BREEDING AND MOLT SCHEDULES OF THE RUFOUS-COLLARED SPARROW IN COASTAL PERÚ

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The Rufous-collared, or Andean, Sparrow (*Zonotrichia capensis*) occurs from the highlands of the state of Chiapas, México, to Cape Horn, Chile, its range spanning approximately 73 degrees of latitude. Further, it is common over most of its range and is often the commonest small passerine where it occurs. A species with such characteristics is an ideal subject for a series of studies of breeding and molt schedules at various latitudes where the populations are subjected to different photoperiodic regimes. Such comparisons make possible an assessment of the relative and changing importance of photoperiod and other environmental features as proximate (timing) factors in the scheduling of the important events in the annual cycles of a single species in different parts of its range. By so doing, a better understanding of the ultimate (adaptive) factors underlying these various annual cycles in this and other species can be achieved.

The first study of the annual cycle of *Zonotrichia capensis* was made in 1958–59 by the late Alden H. Miller (1959a, 1961, 1962) on a population near Cali, Colombia, at latitude 3° 30′ N. There the longest and shortest days of the year differ by only 12 min and photoperiod may be disregarded as a proximate factor. More recently Wolf (1969) has reported on the annual cycle of this species near Las Varas, Costa Rica, at 10° 10′ N, where longest and shortest days of the year differ by 76 min. The present paper reports on the annual cycle near Chilca, Department of Lima, Perú, in the coastal desert at 12° 30′ S, where longest and shortest days differ by 91 min.

MATERIALS AND METHODS

Field work was carried out between 9 October 1968 and 9 August 1969 at Hacienda San Javier Alto, 3 km NE Chilca, 9 km due E of the coast at an elevation of 25 m. This hacienda comprises about 150 ha planted mainly to citrus groves and cornfields. My work was confined to a 20-ha area of citrus orchards and cornfields. Although there was no natural source of fresh water anywhere on the hacienda, extensive deep well irrigation provided an abundance of surface water for the sparrows during the study period.

A Taylor max-min registering thermometer and a Tempscribe thermograph were maintained in a standard instrument shelter near the study area and a Taylor "Clear-Vu" rain gauge was placed nearby. In addition, official government data on temperature, precipitation, and daily hours of sunshine as recorded on a Campbell-Stokes type recorder were obtained for Lima, 35 mi. NNW, and for Cañete, 45 mi. SSE of the study area. Daylength was computed from *The Nautical Almanac*.

Sparrows were caught in mist nets and each bird was marked with a distinctive combination of colored leg bands so that individuals could be identified on recapture. Of 523 birds caught, 133 were juveniles or young first-year individuals. Of the remaining 390, 335 were either adults or mature first-year birds; 55 were not aged. The age of juveniles or birds in part juvenal plumage was determined by feather characters. The ages of birds that had completed the postjuvenal or subsequent molts were determined by the amount of opacity (double-walling) of the skull after the method of Miller (1946). Individuals with extensive clear areas in the skull were classed as young first-year birds, those with small clear areas as mature first-year birds, and those with entirely opaque skulls as adults.

The molt status of each individual was noted, and, as an aid in determining sex, wing length was measured to the nearest 0.1 mm with a dial calipers. (Males have significantly longer wings than do females and the sexes are about 90 per cent separable on the basis of this character.)

In addition to birds which were netted and released after marking, 79 adult and mature first-year males and 23 females of similar ages were collected for direct examination of gonads and stomach contents and preservation of testes for subsequent microscopic examination. Ten of the males and two of the females were collected on the study area and the others within ¼–½ miles. Testes were fixed in Bouin's fluid, stored in 70 per cent alcohol, prepared by the paraffin method, sectioned at 7 μ, and stained with Mayer's hematoxylin and eosin. Each testis was assigned to one of the six spermatogenetic stages described by Bartholomew (1949), as follows: stage 1, resting spermatogonia only; stage 2, spermatogonia dividing, but only a few spermatocytes present; stage 3, many spermatocytes; stage 4, spermatocytes with spermatids; stage 5, spermatids with a few sperm; and stage 6, full spermatogenetic activity with many sperm.

The sex of banded birds was determined primarily on the basis of the presence or absence of a cloacal protuberance (Wolfson 1952). Breeding females were easily distinguished by the presence of an incubation (or "brood") patch and the breeding status of a female could be determined by the nature of the patch: defeathered, vascular, edematous, or recovery (stages 1–4 of Bailey 1952). As regards the breeding status of males, some workers have used testis length as determined by laparotomy as an indicator of level of gonadal activity since in this species, as in passerines generally, there is a significant correlation between testis length and the six stages of spermatogenetic activity previously described. In this study the breeding status of individual males was assessed on the basis of the size of the cloacal protuberance as measured along the anterior wall, and its shape

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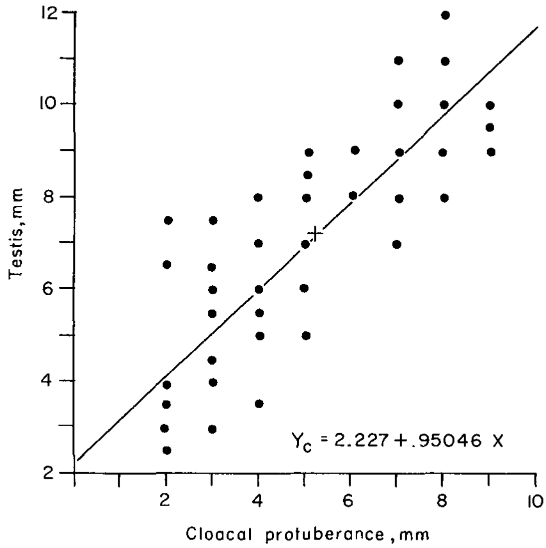

FIGURE 1. Regression of testis length on length of cloacal protuberance of 62 adult male Rufous-collared Sparrows collected near Chilca.

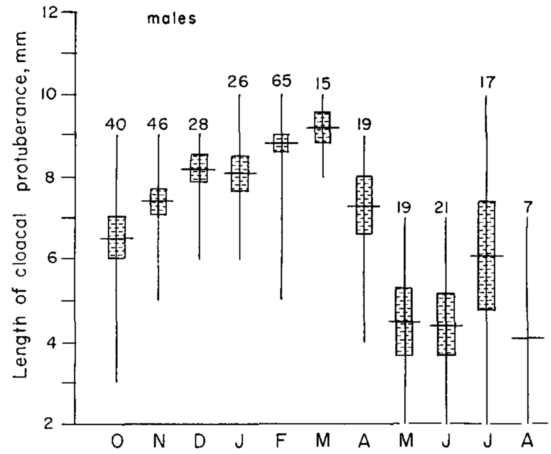

FIGURE 2. Male breeding cycle of Rufous-collared Sparrows near Chilca, based on mean length of the cloacal protuberance of monthly samples of banded adults only. Horizontal line indicates mean, vertical line indicates range, and rectangle indicates two standard errors on either side of the mean. Sample size is given at top of each vertical line. When an individual was captured more than once in a single month, only the first measurement was used.

and consistency (changing from tubular to ovoid to globular, and from flaccid to turgid, as it develops).

Cloacal protuberance is felt to be a more useful indicator of breeding status than testis length for the following reasons. First, there is a very high correlation between the length of the protuberance and testis length in a sample of 62 fully adult males collected on or near the study area ($r = 0.85$; $P < .001$; 99 per cent confidence limits, 0.73–0.92; see also fig. 1). Second, there is a very high correlation in the same sample between protuberance length and the six stages of spermatogenetic activity ($r = 0.75$; $P < .001$; 99 per cent confidence limits, 0.56–0.86). In other words, the length of the protuberance conveys much the same type of information as does testis length. More importantly, Wolfson (1954) pointed out that the testis may be fully active spermatogenetically when the protuberance is at a low level of development. Thus the possibility is always present that one is dealing with a male with fully active testes but without motile sperm in the glomera and thus not in a state of breeding readiness. For this reason the nature of the cloacal protuberance is a more useful indicator of actual breeding condition than is testis length or histology. In the population under study, any protuberance measuring 7 mm or more was fully developed, with rare exceptions noted later. Miller (1958) stated that in his population at Cali, males that were breeding or had recently bred had a protuberance 5–7 mm long.

Although it is possible to obtain motile sperm from the glomera before the protuberance is fully developed (Albert Wolfson, pers. comm.), any male with a fully developed protuberance is definitely in breeding condition; thus, this criterion is conservative and will prevent ascribing breeding readiness to males before they have actually achieved it.

MALE CYCLE

The main features of the male cycle are indicated in figure 2 and table 1. The increase in mean length of the cloacal protuberance from October through December parallels the steady increase in this period in the percentages of males in effective breeding condition (with a protuberance length of 7 mm or more). Continued growth of the protuberance even after individuals have reached breeding condition is indicated by the steady increase in mean length through March. The noticeable decreases in size of protuberance and in percentage of breeding males in April coincided with the start of the complete postnuptial molt in a number of individuals. May and June were months in which nearly all birds were either molting or had recently completed the postnuptial molt; only small percentages of males were in breeding condition and mean protuberance length was small.

TABLE 1. Percentages of male Rufous-collared Sparrows with cloacal protuberance 7–10 mm long.

Month	No. of adults	No. of first-year	Cloaca 7–10 mm	%
Oct.	40	6	21	45.7
Nov.	46	13	45	76.3
Dec.	28	10	35	92.1
Jan.	26	2	26	92.9
Feb.	65	16	78	96.3
Mar.	15	6	20	95.2
Apr.	19	0	14	73.7
May	19	0	3	15.8
June	21	2	3	13.0
July	17	7	10	41.7
Aug.	7	2	1	11.1

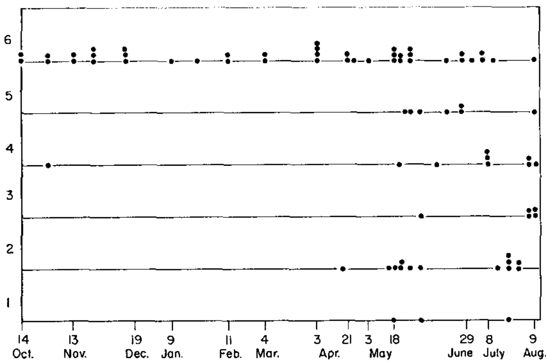

FIGURE 3. Stages of gonadal activity of 79 male Rufous-collared Sparrows collected near Chilca.

Although few males reached actual breeding condition in May and June, the testes of a great majority of males examined histologically showed considerable activity (fig. 3). This probably resulted from two factors. First, the noticeable rarity of males with completely regressed (stage 1) testes suggests that the gonads of most males do not regress completely after the breeding season but return to either stage 2 or 3. Indeed, of the three males that had stage 1 testes, the one collected on 2 June lacked the right testis and the left testis was hard and lumpy and obviously pathologic. Thus, only two of 78 normal males had completely regressed testes. Incomplete regression has been described in other species of tropical birds. Moreau et al. (1947) noted that the annual range of testis size was far greater in temperate zone species than in a number of tropical species which they investigated. As Lofts and Murton (1968) pointed out, this discrepancy may be accounted for in part by the fact that tropical species with long breeding seasons often do not regress completely as do northern birds and the gonads in such species remain relatively large. Second, experimental work done by Miller with birds from his study area in Colombia (Miller 1959b, 1965) and by Miller and O. P. Pearson (MS) on further samples from the same locality indicated that the refractory period in those birds was either negligible or lacking. The same was apparently true of the Chilca population. Most males showed a strong gonadal recrudescence, even to stage 6, as soon as the postnuptial molt had been completed, or in some cases when the terminal stages of molt had been reached.

A marked difference may be noted between the present cycle and that of a small, North Temperate Zone passerine such as the Rufous-sided Towhee (*Pipilo erythrophthalmus*) in central coastal California (Davis 1958, fig. 1). The towhee cycle is noticeably well-ordered compared to that of *Z. capensis*; nearly all birds regressed to stage 1, and when gonadal development started in mid-winter, it started from a stage 1 baseline. Thus, the range of variation was noticeably small at any given point of time, and a number of towhees had testes in a "regression" stage, in transition from full spermatogenetic activity to the resting state. Such testes had the lumina of the tubules filled with degenerating cells and other detritus. No male was collected near Chilca with testes in this stage, another indication that very few males regressed completely after the breeding season ended there.

Whether any male *Zonotrichia* actually reached full breeding condition in May is questionable, and apparently only a few males progressed that far in June and July. Males with cloacal protuberances 7 mm long were examined on 2, 22, and 26 May and on 5 and 9 June. The protuberance examined on 26 May is not described in my notes; the others were described as either flaccid or ovoid, and thus not typical of the fully developed structure.

The only males in undoubted breeding condition after the postnuptial molt were examined between 30 June and 4 July. Of 13 males examined in this period, 11 had cloacal protuberances 7–10 mm long. Eight adults and one unaged bird had fully developed protuberances; they were "nearly globular" and "ovoid" in two mature first-year males. The very restricted period in which breeding birds were examined is undoubtedly the result of sampling error, as a female with a stage 1 incubation patch and a large, yolky egg in the oviduct was collected on 18 June, and the last females with active incubation patches were examined on 15 July. The period in which breeding males occurred after the postnuptial molt probably extended from about mid-June to about mid-July. Relatively few males were involved and this was a minor effort compared to the main breeding period from December through March. It was apparently over by mid-July, as only two of 17 males collected between 14 July and 9 August had testes in stage 6, one collected on each of those dates. The latter bird had the only cloacal protuberance measuring as much as 7 mm; in the other 16, measurements ranged from 2 to 5 mm, averaging 3.3 mm.

Miller (1959a), working at 3° 30′ N in Colombia, followed the annual cycles of a number of color-banded males over long periods and showed beyond doubt that many males, perhaps most, came into breeding condition

TABLE 2. Cloacal protuberance length[a] and type, and testis stage in 16 male Rufous-collared Sparrows before start and after completion of postnuptial molt.

Bird no.	Cloaca before molt date	(mm)	Cloaca after molt date	(mm)	Cloacal type	Testis stage
18	18 Oct.	9	12 July	5	flaccid	4
26	21 Oct.	9	23 June	5	tubular	
41	23 Oct.	7	22 May	5	flaccid	
63	18 Nov.	9	22 May	5		6
88	15 Jan.	9	9 Aug.	5		5
105	8 Nov.	9	1 July	10	globular	
107	14 Feb.	9	22 May	7	ovoid	
			17 June	6	tubular	
125	12 Nov.	7	19 June	5	tubular	
			22 July	3	flaccid	2
224	30 Dec.	9	9 July	5	ovoid	
254	15 Jan.	8	23 June	3	flaccid	
267	31 Jan.	10	4 July	9	globular	
276	4 Feb.	10	4 July	9	globular	
297	6 Feb.	9	20 May	3		2
305	10 Feb.	10	14 July	5	flaccid	6
338	25 Feb.	9	30 May	5	tubular	
344	25 Feb.	10	2 July	8	globular	

[a] When a bird was captured more than once before or after the postnuptial molt, maximum protuberance length is given.

twice in a single year. My records of individual males are much more limited, and are summarized for 16 males examined before and after the postnuptial molt (table 2). Since males regress from breeding condition after the onset of this molt, it is obvious that males 105, 267, 276, and 344 achieved full breeding condition twice within the period of study. Number 107 may have come into breeding condition a second time by 22 May, although his protuberance was not fully developed at that time. By 17 June he had regressed somewhat. The remaining 11 males had failed to reach breeding condition after the complete molt. Number 125 clearly regressed in late June or in July from the level of gonadal activity that he had reached on 19 June. Apparently most, if not all, males show a pronounced recrudescence of gonadal activity after the postnuptial molt, but few reach effective breeding condition.

FEMALE CYCLE

The female cycle is indicated in figure 4. In October 57.5 per cent of the females examined were breeding. The percentage rose to 68 in November and to 96 in December, when only one female examined lacked an incubation patch. In these first three months the female cycle was quite similar to that of the males. From January through March the cycle is difficult to interpret because of the increasing proportion of females with stage 4 patches. Such females may either stop breeding and carry the stage 4 patch until it is refeathered in the postnuptial molt, or they may breed again, the patch again becoming vascular and then edematous (Bailey 1952). Three females definitely bred again after having a stage 4 patch. Number 256 had a stage 4 patch on 16 January and a stage 3 patch on 18 February. Number 270 showed the same sequence on 31 January and 19 February, and number 299 the same on 6 February and 13 March. It is evident that December was the month of most intense breeding, as virtually all females examined on any day were in breeding condition whereas an appreciable proportion of females on any day in January, February, or March were either between nestings or were through breeding for the season.

Three females had breeding seasons lasting at least four months. Number 1 had a stage 1 incubation patch on 9 October, and on 19 February she had a stage 3 patch regressing to stage 4, indicating that she had recently finished breeding. Number 8 had a stage 1 patch on 10 October and a stage 2 patch on 10 February. Number 38 had a stage 3 patch on 23 October, a stage 3 patch on 5 February, and a stage 3 patch regressing to stage 4 on 20 February. Miller and Miller (1968) established an incubation period of 12 days and a mean fledging period of 11 days in the population near Cali, Colombia; they also found that females may spend up to 33 days with dependent young after fledging. Assuming a similar schedule in the Chilca population, these fe-

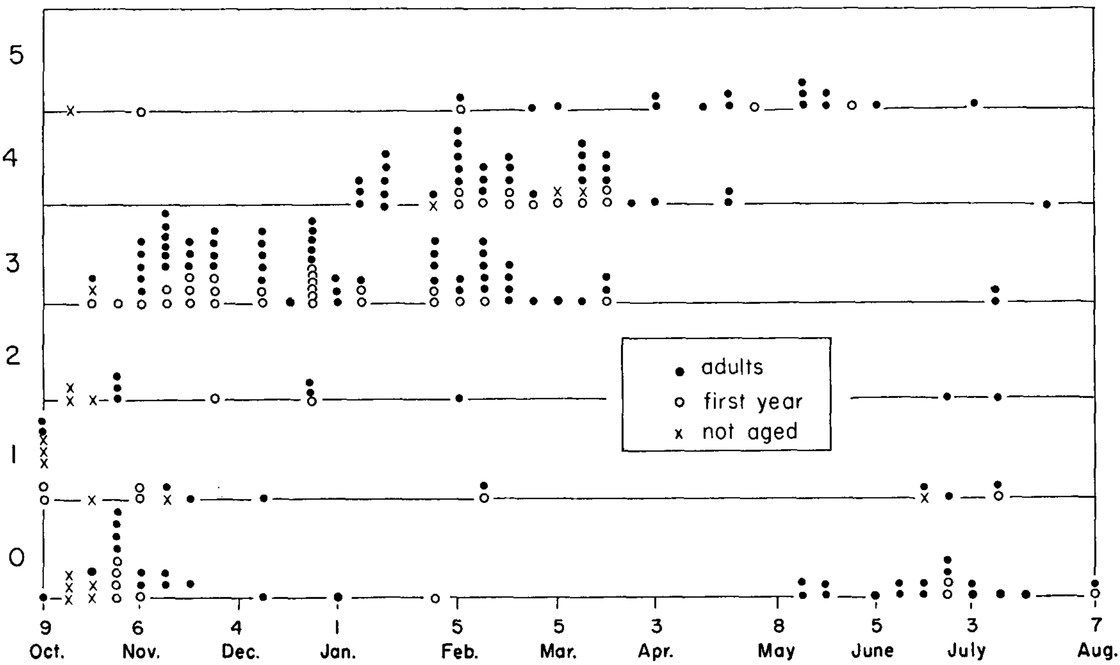

FIGURE 4. Female breeding cycle of Rufous-collared Sparrows near Chilca. Stage 0 indicates absence of an incubation patch. Stages 1–4 indicate the four stages of incubation patch described by Bailey (1952). Stage 5 indicates a refeathering patch. When an individual was captured more than once, at least 14 days elapsed between successive records.

males had time for two successive nestings separated by a lengthy period of attendance on dependent young. A fourth female, number 120, had a stage 3 patch on 11 November and was seen carrying nest material on 7 January. She undoubtedly attempted two broods.

The latest breeding female examined had a stage 3 incubation patch on 13 March. On 13 May a pair of adults accompanied by a single juvenile was seen. One adult held a green caterpillar in its bill, obviously for delivery to the young bird. This juvenile probably came from an egg laid sometime in April. The next breeding female was collected on 18 June; she had a stage 1 patch and a large, yolky egg in her oviduct. The breeding season for most females ended in March, about a month before most males regressed from breeding condition, although there was some breeding in April, as just noted. Between 18 June and 6 August, ten of 23 females examined had active incubation patches, the latest on 15 July. Thus, there was a second period of breeding separated from the first, main peak by three months in most birds and by at least two months in some. Apparently most females did not breed at that time, although the sample is too small to give a good idea of what proportion of females actually bred in winter. As in the males, the second breeding period was much shorter than the first.

AGE OF BREEDING BIRDS

Only one recapture record provides any information on this point. A male, number 52, was in juvenal plumage on 24 October. On 8 January he had completed the postjuvenal molt. Miller (1961) found that Colombian birds completed this molt at four months of age and that the molt occupied a mean of 70 days. If the Chilca population was similar in this regard, number 52 would have been about four months old on 8 January. At that time there was no sign of gonadal activity but on 7 February his cloacal protuberance measured 5 mm and on 14 February, 7 mm. He apparently came into breeding condition at about five months of age. This was the earliest age for which Miller (1959a) found evidence of breeding condition in a Colombian sparrow. On 12 March, number 52 was starting a complete molt and his cloacal protuberance was only 5 mm long and tubular. He had reached breeding condition so late in the season that it is doubtful that he had actually mated. When he was collected on 20 May, he had finished a complete molt and his testes were in stage 6.

Of 82 breeding males of known age examined in October, November, and December, 62 (75.6 per cent) had fully ossified skulls. If the complete double-walling of the skull takes a maximum of 11 months, as established by Miller and Miller (1968) for Colombian birds, about one-fourth of the breeding males in this period were less than one year old. Of 56 breeding females examined in the same period, 35 (62.5 per cent) had fully ossified skulls. The difference between first-year to adult ratios for males and females is not significant in a chi-square test.

SINGING AND FLOCKING BEHAVIOR

Singing behavior showed a high degree of correlation with the testis cycle. Miller and Miller (1968) found that singing was depressed during the molt periods and elevated during the two peaks of breeding in their population. In the Chilca population, singing was at a high level from early October to mid-March. I was absent from the area 19–31 March. Singing fell off noticeably in the first half of April, a time when many birds were starting the postnuptial molt. By the end of the month only a few birds were singing short bouts. In early May a few birds resumed singing and on 20 and 21 May several more birds had started to sing. On 11 June there was a very noticeable resurgence of singing and by mid-June I estimated that the song output was at the level noted in the breeding season. By mid-June, many males had either finished the molt or were in its terminal stages and, as indicated in birds collected or examined, a strong gonadal recrudescence was under way in the males. On 12 and 14 July no singing was heard and there was a virtual absence of song until 7 August. The mean stage of the testes of nine birds collected 12–30 July was 2.6. During my last three days in the area, 7–9 August, several males began to sing much of the time, although song bouts were rather short. The testes of nine males collected in this period were at a mean of stage 4.

Flocking, which occurs in many passerines outside the breeding season, was noted only once. On 15 May a flock of at least 30 sparrows was seen working through a tangerine grove. Three were collected; all were young first-year birds and the gonads of the two birds autopsied were very small and completely inactive. It seems likely that the flock was composed mostly or entirely of young birds. This group was in the area for several weeks although it became smaller as time passed. Miller and Miller (1968) reported that flocking was rare in their population and that males defended territory throughout the year. My data on this point are scanty, although my recapture records indicate that adults and mature first-year birds tended to stay within a rather limited area. Number 26, which had a song peculiarity permitting easy identification, remained in the same area throughout the study period. Further, the fact that adults and mature first-year males have active gonads outside the molt period makes it unlikely that they would enter flocks readily.

MOLT

Two molts were evident in adults and mature first-year birds in the Chilca population. The major breeding period was preceded by a partial molt in some birds and followed by a complete molt in all. This schedule differs from that described by Miller (1961) for his population in which there was a complete molt following each of the two breeding periods. Thus, and this was the striking feature, birds of breeding age replaced the entire plumage twice a year. The Chilca schedule was similar to that described by Wolf (1969) for the Costa Rican population, but there were important differences between the prenuptial molt described by Wolf and the corresponding molt found in my population.

"PRENUPTIAL" MOLT

In October, November, and December 218 adult and mature first-year birds, both breeding and non-breeding, were examined. Of these, 168 were aged on the basis of skull characteristics; 50 were not aged but were assumed to be adults or mature first-year birds because they showed signs of gonadal activity. Of the 218, 108 (49.5 per cent) showed either some active molt or very fresh feathers indicative of recent molt somewhere in the plumage. This molt must have started in some birds in September, as male number 9, caught on 10 October, was replacing primaries 1–5, and males 11 and 13, caught on 11 October, were replacing primaries 1–4 and 1–6, respectively. Birds showing active molt were very rare in December and feather replacement had ended in nearly all birds by the end of November.

There was a highly significant difference in the proportions of males and females taking part in this molt. Of the 130 males, 78 showed active or very recent molt, but only 30 of the 88 females ($\chi^2 = 14.09$; df, 1; $P < .001$). Considering only the 168 birds of known age, there was a significant difference in the proportion of adults to first-year birds among the molting males; 20 of 27 first-year males showed signs of molt, but only 34 of 72 adults ($\chi^2 = 5.71$; df, 1; $P < .02$). Among the females, 11 of 22 first-year birds and 16 of 47 adults showed signs of molt; the difference is not significant, possibly because of the relatively small sample

TABLE 3. Number of primaries replaced by Rufous-collared Sparrows showing discontinuities.

No. of primaries replaced	Males	Females	Total
1	3	0	3
2	10	1	11
3	15	4	19
4	11	5	16
5	16	6	22
6	11	4	15
7	1	1	2
8	2	1	3

size. Thus, the overlap between molt and the onset of breeding condition was less for the adults, which made up the bulk of the breeding population, and for the females, which have much greater demands on their resources in the breeding season than do the males.

This molt invariably involved the primaries and the feathers of the old and new generations were easily distinguishable and formed what Ashmole (1963) termed "discontinuities" in the primary series. Replacement always started with primary 1 and proceeded distally; most birds replaced 2–6 of these feathers (table 3). Primary molt was usually accompanied by light to heavy molt of the crown feathers and/or upper and under tail coverts. Body molt was uncommon and was always light. Rectrix molt was found in only 13 per cent of the birds and ranged from replacement of the central rectrices (1–1) to replacement of the entire tail.

This molt differed markedly from the prenuptial molt described by Wolf (1969), in which replacement of remiges was rare and never involved the primaries. Since primary replacement came early in the complete molts described by Miller (1961) and also in the postnuptial molt of the Chilca population, this limited molt should not be considered a prenuptial molt but an incipient second complete molt which was arrested by the onset of breeding.

Miller (op. cit.) noted four cases in *Z. capensis* in which molt was arrested by breeding activity, and similar arrest has also been described in some seabirds (e.g., *Sterna fuscata*, Ashmole 1963), in a tropical ground-dove (*Columbigallina talpacoti*, Snow and Snow 1964), and in several species of cuckoos of the genus *Clamator* (Friedmann 1948; Payne 1969).

Three birds in the Chilca population clearly showed arrested molt. On 9 October number 2, an adult male, had replaced left primary 1 and right primaries 1–2. On 29 October primaries 1–5 had been replaced bilaterally with 5–5 half-grown. On 6 February 1–5 were full-grown and easily distinguishable from the older primaries 6–9. Number 38, a mature first-year female, was replacing primaries 1–3 on 23 October; 2 and 3 had barely erupted. On 7 November, 2 and 3 were full-grown. On 5 and 20 February no further molt had occurred. On 15 July she had undergone a complete postnuptial molt. In her case there was clear overlap of molt and breeding. When caught on 23 October she had a stage 3 incubation patch; in addition to primary molt she also showed light body molt and some under tail covert molt. Number 63, an adult male, was replacing primaries 1–4 on 29 October; 4–4 were half-grown. On 18 November 4–4 were full-grown; on 10 January and 4 February no further molt had occurred. On 22 May he was in completely fresh plumage.

Birds 38 and 63 not only illustrate arrested molt but also indicate that in the ensuing postnuptial molt, replacement started all over again with primary 1 and not at the point at which molt had been arrested. It is clear that we are dealing with two separate molts and not with a single, suspended molt. In addition to these birds, which were actually molting when first caught, there were many which showed no active molt but had obvious bilaterally symmetrical discontinuities in their primary series indicative of arrested molt (table 3). Such birds could be distinguished at least until mid-March. Three males with discontinuities, caught on 2 December, 15 January, and 6 February, replaced all primaries in the complete postnuptial molt, as did several males and females which were still actively molting when first caught and which had replaced varying numbers of primaries. All these birds indicate that the molts preceding and following the major breeding period were completely separate molts.

Toward the end of my studies at Chilca, between 22 July and 9 August, eight of 12 mature first-year and adult males and two of four females of similar ages showed active molt. Of the 10 molting birds, three were taken in July and the others between 5 and 9 August. There was crown molt in five birds, chin molt in five, throat molt in eight, body molt in two, and tail covert molt in one. This was apparently the beginning of the incipient complete molt between the end of the second breeding period of 1968–69 and the beginning of the major breeding period of 1969–70. If so, it was about a month earlier than in the previous year; as noted previously, some birds must have started this molt in 1968 as early as September. There is evidence that breeding

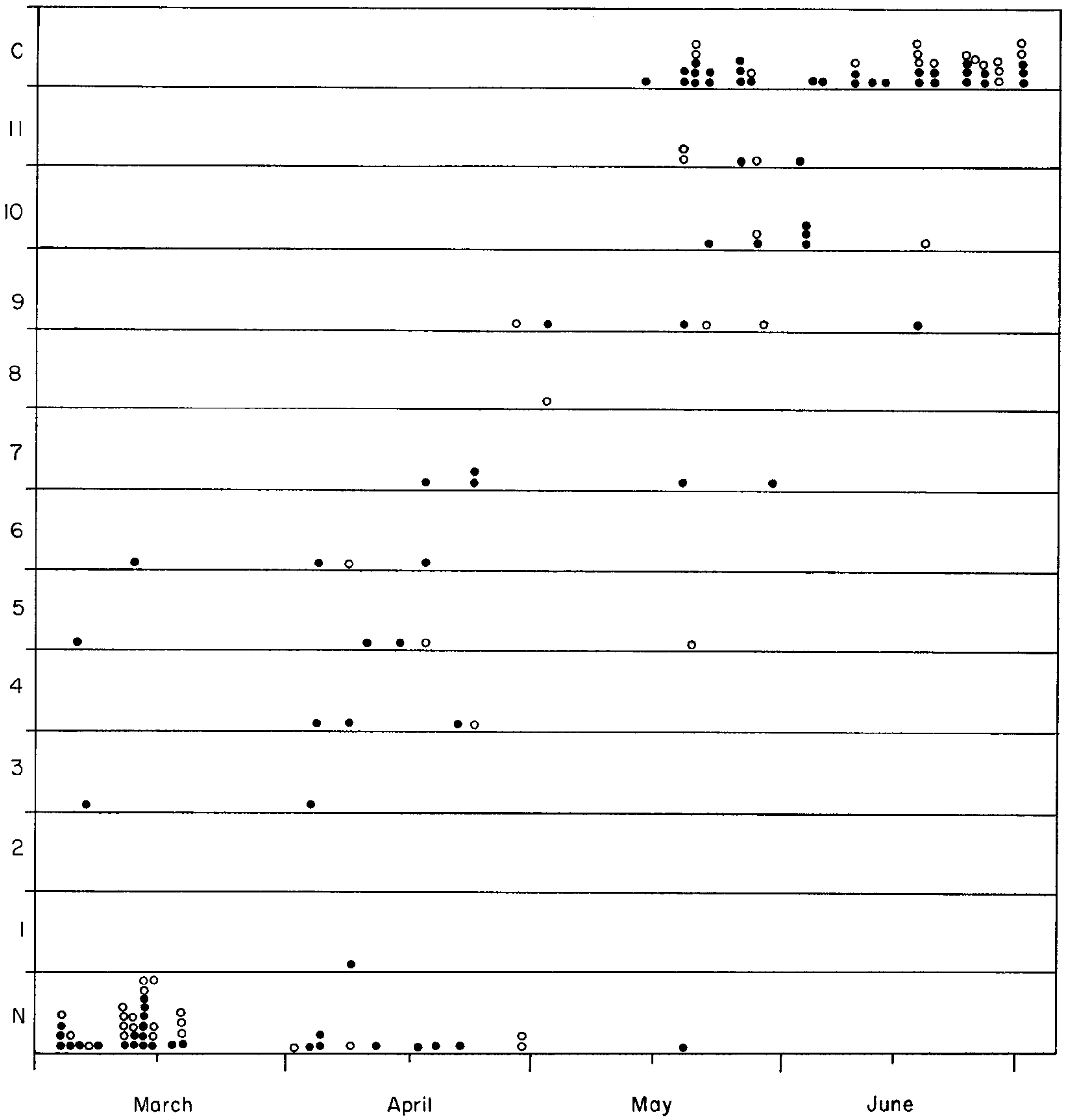

FIGURE 5. Period of the postnuptial molt in the Chilca population of Rufous-collared Sparrows, based on 84 adult and mature first-year males (dots) and 51 females of similar ages (circles). N indicates molt not started and C indicates molt completed. Stages 1–11 are those described by Miller (1961); stages 2–10 refer to replacement of primaries 1–9.

in the second period of 1968 persisted at least until August, and perhaps into early September, as a full-grown juvenile was caught on 9 October and another was seen on 10 October. It is impossible to ascertain the limits of the second breeding period of 1968 with any degree of precision.

POSTNUPTIAL MOLT

The chronology of the postnuptial molt is shown in figure 5, using the 11 stages of molt described by Miller (1961). Feather replacement in adults and mature first-year birds was complete and the molt is similar to the complete molts described by Miller (1961) and by Wolf (1969).

POSTJUVENAL MOLT

The juvenal plumage, figured by Miller (1961: 145, fig. 1), is replaced by adult type plumage at the incomplete postjuvenal molt, in which the remiges are either not replaced at all or are only partly replaced. Of seven juveniles with adequate recapture records, six showed no primary molt and the seventh showed partial primary replacement. This bird was

TABLE 4. Stomach contents of 97 Rufous-collared Sparrows.

Month	N	Green material		Solanum		Amaranth		Other seeds		Insects	
		n	%	*n*	%	*n*	%	*n*	%	*n*	%
Oct.	5	4	80	3	60	0	0	1	20	2	40
Nov.	5	4	80	3	60	2	40	0	0	0	0
Dec.	3	1	33	2	67	2	67	0	0	0	0
Jan.	3	0	0	2	67	3	100	2	67	1	33
Feb.	2	2	100	1	50	1	50	1	50	0	0
Mar.	3	1	33	3	100	2	67	2	67	1	33
Apr.	13	1	8	3	23	8	62	5	38	3	23
May	15	3	20	0	0	12	80	4	27	3	20
June	16	6	37	5	31	11	69	4	25	3	19
July	21	4	19	7	33	19	90	0	0	2	10
Aug.	11	5	45	1	9	11	100	1	9	1	9
Totals	97	31	32	30	31	71	73	20	21	16	16

first caught on 24 October in juvenal plumage with all rectrices but left 5–6 full-grown. On 8 January the plumage was entirely of the adult type; primaries 1–4 were new and full-grown, 5–9 were old. On 12 March his first complete molt had started. Primaries 1–5 were new (the second replacement for 1–4) and the three inner pairs of rectrices were being replaced. Body molt had just started. The skull still had large "windows." This bird was collected on 20 May. It was in completely fresh plumage and all primaries and rectrices were full-grown. The skull was about 40 per cent opaque. In general, the postjuvenal molt appears to be similar to that described by Miller (op. cit.) as "incomplete, most notably failing to involve the remiges."

ANOMALOUS MOLT

A few adults showed heavy general molt at times when such molt was not evident in the rest of the population. A male, 62, had replaced all primaries and was molting heavily on 29 October; primary 9 was about one-fourth grown. Male 113, caught on 8 November, had replaced all primaries; primary 9 was half-grown. All rectrices were new and all but the outermost were full-grown. The remainder of the plumage was fresh. Number 250, a male caught on 13 January, had replaced primaries 1–7 left and 1–8 right, primary 8 being half-grown. All remaining plumage was fresh and this male was apparently in the late stages of a complete molt. Numbers 301 (a male) and 333 (sex undetermined) were also apparently near the end of a complete molt on 7 and 24 February, respectively. Female 373, with a refeathering incubation patch, was about half-way through a complete molt on 28 February.

Without knowing the previous histories of these birds it is impossible to account for the unseasonable nature of their complete molts. Significantly, all were adult and all but one of the five birds of known sex were males. The female may simply have been starting her postnuptial molt early. The most significant birds were 62 and 113, as they may have represented a small group in which the incipient complete molt was not arrested but reached completion. This suggestion is strengthened by the fact that the cloacal protuberance of 62 was only 3 mm long and that of 113 only 5 mm long. In these individuals molt may have delayed the attainment of full breeding condition. This seems most likely for 62, which had the smallest cloacal protuberance of any adult examined in October and November. These two males are also significant in that they were the only birds examined which might have had two complete molts within one year. If so, such a schedule must be very rare in the Chilca population. Including these two, 132 adult and mature first-year males were examined in October, November, and December, and the incipient complete molt proceeded to completion in only two (1.5 per cent).

FOOD HABITS

The stomach contents of 71 adults or mature first-year males, 22 females of similar ages, and four young first-year males were examined macroscopically. Since no pronounced variation in diet among these age and sex groups was noted, the data presented in table 4 are pooled. The diet was predominantly vegetable throughout the study period. Seeds of amaranth (*Amaranthus* sp.) were by far the most important single food item and were found in 73 per cent of all stomachs examined. In 29 stomachs (30 per cent) they were the sole item present. Insects were found in only 16 per cent of all stomachs and were usually represented by small fragments. In only two of 97 stomachs were they a major component, one examined on 18 April, one on 17 June. Although the greatest percentages of stomachs

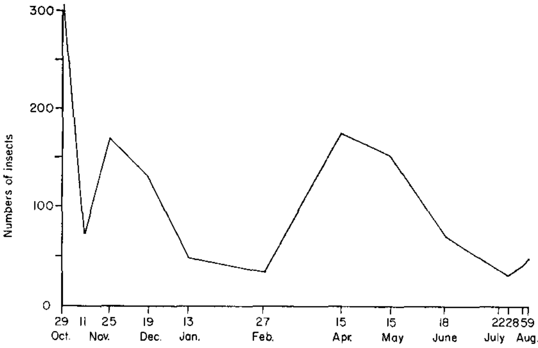

FIGURE 6. Numbers of insects per 10 sweeps of an insect net on a standard sampling area near Chilca, on dates indicated.

containing insects were recorded in October, January, and March, samples in those months were very small. With larger samples from April through early August, the relatively high percentages recorded in April, May, and June may represent increased insect consumption in the molt period. Further, the two stomachs containing large amounts of insect material were taken in that period.

Although adults and independent young birds rely primarily on seeds and green material, nestlings and dependent young are apparently fed an insect diet. On several occasions adults were noted flying with large insects or insect larvae in their bills, undoubtedly for delivery to nestlings or fledglings. Miller and Miller (1968) and Wolf (1969) stated that nestlings and fledglings were fed insects; this is usual in emberizine sparrows.

Food for adults and independent young birds was always readily available on the study area. Both *Solanum nigrum* and *Amaranthus* sp. grew abundantly along the irrigation channels paralleling the rows of fruit trees and they formed luxuriant growths beneath the trees themselves. The same was true of purslane (*Portulaca oleracea*), which may have been an important source of green material. In addition, forbs of other species and grasses were present along roadsides and on the shoulders of main irrigation canals.

To get some idea of seasonal fluctuations in insect abundance, 10 sweeps with an insect net were made at intervals of about one month in a patch of *Solanum*, *Amaranthus*, and tall grass on the study area. The results of this sampling are shown in figure 6. Insects were relatively numerous in October, November, and December, in the first part of the major breeding period, and again in April and May, the period of heaviest molt. Miller (1962) stated, "Although these food sources [grass seeds and insects] were not measured at our field station, the subjective impression gained was that they were always present in abundance." In this study, an abundance of seeds and green material was evident at all times, but it is apparent that there were major fluctuations in the insect population.

BIRDS OF THE LOMAS

Lanning (1967) wrote of the barren hills of the coastal desert, "In areas of dense winter fogs, grasses, bushes, and other plants manage to thrive on trapped and condensed moisture. Such areas of fog vegetation are known as *lomas*." Koepcke (1954, 1963) gives excellent descriptions of the lomas and their vegetation types. She notes that in the summer sunny season, when the vegetation of the lomas is dry and sparse, Rufous-collared Sparrows are rare or absent, but that when the lomas are covered with green vegetation in winter, the sparrows come to such areas in large numbers and breed there commonly. I made the following observations in the Lomas de Atocongo, 15 mi. SE Lima, an area of fog vegetation on a steep, west-facing slope.

On 21 November, I found scattered shrubs still in leaf, a few small trees, some forbs, and scattered small patches of grass. Seven singing male *Zonotrichia* were counted from the base of the slope to the crest, a distance of perhaps ⅔ mi. By 10 January the shrubs had been browsed back severely by goats, no grass was present, and the few sparse annuals remaining were dry and covered with dust. No sparrow was seen or heard along the route previously traversed. On 12 June, the lower third of the slope was still very dry, with little green vegetation present, and little regrowth of the browsed shrubs. However, on the steep upper two-thirds of the slope, there were extensive patches of grass and herbaceous vegetation and the shrubs had leafed out. On the upper third there was nearly continuous ground cover and the vegetation was wet with droplets of condensed fog. Many of the shrubs in this area were now over 5 ft high. One sparrow was heard singing steadily on the census route. Despite the noticeable regrowth of vegetation, no influx of sparrows had yet occurred. On 11 July there was yet a further advance in the vegetation. The shrubs had leafed out more and there was a thick carpet of grass, moss, and low annuals on the upper two-thirds of the slope. The lower third was densely covered with a blanket of blooming amaryllis (*Hymenocallis* sp.) and was thus unsuitable for the sparrows. The soil all the way up the slope was so muddy that footing was difficult and near the crest the fog or low clouds were swirling down to the ground. At least seven steadily singing males were recorded, and perhaps as many as nine. Two pairs were seen and one chase was observed. On 11 August, a conservative count of 11 singing males was made with every attempt to avoid duplicate counts. One juvenile with a full-grown tail was noted. Many sparrows were seen; I estimated a total of at least 25 pairs on the slope. The vegetation was lush and damp and again, at the crest, there was cloud cover down to ground level.

Two visits were made to the Lomas de Lachay, 60 mi. NW of Lima. On 1 March I noted three single sparrows and a flock of 10–12 in a grove of introduced pines and eucalyptus. There was some leaf litter and dry grass beneath the trees. One bird sang a single song and another, or possibly the same one, sang steadily for 5 min. The presence of a flock suggested that the birds were not breeding at that time. On 13 July the ground in the same area was covered with a dense green growth of grasses, forbs, and leafy shrubs. Sparrows were abundant and an estimated 200 were seen. Several chases and numerous displacements were noted. The impression was that of a large population at the beginning of the nesting season.

The derivation of the populations of the lomas is unknown, as is the gonadal status of individuals in that part of the year spent outside the lomas. Such questions will be answered only by extensive color-banding of individuals breeding in the lomas and recovered elsewhere. However, in view of the extremely low recovery rates of North American passerines (see, for example, Cortopassi and Mewaldt 1965), and the virtual absence of ornithologists in Perú, it seems doubtful that any relevant information will be forthcoming in the foreseeable future. The important point relative to the present study is that sparrows are absent from the lomas when breeding is at its height in the coastal river valleys and breed commonly in the lomas when breeding is infrequent elsewhere.

PROXIMATE AND ULTIMATE FACTORS IN THE ANNUAL CYCLE

Avian breeding has traditionally been thought of as being timed to occur in that part of the year in which the prerequisites for successful nesting would be optimal and nesting success would be highest. Such prerequisites as adequate nest sites and supplies of nest materials, an adequate food supply for nestlings and fledglings, a sufficiently low incidence of nest predators, and favorable weather conditions, would be of critical importance. As Lack (1968) notes, at times a compromise must be made. In temperate regions, for example, nest predators, especially snakes, would be most abundant when weather conditions are best for nesting.

However, Pitelka (1957, 1958) was the first to point out that molt may be of considerable importance in the evolution of avian breeding schedules because it demands so much energy that molt and breeding cannot be carried on simultaneously but must be mutually exclusive, or virtually so. There are therefore two alternatives involved. If the ultimate factors in the evolution of an annual cycle pertain to breeding schedule, then breeding coerces the timing of molt by preempting a certain part of the year in which molt cannot occur. If the ultimate factors pertain to molt, then the reverse is true.

Most students of avian breeding schedules agree that an adequate food supply for nestlings and fledglings is probably the single most important prerequisite for breeding success. Since growing young need a high protein diet, and since insects are nearly always the most abundant source of protein readily available to most passerines, it is not surprising that these birds usually feed their young a diet mainly, if not exclusively, of insects. Molt also demands a rich diet to support the synthesis of a new feather coat, and again, availability of insects is an important adjunct to survival in the molt period for many birds. However, molt makes varied demands, and some depend on factors other than diet. There is no doubt that a heavily molting bird suffers from reduction of insulation against heat, cold, and moisture. In a temperate or a cool tropical area this could be critical at night, when temperatures are lowest and foraging is impossible. Again, heavy molt undoubtedly impairs locomotion to some degree just at a time of stress when efficient foraging and effective evasion of predators would be at a premium. Although dietary considerations are undoubtedly the most important in both breeding and molt, weather and shelter factors are also important and should not be overlooked.

Previous studies of the annual cycle of *Zonotrichia capensis* have evoked opposing viewpoints. Wolf (1969) assumed that the ultimate factors in the timing of the annual cycle were associated with breeding and that molt "is relegated, evolutionarily, to periods that are unfavorable for breeding." Miller (1962), on the other hand, believed that molt was the important factor in the annual cycle of his

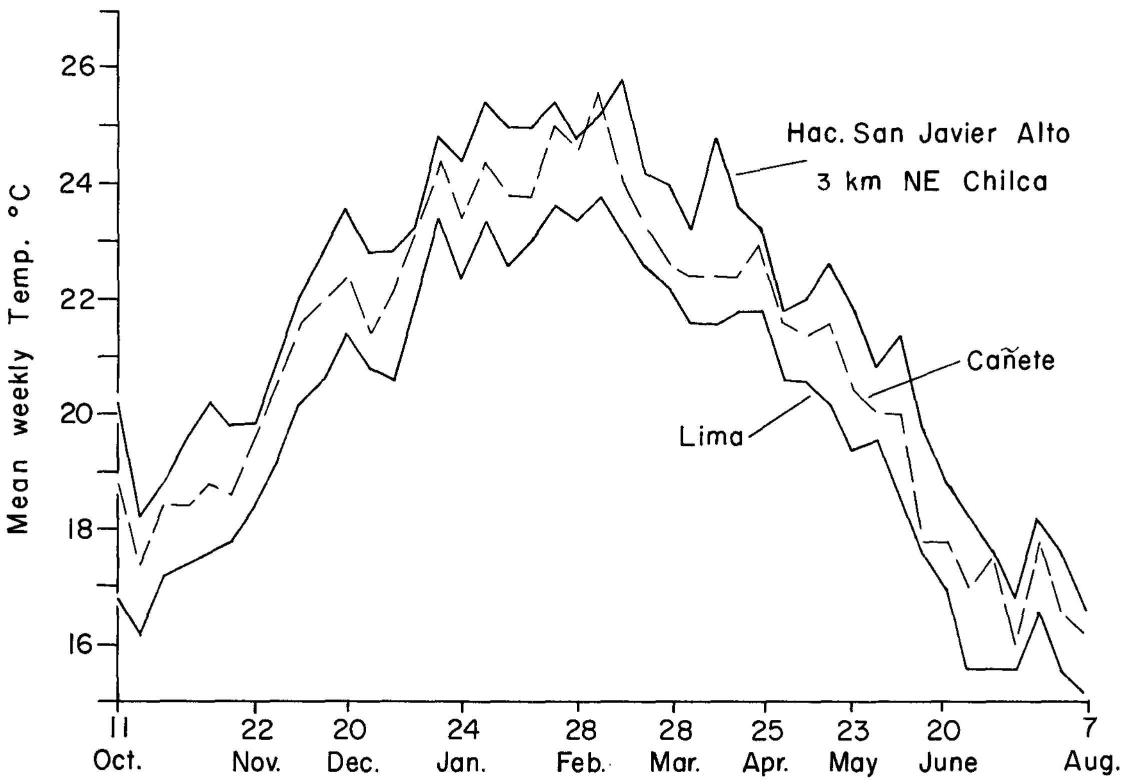

FIGURE 7. Mean weekly temperatures (°C) for Lima, Cañete, and Hacienda San Javier Alto.

population and that it coerced breeding. In the Chilca population there were two distinct breeding periods, a major period extending from October to mid-March in the females and into April in the males, and a second, lesser period, restricted both in extent and in the numbers of individuals involved, from about mid-June to mid-July. The major period was preceded by an incipient complete molt which was arrested by the onset of breeding condition, and followed by a complete molt which occurred from April through June. We may now consider possible proximate and ultimate factors involved in this cycle.

In previous studies of avian breeding and molt cycles, the environmental variables most frequently considered have been the photoperiodic cycle, the annual cycles of temperature and precipitation, and seasonal fluctuations in food supply. Sunshine has been considered in rather few studies but will be considered here.

Precipitation seems to be of no importance as a proximate factor in the Chilca cycle and may be dismissed at the outset. Between 10 October 1968 and 9 August 1969, a total of 15.2 mm of precipitation was recorded. The greatest amount in any 24-hr period was 1.8 mm. The regular irrigation which was carried out was far more important in regulating soil moisture than was precipitation and was therefore critical in regulating food supply, both as regards green and seed-bearing vegetation and the insects which lay their eggs and develop on such vegetation or in the soil. Fresh water for direct consumption was available in abundance throughout the study period and this supply was independent of precipitation. Thus, any possible effect of the extremely low precipitation was overwhelmed by agricultural practice.

Photoperiod also seems to be of no importance. Males came into breeding condition in October and November while daylength was increasing. From 1 October to 30 November daylength increased from 12 hr 13 min to 12 hr 46 min. Whether such a minor increase over such a long period would have any effect is questionable. Most of the major breeding period, from late December to April, was in a period of decreasing daylength. The rapid gonadal recrudescence which followed the postnuptial molt also occurred while the days were getting shorter. The second, lesser breeding period started while daylength was still decreasing and when days were shortest, and it extended into the first two or three weeks of the period of increasing daylength. Between 15 June and 15 July, daylength increased from 11 hr 25 min to 11 hr 30 min; this could hardly have been a factor in causing the onset of breeding in some birds in that period.

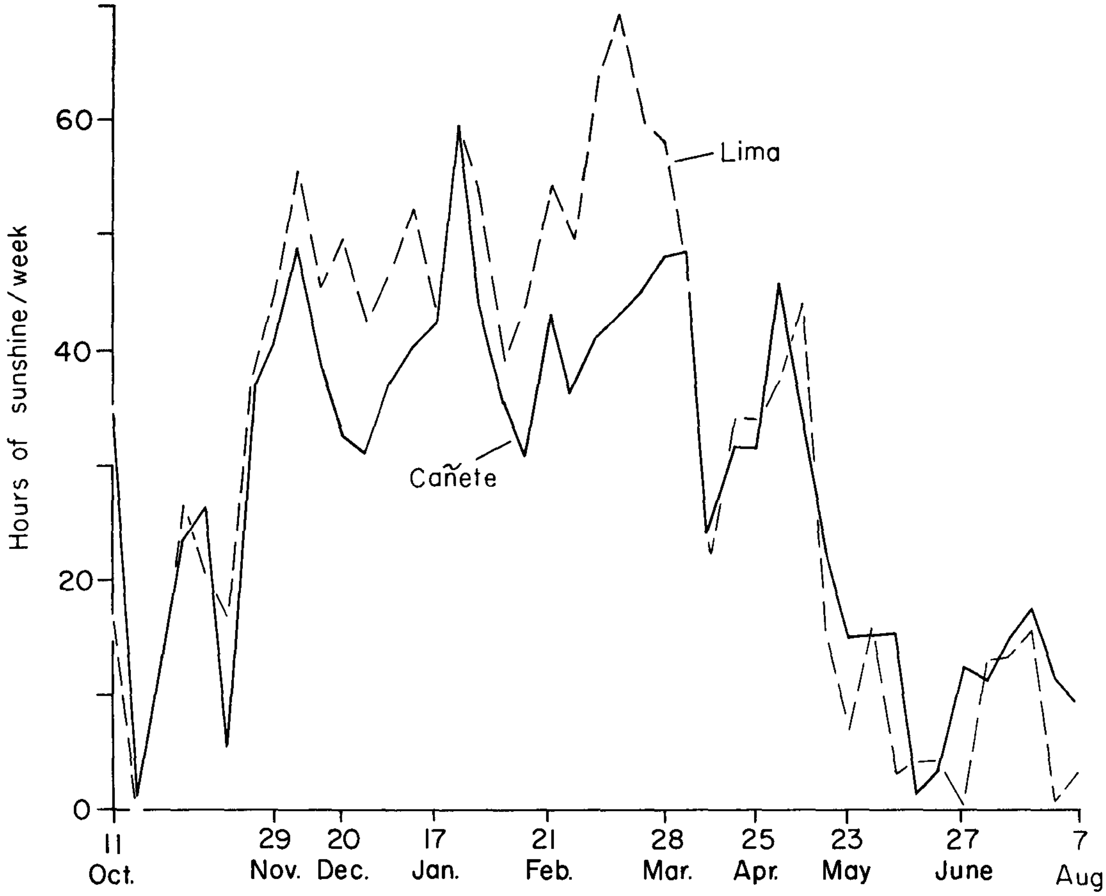

FIGURE 8. Hours of sunshine per week at Lima and Cañete.

The most convincing evidence against the importance of photoperiod as a proximate factor in this study is derived from a comparison of the breeding schedule of *Z. capensis* near Chilca with that reported for this species at Acolla, Provincia de Jauja, Department of Junín, Perú, on the east slope of the Andes at 3400 m, by Blancas Sánchez (1959). Acolla is at 11° 46′ S, or 44 mi. N of Chilca latitudinally, and total daylength at Chilca exceeds that at Acolla by only 4 min a year. Blancas Sánchez reported that *Z. capensis*, abundant at Acolla, nested there in March, April, and May, starting precisely at the time that the sparrows near Chilca were finishing. Further, the entire nesting season at Acolla lay entirely within the period of decreasing daylength. Thus, photoperiod at these latitudes must be so weakly coercive on the breeding of this species, if it is coercive at all, that it is overridden by other factors.

Temperature cycles for Hacienda San Javier Alto, for Lima, 35 mi. NNW, and for Cañete, 45 mi. SSE, are shown in figure 7. The general similarity in pattern among the three cycles is apparent, although the absolute values of the Cañete cycle are closer to those for the hacienda. The males came into breeding condition in October and November in a period of rising temperatures, and relatively high temperatures (22° C or above) prevailed over the major breeding period and over the first three weeks in May, i.e., over most of the molt period. A second, minor peak of elevated temperatures occurred in the last two weeks of July, starting nearly at the end of the second breeding period. Temperature has been shown to influence testis development experimentally in north temperate birds if a stimulatory daylength is provided (see Farner and Wilson 1957:259–260 for discussion). In the study area daylength ranged from 11 hr 22 min to 12 hr 53 min and such a regime would probably permit temperature to act as a proximate factor. Although temperature may have been of some influence in relation to the first breeding period it failed to correlate with the second and could not have been important as a proximate factor at that time.

Sunshine shows a high degree of correlation with both breeding periods. Sunshine records for Lima and Cañete are shown in figure 8. The general similarity of the two cycles is evident. Since there is a rather close correspondence between sunshine and temperature on the Peruvian coastal desert, as may be seen by comparing figures 7 and 8, and since the temperature cycles at Cañete and the hacienda are nearly similar, the sunshine cycles at these two localities must be much the same. As with temperature, the males were coming into breeding condition in a period of increasing incidence of sunshine, the incidence of sunshine was high throughout the first breeding period, and it remained high until mid-May. The sunny period thus included at least the first half of the molt period. Further, there was a lesser, but quite noticeable, period of increased sunshine between 20 June and 18 July which correlated with the second breeding period.

Finally, we may consider fluctuations in insect abundance as indicated in figure 6. October, November, and December were months in which insect numbers were relatively high; this includes the period in which the *Zonotrichia* population was coming into breeding condition, and the first month in which nearly all birds were in breeding condition. There was a noticeable decrease in insect numbers in January and February, despite the fact that actively breeding females were found as late as 13 March. However, females with stage 4 (recovery) incubation patches began to appear in early January and the intensity of breeding began to wane from that point on. It is possible that the decrease in insect numbers coincided with less frequent breeding in January and February. The increase in insect numbers in April and May coincided with the first two-thirds of the molt period and, as previously noted, examination of stomach contents suggests that adults and mature first-year birds were actually consuming more insects in those months. The low numbers of insects in June, July, and the first nine days of August includes the latter part of the molt period and the entire second breeding period.

As regards the males, increasing incidence of sunshine seems to be the proximate factor of major importance. Rising temperatures may act in concert with it. The apparent failure of many males to reach effective breeding condition in the second breeding period may have resulted from the fact that although sunshine increased in this period, it never reached the high levels attained in October and November. It may also be that in part the low level of breeding was caused by the failure of temperatures to rise concomitantly, as they did in October and November. Although sunshine has been largely neglected as a proximate factor, it has been found to be of possible importance in some studies (Baker 1938; Threadgold 1956, 1960). Marshall (1951) found that sunshine and temperature were of considerable importance in accounting for the difference in timing of the gonad cycles of certain passerines from one year to the next at Oxford, England, and he stated that for certain birds resident in areas in which the winter sky is overcast (true of Chilca), sunshine may be a principal long-range environmental influence.

In the permissive climate which prevailed on the study area, and with an abundance of food and water present throughout the year, the energy demands on the males were slight outside the molt period. Kendeigh (1941) has pointed out that, striking though the development of the testes from the resting to the fully active state may be, these organs at maximum size do not exceed 2–3 per cent of the weight of the bird. It is not surprising that, with a refractory period apparently negligible or lacking, there was a pronounced resurgence of gonadal activity as soon as the energy demands of molt had terminated. Thus, the proximate factor or factors which operated in October and November acted on males which were already at an advanced level of gonadal activity. This contrasts with the situation in temperate zone males in which nearly all individuals are in a state of complete gonadal inactivity at the time the important proximate factor, increasing photoperiod, starts to be effective. Such males must be brought from the lowest level of gonadal activity to the highest and, as Wolfson (1942) noted in the Oregon Junco (*Junco oreganus*), the earliest stages of gonadal development are the slowest.

As regards the females, in most species which have been investigated, and nearly all breed in temperate areas, they have a far less pronounced response to photoperiod than do males. Experimental studies suggest that they respond to the visual stimuli presented by the presence of the necessary prerequisites for nesting and to the behavior of the male. It is difficult to think of an environment more stable and generally more favorable for nesting than that in the study area. Predators were rare; the only potential nest predators actually noted on the area were a pair of Sparrow Hawks (*Falco sparverius*) that flew over occasionally. Norway rats (*Rattus norvegicus*) were seen rarely around buildings but never in the study area. Snakes were conspicuous by their absence and no cats were present. The lowest temperature recorded in 10 months was 12.8° C and the highest was 32.8; wind

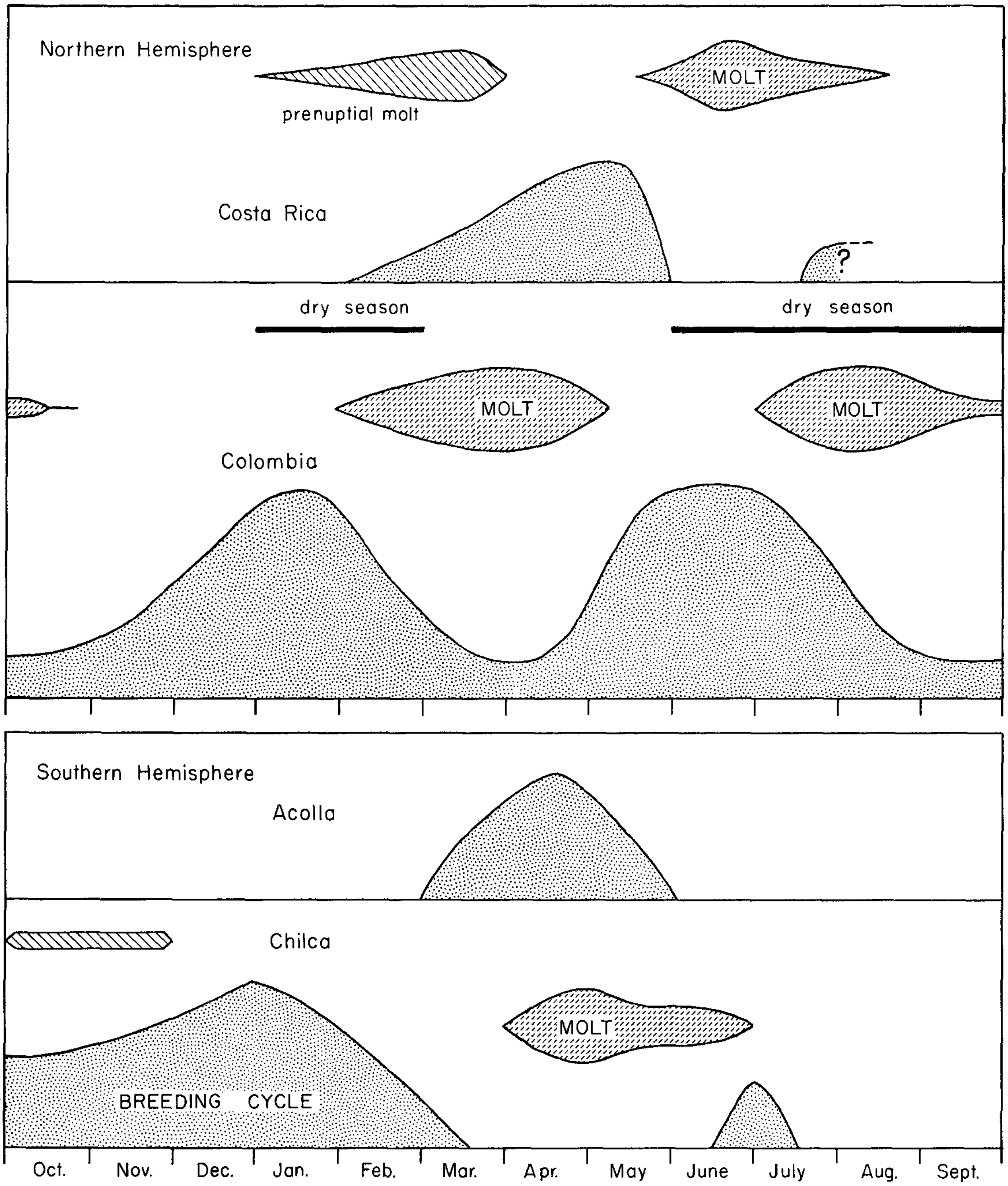

FIGURE 9. Diagrammatic representation of the occurrence of breeding and molt periods of *Zonotrichia capensis* at Las Varas, Costa Rica (Wolf 1969), near Cali, Colombia (Miller 1961, 1962), and near Chilca, and nesting season at Acolla (Blancas Sánchez 1959). Diagrams marked "Molt" refer to complete molts. Cross-hatched bar in Chilca diagram refers to incipient, arrested complete molt.

and precipitation were never prominent. Thus, weather was permissive to nesting throughout the study period. Nest sites were abundant in the thousands of citrus trees and nest materials were common along irrigation ditches and on the shoulders of irrigation canals. Ample supplies of food and water for adults and independent young birds were present at all times. The only prerequisite that varied significantly in the 10 months of study was the level of insect abundance, which would presumably reflect variation in the availability of food for nestlings and fledglings. The proximate factors timing the onset of breeding condition in the females thus appeared to be sunshine, which might have been a potent psychological stimulus, and the increasing numbers of insects, presumably directly evident to the females and another potential visual stimulus.

If the ultimate factors involved pertain to nesting, the conclusion seems inescapable that the breeding schedule was timed to take advantage of increased availability of insect food for the young. Weather factors may also have been involved secondarily, since the major breeding period fell entirely within the warmest and sunniest part of the year. However, such factors were undoubtedly of lesser importance since the climate was generally so mild.

The annual cycle near Las Varas, Costa Rica (Wolf 1969) is shown in figure 9. Correlations with rainfall and temperature were not consistent and it is difficult to point to any proximate factor of outstanding importance. Photoperiod was apparently not coercive as the onset of breeding was about one month later at a station at 2200 m than at a nearby station at 1800 m. However, in his habitat descriptions he stated, "In the early morning there is usually a cloud bank hanging over the eastern slopes of Poás [the higher station] while the western side of Barba [the lower station] tends to be relatively free of such clouds until later in the day." Here is another suggestion that sunshine and/or temperature may be important proximate factors in cool tropical areas near the equator.

The cycle near Cali, Colombia (Miller 1961, 1962), is also shown in figure 9. Breeding periods did not correlate with the weak seasonal photoperiodism which amounted to only 12 min difference between the longest and shortest days of the year. No correlation with temperature was evident but there was a high correlation with rainfall. Miller assumed constant adequacy of food for both maintenance and breeding at all times. This may have been true, but the possibility cannot be dismissed that there might have been periods of increased insect abundance following the peaks of rainfall and that the peaks of nesting were timed to take advantage of them.

In this connection, George J. Wallace (MS) kept notes on the nesting of *Z. capensis* at Popayán, Colombia, 2° 3′ N and at 2092 m, from September 1955 to July 1956. The only active nests were found from April to June, although the presence of a few streak-breasted juveniles, some attended by adults, in the fall and early winter, indicated limited nesting at that time. This suggests that in the year in which Wallace observed there was a major breeding period in spring and early summer and a minor breeding period in the fall and early winter. This schedule would agree with that reported by Wolf in Costa Rica and with

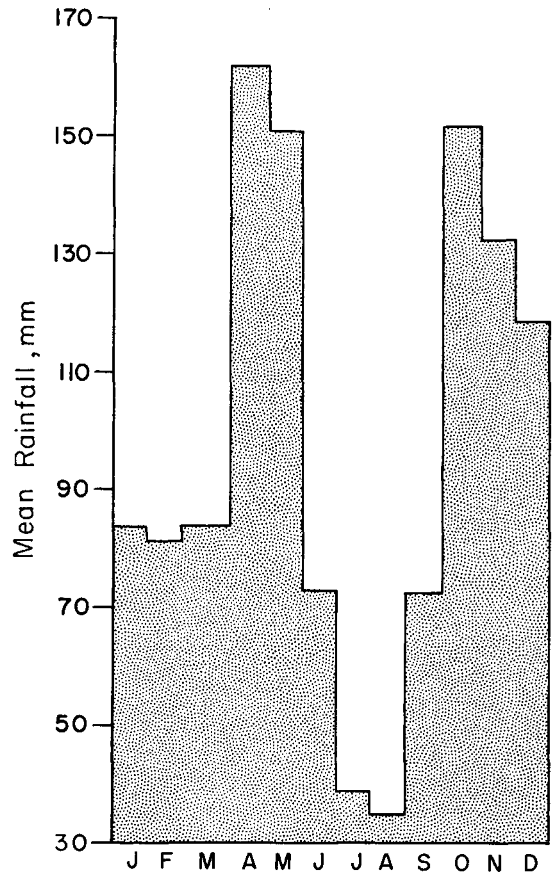

FIGURE 10. Mean monthly rainfall (mm) at Cali, Colombia, July 1934–December 1954.

the schedule at Chilca. Wallace noted that in the fall and winter of 1955–56 at Popayán, unusually heavy and prolonged rains virtually eliminated the usual dry season and may have interfered with fall breeding; they may also have caused earlier breeding in the spring than was evident in Miller's population. This was apparently an unusual year. I have summed up monthly rainfall for Cali, Colombia, near Miller's study area but at lower elevation, from July 1934 through December 1954. The data (fig. 10) clearly indicate a pronounced bimodality of rainfall and the rainiest periods coincide almost exactly with those described by Miller. Apparently, the schedule Miller described is the usual one at his study area.

Miller (1961, 1962) postulated molt as the major factor determining the annual cycle near Cali. In the females the two complete molts followed the two peaks of nesting; in other words breeding and molt were mutually exclusive. In the males, the separation of these two activities was not as clear-cut, presumably because the energy demands imposed on the males by breeding activities were less than those imposed on the females, and some overlap was possible. Nevertheless, it was apparent (Miller 1961) that males in the middle stages of molt, when energy demands were greatest, were rarely in breeding condition and that regressed testes occurred relatively rarely in non-molting males. The onset of molt occurred three or four weeks after the cessation of rainfall at the end of May and at the end of December.

Miller concluded that molt was triggered by the psychological response of the birds "to the changed condition of wetness in the grass" in which they foraged and to a greater incidence of sunshine. The argument that the molt schedule coerced the breeding schedule is made more plausible by Miller's assumption of a constant food supply throughout the year. Presumably other prerequisites for successful nesting were also assumed to be in constant supply. This would almost automatically ascribe ultimate factors to molt.

Miller noted that the population was on a schedule in which molt occurred mainly in the dry seasons and provided fresh plumage for the ensuing wet periods. He stated, "This may have some general advantages, although we have not seen these sparrows badly water-soaked from periods of heavy downpour." However, there are obvious advantages to such a molt schedule. Miller stated that frequent foraging in coarse, perennial grasses by the birds in his population wore the plumage heavily and that the individual, whether it has bred or not, must molt twice a year or become incapacitated. The correlation of molt with rainfall thus assured adequate spacing of the two molts. If they were separated by too short an interval, the lengthy period between the second and third of a sequence of three molts would place far too much wear on the plumage. Further, foraging in wet grass, which might be disadvantageous for a heavily molting bird, would be largely avoided if the molt were timed mainly to those periods in which the grass dries out each day.

Another possibility is that there was a bimodality in the food supply for the young associated with the bimodality of rainfall, and that rainfall adjusts to best advantage the timing of both molt and breeding. With the relatively great outlay of energy that the individual, especially the female, makes in the course of two breeding efforts and two complete molts a year, the premium would be on the proper timing of *all* major energy-demanding activities, or at least on the best compromise possible. Thus, the evolution of a schedule geared to rainfall as a proximate factor might benefit both molt and breeding. Investigations of food supply in relation to rainfall in the area occupied by this population would be of the greatest interest.

The breeding schedule of *Z. capensis* at Acolla, Perú, is also of interest as regards molt. Blancas Sánchez (1959) noted that the birds there nested in March, April, and May. Although he gave no information on the time of molt, we may assume that it began shortly after the end of the breeding season and probably started sometime in June for most birds. In his descriptions of the four seasons at Acolla, Blancas Sánchez notes that winter (22 June–22 September) is the dry season, with no rain. This would also be the season of most sunshine. Unfortunately, he presents few temperature data. The mean minimum for 7–16 May was 7.5° C and for 7–22 August, 6°. These few data suggest that the cold stress on the population would not be appreciably greater in winter than in fall, when breeding occurred. Again, molt appeared to be timed to coincide with the season of greatest dryness of vegetation and most sunshine.

Snow and Snow (1964) hypothesized that the breeding seasons of the numerous species which they studied in Trinidad (10° 40′ N) were "ultimately adapted to take advantage of the periods of greatest food supply and, in some species, to the period of greatest safety of the nest." They concluded that none of the proximate factors considered (daylength, rainfall, temperature, and seasonal fluctuations in food supply) was important in controlling the whole annual cycle. Further, they pointed out that despite the great variation in time of onset of breeding, nearly all of the species which they studied molted in the same months of the year. They therefore suggested that the molt schedule was the major factor in timing the annual cycle, with the breeding season timed in each species according to the specific refractory period which would determine the amount of time elapsing between the end of molt and the onset of breeding. The annual variation in breeding season for a given species would result from modification by "environmental factors which sometimes may be obvious . . . but more often are too subtle to be apparent to the observer" (Snow and Snow, op. cit.). This is something of a compromise, in which the ultimate factors are still related to breeding but with molt itself acting as the major timing factor. This, of course, demands a set of proximate factors for molt. There is some evidence that the beginning of the wet season is the major proximate factor timing the molt of *Manacus manacus* in Trinidad, but information is lacking for other species.

As regards the Chilca population, one may assume, as I have, that the ultimate factor in the timing of the entire annual cycle is the coincidence of breeding with insect abundance. However, to consider the opposite possibility, let us assume that my insect sampling, admittedly minimal, was inaccurate, and let us assume, as Miller did, that a food supply adequate for both breeding and maintenance was present at all times. The other important prerequisites for successful nesting, as noted previously, were indeed present at all times, so we are assuming that effective breeding could occur at any time of year. Thus, ultimate factors would pertain to molt rather than to reproduction.

In this case, with precipitation virtually nonexistent, the foraging milieu would be dry save for perhaps 30–35 daylight hours a year. Temperature would then be the ultimate factor of importance, with molt occurring in a warm, sunny season so that individuals in heavy molt would not have to contend with overcast skies and relatively low temperatures. The period of relatively high mean temperatures, high mean minima, and high incidence of sunshine starting in October was amply long to include most of the nesting effort and most of the period of molt (fig. 8, 9). This is in sharp contrast to the situation at high northern latitudes (Morton et al. 1969) in which birds have a short season in which to breed and molt. The lack of urgency of molt in the Chilca population was exemplified by the fact that the females finished breeding at about mid-March but did not start the postnuptial molt until April (fig. 5). In contrast, at Point Barrow, Alaska, 71° 20′ N, female Lapland Longspurs (*Calcarius lapponicus*) losing a nest or young after 20 June will, with rare exceptions, not renest but start the postnuptial molt (Frank A. Pitelka, pers. comm.).

If the ultimate factors in the Chilca cycle did indeed pertain to molt and involved high temperatures and high incidence of sunshine, then molt was not timed optimally, as the weather started to become cooler and more overcast in May, well before the molt period was over. December, January, February, and March were the months of most sunshine and January, February, March, and April were the months of highest mean minima. Thus, January, February, and March would have been the months best suited to molt. The most compelling reason for the occurrence of molt in April, May, and June, on the basis of the evidence in hand, would be the timing of molt to coincide with an increased abundance of insects. But this is no more compelling a correlation than is the timing of the onset of breeding condition and the month of most intense breeding (December) also to occur at a time of increased insect abundance.

In evaluating molt as a major factor in the timing of nesting (as suggested for Trinidad by Snow and Snow 1964), in October and November at Chilca, when these two activities were actually competing for the energy resources of the individual, it was molt that was arrested rather than breeding. The only possible role that molt might have had in the timing of breeding would have been to terminate it. Here we are on dangerous ground for we are dealing with a population that is apparently uninfluenced by the slight photoperiodic changes in its environment, and one that appears to have a negligible refractory period. Considering all of the evidence in hand, it seems most likely that the ultimate factors involved in this cycle pertain to breeding and not to molt, that the ultimate factor of primary importance is the timing of nesting to an adequate supply of insect food for the young, and that the sunshine and temperature cycles are the proximate factors of greatest importance.

The birds breeding in the lomas must remain an intriguing mystery. There is considerable anthropological evidence indicating that the lomas were much more widespread in the central coast, at least up to 6000 B. C. (Lanning 1967). The numbers of birds presently involved are apparently only a fraction of those involved in earlier times. Whence they are derived, and what they do away from the lomas, are unknown. One may hypothesize only that for these birds, the breeding period, which is a second, minor reproductive effort for populations resident elsewhere along the coast, is a major, and possibly the major, breeding period.

SUMMARY

The annual cycle of a population of *Zonotrichia capensis* was studied in the coastal desert of Perú at 12° 30′ S from early October 1968 to early August 1969. Both sexes came into breeding condition in October and November, and by December virtually all birds were breeding. Females stopped breeding at mid-March and males in April.

In October and November an incipient complete molt involving the primaries as well as other parts of the plumage was arrested by the onset of breeding condition. The postnuptial molt started in April in both sexes and

was completed in some birds by the end of May and in nearly all birds by the end of June.

Testes regressed incompletely at the beginning of the postnuptial molt but rapidly returned to high levels of spermatogenetic activity when the molt had been completed. A second breeding period involving relatively few birds occurred from about mid-June to about mid-July.

Precipitation and photoperiod were unimportant in timing the annual cycle. Increased incidence of sunshine appeared to be of primary importance in bringing both sexes into breeding condition, with temperature probably of secondary importance.

Greater insect abundance in October, November, and December may also have been important as a proximate factor for the females and was probably the most important ultimate factor in this cycle.

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