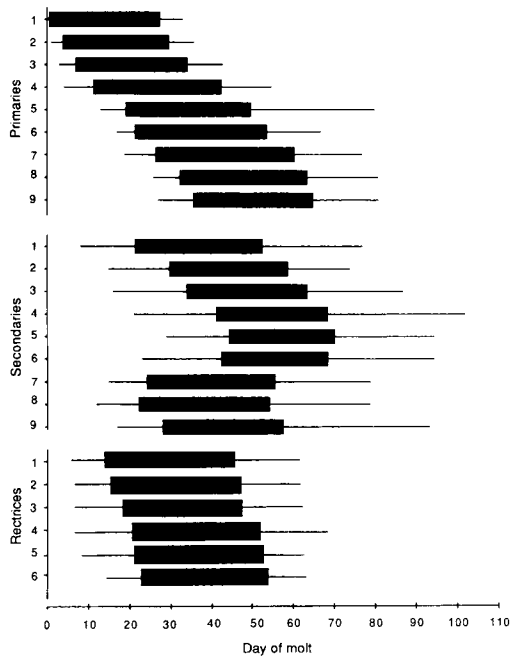

FIGURE 3. Timing of molt in primary and secondary remiges and rectrices of captive Harris' Sparrows (eight males, six females) exposed to simulated natural photoperiods. Horizontal bars show mean onset, finish, and duration of molt of each feather; horizontal lines show the range of days during which each feather was replaced. The upper series of numbers is molt intensity (molt index) in the contour plumage; the lower series is molt intensity (molt index) for the entire plumage (wings, tail, and body).

tial molt (e.g., *Z. l. gambelii,* Morton et al. 1969). The sequence and phasing of feather replacement is summarized in Figure 3 and will be described by tract below. Overall, molt intensity was highest between 28 July and 26 August or on days 28–59 (average = 41) of molt.

Primary remiges and their coverts. Onset of postnuptial molt was signaled by the loss of the first primary (P1) and conforms in this respect to onset in other *Zonotrichia* examined thus far (Morton et al. 1969, King 1972, Morton and Welton 1973, Sheffield 1975, King and Mewaldt 1987), although body molt sometimes anticipates the primary molt in some populations of *Z. capensis* (Miller 1961).

Males and females began to shed the primaries at the same time, as they do in some (but not all) captive *Z. oriantha* (Morton and Welton 1973, King and Mewaldt 1987). However, males commonly begin to molt earlier than females in free-living populations of this race (Morton and Welton 1973), the *Z. nuttalli-pugetensis* group (Mewaldt and King 1978), and *Z. capensis* (Miller 1961), but not in *Z. l. gambelii* (Morton et

al. 1969). In contrast to our findings, Sheffield (1975) found that captive male Harris' Sparrows began to shed primaries about 9 days earlier than females (*P* < 0.05), again possibly because of differences in experimental design between his study and ours.

Primaries were replaced symmetrically in the two wings and in sequence from P1 through P9 (Fig. 3), which is the normal sequence not only among all other crowned sparrows that have been studied, but also among passerines generally (Stresemann and Stresemann 1966). However, the rate of replacement was not uniform over time as reflected by differences in shedding intervals (Table 1). P2–P4 were lost quickly (average interval between successive feathers = 3.6

TABLE 1. Growth rates of primary remiges in captive *Zonotrichia querula*. Sample sizes are eight males and six females unless otherwise indicated in parentheses.

Primary number	Final length (mm)[a,b,c]		Growth to 60% (mm/day)[b,d]	Days to grow 60%[d,e]		Shedding interval (days)[d,f]	
	Male	Female	Male and female	Male	Female	Male	Female
1	59.2 ± 2.4 A	56.8 ± 1.5 A	4.0 ± 0.4 (13) A	8.2 ± 0.4	8.4 ± 1.0	3.4 ± 3.3	3.2 ± 1.6
2	60.8 ± 2.7 A	58.3 ± 1.5 A	4.3 ± 0.2 A	8.5 ± 0.4	8.3 ± 0.5	3.0 ± 0.5	3.3 ± 2.8
3	62.8 ± 1.9 AB	59.8 ± 1.3 AB	4.2 ± 0.4 A	9.1 ± 0.8	8.8 ± 0.8	4.3 ± 2.3	4.3 ± 4.8
4	65.5 ± 1.4 BC	62.3 ± 1.4 BC	4.1 ± 0.4 (13) A	8.9 ± 1.4	9.1 ± 1.3	5.7 ± 2.9	5.7 ± 1.8
5	62.9 ± 2.0 BC	65.5 ± 1.2 D	4.2 ± 0.3 A	9.8 ± 0.5 *	9.4 ± 0.7	4.8 ± 2.0	4.9 ± 1.2
6	70.4 ± 1.8 D	66.3 ± 1.0 D	4.0 ± 0.2 (13) A	10.2 ± 0.6	10.0 ± 0.7	5.9 ± 2.6	5.4 ± 1.6
7	69.9 ± 1.2 D	65.3 ± 1.0 CD	3.9 ± 0.3 (13) AB	10.7 ± 0.7	10.5 ± 0.9	5.3 ± 2.0	1.4 ± 3.1
8	68.9 ± 1.4 CD	65.0 ± 1.1 CD	3.6 ± 0.3 BC	11.3 ± 1.0	11.0 ± 1.1	5.6 ± 1.5 *	1.0 ± 4.7
9	61.9 ± 1.6 AB	57.7 ± 1.5 A	3.4 ± 0.7 C	11.2 ± 1.6	10.7 ± 1.6		

[a] Underlined pairs of values are not significantly different (*P* < 0.05); those pairs *not* underlined differ at the 0.5 or a higher level of significance (Student's *t*-test, two-tailed).
[b] Values are averages ± SD for left *and* right wing feathers combined.
[c] Values in each column followed by different letters differ significantly at the 0.5 or a higher level; those followed by the *same* letter are not significantly different (one-way ANOVA followed by Student-Newman-Keuls or Scheffé's tests).
[d] Values are for primaries in the left wing only.
[e] Values separated by asterisks (*) differ significantly at the 0.05 level; other pairs of values are not significantly different (Student's *t*-test, two-tailed).
[f] Shedding intervals are for successive feathers dropped.

days), but not as quickly as reported in *Z. l. oriantha* (1.5 days; Morton and Welton 1973), while P5–P9 were shed more slowly, at intervals of 4.7 (females) and 5.5 (males) days on average. This two-phase pattern of shedding primary remiges deviates from that typically observed in other passerines (Stresemann and Stresemann 1966), as well as in *Z. l. gambelii* (Morton et al. 1969), *Z. l. oriantha* (Morton and Welton 1973), *Z. capensis* (Miller 1961, King 1972) and another group of *Z. querula* (Sheffield 1975) in which the central primaries are lost more slowly than primaries at *both* ends of the series.

Among our birds, the shedding intervals were generally similar in the two sexes and ranged between 1.0 (P8–P9 interval of females) and 6.4 days (P7–P8 interval of females; see Table 1). King (1972) reports intervals of 2.8–9.0 days for *Z. capensis*.

Growth of primary feathers was linear for the first 60% of the final feather length and then tapered off (Fig. 4). King (1972) also observed this linearity in *Z. capensis*. Rates of growth to 60% were similar in both sexes but not uniform throughout the primary series: P2 exhibited the fastest growth (4.3 mm·day^{-1}), P7–P9 the slowest (3.4–3.9 mm·day^{-1}; Table 1). Hence, the time (8–11 days) required for individual feathers to grow to 60% of their final length was similar in both sexes even though the mature feathers of males were longer than those of females (Table 1). In *Z. capensis,* primaries grow much more rapidly (5.8–9.5 mm·day^{-1}) and reach 60% of their final size much more quickly (in 7–9 days). Rates of growth were also variable in *Z. l. gambelii*: averaging 0.6 and 5.4 mm·day^{-1} for P1 and P9, respectively (Morton et al. 1969), although these rates are based on the time required for primaries to reach their final length rather than 60% of it.

Primary molt lasted as long as 81 days and averaged 66.2 ± 7.8 days. Replacement required a similar amount of time in another group of *Z. querula* (61 days on average; Sheffield 1975) and *Z. capensis* (54–64 days; Miller 1961, King 1972), but more time than it does in *Z. l. gambelii* (37 days; Morton et al. 1969) and *Z. l. oriantha* (46 days; Morton and Welton 1973).

Replacement of the primary coverts began at P1–P2 and progressed outward, the usual pattern for passerines including *Z. capensis* (Miller 1961, King 1972). In *Z. capensis,* the coverts molt sequentially from 1 through 9 concurrent with re-

placement of the corresponding primary remiges. In our birds, molt of covert feathers began on average on day 9.8, finished on day 55, and lasted 44.5 days. Onset was concurrent with replacement of P_1–P_3 and finish with the completion of molt of P_6–P_7.

Secondary remiges and their coverts. Replacement of the secondaries was symmetrical, but characterized by its irregularity compared with that in passerines generally and other *Zonotrichia* specifically where the tertials (S_7–S_9) and S_1 are shed first, followed later by S_2–S_6 in sequence (Miller 1961, Morton et al. 1969, Morton and Welton 1973, Sheffield 1975).

Eight of our 14 birds lost S_1 first, and six of them lost S_7 or S_8 first. In a larger sample of captives (including these 14 sparrows; $n = 33$), only 27% began secondary molt with S_7 or S_8, whereas 58% began with S_1 (deGraw and Kern, unpubl. observ.). This contrasts with Sheffield's earlier (1975) study of captive Harris' Sparrows in which all 10 birds began secondary molt by shedding S_8. However, King (1972) observed similar irregularities, as well as asymmetry, in the secondary molt of *Z. capensis*.

Nonetheless, we usually found early renewal of S_1 and S_7–S_9 followed later by replacement of the other secondaries (S_2–S_6; Fig. 3). However, S_2–S_6 were not renewed in sequence, S_6 commonly preceding S_5 (64% of our birds).

Secondary remiges grew at rates between 2.2 (S_9) and 3.8 (S_3) mm·day^{-1} and showed no differences by sex (Table 2). Early growth was linear, but slower than that of the primaries. The tertials grew much more slowly than S_1–S_6. Except for S_9, secondary feathers of males were significantly longer than those of females, differences ranging from 1.8 mm (S_1) to 4.5 mm (S_5).

Secondaries were shed at intervals of 1.6–6.7 days in males, 1.0–4.5 days in females. Intervals between loss of successive feathers were similar in both sexes, as well as highly variable (Table 2), the longest being 11–12 days.

Males and females began to replace the secondaries (at day 21–22) and finished replacing them (day 74–76) at the same time and as a consequence the duration of secondary molt (55.0 ± 10.4 days; range = 44–85 days) was also similar. Secondary molt typically began while P_5 or P_6 were being replaced, as it did in Sheffield's (1975) earlier study of *Z. querula*. However, he found that captive male Harris' Sparrows began to replace the secondary remiges about 13 days
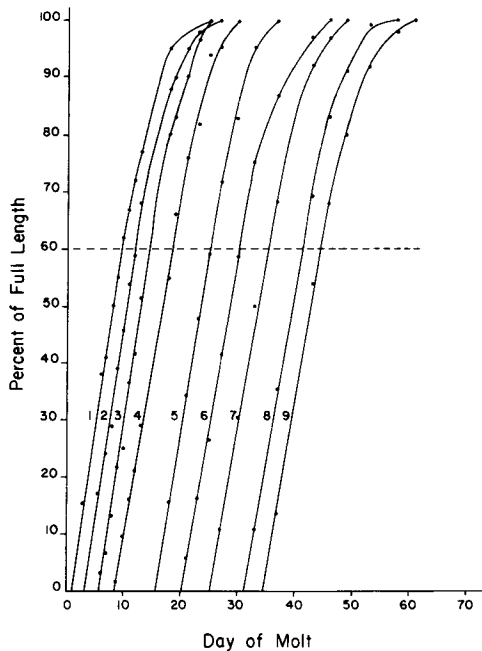

FIGURE 4.   Growth of individual primaries of a captive female Harris' Sparrow during postnuptial molt. Growth of each feather to 60% of its final length was linear.

earlier than the females and that secondary molt lasted only 42 days. In other crowned sparrows, except *Z. c. hypoleuca* (King 1972), its duration is also shorter: 26–38 days (Miller 1961, Morton et al. 1969, Morton and Welton 1973).

Molt of secondary greater covert feathers started at the wrist and progressed medially. It began on day 12 ± 5 concurrent with renewal of P_4, and concluded on day 65 ± 14, near the end of primary molt (Table 3). Hence, it lasted 53 ± 12 days. It began earlier and lasted considerably longer than reported in *Z. capensis* (through renewal of P_8, Miller 1961; days 23–24 or 17 days in duration, King 1972). In contrast to our observations, there is apparently no fixed pattern of molt either in this tract or in the middle and lesser coverts in *Z. capensis* (Miller 1961, King 1972). No descriptions are available for other *Zonotrichia*.

Middle secondary covert replacement began at the wrist concurrent with molt of the greater coverts and progressed both laterally and medially at the same time (Table 3). Molt of the lesser secondary coverts began later (day 21 ± 4) and concluded sooner (day 56 ± 5). Pins first

TABLE 2. Growth rates of secondary (and tertial) remiges in captive *Zonotrichia querula*. Sample sizes are eight males and six females unless otherwise indicated in parentheses.

Secondary number	Final length (mm)[a,b,c]		Growth to 60% (mm/day)[c,d]	Days to grow 60%[b,c,e]		Shedding interval (days)[c,e,f]	
	Male	Female	Male and female	Male	Female	Male	Female
1	58.5 ± 1.5 A	55.7 ± 1.2 A	3.7 ± 0.3 A	22.9 ± 5.6	21.6 ± 2.8	3.5 ± 2.0 (7)	1.0 ± 0.5 (5) *
2	58.9 ± 0.8 A	55.0 ± 1.1 A	3.7 ± 0.5 A	28.0 ± 6.0	27.0 ± 5.4	1.6 ± 1.3 (6)	2.4 ± 1.8
3	58.2 ± 1.2 A	53.8 ± 0.4 AB	3.8 ± 0.4 (11) A	32.5 ± 5.0	26.6 ± 9.1	3.3 ± 5.1 (5)	1.3 ± 0.8 (5)
4	56.9 ± 1.0 AB	53.2 ± 1.5 ABC	3.8 ± 0.3 A	34.7 ± 4.8	33.2 ± 10.2	5.4 ± 2.8 (6)	4.5 ± 4.6 (5)
5	56.2 ± 1.6 AB	51.7 ± 1.0 BCD	3.6 ± 0.3 (13) A	36.9 ± 4.5 *	30.8 ± 3.4	6.7 ± 3.5 (7)	4.1 ± 3.9
6	54.6 ± 0.7 BC	50.7 ± 0.8 CD	3.5 ± 0.3 (13) A	37.4 ± 5.1 *	28.4 ± 5.6	1.8 ± 1.1 (6)	3.5 ± 2.2 (5)
7	53.0 ± 2.1 C	49.3 ± 0.8 D	3.1 ± 0.4 (10) B	25.0 ± 4.8	24.3 ± 1.8	3.0 ± 1.3 (7)	4.3 ± 2.8 (5)
8	42.6 ± 1.5 D	39.8 ± 1.0 E	2.6 ± 0.4 (13) C	22.8 ± 4.1	23.5 ± 4.3	2.4 ± 2.2 (7)	2.8 ± 2.8 (5)
9	30.9 ± 1.4 E	29.8 ± 1.7 F	2.2 ± 0.6 D	27.2 ± 6.4	24.0 ± 3.6		

[a] Underlined pairs of values are not significantly different (*P* < 0.05); those pairs *not* underlined differ at the 0.5 or a higher level of significance (Student's *t*-test, two-tailed).
[b] Values are averages ± SD for left *and* right wing feathers combined.
[c] Values in each column followed by different letters differ at the 0.5 or a higher level of significance; those followed by the *same* letter are not significantly different (one-way ANOVA followed by Student-Newman-Keuls or Scheffe's tests).
[d] Values are for secondaries in the left wing only.
[e] Values separated by asterisks (*) differ significantly at the 0.05 level (Student's *t*-test, two-tailed).
[f] Shedding intervals are for successive feathers dropped.

appeared in the center of the tract and then as a wave advanced toward the leading edge of the wing in lateral and medial directions simultaneously.

Rectrices. Replacement of the tail feathers typically began with loss of R1 (day 17; range = day 6–38) when P4–P5 were being replaced (Fig. 3). Molt was symmetrical in most birds, but two or more feathers on each side were often dropped simultaneously, rather than sequentially. It was characteristic for all of the tail feathers to be growing concurrently. Miller (1961) and King (1972) noted the same irregularity in replacement of the tail feathers in *Z. capensis*. Morton et al. (1969) observed rapid loss of all tail feathers in *Z. l. gambelii* leaving the bird temporarily tailless.

The decks grew significantly (*P* < 0.02) faster in males than in females (3.4 vs. 3.1 mm·day⁻¹), and when mature were significantly (*P* < 0.001) longer in males (82 ± 3 mm vs. 74 ± 1 mm). Consequently, replacement concluded at approximately the same time (days 50–56 on average) in both sexes; the same was true for other rectrices as was reported in *Z. l. gambelii* (Morton et al. 1969).

The duration of tail molt (40.2 days overall; Table 3) varied between 29 (R6) and 35 (R1) days; shedding intervals from 0.9 (R5) to 3.8 (R6) days. R2 was lost 3 days after R1 and R2–R6 within the next 7.5 days on average. This sequence and tempo is similar to that reported for *Z. l. oriantha,* in which the respective intervals are 2.9 and 5.5 days (Morton and Welton 1973).

Contour plumage. Replacement of body feathers began in the dorsal tract on day 10 of molt, i.e., during replacement of P1–P3, and ended 70–72 days later in this and the ventral tract (Table 3). The pattern is similar to that in other crowned sparrows (Morton et al. 1969, King 1972, Morton and Welton 1973, Sheffield 1975): replacement of the contour plumage begins soon after P1 is replaced (on average at day 10 of molt) and marks the end of postnuptial molt later. Miller (1961), however, found that it can begin before loss of P1 in *Z. capensis*.

Its origin in the dorsal tract in our study confirms Sheffield's (1975) observations in another group of Harris' Sparrows and corresponds to the origin in some populations of *Z. capensis* (Miller 1961). However, in other populations of the latter, body molt starts in the tail coverts and scapular tracts (King 1972) and in *Z. l. oriantha*

TABLE 3. Onset, conclusion, duration, and maximum intensity of postnuptial molt in feather tracts of captive Harris' Sparrows on simulated natural photoperiods. Numbers for remiges, rectrices, and coverts are average values for eight males and six females. Numbers for the contour tracts are average values for eight males and three to four females.

Feather tract	Onset of molt (day of molt)	End of molt (day of molt)	Duration of molt (days)	Maximum intensity (day of molt)
Primary remiges	0.1 ± 0.5	66.4 ± 8.0	66.2 ± 7.8	24
Primary coverts	9.8 ± 4.1	55.0 ± 7.6	44.5 ± 5.2	22
Secondary remiges	18.1 ± 7.8	73.1 ± 12.8	55.0 ± 10.4	44
Secondary coverts	12.7 ± 6.1	66.8 ± 11.9	54.2 ± 11.5	24
Rectrices	14.9 ± 5.4	55.4 ± 9.4	41.1 ± 5.9	36
Contour tracts				
Capital				
Crown	25.6 ± 6.6	73.0 ± 10.6	47.4 ± 7.4	40
Cheek	26.1 ± 3.8	79.9 ± 10.7	54.4 ± 10.3	40
Chin	20.2 ± 4.2	63.2 ± 6.6	43.0 ± 5.1	32
Dorsal	9.8 ± 5.4	77.3 ± 10.1	67.5 ± 12.6	32
Scapulohumeral	12.7 ± 5.5	66.2 ± 8.1	53.6 ± 8.4	24
Femoral	16.4 ± 7.1	67.8 ± 7.5	51.3 ± 7.8	40
Ventral	13.9 ± 4.3	81.5 ± 9.7	68.4 ± 8.0	34
Crural	27.0 ± 5.4	64.8 ± 7.8	37.8 ± 7.4	40

it begins in the cervical region (Morton and Welton 1973). Replacement of the capital tracts characterizes late stages of body molt in *Z. capensis* (Miller 1961, King 1972), but not in *Z. querula*. Like Sheffield (1975), we found that this molt lasted somewhat longer than 60 days (Table 3), and considerably longer than the 49 days in *Z. l. gambelii* (Morton et al. 1969) and 42–54 days in *Z. capensis* (Miller 1961). No sexual differences in onset or end of body molt, like those reported for *Z. querula* by Sheffield (1975, males began body molt 8 days earlier than females), were evident in any body tract.

As a whole, contour feathers in the body tracts began to renew at day 9.9 ± 5.7 days. Body molt was most extensive during days 19–44 or for about 25 days and less intense before and afterwards. Sheffield (1975) reported peak intensity in this race about day 30. In *Z. l. oriantha* it is heaviest on days 25–35 (Morton and Welton 1973), and in *Z. l. gambelii* on days 25–40 (Morton et al. 1969), periods remarkably similar to that of *Z. querula* given the differences among these races in duration of postnuptial molt (Table 4).

(1) *Dorsal tract* (onset = day 10). Feather replacement typically began in the saddle or posterior element and spread anteriorly and posteriorly. Occasionally, a secondary wave of molt appeared in the anterior element and moved posteriorly. In the wide saddle element, feather replacement began in the midline and progressed laterally.

(2) *Scapulohumeral tract* (day 13). Molt began in the dorsal center of this tract and progressed anteriorly and posteriorly.

(3) *Ventral tract* (day 14). Pins appeared first in the anterior part of the main element and then spread anteriorly, posteriorly, and laterally (i.e., toward the margins of the tract) to involve the remainder of this element and the flank element.

(4) *Femoral tract* (day 16). There was no consistent point of origin of molt here, although replacement was usually from medial to lateral margins.

(5) *Capital tract.* (a) *Chin* (day 20). Pins first appeared in the nuchal area and spread rostrad. Within days, however, a secondary front appeared at the base of the bill and spread posteriorly. Some pins and brushes were frequently present in this part of the capital tract until the very end of postnuptial molt, as reported in *Z. capensis* (Miller 1961, King 1972). (b) *Crown* (day 26). In most cases, feather renewal began in the center of the middle third of the crown and spread centrifugally. Pins were present at the lateral margins of the crown within 14 days of onset. This pattern differs somewhat from that in *Z. capensis* in which crown molt begins near the bill and spreads posteriorly (King 1972). (c) *Cheek* (day 26). The first evidence of molt in the cheek was often the appearance of pins and brushes in

TABLE 4. Duration of postnuptial molt in *Zonotrichia* for which data are available.

Species or race	Latitude of breeding area	Elevation of breeding area (m)	Duration of postnuptial molt (days)[a]	Source
Z. leucophrys gambelii	65°N	140–280	33	DeWolfe (1967)
			49	Morton et al. (1969)
Z. querula	57–67°N[b]	35[c]	63	Sheffield (1975)
			82	This paper
Z. l. oriantha	42°N	1,890	53–61	King and Mewaldt (1987)
	38°N	3,000	49	Morton and Welton (1973)
Z. l. nuttalli	37°N	60–300	68	Mewaldt and King (1978)
Z. l. pugetensis	41–49°N	10–30	47–68	Mewaldt and King (1978)
Z. capensis costaricensis	10°N	1,900	ca. 60	Wolf (1969)
	3.5°N	2,000	60	Miller (1961)
Z. c. peruvianus	12.5°S	25	60–70	Davis (1971)
Z. c. hypoleuca	27°S	550	80	King (1972)

[a] Underlined numbers were obtained from studies of caged sparrows; numbers not underlined from birds captured in the field.
[b] Since we do not know where our birds or those of Sheffield (1975) spent the summer, we include the entire breeding range of *Z. querula*.
[c] Elevation at Fort Churchill, Manitoba, near the southern limit of the breeding range.

the eye ring. Later, the gray nuptial plumage was replaced by brown eclipse plumage in a wave from posterior to anterior.

(6) *Crural tract* (day 27). No consistent pattern of feather replacement was evident in this tract: scattered pins appeared throughout the tract beginning on day 27 of molt.

SUSPECTED INTERRELATIONSHIP BETWEEN BREEDING ACTIVITIES AND POSTNUPTIAL MOLT IN FREE-LIVING HARRIS' SPARROWS

Comparative studies of *Zonotrichia*, especially of the North American races of this sparrow, indicate that periods of breeding and postnuptial molt are mutually exclusive processes in the annual cycle. This is especially the case in females, because of the high energy demands each places on the birds (Miller 1962, DeWolfe 1967, Mewaldt et al. 1968, Morton et al. 1969, Wolf 1969, Davis 1971, Morton and Welton 1973). In this group as well, latitudinal trends exist in the duration and onset of molt that are apparently adaptive in nature. In *Z. l. nuttalli* and *Z. l. pugetensis*, e.g., molt is shorter at higher northern latitudes than at more southerly ones, probably because of the shorter growing (i.e., frost-free) season there (Mewaldt and King 1978). In *Z. l. gambelii*, postnuptial molt begins 1–2 days later for each degree of latitude as one moves north from southern California to Alaska (Morton et al. 1969). Populations summering at high elevations (Morton and Welton 1973), like those at high northerly latitudes, also have relatively short periods of postnuptial molt lasting only 33–49 days (Table 4).

In contrast, postnuptial molt in Harris' Sparrows lasts 82 days on average and is longer than that of other crowned sparrows studied to date from all latitudes (Table 4). Postnuptial molt of captive crowned sparrows faithfully replicates what happens in free-living birds (Morton et al. 1969, King 1972, Morton and Welton 1973, Mewaldt and King 1978). Although parallel assessment of molt in free-living and captive Harris' Sparrows was not possible in this study, we believe our data on captives exposed to simulated natural photoperiods reflect the time-course of events occurring on the breeding grounds in northern Canada. Hence, in Harris' Sparrows breeding at high northern latitudes molt may be about twice as long as that of other *Zonotrichia* nesting under similar conditions or at high altitudes. In these other forms, periods of breeding and molt are by and large rigidly separated. It does not seem probable that they are separated, however, in Harris' Sparrows given what we know of their summer and fall program. It is possible that the beginning of postnuptial molt overlaps the end of the breeding period in this finch as it sometimes does, in fact, in males (but not females) of other *Zonotrichia* (Miller 1961; King 1972; Morton, unpubl. observ.).

Harris' Sparrows that nest near Fort Churchill, Manitoba (58°N), have fledged most of their chicks before 12 July (Rees 1973), although renesters may not even hatch chicks until as late as 21 July and therefore not get them out of the

nest for another 14 days (4 August). Banding data indicate that migrants have completed the postnuptial molt when they arrive in southern Saskatchewan, the Dakotas, Nebraska, and Iowa between late September and mid-October (Swenk and Stevens 1929; deGraw, pers. observ.). Most *Z. querula* must therefore depart Churchill in mid-September at the latest. The interval between 12 July and mid-September is barely adequate to allow the birds to finish molting before they leave Churchill if the duration of the postnuptial molt were about 60 days as Sheffield (1975) suggests. However, his data were not obtained from birds exposed to photoperiodic conditions typical of the summering areas. If our 82-day period is accurate, and we think it is, it is not possible for Harris' Sparrows to finish breeding before they begin to molt. Molt in our captives began as early as 5 July or roughly when the birds would be brooding chicks in Churchill. Even if the birds begin to molt this early, they will not finish until mid-September.

The implications of this protracted postnuptial molt, as we see it, are (a) that periods of breeding and postnuptial molt normally overlap, (b) that postnuptial molt is completed while the birds move south at the end of the summer, and (c) that most renesting attempts, particularly very late ones, are unsuccessful. In this regard, it is worth noting that some migrating *Z. l. gambelii* arrive in Washington in the fall with light body molt (Morton et al. 1969; Kern and deGraw, unpubl. observ.).

However, since (1) most wing, tail and body feathers are replaced early in the period of molt (Table 3, Fig. 2)—between 28 July and 26 August (days 28–59 of molt), and (2) since wing and tail feathers regrow to 60% of their final length in 11 (primary remiges), 14 (retrices), and 37 (secondary remiges) days (Tables 1, 2), the most important part of the plumage is renewed before the birds must leave the nesting areas. A long postnuptial molt may not therefore be maladaptive.

ACKNOWLEDGMENTS

LITERATURE CITED

BANKS, R. C. 1964. Geographic variation in the White-crowned Sparrow *Zonotrichia leucophrys*. Univ. Calif. Publ. Zool. 70:1–123.

BAUMGARTNER, A. M. 1968. *Zonotrichia leucophrys*: Harris' Sparrow, p. 1249–1273. *In* O. L. Austin, Jr. [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 3. U.S. Natl. Mus. Bull. 237.

BLANCHARD, B. D. 1941. The White-crowned Sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool. 46:1–178.

CHAPMAN, F. A. 1940. The post-glacial history of *Zonotrichia capensis*. Bull. Am. Mus. Nat. Hist. 77:381–438.

CORTOPASSI, A., AND L. R. MEWALDT. 1965. Circumannual distribution of White-crowned Sparrows. Bird-Banding 36:141–169.

DAVIS, J. 1971. Breeding and molt schedules of the Rufous-collared Sparrows in coastal Peru. Condor 73:127–146.

DEGRAW, W. A., AND M. D. KERN. 1985. Changes in the blood and plasma volume of Harris' Sparrows during postnuptial molt. Comp. Biochem. Physiol. A. Comp. Physiol. 81:889–893.

DEWOLFE, B. B. 1967. Biology of White-crowned Sparrows in late summer at College, Alaska. Condor 69:110–132.

KERN, M. D., AND W. A. DEGRAW. 1986. Thyroid-molt relationships in Harris' Sparrow (*Zonotrichia querula*). Comp. Biochem. Physiol. A. Comp. Physiol. 85:49–55.

KING, J. R. 1972. Postnuptial and postjuvenal molt in Rufous-collared Sparrows in northwestern Argentina. Condor 74:5–16.

KING, J. R. 1973. The annual cycle of the Rufous-collared Sparrow (*Zonotrichia capensis*) in three biotopes in north-western Argentina. J. Zool. (Lond.) 170:163–188.

KING, J. R., AND L. R. MEWALDT. 1987. The summer biology of an unstable insular population of White-crowned Sparrows in Oregon. Condor 89:549–565.

LEWIS, R. A. 1975. Reproductive biology of the White-crowned Sparrow. II. Environmental control of reproductive and associated cycles. Condor 77:111–124.

MEWALDT, L. R., AND J. R. KING. 1978. Latitudinal variation of postnuptial molt in Pacific coast White-crowned Sparrows. Auk 95:168–179.

MEWALDT, L. R., S. S. KIBBY, AND M. L. MORTON. 1968. Comparative biology of Pacific coastal White-crowned Sparrows. Condor 70:14–30.

MILLER, A. H. 1961. Molt cycles in equatorial Andean Sparrows. Condor 63:143–161.

MILLER, A. H. 1962. Bimodal occurrence of breeding in an equatorial sparrow. Proc. Natl. Acad. Sci. 48:396–400.

MORTON, M. L., J. R. KING, AND D. S. FARNER. 1969. Postnuptial and postjuvenal molt in White-crowned Sparrows in central Alaska. Condor 71:376–385.

MORTON, M. L., AND D. E. WELTON. 1973. Postnuptial molt and its relation to reproductive cycle and

body weight in Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*). Condor 75:184–189.

REES, W. E. 1973. Comparative ecology of three sympatric sparrows of the genus *Zonotrichia*. Ph.D. diss., Univ. of Toronto, Toronto, Canada.

SHEFFIELD, M. V. 1975. A quantitative examination of normal molt and inhibition of molt by prolactin in Harris' Sparrow, *Zonotrichia querula*. M.A. thesis, Univ. of Nebraska at Omaha, Omaha.

STRESEMANN, E., AND V. STRESEMANN. 1966. Die Mauser der Vögel. J. Ornithol. 107:1–447.

SWENK, M. H., AND O. A. STEVENS. 1929. Harris's Sparrow and the study of it by trapping. Wilson Bull. 41:129–177.

WOLF, L. L. 1969. Breeding and molting periods in a Costa Rican population of the Andean Sparrow. Condor 71:212–219.

WOLFSON, A. 1954. Notes on the cloacal protuberance, seminal vesicles, and a possible copulatory organ in male passerine birds. Bull. Chicago Acad. Sci. 10:1–23.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.