

MOLT CYCLES IN EQUATORIAL ANDEAN SPARROWS

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A principal finding in a year-long study of an equatorial population of Andean Sparrows (*Zonotrichia capensis*) in Colombia was that each individual displays two breeding periods in one year (Miller, 1959). This is particularly clear in males in which there are two complete regressions and two full regrowths of the testis over a 12-month period, the 6-month norm for the completed cycle reflecting an innate cyclic tendency which is only partly coerced by the rainfall cycle. At least some individuals in full reproductive capacity and some actual nestings may be found in every month of the year.

In north temperate and arctic passerine birds it has long been recognized that among the non-migratory species the single, complete, annual molt follows the nesting period, and it has often been thought that this molt was physiologically related to the reproductive cycle, being an expression in part of the drastic changes in hormonal balance that inevitably occur in the regressive period of the hypothalamic-pituitary-gonad mechanism. Experimental results in recent years, particularly in respect to the prenuptial molt, have tended to show a partial independence of the physiologic control of molt and the gonadal cycle (see, for example, Miller, 1954:18, and Selander, 1958:366). But in any event from the ecologic and adaptive standpoint it has become increasingly clear that molt and nesting are functions which compete for energy and food resources and that the two, by whatever stimulating and physiologic mechanisms, are neatly timed in various ways to avoid a simultaneous drain on the bird and its environment. These matters have been especially brought to notice and analyzed by Pitelka (1958).

In the light of these several circumstances it was surprising to find in equatorial populations of *Zonotrichia capensis* that two complete "annual" molts occur each year and that there are no partial, prenuptial molts. Moreover both a linking and a degree of independence of the schedules of molts and breeding states were observed and these matters require detailed exploration for their various implications. The complete molt in equatorial passerines is no less taxing a process than in northern species, if, as often proves true, it is pursued almost as rapidly as in northern types. Pitelka (1958) has shown that in the Steller Jay (*Cyanocitta stelleri*) the dry weight of the plumage mass represents about 10 per cent of the total weight of the bird and the assumption of a similar relation in Andean Sparrows suggests the appreciable energy drain in producing the plumage over a two-month period in addition to other normal activities.

METHODS

The general setting for this work and the procedure in following the cycles of individuals has been described in part in earlier papers (1958; 1959). Throughout I was aided in trapping birds and recording weather by Virginia D. Miller and our daughters, Barbara and Patricia. Acknowledgment also is gratefully made of support by a Guggenheim fellowship and of aid by F. Carlos Lehmann V. of the Universidad del Valle, Colombia.

The particular data on molt were derived in three ways. (1) The 160 banded individuals trapped and marked in an area of about 4 acres, from February 10, 1958, to January 22, 1959, were retrapped as often as possible, and on almost all occasions they were examined for molt. Thus in the year a total of 720 capture and recapture records was made; multiple captures on a single day are not included. (2) Color-marked birds identified as individuals and closely followed with binoculars at close range were recorded as in molt when they showed conspicuous breaks in plumage of the body, wing, and tail.

(3) A total of 78 individuals was collected off the study area but within 2 miles of it in similar pasture areas and second-growth bush lots. These were preserved as skins or skeletons and the gonads and some other organs saved for histologic sections. Molt stages were recorded for each.

A series of molt stages has been devised (table 1) to which our raw data on condition of feather replacement can be related. Concordance of molt activity in different feather tracts is broadly similar to that in other northern passerines (see, for example, Miller, 1928:411, table 5, and Pitelka, 1945:245, table 4), but there is greater variability (see p. 147) such that one cannot combine data effectively from different tracts in recording stages as Pitelka (1958:39-41) did for Steller Jays. The most meaningful, protracted replacement process is that of the primaries and this will be used as a basis for registering stages of molt. The orderly sequence of replacement from primary no. 1 to no. 9 is seldom violated, and then only in a minor way, and the replacement of these feathers almost spans the entire molt process.

TABLE 1
STAGES OF COMPLETE, ADULT MOLT

1. Body feather replacement started or replacement in progress in tracts other than primaries (this stage may be omitted and the molt begin with stage 2).
2. Primary 1 (innermost) dropped or regrowing; nos. 2-9 old.
3. Nos. 3-9 old.
4. Nos. 4-9 old.
5. Nos. 5-9 old (inner secondary molt, nos. 7, 8, 9, usually begins).
6. Nos. 6-9 old (outer secondary molt, nos. 1 and 2, usually starts).
7. Nos. 7-9 old.
8. Nos. 8-9 old.
9. No. 9 old.
10. Nos. 8 and 9 new, short; several secondaries still molting.
11. A few secondaries still not full length and/or late traces of body molt and sheath remnants present on outer primaries.

In addition, in the appraisal of the history of an individual, stage of wear, especially of the remiges, was made in order to judge whether a complete molt had or had not occurred recently. It is to be recalled that since there is no perfect coordination of gonad or molt cycles in all individuals of a population, no assumptions about recent molt history can be made on the basis of date alone.

As explained elsewhere (Miller, 1958) age of many of the birds captured was determined by a simple skull operation and reproductive state was ascertained by external evidence in the form of brood patches and the development of the male cloacal gland and by laparotomies. These approaches often enabled us, using also observational records at nests, to relate quite closely age and reproductive and molt histories of individuals.

SEQUENCE OF MOLTS AND PLUMAGES

The sequence of molts and plumages is simple in this species. The natal down is largely lost just after the fledgling period when it wears off the tips of the juvenal feathers to which it adheres, as is usual in passeriform birds. The juvenal plumage is followed by a postjuvenal molt which is incomplete, most notably failing to involve the remiges. The next molt is the complete or adult type of molt engaged in thereafter at approximately six-month intervals. There are no special, partial prenuptial molts. Moreover, once the juvenal body plumage is fully replaced in the postjuvenal molt, the appearance

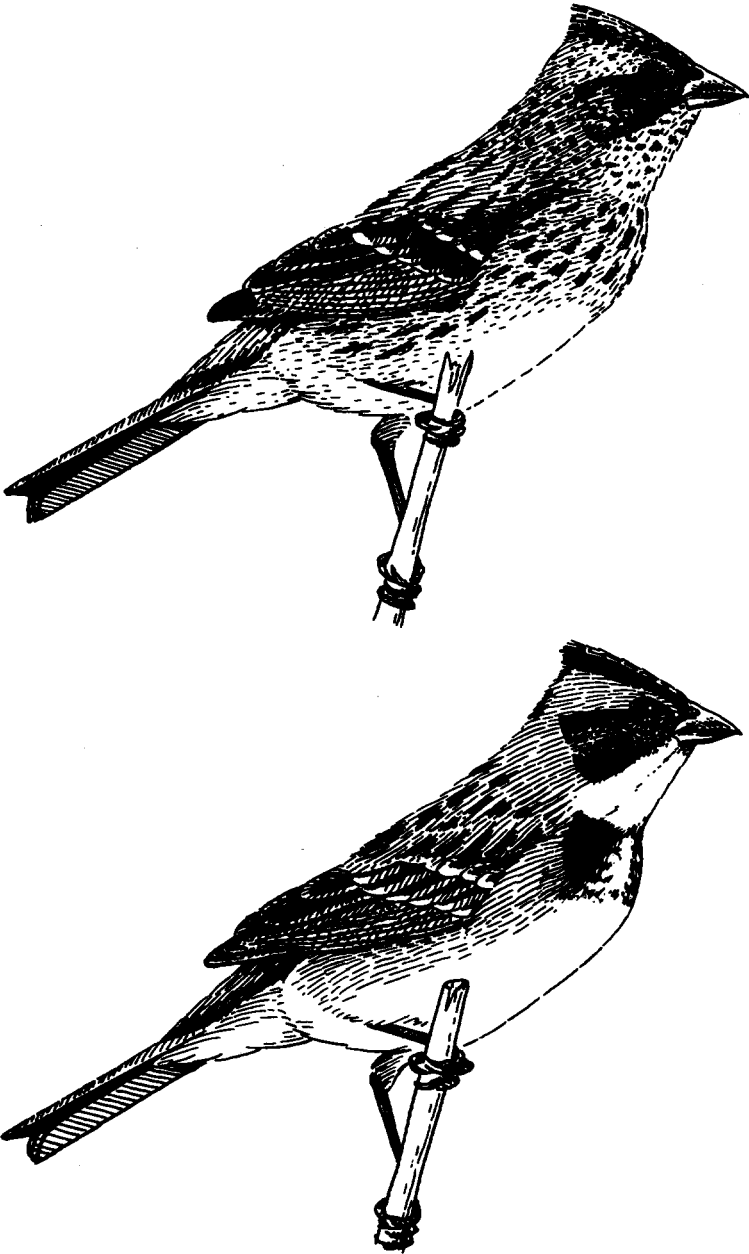


Fig. 1. Plumages of Andean Sparrows (*Zonotrichia capensis*), three-fourths natural size. Drawings by Gene M. Christman based on live birds and showing crest elevated in normal alert attitude. Areas posterolateral to black spot at base of neck are rufous in adult.

of the bird is stabilized in pattern and color at the adult level. An adult-appearing bird, still showing immaturity in the skull, may then at approximately 6 to 8 months of age molt fully from an adult-type plumage to an identical plumage, whether or not it has reached breeding level or engaged in breeding in the preceding interval.

TIME REQUIRED FOR ADULT MOLT

Case histories in some instances are complete enough to show the span of time required for the entire adult molt. There are five records of such molts (table 2) which either run from stage 1 to 10 or 11, or at one or both ends of the process involve records of known lack of molt. These full records indicate minimum spans of 2 months, plus or minus a few days; the case which lacks stage 11 is shorter, at 1 month and 10 days, a history that might well represent a molt completed in 10 days less than 2 months. It is to be noted that this same individual required 2 months for another complete molt six months earlier.

TABLE 2
HISTORIES OF INDIVIDUAL ADULT MOLTS

No. of individual	Stages recorded	Elapsed time*
472 (molt 1)	none-5-6-10-11-none	2 mos., 1 day
472 (molt 2)	none-2-3-10	1 mo., 10 days
466 (molt 1)	none-3-5-none	2 mos., 4 days
482	1-11	2 mos., 2 days
460 (molt 1)	none-M-M-M-M-M-11	1 mo., 29 days
460 (molt 2)	3-9	1 mo., 8 days
466 (molt 2)	3-M-M-10	1 mo., 26 days
840	4-none	1 mo., 17 days
806	none-6-9	1 mo., 27 days
496	4-10	1 mo., 20 days
495	4-6-11	2 mos., 11 days
494	1-3-9	1 mo., 23 days

* Months are all calculated as 30 days.
M = obvious molt seen in field at close range.

Seven other less extended records (table 2), which nonetheless span about four-fifths of the molt stages, are consonant with the foregoing. These show durations of 1 month and 8 days to 2 months and 11 days. Obviously the latter is a case in which the complete molt would extend over at least 2 months and 20 days.

The conclusion to be drawn is then that the adult molt in free-living individuals normally requires 2 months and that the variation, which is rather less than was expected, is represented in probable extremes of 1 month and 20 days and 2 months and 20 days.

The ten stages of the molt, or the eleven stages when number 1 is counted, should require about 6 days each. We have closely examined the record of intervals between stages that are two or three units apart. In calculating the time involved for these short spans, one encounters the danger that the observations could have fallen for any one stage close to the beginning or end of that stage, thus augmenting the apparent variability. Thus if in fact the period from the start of stage 1 to the start of 3 consists of 12 days, at 6 days per stage, the record of successive captures in stages 1 and 3 could be as little as 7 and as much as 18 days apart. Actual inspection of 10 clear-cut two- or three-unit spans shows average time in each ranging from 5 to 12 days per stage with a general average of 8 days. In view of the chances of error in reflecting the exact interval, this figure is not far out of line with that obtained by division of the total time required for molt by the number of stages.

More significant is an inspection of the records to see if longer intervals prevail in the early or late stages of the molt both for two- and three-unit spans and the longer spans (total number of molt history sequences examined is 24). This reveals that most of the 10- to 12-day intervals per stage relate to stages 6 to 11 and most of those

of 5 to 7 days are for stages 1 to 5. We are quite convinced of the trend here indicated, but there are exceptions such that this matter cannot be rigorously quantified. For example, there is one case in which a bird progressed from 6 to 11 at an average of 2 days a stage. But there are no instances of long intervals such as 9 to 12 days for the first four stages whereas there are three instances involving intervals of 2 to 4 days per stage.

It is safe to assume that normally the first four stages proceed more rapidly than the terminal ones, averaging probably 4 days, and that later stages normally are 7 or 8 days. I suspect that stage 11 as defined is usually 10 days long. It is to be recalled that stage 1 may sometimes be skipped.

It is well to note that the total time of 60 days for the complete molt in *Zonotrichia capensis*, here determined directly from living birds, is surprisingly close to Pitelka's calculation of 60 to 70 days for Steller Jays based on molting birds saved as skins. The latter is of course a larger species, but the sample studied was living at 52° to 54° north latitude. Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*), more closely related as fringillids, at 71° N, require 50 to 55 days for the molt (Pitelka, MS). Yet individual House Finches (*Carpodacus mexicanus*) in southern California are occupied for 120 to 150 days with the annual molt (Michener and Michener, 1940:141), and Hawaiian honeycreepers seem to require 3 or 4 months (Baldwin, 1953:322-330).

CORRELATION OF MOLT IN FEATHER TRACTS

The broad relations between activity in the several feather tracts that is generally characteristic of passerine birds prevails in *Zonotrichia capensis* but there is a greater variability in this respect than is usual (compare Miller, 1928:411, and Michener and Michener, 1940:142). If the standard stages based chiefly on the primary molt are used as a base of reference, norms and extremes in certain of the other tracts may be indicated. I gave no detailed attention to precise sequence in certain of the covert series and estimated body replacement as fractions of completion rather than indicating the exact section of the tracts entailed.

Secondaries.—Molt begins in the group of inner secondaries, numbers 7 to 9, and starts separately, always later, with no. 1 and then proceeds in order to no. 6. Thus in fact two sets of replacements occur in this series, probably quite independently. The inner secondaries start molting at stage 5 or 6 (9 instances) and their regrowth probably spans about three stages. Two exceptional initiations at stages 2 and 3 were recorded. We saw no instances of inner secondaries molting or growing later than stage 9.

The outer secondaries in no instance started dropping before stage 6 and never later than stage 7. In one bird they were all replaced by stage 9, but in most individuals two to four old secondaries remain in stage 9 and 1 to 4 in stage 10. By definition, all have at least dropped, although they are not necessarily fully grown, in stage 11. In half of the twelve examples of stage 11, however, all outer secondaries were fully grown.

Wing coverts.—The greater primary coverts molt sequentially from 1 to 9 in coordination with their respective primaries. We saw no exceptions. The alula was noted molting with the outer three primaries.

Greater and middle upper secondary coverts molt in no fixed sequence that could be detected, but more or less en masse. Probably a span of only three stages is required for completion of their growth. Four of ten birds in stages 1 and 2 had begun molting these tracts. Yet six others had not begun by stage 4. A tally of all cases of molt of these coverts shows them fairly evenly spread from stages 1 to 9, but none later. This spread

then reflects chiefly the variation in initiation of the molt over the period from at least stage 1 to 4 and probably from 1 to 5 or 6.

Rectrices.—The tail molt was divided into three stages only since the sequence of dropping of feathers was very irregular even though it tended to be centrifugal. The tail becomes extremely worn in this species and probably it is often partly or entirely removed by accidents. This explains part but not all of the variation in molt. The progressive stages of tail replacement are: A, some or half of old feathers dropped; B, all or nearly all dropped and many partly regrown; C, all old feathers gone and some new feathers fully grown but others short. The correspondence with general molt stages is plotted in table 3; O=no molt as yet; N=fully grown new tail.

TABLE 3
TAIL MOLT IN RELATION TO GENERAL MOLT STAGE

General stage	1	2	3	4	5	6	7	8	9	10	11
	A	A	B	O	A	A	B	B	B	A	C
	A	O	O	O	A	A	B	B	B	B	C
	O	O	O	O	B	A	B	C	B	C	N
	O		O	O	B	A	C	C	C	C	N
	O		O	O	O	B		C	C	C	N
	O		O	O		B		C	C	C	N
	O		O	O		B		C	C	C	N
			O			B		C	C	C	N
						B			N	N	N
						B			N	N	N
						C			N	N	N
									N	N	N

Thus it is clear that the tail normally molts in the period from stage 5 to 10 but that it can begin with stage 1 or 2; we did not find a case of completion before stage 9.

Body.—As expected, we found that the body molt starts in the center of the ventral and dorsal tracts at about the level of the wings and tends to spread forward and back and to the inner and outer edges of the tracts. Head and neck molt typically marks the late stages of the entire body molt. The downs of the brood patch of females are regrown soon after the start of body molt.

Body molt is designated as follows: O, not yet started; I, started; II, $\frac{1}{4}$ through; III, $\frac{1}{2}$ through; IV, $\frac{3}{4}$ through; V, late remnants; N, complete.

Stage 1 of the general molt by definition consists of those cases in which body molt has at least started but the dropping of primaries has not. This early beginning of body molt is unusual in comparison with other passerines such as House Finches, Loggerhead Shrikes (*Lanius ludovicianus*) and Scrub Jays (*Aphelocoma coerulescens*), in which it starts after two primaries have been lost. However, the delayed beginning of body molt is not rare in *Zonotrichia* as shown in table 4 where at least four cases are shown of delay until after stages 3 or 4. Rarely body molt is complete by stage 9 but normally not until stages 10 or 11. Stage 11, it is to be recalled, is partly marked by late remnants of growth either of the remiges or body feathers or both. The usual span of a body molt is over 7 to 9 stages.

Special abnormalities.—Aside from arrested molt and the special circumstances attending it (see p. 154), there are occasional instances of irregular sequence or procedure in the molts of remiges. Occasional instances were noted of replacement of single outer secondaries out of the normal sequence of 1 to 6, and there were two instances of single primaries (nos. 2 and 4, respectively) molting out of sequence in both wings. Also

TABLE 4

BODY MOLT IN RELATION TO GENERAL MOLT STAGE

General stage	1	2	3	4	5	6	7	8	9	10	11
I	I	O	O	I	II	III	III	III	III	III	V
I	I	O	O	III	II	III	III	III	III	IV	V
I	I	I	I	III	III	III	III	III	IV	IV	V
I	II	I	I	III	III	III	III	III	IV	IV	V
I	II	I	I		III	V	III	IV	IV	IV	V
I	II	I			III		III	IV	IV	IV	V
I		I			III		IV	V	V	V	V
I		I			III			V	V	V	V
I		II			III			V	V	V	V
I		II			IV			N	V	V	V
I		II							V	V	V
I										V	V
I											V
II											N
											N
											N
											N
											N

occasionally the two wings are one stage apart in dropping primaries. The most surprising and functionally significant abnormality was shown by a female that had five new inner primaries and which had dropped numbers 6 to 9 almost simultaneously. These latter were either lacking, distally, in the wing or were so short as to be hardly functional; the bird could barely fly, for this situation prevailed in both wings. In another instance a male had primaries 6 to 9 all short, but irregularly so and with details different in the two wings. Its flight was not seriously impaired at the time, but it may have been earlier as in the female just described.

Summary.—In review, we may point out that the secondary molt, in its sequence and relation to primary molt, is very similar to that of well studied northern passerines. The variations and abnormality in it are no greater than expected from experience with other species. The tail molt is not much more erratic than in other passerines. However, the initiation of body molt shows distinct departure from the norm for passerines, both in the degree of individual variability and the prevalent, perhaps usual, commencement before the inception of the primary molt. The highly irregular schedule of the secondary covert molt is unusual, yet since it seems to be linked with active body molt, its irregularity is perhaps only another expression of the variation in timing of the latter. The two striking instances of abnormalities of primary molt in which a nearly simultaneous loss of four outer feathers occurred, is a situation I have never encountered while examining hundreds of molting passerines in north-temperate areas.

THE DOUBLE ANNUAL CYCLE OF COMPLETE MOLTS

The evidence proving that two adult molts occur each year is presented in table 5. In 20 adult individuals the records show that two complete molts had occurred. These are birds which were far past their postjuvenile molt and the immature period when their trapping and observational histories began. In two instances the records are lengthy enough to show three successive, complete molts spaced roughly at 6-month intervals. Moreover, in no instance did an adequate record of captures of an adult over a span of eight months fail to show evidence of a complete molt. Thus it seems safe to conclude that the double molt is normal, and in so far as we know it always takes place.

The dates entered in table 5 mark the inception of molt at stage 1. When our first record of a molt was for a later stage, the time of stage 1 was estimated on the basis of

the average of 6 days a stage unless a definite record of lack of molt necessitated placing stage 1 subsequent to that date. In two instances stage 1 was estimated partly from close-range observation of a bird outside the trap in which there obviously was a complete-type molt in progress. The extrapolated dates of stage 1 have an estimated reliability of ± 5 days. In many instances the date must be much more accurate than this. In two or three cases possibly an error of 10 days is involved. Where no precise date is

TABLE 5
HISTORY OF ADULT BIRDS SHOWING TWO COMPLETE MOLTS IN ONE YEAR

Bird no.	Molt 1 Date of stage 1	Molt 2 Date of stage 1	Molt 3 Date* of stage 1	Interval between molts in days
844 ♀	Feb. 19	Aug. 10		172
806 ♂	Mar. 10	Aug. 20		163
498 ♀	Feb. 3	X		-----
495 ♂	Feb. 2	X		-----
494 ♀	Feb. 26	Aug. 6		161
488 ♀	Jan. 22	Aug. 2		190
485 ♀	X	Sept. 15		-----
484 ♂	Feb. 28	Sept. 3		185
483 ♀	Jan. 15	July 1		167
482 ♂	Feb. 20	Aug. 2		163
480 ♂	Feb. 19	July 30	Jan. 19	161, 173
478 ♀	Feb. 18	July 6		138
477 ♀	X	July 20		-----
475 ♂	Jan. 10	X		-----
472 ♂	Feb. 17	July 10		143
471 ♀	Feb. 16	Aug. 3		168
470 ♀	Mar. 12	Aug. 1		142
468 ♂	Jan. 15	July 19	Jan. 4	185, 169
466 ♂	Feb. 20	Aug. 13		174
460 ♂	Mar. 7	Aug. 13		159
Total measured intervals				17
Average interval				165.4 days

* Dates are in 1959 for this molt; all other molts in 1958.
"X" indicates molt known to occur; see text.

entered, but only an X mark, we have conclusive evidence that a complete molt occurred roughly in the same period as other dates in the column but without any possibility of fixing a date of inception. Evidence in these instances was derived from a conspicuous shift from totally worn remiges to new ones and in females by the refeathering of a brood patch. In the latter connection we have abundant evidence that a brood patch refeathers only at the time of the general molt. In the interval between molts it may undergo several alternating periods of activity (edematous state) and inactivity but not refeathering.

The interval between initiation of molts averages 165.4 days or about 5 months and 15 days. Extremes are 138 and 190 or about $4\frac{2}{3}$ months to $6\frac{1}{3}$ months. It is to be noted that all but two of the records are for the interval between a January-March inception and a July-September inception. We may expect that similar records between July-September and January-March would average a little greater, probably about 190 days. Thus there is indication that the year is not divided quite equally. Further evidence in support of this is supplied in figure 3, and the implications of it are discussed in relation to rainfall (p. 155).

The reason for this species having two complete molts a year is not because of the

impact of the double breeding cycle, for the two are not tied together rigorously in a physiologic sequence. However, ecologically there is an apparent reason for the evolution of such a dual molt program. The birds forage in coarse, perennial grasses and the plumage becomes heavily worn in an interval of 5 to 6 months even if the bird has not engaged in the work of feeding a normal, successful brood of one or two young. In some individuals the wing and tail become so abraded that the birds experience obvious difficulty in flight. It was quite evident to us in watching and handling the species that if a year had elapsed between complete molts, the birds would have become incapacitated. The peculiar double molt schedule appears then to be one necessary for survival under the mode of life of the species in this area.

DEGREE OF CORRELATION OF MOLT AND REPRODUCTIVE CYCLE

Female.—The reproductive cycle of the female shows a simple relation to the molt cycle consisting of mutual exclusiveness. The state of reproduction in females was judged only by the presence of an active, edematous brood patch or the presence of an egg in the duct which was evident by an external bulge coupled with a loosening of the cloacal sphincter. Such females were classed as nesting or breeding. All others were regarded as nonbreeding. An inactive brood patch or lack of any bare area could be associated with the nest-building stage and an inactive patch could of course be present when nestlings were in the last half of their nestling period at 7 to 12 days of age.

Few laparotomies of females were undertaken. We are not sure that the ova reduce below 1 to 1.5 mm. in diameter in a nonbreeding interval and their substantial increase above this level would be in a brief period, perhaps 10 days, preceding laying. Thus seldom would worthwhile evidence be derived by laparotomies of this sex where we were dependent to considerable degree on chance in the time of recapture of free-living birds.

From the records of trapped females and those collected for tissue samples, 29 instances of birds with active patches and/or laying can be listed in which data on plumage are explicit. These 29 instances contain no duplications of the same breeding or laying period of a given female. Of the 29, 28 show no molt. The other bird is in molt stage 1, meaning only that body feathers and no remiges were involved. Furthermore it was not at the laying stage. Another individual had an asymmetrical molt of a few inner primaries accompanied by no activity in the other wing or elsewhere on the body. It must be regarded as an accidental feather replacement due to extraction of feathers rather than to true molt. An additional 27 records of females show molt, from stages 2 to 11. All of these birds had either no brood patch or an inactive brood patch at the time.

Thus there is a near-perfect negative correlation between molt and the active laying and brooding period of females. The single exception involves only the earliest stage of molt and may well represent an individual in transition, just at the conclusion of a brooding period. This fact, coupled with evidence of arrested molt (p. 154) associated with breeding in a female, strongly indicates in this sex that the two processes at their peak level are physiologically incompatible. There is an obvious "competition" for nutrients by the two processes in the female. It may be noted that the males do not incubate or brood and thus have neither the energy drain of egg production nor that of brooding. Indeed many, but not all, males take no part in bringing food to the young.

Male.—The male cycle as reported earlier (1959) can be ascertained principally in two ways, by laparotomy and by measurement of the cloacal gland or protuberance. If the testis measures 7 or more millimeters in total length, it is in full reproductive state with mature sperm present. Testes 6 mm. long often possess sperm also but in some they may not yet be quite fully functional. Testes 2 to 5 mm. in length are in various re-

gressed stages or are progressing in recrudescence toward breeding. The decline is very rapid so that the intermediate stages measuring from 3 to 5 mm. probably almost always represent regrowth and progressive stages in maturation of germ cells. For purposes of this study of molt correlation, then, testes 7 mm. or over represent the breeding plateau which is of $3\frac{1}{2}$ to $4\frac{1}{2}$ months' duration, and measurements from 2 to 6 mm. represent regression and recovery, chiefly the latter, with 6 mm. conservatively rated as just short of breeding. The regression and recovery period averages about 2 months, varying from $1\frac{1}{2}$ to 3 months. Moreover the invariable association, in over 100 instances, of a large, 7+ mm. testis with a cloacal protuberance 6 mm. or more in diameter means that a breeding state of the testes can be assumed from such external evidence; probably a protuberance 5 mm. in diameter reflects this level but one or two possible exceptions led me to set the 6 mm.-level as more reliable.

		Testis Length (mm)					
		2	3	4	5	6	7
Molt Stages	no molt		4	1	4	3	65
	1		1			1	4
	2		1				4
	3	2	1			1	4
	4						2
	5	1				1	
	6	2	2			1	
	7			1	1		
	8						1
	9	1	1				1
	10		3	1	1		1
	11	1	2	1		1	2

Total in molt = 47

Fig. 2. Correlation chart showing relation of breeding state to molt in males of *Zonotrichia capensis*.

The combined evidence on breeding state and molt status is shown in a correlation chart (fig. 2). In this the breeding stages range from testis lengths of 2 to 7 mm., the latter alternatively being indicated by the cloaca, and molt stages are the units already standardized from 1 to 11. Since a testis of 7 mm. normally is sustained for 8 months out of the year in each individual and lack of molt similarly prevails for 8 months, and whereas each molt stage has an average duration of only 6 days, refined statistical manipulation of these data on correlation would be unsound.

There is nevertheless evident a partial inverse correlation. The imperfection of it is obvious from tracing the record of testis stages of 6 and 7 mm. At least occasional molt of all stages except no. 7 can occur in combination with testis 6 or 7 mm. The lack of evidence for molt of stage 7 coupled with enlarged testes may well be a gap owing to sampling. Still the chart does show that the middle stages of the molt process, from 5 to 7, when perhaps the greatest demands are put on the bird for feather growth, are rarely associated with breeding state. Note also that there is a lack of instances of fully reduced testis when no molt is in progress.

The partial exclusion of one state by the other is further reflected in these facts. Of the 47 cases of molt tabulated, one third or only 15 should by chance alone coincide

with a stage of regressed testes (1 to 6 mm.) since both these aspects of the cycles each occupy only a third of the bird's year. As a matter of fact, however, 28 rather than 15 are in regression or recovery phases of the testis cycle. Conversely 40 individuals sub-maximal for testis should have about 13 in molt stages whereas 28 are in molt.

In the large group of 77 records in which no molt occurs, a status that prevails on the average for 8 months in the year per individual, one would expect that regression, which occupies 4 months' time, should show up in 17 of them if randomly distributed. In fact it occurs in but 12.

Four case histories of adults that are reasonably complete throw further light on this matter. No. 478 on February 14 was in molt stage 5 with testis at 6 mm.; on March 9 it showed molt 8 and testis 7 mm. with obviously no testis recession intervening between molt stages 5 and 8; yet in a later molt, on September 7 it was in stage 10 with testis 2.9 mm. and in a still later molt on January 16, it was in stage 3 with the testis at maximum. Thus even in one individual the processes do not correlate in just the same way from one molt to the next.

No. 472 on July 16 and 19 was in molt stage 2 with maximum testis; on July 19, molt 3 and testis 7 mm. were recorded; August 23, molt 10 and testis 2.8 mm. This type of case history is probably rather frequent with regression during the latter part of the molt.

No. 495 had a somewhat abnormally protracted molt during which a complete regression and recovery of the testes took place. On February 26 and March 4 it was in molt stage 4, but one in which body molt was just then starting, and the testis was 7 mm.; March 27, molt 6 and testis 3.3 mm.; May 8, molt 11 and testis 6+ mm.

No. 806 on March 8 had no molt but the testis was 2.9 mm.; March 25, molt 6; April 24, molt 9 and testis 7+ mm. This bird, like the preceding, had clearly recrudesced in the latter half of the molt.

Discussion.—In summary it should be stressed that molt in adult males does not interfere in all instances with the testis cycle or the converse. The two do have an influence on each other, regressed periods corresponding with molt much more often than would be true by chance alone. The fact that females avoid coincidence of molt and the nesting cycle is not incongruous with the imperfect inverse correlation in males, because it should be realized that the male has long plateaus of breeding potency and the female short periods of actual reproductive activity. A mated pair may spend many weeks together with the male at its high reproductive plateau and yet engage in no nesting. This was particularly true in a well studied pair, ♂ 460 and ♀ 488, which was watched almost daily. The male was at breeding state and singing heavily from May 4 to at least July 29 and yet only one nesting was undertaken, with eggs laid on June 8; this nest was successful.

Although males are somewhat more active in territorial defense and singing during their high plateau than at other times, they are not putting out the effort that the female does in brooding, nor in many instances in the gathering of food for the young. Also only two eggs are laid and rarely does more than one young reach the stage of freely following about after the parents subsequent to leaving the nest. Thus there is less competition for energy between the breeding activity of the male and the molt than in the female, or it may be said that his breeding activity load is spread widely so that competition with molt is slight. Compared with north-temperate relatives the male's breeding activity never reaches so sharp a peak as that entailed in simultaneous population-wide territorial establishment and strife and in the frequent feeding trips by both parents necessary for a large brood of nestlings.

ARRESTED MOLT

Four instances came to notice of adult molt that started and then ceased at an early stage coincident with breeding. Three males and one female were involved.

No. 460, a male, on February 10 was in early body molt and primary 1 had dropped and was in a 2 cm. sheath; it was thus in molt stage 2. It had a mate and nest in which eggs had been laid about January 30. On March 6 and 8 there was no molt and the preceding activity had stopped at stage 2. Then on May 4 it was in stage 11, just completing the arrested molt. From February 12 on to March 15 it had engaged in feeding juveniles, in and out of the nest, and on March 26 it was seen at a distance to be molting.

No. 480, a male, started body molt normally in the center of the back on July 30 and thus was in stage 1. Its female had a nest and eggs at that time, the eggs having been laid about July 22. This set did not carry through to hatching, but the male evidently suspended its molt. On October 20 this male was again in stage 1 with reactivation of further replacement in the centers of the spinal and sternal tracts.

No. 484, a male, was at stage 1 of molt on July 8 and the cloacal protuberance was maximum. On July 23, it was in arrested molt at stage 2 and the cloaca was maximal. On August 26 it had obviously resumed molt, as judged from appearance at a distance, and on November 3 it was in stage 11 at the end of this molt.

No. 483, a female, was in stage 1 on July 14 following a laying estimated to have occurred on June 29. On July 16 she was in stage 2 and the brood patch was refeathering. On July 28 she had a new active brood patch and molt had been arrested at stage 2. The molt must have resumed soon after, as it was in stage 11 near completion on September 20 and was entirely finished on October 3.

In each of these histories the correlated breeding conditions or nesting activity strongly suggest that these actively suppressed the molt. There must be some physiologic mechanism for this in both females and males even though it clearly does not always operate in males as the imperfect correlation of molt and breeding in this sex shows. The intervals of suspension of the molt in these four cases seemed to be approximately 20 to 80 days in the males and about 15 days in the female.

ANNUAL OCCURRENCE OF MOLT IN THE POPULATION

Inasmuch as the two complete molts of each adult tend to fall during non-reproductive states of the individual, it follows that on a population-wide basis molt is encountered in two principal segments of the year and that these occur chiefly when nesting is at its lowest levels. What we were not prepared to find was that these two molt periods show sharper "peaking" than do the major nesting periods for the population and that there is a more evident coercion of the molt cycle by the environment than in the case of the breeding cycle.

Figure 3 shows a plotting for a 12-month period of the recorded stages of molt derived from all individuals handled or taken as specimens and from those observed in which obvious, heavy molt was in progress. There are 135 molt records thus involved. There is no duplication of individuals within each 10-day period of the chart except that if the same individual showed two different numbered molt stages when in hand in these 10 days, each is plotted; there are only 5 instances of this. The reciprocal situations where a positive record of no molt was entered for birds examined in hand is shown at the top; there are 144 such positive records. One would expect twice as many non-molt records as molt records for the year; the discrepancy from this expectation is due to failure to record the negative evidence of lack of molt and the fact that absence of molt could never be recorded by observation at a distance to balance the distant visual recording of molt.

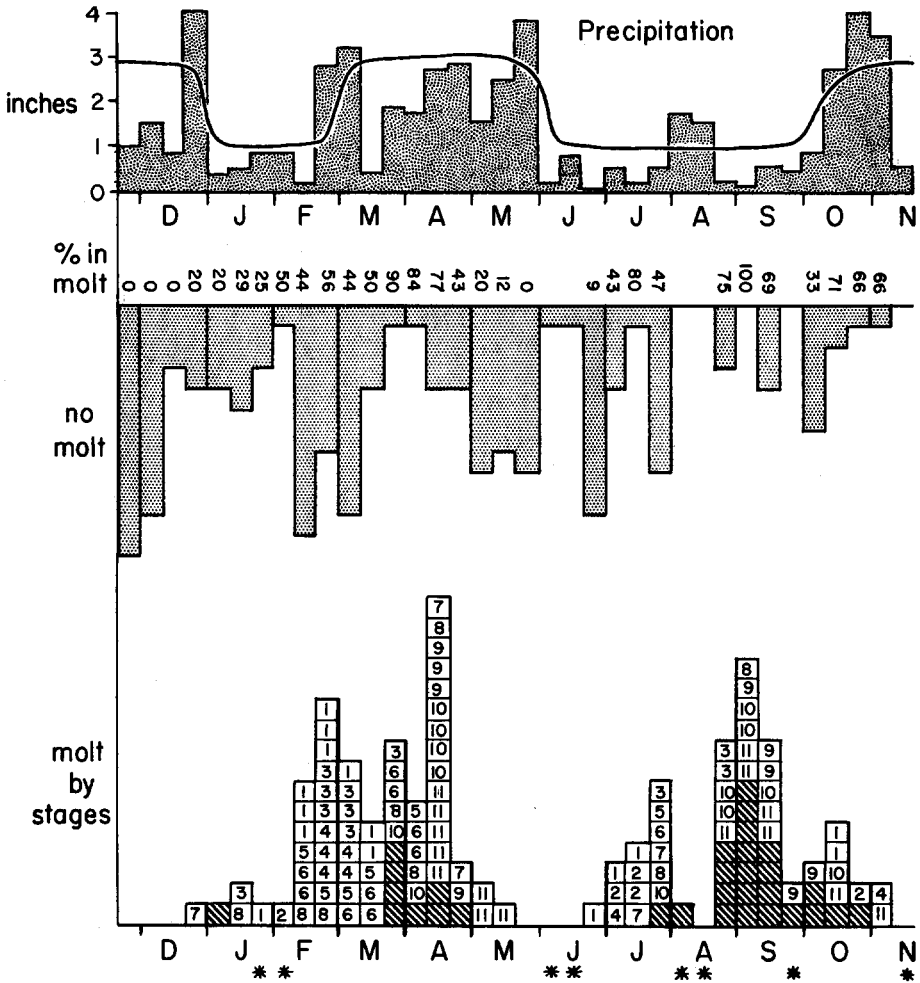


Fig. 3. Seasonal occurrences of molt and molt stages in a population of *Zonotrichia capensis* in correlation with rainfall. Data derived from records at 4 kilometers northwest of San Antonio, 6500 feet, Valle, Colombia. For explanation, see text. Cross-hatched squares indicate birds observed from a distance to be in general molt. Stars indicate 10-day periods in which, due to our absence, few or no data were obtained.

Figure 3 clearly demonstrates that there are two well defined seasons of molt, one from February through April and the other from July through October. There was no evidence whatsoever of adult molt from May 12 to June 25 and similarly none from November 4 to December 20. On the other hand, non-molting birds are recorded for every month and in every 10-day period except those when we were absent or worked at the station only one or two of the 10 days. A total of the individuals recorded with respect to molt or its absence in any 10-day period may be approximated by adding the columns in the two segments of the graph; from this may be figured the percentage of the sample in molt. This is shown at the top and is another reflection of the two definite periods of the year when most molt occurs.

In contrast with the annual distribution of dates of completed sets of eggs (Miller,

MS), the data on molt occurrence show the two gaps just referred to above, each of about 6 weeks' duration. Gaps in nesting occurrences in no instance represented more than single 10-day periods during the "lows," and these can be ascribed to sampling. In general, nest starts varied in the proportion of 1 to 5 between low and high periods, whereas molt comparably varied from levels of zero to 10 or somewhat above.

Figure 3 also reflects by means of the recording of molt stages the expected general, but imperfect, progression of the population from early stages to late stages in each molt period. Thus in the July to October molt, stages 1 to 5 dominate in July but in September stages 8 to 11 prevail. The February to April molt shows the same thing quite as distinctly. Thus this circumstance makes it clear that the curve would have evened out in August if data had been available and that molt must have been extensive in that month; we were absent from the station for almost all of the first 20 days of August.

CORRELATION OF MOLT AND WEATHER

The correlation most obvious between molt and weather is with the rainfall, which although erratic, shows two high and two low periods annually. Our weather data for the one year (fig. 3) do not necessarily represent the average rainfall pattern, although local accounts of wet and dry seasons and data from lower elevations, as at Cali, support the view that the year we experienced was broadly representative. Two conspicuous cessations of frequent, nearly daily, heavy rain occurred—one precisely at the end of May and the other at the end of December. The conspicuous upswing in molt began at a time 3 or 4 weeks later in each instance, even though these events were not quite evenly spaced at six-month intervals. Since molt when once started seems to go through to completion at a rather fixed rate, except for occasional arrest by nesting, the initiation of this physiologic process seems to be most critical and the environmental stimulus for molt control is properly to be sought in association with it rather than with subsequent molt rates and environmental events prevailing during middle and later stages.

Associated with each cessation of frequent rain is an increase in average daily maximum temperature of about 1.7 degrees F. This is of course a small differential and the absolute values for the two molt-initiation periods are in fact 3.8 degrees different (see Miller, 1959:table 2). Still the temperature shift does reflect at our station an even greater increase in the period of the day when the sun is out. The diminution of rains also means substantial periods of each day when the grass is free of drops of water, even though it is wet by precipitation or dew each morning and evening from the almost nightly fog or cloud cover.

If the molt is triggered by the cessation of frequent rain, we are at this stage of our knowledge uncertain whether this is (1) a behavioral and activity response by the bird to stoppage of actual precipitation; (2) the effect of small increase in the temperature itself experienced during the day, but not an absolute temperature level or nighttime temperature change, (3) the changed condition of wetness in the grass in which the birds forage and to which they may react psychologically, or (4) the greater clearing of the skies and the exposure to sun which results. I am inclined to favor the last two possibilities, perhaps in combination, which the bird responds to psychologically with ultimate effect therefrom on endocrine and metabolic balances. The grass itself, it should be understood, never dries out in this area, but remains green, and there is always seeding of the grass, although possible seasonal fluctuations in amount of this were not investigated. The grass is wearing on the plumage at all times.

Frequent although not invariable occurrence of nesting prior to the molt might be thought of as leading to an especially worn state of plumage which stimulates molt, but

in this connection it should be realized that the small broods and widely spaced nestings of a pair do not produce the striking peaks of plumage wear we associate with northern passerines. Moreover there are many cases in which molt starts while young are in the nest and others in which it is delayed for many weeks after one or more nesting efforts. Also it should be recalled that some males do not participate at all in feeding the young.

Apart from the controlling stimulus of the initiation of molt, it should be observed that the population on the average has by this stimulus achieved a schedule in which molt occurs chiefly in the drier seasons and fresh plumage is provided for the ensuing wet seasons. This may have some general advantages, although we have not seen these sparrows badly water-soaked from periods of heavy downpour.

AGE OF INITIATION OF COMPLETE MOLT

Case histories of nine young birds provide the basis for determining age when the first adult molt occurs following the postjuvinal molt. These birds were all handled in the juvenal plumage or at a stage in the postjuvinal molt which permitted a close estimate of their age. Subsequent capture then showed them in some stage of the first adult molt and from knowledge of the time involved in such a molt, that is, two months, the approximate age of initiation of it was established. The figure for age thus derived of course lacks precision, but it probably is within two weeks of the true value. Two of the nine had obviously completed a molt recently, judged by the fresh condition of the remiges, and their age for initiation of the first adult molt can be stated only as possible maxima. It should be noted that no evidence has ever been obtained to indicate that the remiges, other than the inner secondaries are molted in the postjuvinal molt, and therefore in the subsequent three or four months a condition of wear of the juvenal remiges permits determining that the first adult molt has not occurred.

The recorded ages for stage 1 of the first adult molt are as follows, in months: $6\frac{1}{4}$, 7, $7\frac{1}{2}$, $7\frac{1}{2}$, $8\frac{1}{2}$, $8\frac{1}{2}$, $8\frac{3}{4}$, no more than $5\frac{3}{4}$, and no more than $8\frac{1}{2}$. These ages, ranging essentially from 6 to $8\frac{1}{2}$ months, represent molts initiated 2 to $4\frac{1}{2}$ months following termination of the postjuvinal molt, since the latter event occurs at about 4 months of age. The average interval of $3\frac{1}{2}$ months is thus the same as that between adult molts.

In the interval between postjuvinal and first adult molts, the bird, of whatever sex, may attain breeding condition or not. Some that do reach this condition actually engage in nesting. Such was true, for example, of one of the females that had her first adult molt start at $8\frac{1}{2}$ months.

The first molt following the postjuvinal molt is ordinarily a complete molt involving all remiges and the primary coverts as is true invariably of subsequent adult molts. However, some birds in the first adult molt fail to molt the primaries, their coverts, and secondaries 1 to 6. Among the 9 case histories mentioned and 8 skins of immatures (skull evidence of age of 6 to 8 months), 14 showed sure evidence of a complete molt that involved the remiges. Two of the 17 had had incomplete molts and were retaining juvenal remiges and a third, represented by a skin, probably was doing so. A rough estimate of the frequency of completeness of the first adult molt is, then, 80 per cent.

THE POSTJUVENAL MOLT

This partial molt, in which the juvenal patterning, and especially the ventral streaking, is lost, is an important series of changes which aids in estimating the age of an individual. In the early stages of this molt estimates of age are accurate to about 10 days. Preceding the molt, the time required for full growth of the juvenal remiges and rectrices is a reasonably constant period except in obviously sick or runt individuals.

Based on data from the vigorous growth of three hand-raised nestlings, of two broods, which accorded closely with a few case histories of wild juveniles traced from early nestling stages on, a chronology of stages may be established (table 6).

At the conclusion of the growth of the juvenal plumage at about 50 days of age, the postjuvenal molt may begin, but normally it starts after a short interval. We have two

TABLE 6
CHRONOLOGY OF EVENTS IN DEVELOPMENT

Age in days*	Events and stages
12 ± ½	Hatching
21 - 24	Fledging
28 ± 1	Rectrices 32 mm. long
33 ± 2	Rectrices 45 mm. long
40 ± 3	Rectrices essentially full length (52 mm. ± 2), but sheaths present at bases of both rectrices and primaries
45 ± 3	Sheaths at bases of rectrices only
50 ± 5	No sheaths on rectrices (approximate end of dependency)

*Age is from beginning of incubation, which coincides with completion of the two-egg clutch.

clear cases of juveniles starting this molt in the center of the breast and back while still showing sheaths on the rectrices and probable traces on a primary (45-48 days). However, the interval normally is none (without overlap) to 11 days. Fairly certain individual records are as follows: 0, 0, 0, 3, 4, 5, 5, 6, 7, 7, 8, and 11 days. Doubtless there are occasional long retardations, but the normal interval is about 5 days and in estimating age the interval of 5 days may be used. Accordingly the postjuvenal molt may be said to begin at ages from 45 to 60 days, and 54 days is regarded as approximately the modal time for this event.

The time involved in postjuvenal molt must be estimated from a series of stages in the completion of the body feather replacement since the remiges are never molted in more than accidental or sporadic fashion and the rectrices are only involved in part of the cases. The stages employed for the body are the same as the five stages for this process in the adult molt and the spread of the molt through the tracts is similar.

Duration of the postjuvenal molt, judged from adequate histories in which details were recorded, is probably rarely less than 60 days. About eight case histories, most of them running from stage I or II to completion or from stage I to late stage V, indicate two months are occupied; actually most of these would probably require for absolute completion about 70 days. There is one instance of a bird occupying only 30 days from stage II to completion and another that went from I to IV in 32 days. Probably these two individuals completed the process in 50 days. There were two other histories when the molt must have occupied 91 days and 100 days, at least. A range of 50 to 100 days is thus shown and a normal of 70 days indicated. Probably most cases fall in the range of 60 to 80 days. Compared with the adult molt, the normal duration of the incomplete postjuvenal molt is about the same, but the variation in span is almost twice as great.

The age at which young birds complete the postjuvenal molt accordingly is about 4 months. It may rarely be 3 months, as was true in one case (no. 486) where the history from stage II was known; this was the individual that passed from stage II to completion in 30 days. Unless there was an unusually long interval between growth of rectrices and stage I, this bird was indeed rapid in attaining full adult plumage. One female that completed the molt at 4½ months had an active brood patch at 5½ months, and thus was nesting and must have started nest building at close to 5 months of age. On the other

hand, the two individuals with long-protracted postjuvenile molts must have completed them at ages of 5 months or a little more.

The postjuvenile molt in no instance discovered by us involved a regular sequential replacement of the primaries or of secondaries 1 to 6. In 56 birds in stage III or later of the postjuvenile molt or in which this molt recently was completed, there was no instance of orderly molt of these feathers. The same may be said of the greater primary coverts although these coverts were not always specifically checked and the juvenile and replacement feathers of this series are not readily separable on the basis of color. Four instances of replacement of single primaries and two of a single outer secondary were recorded, but the fact that these were odd replacements, occurring only in one wing, indicates they were fortuitous.

In contrast, the inner secondaries, 7, 8, and 9, in four instances were undergoing molt on both sides and since these feathers are often associated in molt with the greater secondary coverts, these cases seem to reflect a true molt. We have no accurate estimate of the frequency of inner secondary replacement in the postjuvenile molt. Probably it occurs in no more than 10 to 15 per cent of the population.

The greater, middle and marginal coverts of the secondary or arm area apparently always are replaced. As in the adult molt this may be early or late in the total process.

The juvenile rectrices were recorded as molted in 9 cases and definitely as retained in 13 instances. Probably there are many more instances of the failure to replace rectrices that went unnoticed, as we often neglected to make a specific record on this score, or the rectrices were worn or wet so that judgment of their newness could not be made. Accordingly the proportion of replacement in the postjuvenile molt cannot be well indicated. Probably it is considerably less than the 40 per cent that the foregoing figures would suggest. It is very likely in the order of 25 to 30 per cent.

COMMENT ON MOLT TERMINOLOGY

It will be observed that names for molt here used for *Zonotrichia capensis* are the same as those in long established usage or represent relatively simple adjustments thereof fitted to the situation. Humphrey and Parkes (1959) in proposing a new system of nomenclature of molts and plumages have sought to overcome some three presumed defects of the terms that are prevalent. First, they seek to have names of the molts always reflect the plumage that is to follow rather than that which is lost. This may have some appeal in logic, but language does not always grow logically and does not have to do so for clear understanding and communication. I have never found new students particularly confused by the terms "postjuvenile," "prenuptial" and "postnuptial" molts. These are obvious descriptive terms even though some relate to loss, partial or entire, of a feather generation and others to the gaining of a plumage.

Second, they seek to divorce terminology from seasonal events or other possibly independent events in the life of the bird. Such a need is partly necessary in tropical species and the situation in *Zonotrichia capensis* is a case in point. But the obviously invariable juvenile plumage needs no replacement in terms, all agree, and I would submit that postjuvenile molt is accordingly the most meaningful and direct description of the molt that follows the juvenile state. It is therefore used here and elsewhere in my dealing with tropical or equatorial birds. I have never found it particularly confusing that some molts are complete and others incomplete and that individuals subsequent to an incomplete molt have a mixture of two or more feather generations. These matters can be readily explained and diagrammed for elementary classes and do not need elaborate explanation or special nomenclature.

Third, Humphrey and Parkes attempt to resolve homologies of the postjuvinal plumages in the situation where some species have one plumage a year and others two alternating plumages by naming one as basic and the other as alternate. This effort and the selection of the word basic is what leads to difficulty and this is pointed up by examples in *Zonotrichia*. In the northern *Zonotrichia leucophrys* and *Zonotrichia atricapilla* the first plumage after the juvenal would be called "basic" by their system as also that of the autumn a year later, with the intervening brightly patterned but non-sexually dimorphic plumages that serve the nuptial functions called "alternate" plumages. In *Zonotrichia capensis* there is then no "basic" plumage, a situation that to this author seems most anomalous from what is implied by the word. The postjuvinal, highly patterned plumages of *capensis* used during nuptial activities are the obvious homologs of the "alternate" plumage of the other *Zonotrichias*. This is in fact the stable and one could say basic plumage of the species and the genus. Why not merely call it the adult plumage as I have done for *capensis*, descriptively, and so also describe the molt which changes it as the adult, complete molt. The meanings seem to be clear and free of ambiguity.

In tropical passerines very generally the postjuvinal, so-called basic plumage is lost or was never possessed, which alternative we do not surely know. The "basic" plumage of Humphrey and Parkes may well then be in them an alternative feature, a retarded type of plumage, added or accentuated in relation to the seasonality evolved in the temperate latitudes. If this follows, their "basic" plumage is the alternate plumage and their "alternate" plumage is the truly basic one. Obviously I do not favor their terms.

SUMMARY

The Andean Sparrow, *Zonotrichia capensis*, at equatorial latitudes undergoes a double molt cycle in a twelve-month period. Two complete, adult-type molts occur, each of about 2 months' duration and spaced at approximately 6-month intervals. The duration of each molt is equivalent to that of several northern passerine species and is shorter than in some tropical and north-temperate types.

The program of replacement in tracts and the duration and timing of molt were ascertained from case histories of retrapped birds, observation of color-banded birds at close range, and prepared study specimens.

Sequence of feather replacement is generally similar to that for north-temperate passerines but greater variability of timing of events within the molt period is evident. Thus the body molt may initiate the molt period or be delayed until the third or fourth primary is dropped, and the replacement of secondary coverts may occur very early or late in the sequence of molt stages defined on the basis of primary replacement.

No instances were found in which adults failed to molt twice in a year. The molt is invariably complete after the first adult-type molt. The first adult molt normally occurs at ages from 6 to 8½ months and 2 to 4½ months after conclusion of the postjuvinal molt. This first adult molt is normally complete, but in two and possibly three out of 17 adequate records there was no replacement of the primaries and outer secondaries.

The terminology of Humphrey and Parkes for postjuvinal plumages as "basic and alternate" is confusing and not usefully applicable in reference to *Zonotrichia*.

The molt season is not sharply defined in the way that it is in higher latitudes, yet most of the population engages in adult molt in a period from February through April and from late July through October. Molt may occur at other times but none of the adult type was found from May 12 to June 25 and from November 4 to December 20.

Correlation of the principal molt periods with rainfall is evident. Molt is probably triggered by the end of the rainy season or the cessation of more or less daily rainfall.

In the year under surveillance, cessation was abrupt at the end of May and at the end of December. Molt became prevalent in the populations 3 or 4 weeks following such cessation. There were no associated differences in photoperiod or absolute values of temperature. The most likely postulated mechanisms involve either a stimulus to the bird resulting from changes in degree of wetness of the grass in which it forages or one derived from greater periods of clear sky and exposure to direct sunlight. Such stimuli occurring at the end of the rains may actually work in combination to initiate molt.

The postjuvinal molt is always incomplete in respect to replacement of the primaries, primary coverts, and outer secondaries. The tail is molted in about one-fourth of the individuals. The molt normally begins at an age of 54 days from the start of incubation and lasts 50 to 100 days but usually about 70 days.

Postjuveniles terminate the postjuvinal molt at ages of 4 months usually and between this molt and the ensuing first adult molt they may or may not breed. One female is known to have started breeding at 5 months of age.

Molt essentially never occurs in females while they are laying, incubating or brooding, and if they undergo these processes while in molt, the molt is arrested.

The reproductive periods of males, in which the testis is at the enlarged, fully functional level for approximately 4-month spans, occur twice a year. These high functional plateaus of males and their molt periods may coincide. However, there is a partial correlation of regressed testis with molt. The occurrence of molt at this time is about twice as great as would be indicated by chance alone. Thus the two cycles may be supposed to have some influence on each other. Contrasted with females, there is in males less competition for energy between the breeding state and the molting process.

A dual molt program is an apparent necessity in that the plumage of this species in this area, because of its grass-land foraging procedures, becomes worn to a point where less frequent molt would lead to incapacitation.

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