POSTNUPTIAL AND POSTJUVENAL MOLT IN RUFOUS-COLLARED SPARROWS IN NORTHWESTERN ARGENTINA

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The Rufous-collared Sparrow, *Zonotrichia capensis*, inhabits brushlands and open woodlands in Latin America from central México to Cape Horn. It is a polytypic species in which more than 20 taxonomic forms have been proposed to date (Chapman 1940; Koepcke 1963, 1971; Phelps and Phelps 1955; Wetmore 1951). Owing to this diversity the *Zonotrichia capensis* complex is an especially attractive model for examination of adaptive radiation in various functional attributes. The investigations by Chapman (1940), Miller (1961), Wolf (1969), and Davis (1971) provide the basis for an initial survey of the patterns of molt in populations of *Z. capensis* extending from Costa Rica to Perú. To these reports I am now able to add data from *Z. capensis* in northwestern Argentina. Attention will be confined here mainly to the pattern and tempo of molt. The phasing and regulation of molt cycles as components of the entire annual cycle will be considered in a separate report.

MATERIALS AND METHODS

THE STUDY AREAS

Rufous-collared Sparrows of the race *hypoleuca* (Chapman 1940:402) were studied in the Province of Tucumán, in northwestern Argentina, from late August 1969 to mid-June 1970. Three study stations were established along an east-west line of about 100 km at latitude 26.9°S, extending from chaco parkland near Las Cejas (400 m above sea level) through transition-zone vegetation to the lower edge of the Andean rain forest at Horco Molle (550 m), and to the high-altitude semi-desert at Tafí del Valle (2000 m). The floristic and physiographic characteristics of these zones are described by Digilio and Legname (1966) and by Hueck (1966). Most of the work described in this report was accomplished at the station at Horco Molle, but data from other stations will also be mentioned. Rufous-collared Sparrows were present throughout the year in the lowlands, but they disappeared from Tafí del Valle in mid-April, after the end of the breeding season. The scant evidence available indicates that *Z. c. hypoleuca* is only an altitudinal migrant.

METHODS OF STUDY

The patterns and seasons of molting were studied by three integrated procedures, including (1) serial examination of captive birds, (2) periodic sampling of free-living populations by shooting and by capture in mist nets, and (3) observation of free-living birds with the aid of binoculars. Owing to limitations of time and manpower it was not feasible to band and recapture a significant number of birds, and only slight information was obtained from returns or observation of 16 color-banded adults and 12 juveniles.

Twenty Rufous-collared Sparrows were captured near Horco Molle in late August and early September and were caged individually in an outdoor shelter until 26 January 1970, when they were sent to the University of Washington for experimental studies. They were replaced by 16 birds (11 adults and 5 juveniles) caught in early February. A few additional birds were caught and caged later in the season, after molt had begun. All birds were weighed and examined every seventh day until the onset of molt, during which they were examined every third day. Molt condition was recorded on a standard form including the following data: condition of each flight feather (old, empty socket, pin just visible, growing by estimated tenths of full length, new with persistent basal sheath), intensity of body molt and head molt (L, M, H, per cent black in crown if in postjuvenal molt), with notes on individual tracts and condition of molt in coverts. Shed remiges and rectrices were recovered daily from each cage and were noted in the written records. The conventional American molt terminology was used uniformly. The primaries were numbered (P1–P9) from proximal to distal, and the secondaries (S1–S9) from distal to proximal, including the "tertials" (S7–S9). The rectrices were numbered from the central pair (R1–1) outward.

The molt condition of birds obtained by shooting or netting was recorded by the same procedure. Altogether, about 270 individuals from the free-living populations were examined; 143 of these were in some stage of postnuptial or postjuvenal molt.

Finally, it was possible to make some useful supplementary observations of molt in free-living birds by use of binoculars at certain times of the year. In adults the plumage becomes very worn and faded by the last third of the breeding season. The buffy-cream edges of the greater secondary coverts are worn off and the wing lacks the bar characteristic of the fresh plumage; the nuchal area is commonly almost bare so that in profile the crest when erect appears as a flat plate rather than a wedge; and finally, the breast plumage becomes very worn and soiled, lacking the clear, pearly gray of the fresh condition and the sharp contrast with the black lateral breast patches. The latter may become so worn as to be almost invisible. The distinction between worn, transitional, and fresh plumage is very clear to an experienced observer, and can be used as an index (disappearance of worn plumage in the population) of the progress of postnuptial molt. Similar field observations of the transition between juvenal and adult (first-year) plumage can be made, and the duration

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of molt in an individual in certain stages of postjuvenal molt can be estimated roughly on the basis of criteria obtained from study of captives (see table 4). It was possible to distinguish between adult and immature birds in the field until late April or early May on the basis of plumage condition and (or) behavior. As territories disintegrated and adults joined the free-ranging flocks of immatures, the recognition of the two age groups became progressively more difficult and field data on molt condition therefore became unreliable. The method was not used after 9 May.

RESULTS AND DISCUSSION

The pattern and tempo of molt will be analyzed first for the captive birds, where the process was followed in detail in individuals. Comparisons will then be made with molt condition in samples of the free-living population in an attempt to learn if captive *Z. capensis* kept outdoors provide a reliable model of normal molt, as is the case with *Z. leucophrys gambelii* (Morton et al. 1969). There was no evidence of prenuptial molt in the populations at the three study areas, and the ensuing discussion concerns only postnuptial and postjuvenal molt.

Rufous-collared Sparrows, like crowned sparrows generally, adapt well to captivity (3 of 38 *Z. capensis* died while in captivity). However, the birds in Tucumán resist handling much more vigorously than do any of the North American forms of *Zonotrichia* with which I have worked previously. In five particularly fractious *Z. capensis* the struggling during detailed examination of the plumage (which sometimes required 8–10 min per bird) evidently caused slight to substantial irregularities in the shedding and replacement of flight feathers. Similar irregularities were not found in the free-living population, and they are judged to be abnormal. These birds are therefore omitted from the following analysis, which is confined to five adults and five juveniles that were relatively placid and for whom there is no evidence of damage to plumage or irregularity in its replacement during molt.

THE ONSET OF POSTNUPTIAL MOLT: HORCO MOLLE

The mean date for the beginning of the postnuptial molt (shedding of P1) in nine captive adults (including four that subsequently were excluded from the analysis) was 21 February (range, 11 February–6 March). The late date in the range was from a female (6635) with a vascular brood patch at the time of capture on 2 February. One female (6631) on the date of capture (1 February) was in suspended molt (see beyond) at P5, but resumed a regular molt with the shedding of P6 on 22 February.

TABLE 1. The temporal course of postnuptial molt in free-living *Zonotrichia capensis* at Horco Molle, as indicated by the regeneration of wing bars.

		Wing-bar pattern[b]	
Date[a]	No. birds	old	new
9 March	17	85	15
20 March	23	57	43
1 April	20	43	57
16 April	26	8	92
8 May	19	—	100

[a] Sample occasionally obtained during two consecutive days.
[b] Percentages, rounded to nearest whole number.

The mean date for the beginning of postnuptial molt in the captives reflects with reasonable fidelity the beginning of molt in the free-living population at Horco Molle. The captives were very much better synchronized, however, owing probably to the arrest of reproductive activity. Three of five adult *Z. capensis* collected at Horco Molle on 24 February were not yet molting, nor were three of six adults collected on 7 March. All adults collected or examined on or after 19 March had begun the molt. Estimates based on extrapolated dates of molt onset (for method, see beyond) indicate that about 30 per cent of the free-living population had begun the molt by 15 February, about 50 per cent by 22 February, and about 90 per cent by 14 March (see fig. 3).

Field observations of plumage condition in adults tend to confirm the timing of molt onset indicated by the captives and the collected specimens. The regeneration of the wing bar with the growth of the greater upper secondary coverts is the best field mark for this purpose. Data from captives show that these feathers begin, on the average, to grow on day 23 (range, 21–28) after the beginning of molt, and complete their growth, on the average, by day 41 (range, 31–50). The wing bar is visibly complete by about day 30. Data based on this criterion are shown in table 1, where it is evident that the temporal pattern of change conforms approximately to the pattern expected if the molt had begun in the free-living population on the schedule suggested by the collected samples. The line defined by the percentage of new wing bars in the population of adults is shown in figure 3. In general, the wing-bar line, as expected, lies 30–35 days later than the line for molt starts. These independent sets of data are therefore mutually consistent.

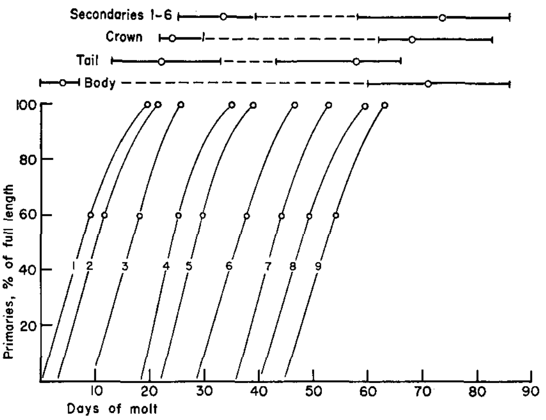

FIGURE 1. The sequence of plumage replacement during the postnuptial molt in five captive *Zonotrichia capensis*. At the top, horizontal lines represent the span of growth in plumage categories; circles, the mean dates of beginning and end of growth; solid bars, the range of dates.

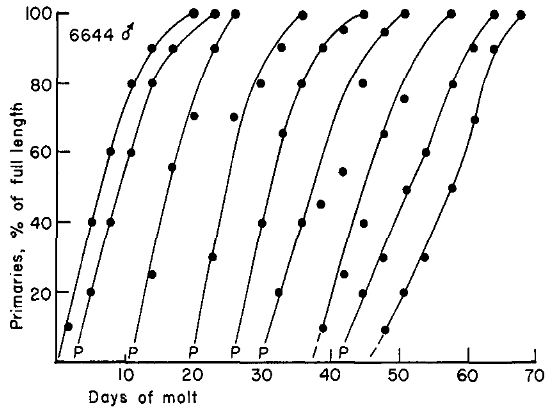

FIGURE 2. The growth of the primary remiges during postnuptial molt in a typical captive *Zonotrichia capensis*. A pin just emerging from skin is indicated by *P*.

Individually, each of the three methods (captives, field samples, field observation) is statistically weak or is not fully satisfactory for other reasons; but collectively these methods provide consistent results and a reliable estimate of the calendar of molt.

THE PATTERN OF POSTNUPTIAL MOLT: HORCO MOLLE

The sequence and phasing of plumage replacement during postnuptial molt in the birds in Tucumán did not differ from that reported by Miller (1961) for Z. *capensis* in Colombia. However, the serial examination of individual captives in Tucumán makes it possible to present the following more detailed analysis and a more reliable calendar.

Primaries and their coverts. A summary of the temporal phase relationships in the major feather tracts for five adult Z. *capensis* is shown in figure 1. Day zero in the presentation is taken as the day on which P1 is shed. For the analysis, all birds were set in phase on day zero regardless of the calendar date on which molt began. The shedding of the first primary was always the first evidence of postnuptial molt. The schematic graph for the growth of primaries (fig. 1) was obtained in the following way. The growth of each primary remige in each bird was first plotted separately. An example of original data for a typical bird is shown in figure 2. It was noted that growth to 60 per cent of full length was essentially linear with time in nearly all feathers and birds. The mean day for reaching 60 per cent of full length was therefore computed for each of the nine primaries and five birds by taking exact or interpolated values from the individual graphs. The average days on which growth began and on which full growth (100 per cent) was reached were estimated in the same way. The three averages for each feather were then connected by lines as shown in figure 1. The sample sizes are too small for meaningful statistical analysis, but an estimate of variability can be obtained by inspecting typical ranges of values. For instance, in the order P1, P5, P9, the ranges for dates of beginning growth are 0 (by definition), 18–25, 39–50; for 60% of full length, 8–12, 25–32, 47–59; and for full length, 16–24, 35–42, 56–68. In general, the maximum full-range error is about ± 5 days.

The rate of growth in the primaries was not uniform through the series, but was most rapid in the middle three, decreasing from the middle toward each end. The mean interval between feather emergences in the series seems likewise to be arranged by functional triplets (table 2).

TABLE 2. Growth rates in primary remiges of five captive *Zonotrichia capensis*.

Primary no.	Length[a] mm	Growth to 60%		Shedding interval[b]
		Days	mm/day	
1	58	9.0	6.4	2.8
2	60	8.6	7.0	6.6
3	61	8.6	7.1	9.0
4	63	6.6	9.5	3.6
5	65	7.6	8.6	6.6
6	65	8.8	7.4	7.2
7	64	8.6	7.4	4.2
8	62	9.2	6.6	4.6
9	55	9.4	5.8	

[a] Lengths of the plucked feathers, straightened and flattened, from a specimen having the same mean wing chord as the captives.

[b] Mean interval, in days, between dropping of successive feathers.

TABLE 3. Postnuptial molt profiles of six *Zonotrichia capensis* collected at Horco Molle (representative examples).

Date collected	Sex	Condition of primaries[a]									Body molt[b]	Tail molt	Crown molt	Sec 7–9	Sec 1–6	Day in molt
		1	2	3	4	5	6	7	8	9						
24 Feb	m	N	N	80	50	P	X	X	X	X	+	X	X	+	X	23[c]
16 Mar	f	N	N	90+	80	50	0	X	X	X	+	+	+	+	X	27
16 Mar	m	N	N	90+	80	60	0	X	X	X	+	+	+	+	X	27
10 Apr	m	N	N	N	N	90	50	10	X	X	+	+	+	N	+	37
30 Apr	m	N	N	N	N	N	90+	80	40	10	+	N	+	N	+	47
2 May	f	N	N	N	N	N	N	90+	90	50	+	N	+	N	+	53

[a] N = new, fully cornified feather; P = a pin just emerging; 0 = an empty feather socket; X = an old, worn feather; numerical values = percentage of full length.

[b] For body, tail, crown, and secondaries (Sec), + = growing feathers, X = old feathers and no growth, N = new feathers and molt ended.

[c] Estimated day since beginning of molt.

The renewal of the upper primary coverts invariably accompanied the renewal of the corresponding quill, as is the usual pattern in passerines.

Secondaries and their coverts. In general, the renewal of the secondary remiges followed the sequence expected in passerines, but it was much less regular in sequence and in rate than the pattern found, for instance, in *Z. l. gambelii* (Morton et al. 1969). In the captive *Z. capensis* the molt of the secondaries was commonly asymmetrical and did not always show a smooth gradation of growth from S1 through S6. On the average, the renewal of the secondaries began in the "tertials" with S8, which appeared as a pin on the average on day 18 (range, 12–22), followed by S9 on day 25 (range, 16–30), and S7 on day 35 (range, 14–44). Shedding of S1 occurred on the average on day 33 (range, 25–40), and S2–S6 sometimes followed in ascending order but commonly involved two or three feathers at once. Average renewal of the secondaries was completed on day 74 (range, 58–86).

Renewal of the greater upper secondary coverts typically began about 10 days before the first growth of the new quills themselves, on the average on day 23 (range, 12–28), and continued to day 41 (range, 31–50). There was no regular gradation or consistent sequence of secondary covert renewal among the specimens examined. Replacement of the lesser upper secondary coverts occurred later than that of the greater coverts.

The rectrices. Growth of the new tail typically began with the shedding of the central rectrices (1–1), on the average on day 22 of molt (range, 13–33). In some individuals there was a discernible sequence of shedding and renewal from R1 through R6, but it was common to find that all rectrices were growing concurrently without orderly gradation.

The contour plumage. Molt of the body feathers usually began soon after the shedding of P1, appearing first in the upper and lower tail coverts and scapular tracts, and involving next the interscapular region of the dorsal tract. Body molt then proceeded through other regions and tracts, reaching last the cervical and nuchal regions. Molt of the head plumage typically began with the auricular and malar tracts, then appeared in the rostral region of the coronal tract, spreading backward. The last residues of molt (long-persisting basal sheaths) were found in the auriculars and chin.

Phase relationships in plumage categories. The schematic model of phase relationships in molt (fig. 1) is a useful statistical abstraction of molt in captives, but it remains to be shown whether or not it reliably represents the pattern and pace of molt in free-living birds. A comparison can be made by what I will call the "method of profiles." Vertical lines drawn through figure 1 on selected days give molt-pattern profiles of the typical captive bird on these days. For instance, on day 5 after the beginning of molt, P1 = 30, P2 = 10, body molt may or may not have begun, and there is no molt in other tracts. On day 35, P1–3 are new, P4 = 90+, P5 = 80, P6 = 40, the body, head, and tail are in molt, and molt may or may not have begun in S1–6. Such profiles can be supplemented by information, such as the molt of S7–9 and of the secondary coverts, not included in figure 1.

Similar profiles can be written for each specimen obtained from the free-living population. It should be possible to match such profiles with the standard diagram, and thus to estimate days since the start of molt, if in fact the phase pattern of the captive group is a faithful replica of that of the free-living population. A good match will also be strong evidence that the pace of molt is similar in the captive and free populations. If birds in the free-living population molt significantly faster than captives, then profiles from the latter can be expected to include more than three primaries growing concurrently, and conversely (Stresemann and Stresemann 1966:33), with attendant differences in the proportionate lengths of the quills.

In fact, a very good match is found between the standard molt profile and the profiles of collected birds, providing a reliable basis (in specimens lacking evidence of suspended molt; see beyond) for estimating the dates on which postnuptial molt began in the free-living population. This is the basis for the estimates already mentioned. Some examples of molt profiles taken at random but spanning the molt season are shown in table 3. Readers will note that all of these profiles are easily accommodated by the standard diagram in figure 1. There is no evidence in these data or in complementary data that the duration of molt changed in the free-living population during the season (see also fig. 3). Within the span of molt in the primaries the maximum error of estimate is about ± 5 days.

The duration of postnuptial molt. The average duration of postnuptial molt in the five captives included in figure 1 was 78.5 days (range, 69–91 days), or an average of 82.9 days (SE = 4.13 days) if to these five are added three other adults showing only minor irregularities of molt attributable to handling. A round number estimate of 80 days is a reasonable compromise.

For free-living birds I do not have sufficient data from banded and recaptured specimens to allow estimate of molt duration in individuals. An indirect approximation can be made on the basis of the following data (see fig. 3). The temporal course of molt starts in the population at Horco Molle is indicated by the cumulative percentage of starts, shown by the second curve from the left in figure 3. The dates for molt start were estimated in most cases by the method of profiles. If it is assumed that the complete molt requires 80 days on the average, then the temporal course of molt termination should resemble that of initiation, displaced to 80 days later, as shown by the curve at the right in figure 3. The data from the free-living population are confounded by cases of suspended molt and are not adequate to trace the entire course of molt termination, but only to estimate its beginning and end. As indicated in figure 3, the earliest observed cases of terminating molt were found in the field on 21 April, exactly 80 days after the earliest estimated (and observed) cases of molt start. The latest cases of terminating molt were found in the field on 7 June, about 10–12 days before the predicted date. This could indicate a slight shortening of the duration of molt to about 70 days late in the season, but it is equally likely that the discrepancy is a result of sampling error. Only about 5 per cent of the population was still molting in early June, and the small sample of adults (9 birds) collected at Horco Molle in the first half of June could easily have missed molting birds. In any event, the field data give no reason to believe that the patterns or rates of molt observed in the captives do not accurately reflect the condition in the free-living birds.

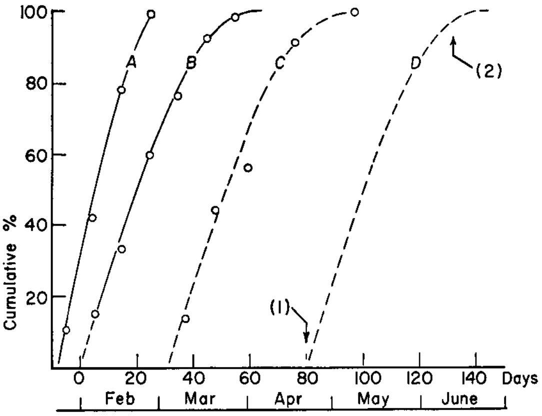

FIGURE 3. Estimates of the course of postnuptial molt in free-living *Zonotrichia capensis.* Line A = cumulative per cent of molt starts at Tafí del Valle ($n = 19$); line B = cumulative per cent of molt starts at Horco Molle ($n = 21$); line C = per cent of birds with new wing bars at Horco Molle (see table 1); Line D = line C displaced 80 days and representing predicted course of molt termination at Horco Molle. Date (1) = 21 April, when the earliest adults ending the molt were collected; date (2) = 7 June, when the last adults ending the molt were collected.

Miller (1961) estimated that the postnuptial molt required 50–80 days in individual free-living *Z. capensis* in Colombia, averaging about 60 days. From the data obtained by Davis (1971: fig. 5) for *Z. capensis* in Perú it is possible to estimate that the duration of molt in an individual bird was 60–70 days. These values are somewhat lower than the range (69–91 days) found in captives in Tucumán, but the data do not allow a rigorous statistical comparison.

POSTJUVENAL MOLT: HORCO MOLLE

Rufous-collared Sparrows molt directly from the juvenal plumage to an adult plumage, without the transitional first-winter plumage that is characteristic of North American forms of *Zonotrichia.* The contrast between juvenal

TABLE 4. The calendar of postjuvenal molt in five captive *Zonotrichia capensis* from Horco Molle.

Plumage category	Days after day zero[a]	
	Mean	Range
Body molt		
begins[a]	0.0	—
ends	51.0	48–54
Crown molt		
begins	5.4	0–12
ends	46.0	37–50
Throat spot complete[b]	22.8	21–24
Rufous collar complete[b]	29.2	24–34
Adult pattern complete[b]	30.8	28–35

[a] Day on which molt was first detected; mean day zero = 24 February (range, 22–25 February).

[b] Visibly complete, but feather growth continues.

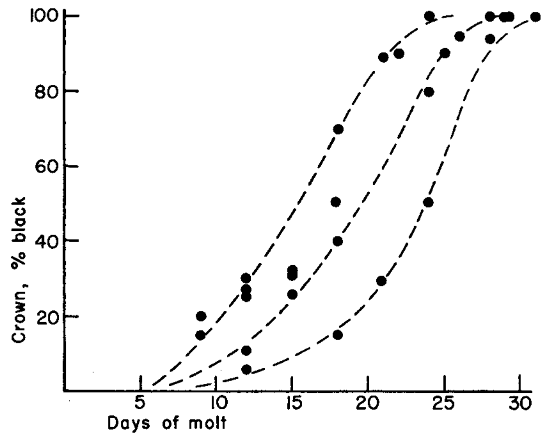

FIGURE 4. The time-course of replacement of brown by black crown feathers in five captive *Zonotrichia capensis* during postjuvenal molt. Points = empirical estimates for individual birds; curves = suggested mean and limits.

and adult plumage patterns in *Z. capensis* is depicted by Miller (1961:145).

There were no discernible differences in the plumage patterns or coloration of the adult and first-year *Z. c. hypoleuca* that I examined. Chapman (1940:413) states that the first-winter plumage of *Z. capensis* resembles that of adults, "but in the younger bird the remiges and rectrices are usually browner, the wing coverts not so black, their tips less sharply white."

These differences result from fading of the first-winter plumage, which at any time of collection following the postnuptial molt of adults will have been worn from several weeks to several months longer than the new plumage of the adults. The difference is not a reliable criterion of age, since the subsequent fading of the adult plumage soon brings the two age groups to a similar condition.

The pattern of the postjuvenal molt. Analysis of the postjuvenal molt, as in the case of the postnuptial molt, will begin with a consideration of its pattern and pace in five captives. The immature birds were less fractious than the adults and they were handled less extensively. The patterns of molt were alike in all five birds, and there was no evidence of abnormality. The sequence of plumage replacement is summarized in table 4. Bilateral replacement of S7–9 occurred in four of the five birds, and bilateral replacement of S8–9 occurred in the fifth. Replacement of secondaries in the field specimens was found only in S7–9. The secondary coverts (upper greater and lesser) were replaced but the primary coverts were not. There was evidence of replacement of rectrices 1–1 in 2 of 28 field specimens (all three study stations) in which this event could have been detected, but none of the captives replaced rectrices. Miller (1961) thought that 25–30 per cent of the population of *Z. capensis* that he studied in Colombia replaced rectrices in the postjuvenal molt.

The temporal course of transition from immature to adult crown pattern is shown in figure 4. The estimate "per cent black" is imprecise and there is considerable individual variation. These data, used in conjunction with other criteria (table 4), nevertheless aid in estimating the time of molt in individuals.

I examined 23 specimens of immature *Z. capensis* from the free-living population at Horco Molle. Only two of these were in transitional molt stages allowing estimate of the time since the start of molt. The other specimens had either completed the molt or had not yet started, aiding only in setting temporal limits on the molt calendar. Some information on the calendar of molt in the free-living population can be gained, nevertheless, from observational sampling of flocks of juveniles with the aid of binoculars. The data are assembled in table 5. Visible transition toward the adult plumage began between 9 and 13 March, indicating (see table 4) that molt had begun about 23 days earlier, or on about 16 February (range, about 14–18 February). The first birds in visibly complete first-year adult plumage were detected on 20 March, indicating that molt began about 31 days earlier, or on about 17 February (range, about 14–21 February). These partially independent estimates thus reinforce one another.

The captive juveniles began the postjuvenal molt on the average on 24 February (range,

TABLE 5. The temporal course of postjuvenal molt in free-living *Zonotrichia capensis* at Horco Molle.

Date[a]	No. birds[a]	Patterns observed[b]		
		Juv.	Trans.[c]	FY[c]
10 Feb	18	100	—	—
16 Feb	21	100	—	—
24 Feb	26	100	—	—
9 Mar	24	100	—	—
13 Mar	31	85	15	—
20 Mar	40	75	17	8
26 Mar	36	60	25	15
1 Apr	22	45	33	22
16 Apr	34	20	38	42
8 May	21	—	10	90

[a] Sample occasionally obtained during two consecutive days.

[b] Percentages, rounded to nearest whole number.

[c] Transitional = birds with incomplete collar but unstreaked breast; FY = first-year adult plumage.

22–25 February). Data from the collected samples are not inconsistent with the information yielded by the captives and by the field observations. All available evidence indicates that postjuvenal molt began in a large proportion of the immature birds soon after mid-February, and that there was no molting before that time.

Postjuvenal molt and age. Miller (1961: 158) showed that postjuvenal molt in *Z. capensis* in Colombia begins soon after the completion of growth of the juvenal plumage, with a lag in 12 cases ranging from 0 to 11 days and averaging about 5 days. The age relationship was different in the populations that I studied in Argentina. Nesting began in late September and the first fledglings were seen on 18 October. Reckoned from the beginning of incubation, the age of these birds and others from early clutches was four to five months when postjuvenal molt began in mid-February. Juveniles that hatched at a later time obviously would be younger when the postjuvenal molt began. The span of incubation starts was about six months in 1969–70, but the span of postjuvenal molt starts was only a little more than two months at a maximum.

Data from captives substantiate the conclusion that there is no fixed age at which postjuvenal molt begins. Three juveniles captured on 1 and 4 February were in a subadult range of body weight (16.2, 16.7, and 17.8 g, respectively). One bird had rectrices still in postnatal sheaths and it begged for food from an adult male with which it was initially caged. These birds began the postjuvenal molt on 22, 25, and 25 February, respectively. Skull ossification, examined on 10 May, was about 20, 40, and 80 per cent complete, respectively.

In contrast, two juveniles captured on 1 and 8 February were older, with faded and worn plumage, and weighing 18.8 and 19.4 g. Skull ossification, examined on 12 May, was complete in one bird, and the cranium was hard and inflexible (but without trabeculae, an anomalous condition) in the other bird. These birds, like the younger ones, began the postjuvenal molt on 22 and 25 February.

Finally, observation of immatures color-banded as nestlings adds some data that are consistent with the foregoing evidence. Juvenile 6628 was fledged on 11 November, and was seen again on 7 February, when there was no visible evidence of molt, and again on 26 March, when the breast was without streaks but the rufous collar was still incomplete. This bird must have been about four months old when the postjuvenal molt began (roughly, on 4 March).

Juvenile 6647 was fledged on about 7 February. It was seen again on 13 March still in juvenal plumage, again on 4 April when the breast and throat were of the adult pattern but lacking the rufous collar, and finally on 20 April, when the adult plumage pattern was visibly complete. This bird was about 1.6 months old when postjuvenal molt began (roughly, on 4 March), in which case the postjuvenal molt must have followed immediately after the completion of the juvenal plumage.

The duration of postjuvenal molt. Postjuvenal molt lasted an average of 51 days (range, 48–54 days) in five captives in Tucumán (table 4). I have no information on the duration of postjuvenal molt in individual free-living birds. In Colombia, Miller (1961) estimated that postjuvenal molt occupied about 50–100 days (average, about 70 days) in individual free-living *Z. capensis*.

MOLT AT OTHER STATIONS

Las Cejas (in the chaco woodland) and Tafí del Valle (in the mountain semi-desert) were visited at 3- to 6-week intervals, and the pattern and schedule of molt cannot be reconstructed in the detail made possible by the more abundant data from Horco Molle. Furthermore, the density of Rufous-collared Sparrows was much less in these habitats than in the lush vegetation at Horco Molle, and attempts to accumulate observational data and banding-recapture data did not produce statistically useful amounts of information except in a few cases. Nevertheless, as will be shown, the spans of the molting seasons can be estimated with rather good reliability.

Las Cejas: postnuptial molt. Nineteen adults in various stages of molt are represented in the collections from Las Cejas. Ten of these birds were in suspended molt or showed evidence of previous suspended molt. Three additional birds showed evidence of incipient suspended molt (e.g., one primary still growing but body molt suspended). The molt profiles in the remaining six specimens conform very well with the scheme for Horco Molle shown in figure 1, leading to the conclusion that the basic pace of molt was about the same at the two locations. All of the birds in "normal" postnuptial molt were collected on 21 March. The average estimated date for molt starts in these six birds was 23 February (range, 10 February–12 March). This corresponds closely with the mean date for molt start in captives at Horco Molle (21 February) and falls within the span of molt starts in the free-living population there (see fig. 3).

Additional collections were not made at Las Cejas until 27 April. On and after that date and until 14 June (when three adults were collected in the terminal stages of molt), all adults were in suspended molt or showed discontinuities indicating previous or incipient suspension. The period of molt suspension probably corresponds with a second seasonal peak of intense nesting, but I have no satisfactory data on this subject at Las Cejas.

Las Cejas: postjuvenal molt. I have 12 specimens of immatures from Las Cejas about which some statement of molt timing is possible. The earliest estimated date of molt starts is 23 February, and the latest is "after 27 May." On that date a juvenile was collected that was just completing the growth of the juvenal plumage. Four of the 12 records indicate molt starts before 8 March, and 10 of them indicate starts before 7 April. It is evident that the large majority of the juvenile population completed the molt, or at least visibly reached the adult stage, by mid-June. Observational data and a small collection (three juveniles in the last stages of postjuvenal molt) on 14 June support this prediction. In short, the season for postjuvenal molt at Las Cejas was not temporally distinguishable from the season at Horco Molle.

Tafí del Valle: postnuptial molt. I have 21 specimens from Tafí del Valle that yield information about the postnuptial molt. Four of these had completed the molt or were in its terminal stages; 17 showed pattern profiles conforming very well with the standard scheme shown in figure 1. It is therefore assumed that the pace of molt at Tafí del Valle did not differ appreciably from that at Horco Molle. The estimated average date of molt start for 17 birds was 9 February (range, 24 January–27 February). The estimated temporal trend for molt starts is shown by curve *A* in figure 3.

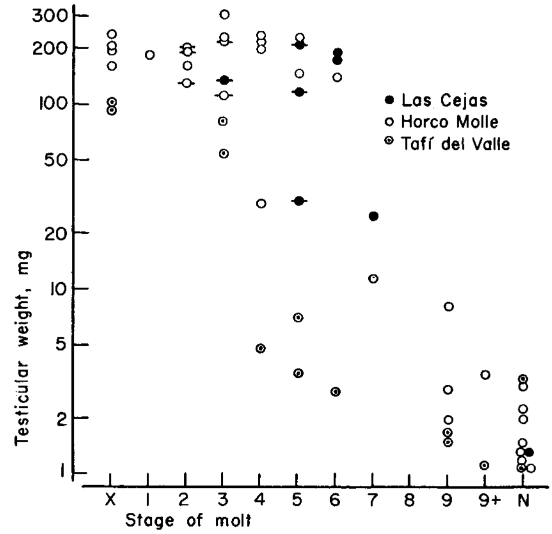

FIGURE 5. Testicular weight in relation to stage of postnuptial molt in free-living *Zonotrichia capensis* in Tucumán. Numerals along the abscissa indicate the most distal growing primary; X = old plumage, no molt; 9+ = molt still active beyond full growth of P9; N = new plumage, no molt. A symbol with lateral bars indicates a bird in suspended molt.

Tafí del Valle: postjuvenal molt. I have data relevant to molt from only 10 juveniles at Tafí. The average date for molt onset, estimated for six of these on the basis of plumage pattern, was 15 February (range, 5–24 February). The plumage condition in the four others does not indicate dates outside this span.

POSTNUPTIAL MOLT AND GONADAL ACTIVITY

Wing molt may occur at all stages of testicular size in equatorial and subequatorial populations of *Z. capensis*, although testicular size tends to diminish during the molt period (Miller 1961; Wolf 1969). In females, on the other hand, wing molt and egg-laying, incubation, and brooding are mutually exclusive (Miller 1961). Data for *Z. capensis* in Tucumán are shown in figures 5 and 6. It is evident that molt can proceed at least to the growth of P6 while testicular size is still maximal, but that the last third of postnuptial molt is associated in all males with regressing testes. At this time of the reproductive cycle, testicular weights greater than 100 mg are uniformly associated with histologic stage VI (full spermatogenic activity) of Bartholomew (1949), and testicular weights less than 40 mg are

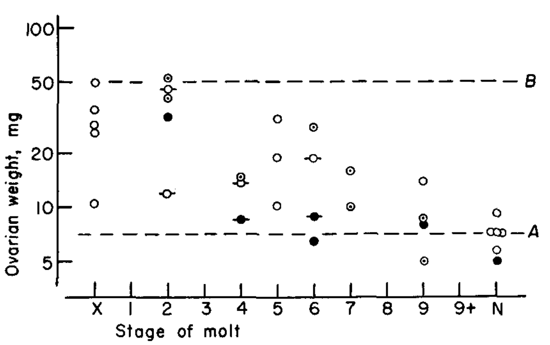

FIGURE 6. Ovarian weight in relation to stage of postnuptial molt in free-living *Zonotrichia capensis* in Tucumán. Weight-level A = mean weight of inactive ovary; weight-level B = mean pre-ovulatory weight (see text). Symbols as in figure 5.

uniformly associated with testicular involution (unpubl. data). The data for birds in Tucumán are similar to those obtained by Miller in Colombia and by Wolf in Costa Rica, except that there was no resurgence of testicular size in the terminal stages of molt, as was found in the subequatorial populations.

The relationship between molt and reproductive condition in females is not so easily assessed, but the following observations are pertinent. The mean weight of the quiescent ovary was about 7 mg (fig. 6); that of the active but non-ovulating ovary was about 50 mg, with follicles graded up to about 3 mm in diameter, preceding the rapid growth phase of the activated follicle. Molt beyond the growth of P2 was always associated with ovarian weight below the average pre-ovulatory level and with maximum follicular diameters below 1.6 mm. An active (edematous) brood patch was found in only one female, in which molt was suspended. All other females in active or suspended molt had inactive brood patches.

As in the more northerly populations of *Z. capensis*, the birds in Tucumán show a partial antagonism, mostly evident in females, between molt and reproductive activity. This antagonism may be further expressed by cases of suspended molt.

SUSPENDED POSTNUPTIAL MOLT

The term "suspended molt" as used in this report refers to a temporary interruption in the sequence of feather replacement, which is subsequently resumed at the point of suspension. I distinguish this from "arrested molt," in which the process is permanently stopped before feather replacement is completed (as in the case of the "prenuptial molt" of *Z. capensis* in Perú, described by Davis, 1971). Miller (1961) notes four cases in Colombian *Z. capensis* that appear to represent suspended molt.

In Tucumán, suspended molt was found only at Horco Molle and Las Cejas, where it occurred in 24 per cent of 87 individuals (11 males, 10 females) in which the condition could have been detected after early February. These cases could easily be identified by aberrations in the growth pattern coupled with discontinuities in the color and wear of the primaries, or by the presence of an empty remigial socket preceded in the series by a new quill. Evidently, once a feather germ begins to grow it continues to completion. I found no cases of suspended molt involving partly grown quills.

All but one of the 21 cases of suspended molt were found after 19 March. The molt was suspended with the completion of P1 in 5 cases, P2 in 2 cases, P3 in 4 cases, P4 in 3 cases, P5 in 5 cases, and P6 in 1 case. The date on which molt was suspended is of course not known, but it is significant that 27 molting adults of the lowland populations that were examined before 19 March showed no evidence of suspended molt (with the exception noted below), indicating that this phenomenon was concentrated in the middle of the molting season, and late in the nesting season. As mentioned previously, *Z. capensis* in Tucumán has no prenuptial molt, and none of the 88 specimens from the lowland populations examined in the pre-nesting and early-nesting periods showed any molt. The cases of suspended molt therefore do not represent merely a belated detection of a "prenuptial molt" arrested by the onset of nesting, of the type described by Davis (1971).

An exception to the general timing of molt suspension was found in adult female 6631, captured and caged on 1 February with molt suspended at the completion of P4 (P5 with empty sockets bilaterally and P1–4 obviously browner and less worn than P6–9). At the time of capture this bird had a vascularized but nonedematous brood patch. Molt resumed at P5 on 20 February and subsequently followed a normal sequence. This bird was also unusual in the fact that molt must have begun initially in early January at the latest, a month before molt started in the population generally.

A slight amount of additional information about suspended molt can be gained from one adult male (6621) that was color-banded and

TABLE 6. The calendar of molt in *Zonotrichia capensis* at three localities in the Province of Tucumán.

Locality	Postnuptial molt Earliest start	 Mean start	 Duration, days[a]	Postjuvenal molt Earliest start	 Mean start
Las Cejas	10 Feb	23 Feb	118	23 Feb	?
Horco Molle	1 Feb	21 Feb	115	16 Feb	24 Feb
Tafí del Valle	24 Jan	9 Feb	110	5 Feb	15 Feb

[a] Estimated duration in the population.

TABLE 7. Comparison of molts and plumages in forms of *Zonotrichia*.

	First-year plumage[a]	Prenuptial molt	First nuptial plumage[b]	Postnuptial molt	First postnuptial plumage
Z. capensis					
Costa Rica	Adult	Yes	Adult	Yes	Adult
Elsewhere	Adult	No[c]	Adult	Yes	Adult
Z. leucophrys					
pugetensis[d]	Imm.	Yes	Adult	Yes	Adult
nuttalli	Imm.	±No[e]	±Imm.[e]	Yes	Adult
Z. albicollis					
White morph	Imm.	Yes	Adult	Yes	Adult
Tan morph	Imm.	Yes	±Imm.	Yes	±Imm.

[a] Type of plumage acquired during postjuvenal molt.

[b] Type of plumage worn during first breeding period.

[c] Excludes the abortive complete "prenuptial" molt described by Davis (1971).

[d] Represents also all other North American forms of *Zonotrichia.*

[e] Predominantly in southern populations. See text.

released on 12 October. At this time the bird was paired and showing the apprehensive behavior characteristic of an adult with a nest, but the nest could not be found. This bird was subsequently associated with a nest from which two Shiny Cowbirds (*Molothrus bonariensis*) were fledged on about 10 January. It was captured and examined on 2 February, when the plumage was very worn and molt had not yet started. It was subsequently observed as often as possible, and by 5 March the secondary coverts had grown sufficiently so that the wing bar was restored, indicating initiation of molt in early February. This bird was inadvertently shot in collections made on 19 March, at which time the molt was suspended with the completion of P3. The bird had been associated with a nest (no. 70–38) containing two fresh sparrow eggs on 26 February, and from which two fledglings disappeared between 18 and 24 March. It seems clear from this history that molt was suspended slightly before or during this nesting, which probably was at least the third attempt of the season.

On the basis of the correlation between the nesting seasons and suspended molt at Horco Molle and at Las Cejas it is reasonable to conclude that molting was suspended in many individuals during the terminal nesting of the year, as illustrated by the case history just described.

COMPARISONS AMONG THE STUDY STATIONS

Some estimated dates in the calendars of molt are shown in table 6. On the average, postnuptial and postjuvenal molt began earlier at Tafí del Valle than at the lowland stations, a difference correlated with the earlier termination of nesting at Tafí del Valle and with the departure of the birds from that region soon after mid-April. Nevertheless, similarities in timing are more conspicuous than the differences, which are slight. The duration of postnuptial molt in individuals was apparently about the same (about 80 days) at the three stations, as was the duration of molt in the population as a whole (table 6). This synchrony of molt among individuals and populations in Tucumán is much more notable than synchrony in reproduction. Nesting began at least two months earlier at Horco Molle than at the other two stations. The implications of this difference in relation to the control of the annual cycle will be considered in a separate report.

COMPARISONS WITH OTHER POPULATIONS OF CROWNED SPARROWS

Data already presented show that the sequence and duration of the postnuptial molt do not differ markedly in populations of *Z. capensis* from about 10°N (Costa Rica) to about 27°S (Tucumán), although the duration of molt in individuals may be somewhat shorter in the subequatorial populations. Nevertheless, there are some interesting variations in the population patterns of molt, both within and between northern and southern hemisphere forms of *Zonotrichia*, that merit additional attention.

As a pivot for this discussion it may be assumed, strictly as a working hypothesis, that the progenitors of Z. *capensis* originated in North America and radiated southward in Pleistocene and post-Pleistocene time, as argued by Chapman (1940). It is unlikely that robust evidence concerning this subject will ever become accessible, but some insights into the probable evolutionary history of the crowned sparrows may be gained by comparison of present-day functional attributes, in this case the molts. An attempt to summarize our current understanding of molt schemes in crowned sparrows is shown in table 7.

Partial ("prenuptial") molt. A partial molt like the prenuptial molt of typical Z. *leucophrys* has been found in Z. *capensis* only in Costa Rica (Wolf 1969). Chapman's (1940) investigation of about 1150 specimens of adult Z. *capensis* from throughout Latin America, as well as the more recent field studies already mentioned, failed to detect any traces elsewhere of a partial prenuptial-like molt in Z. *capensis.*

In contrast, all North American forms of *Zonotrichia* have a prenuptial molt leading to the adult plumage-pattern, although there are variations of intensity and effect among populations (table 7). For instance, in the Z. *l. nuttalli-pugetensis* complex inhabiting the Pacific Coast there is a decrease in the extent and intensity of prenuptial molt from north to south (Banks 1964; Mewaldt et al. 1968), and some individuals in southern California evidently breed in the first-winter plumage (Blanchard 1941:11). In Z. *albicollis,* one of the two known morphs retains throughout its life a plumage pattern resembling that of the first-winter plumage (Lowther 1961; Lowther and Falls 1968; Thorneycroft 1966).

The adaptive significance of a relatively drab first-winter plumage is an intriguing question, but one that is beyond the scope of the present report. It is apparent, however, that differing selective pressures have been operating with respect to first-year plumage in different populations of *Zonotrichia.* During the hypothetical spread of *capensis* through the funnel of Middle America it evidently encountered pressures causing evolution of a postjuvenal molt leading directly to adult plumage (or, conversely, it escaped from pressures favoring retention of a distinct first-winter plumage), and leaving the partial prenuptial molt as a relict producing merely partial renewal of an adult-like plumage. We can surmise that additional modification of the ancestral gene pool in southerly populations led to a deletion of the molt itself. If this interpretation is correct, then it is likely that forms of Z. *capensis* north of Costa Rica should also retain a partial prenuptial molt.

In the *nuttalli-pugetensis* complex in North America a different evolutionary pattern may be apparent, in which the prenuptial molt is markedly reduced or is eliminated from the annual cycle, and the fully adult plumage is acquired only in the first postnuptial molt (table 7). It is also noteworthy that these birds (*nuttalli,* at least) have the potential to produce black crown feathers at the time of the postjuvenal molt, even though they do so only in experimental conditions (Morton 1962). It seems that this genetic potential has become expressed in the postjuvenal molt of Z. *capensis.*

Still a different molt scheme is evident in Z. *albicollis,* in which both the white-striped and the tan-striped morphs uniformly show a prenuptial molt, but in which the tan-striped form permanently retains elements of the immature (first-winter) plumage.

In short, it appears that opposite evolutionary trends have developed in northern (toward neoteny in some populations) and southern (toward early maturation of the plumage pattern) forms of *Zonotrichia.* The adaptive significance of these differences is enigmatic at the present time, and the subject invites further exploration.

Complete ("postnuptial") molt. The patterns of "annual" molt in various populations of Z. *capensis* present a rather complex picture at present. Wolf (1969) detected no unusual aspects in Costa Rica, compared with postnuptial molt in North American crowned sparrows; but Miller (1961) showed that in Colombia individual Z. *capensis* completely replace the plumage twice each year, following the two annual breeding periods. Davis (1971), in coastal Perú, found a molt scheme in which, in addition to a typical postnuptial molt, there was a prenuptial period in which a molt like a typical annual molt was begun (at P1, following the usual sequence) but was arrested at the onset of nesting. In those individuals for which histories are adequate it is clear that the complete postnuptial molt started at P1, and not at the point of arrest. This abortive "prenuptial" molt occurred in about half of the individuals ($n = 218$) in which it could have been detected. Davis (1971:133) describes this molt as an "incipient second complete molt," and it is tempting to interpret it as a relict of a double annual molt (Miller 1961) acquired by Z. *capensis* as it invaded the equatorial zone and subsequently radiated southward. The suspended postnuptial molt found in Z. *capensis* in Tucumán, which is apparently unknown in any North American crowned sparrow except perhaps Z. *l. nuttalli* (Mewaldt et al. 1968:26), can also be interpreted as a functional residue of the double annual molt of the equatorial-zone populations. The plausibility of these speculations can be tested by data from additional populations at other latitudes, and it seems unprofitable to extend them further at the present time.

SUMMARY

The molts of *Zonotrichia capensis* were studied in populations inhabiting three biotopes (chaco woodland, transition-zone savannah, and mountain semi-desert) at 27°S latitude in northwestern Argentina. There was no prenuptial molt in any population. Postnuptial molt required about 80 days in individuals in all populations, and 110–120 days in the populations. Molt was begun late in the breeding season in the lowland populations but was then suspended temporarily in about one-quarter of the individuals, apparently during the terminal breeding effort of the year. There was no suspended molt in the mountain population.

Postjuvenal molt required about 50 days in individuals and led to a plumage indistinguishable from that of adults. Replacement of the "tertials" (S7–9) was common, but replacement of the central rectrices was not. Postjuvenal molt began synchronously in the majority of immature birds, regardless of age. Some individuals were four to five months old at the start of postjuvenal molt, while others were only six to seven weeks old (reckoned from the beginning of incubation).

Patterns of molt are summarized and compared for *Zonotrichia* spp. in Costa Rica, Colombia, Perú, northern Argentina, and North America. Some hypotheses are offered concerning evolutionary trends in molt patterns.

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LITERATURE CITED

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

Bartholomew, G. A., Jr. 1949. The effect of light intensity and day length on reproduction in the English Sparrow. Bull. Mus. Comp. Zool. 101: 433–476.

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. M. 1940. The post-glacial history of *Zonotrichia capensis*. Bull. Amer. Mus. Nat. Hist. 77:381–438.

Davis, J. 1971. Breeding and molt schedules of the Rufous-collared Sparrow in coastal Perú. Condor 73:127–146.

Digilio, A. P. L., and P. R. Legname. 1966. Los árboles indígenas de la Provincia de Tucumán. Opera Lilloana 15.

Hueck, K. 1966. Die Wälder Südamerikas. Fischer Verlag, Stuttgart.

Koepcke, M. 1963. Zur Kenntnis einiger Finken des peruanischen Küstengebietes. Beitr. Neotrop. Fauna 3:2–19.

Koepcke, M. 1971. *Zonotrichia capensis markli* nov. subspec. (Fringillidae, Aves), una raza geográfica neuva del gorrión americano de la costa norte del Perú. Publ. Mus. Hist. Nat. "Javier Prado," Ser. A Zool., No. 23, pp. 1–11.

Lowther, J. K. 1961. Polymorphism in the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Can. J. Zool. 39:281–292.

Lowther, J. K., and J. B. Falls. 1968. *Zonotrichia albicollis* (Gmelin): White-throated Sparrow. P. 1364–1392 *in* O. L. Austin, Jr. [ed.] Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus., Bull. 237, Pt. 1.

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.

Morton, M. L. 1962. A plucking experiment with White-crowned Sparrows. Condor 64:327–328.

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.

Phelps, W. H., and W. H. Phelps, Jr. 1955. Seven new birds from Cerro de la Neblina, Territorio Amazonas, Venezuela. Proc. Biol. Soc. Washington 68:113–123.

Stresemann, E., and V. Stresemann. 1966. Die Mauser der Vögel. J. Ornithol. 107 (Sonderheft).

Thorneycroft, H. B. 1966. Chromosomal polymorphism in the White-throated Sparrow, *Zonotrichia albicollis* (Gmelin). Science 154:1571–1572.

Wetmore, A. 1951. Additional forms of birds from Colombia and Peru. Smithsonian Misc. Coll. 117(2):1–11.

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

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