BREEDING AND MOLTING PERIODS IN A COSTA RICAN POPULATION OF THE ANDEAN SPARROW

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Photoperiodic changes have been established as an important environmental component controlling breeding cycles in north temperate birds, but there has been little detailed investigation of the factors controlling breeding seasons of tropical birds. The lack of much experimental examination of the controlling factors in part is explained by the deficiency in detailed knowledge of cycles of populations in the wild and the apparent exogenous correlates of these cycles. There have been some studies in the Old World tropics (e.g., Baker et al. 1940; Moreau et al. 1947). However, the number of studies from tropical America is very limited. Three exceptions are the studies of Miller (1959, 1961, 1962) on the Andean Sparrow (*Zonotrichia capensis*) in the highlands of Colombia and the work by Snow and Snow (1964) and Snow (1962) on the island of Trinidad. This paper presents data from a resident population of *Zonotrichia capensis costaricensis* in the highlands of Costa Rica and attempts to identify some important relations to environmental parameters which the breeding season of this widespread species shows.

METHODS AND MATERIALS

The Andean Sparrow ranges from southern México south to the tip of South America and to several islands of the West Indies. Within this area the altitudinal range extends from sea level to above 3300 m. However, this altitudinal range rarely is realized over a short geographic distance. The birds of the present study belong to the subspecies *costaricensis,* which occurs in the mountains of Costa Rica and western Panamá (Slud 1964) from about 500 m to over 3300 m above sea level. The center of its abundance, however, is at the middle elevations (Skutch 1967). Within this range, it is numerous wherever the area has been cleared and the second growth vegetation is relatively open. It is one tropical bird which seemingly has benefited from the destructive presence of man.

Collections of birds were made approximately monthly on the following dates in 1966 (sample size in parentheses): 26 June (9); 20 July (11); 30 August (10); and in 1967: 4 January (6); 31 January (16); 25 February (19); 27 March (19); 23 April (25); 21 May (30); 25 June (29), and 14–17 August (12). All collections were made within five miles of Vara Blanca, Heredia Province, Costa Rica. The birds taken were usually sighted along the highway from Heredia to Volcán Poás. The specimens were obtained almost exclusively from pastures, especially ones that contained some brush. No attempt was made to sample one area systematically or to sample all areas. This may have biased the results slightly when we initially selected territorial birds and then, since we traversed the same area each time, we later collected the replacement birds. Any floating population of non-breeders early in the season may have been allowed a place in the breeding population. Later samples conceivably could have been obtained from a population in which there were birds that initially had been excluded from the breeding population. Often in passerines, non-breeders are first-year birds which, for some species, are somewhat retarded in reaching full breeding capacity (Wright and Wright 1944; Selander and Hauser 1965). However, this probably would affect only April to June samples in 1967. The specimens were saved as flat skins and are in my possession.

PHYSICAL ENVIRONMENT

The elevation at which most of the birds were collected varied from 1800 to 2000 m; Vara Blanca is at 1810 m. Eleven specimens were taken in late January, February, and March at 2200 m. The latitude of Vara Blanca is 10° 10′ N. The difference between the longest and shortest days was on the order of 76 min.

Temperature and rainfall data for Vara Blanca are presented in table 1. There is a short dry season of about three months duration from February to April, with obvious annual variation in timing and severity. Another, even shorter "dry" period usually occurs in July and August; this also varies somewhat in severity and duration each year. The peak periods of rain are in June and July and from September to November.

The average monthly temperature varies only slightly throughout the year. There are minor variations in

TABLE 1. Temperature and rainfall at Vara Blanca, Costa Rica.

	Rainfall (mm)		Temperature 1964 (°C)				
	1964	1965	$\bar{x}$	$\bar{x}_{max}$	$\bar{x}_{min}$	Abs. max.	Abs. min.
Jan.	115.7	322.8	15.4	19.7	11.1	22.5	6.3
Feb.	9.6	169.0	16.4	22.0	10.8	25.8	7.9
March	23.8	99.7	16.8	22.2	11.4	26.4	8.0
April	>107.9	10.6	16.7	22.4	11.0	24.9	6.9
May	117.9	293.0	17.4	22.0	12.8	25.8	11.1
June	413.1	289.1	16.9	21.8	12.0	24.9	11.2
July	463.1	375.7	17.1	22.6	11.7	25.4	10.7
Aug.	232.5	291.1	17.2	22.2	12.3	24.4	11.0
Sept.	379.2	441.3	17.3	22.8	11.8	25.0	10.4
Oct.	303.0	473.9	16.4	20.5	11.7	24.4	10.4
Nov.	161.1	446.5	16.1	21.2	11.6	24.3	6.2
Dec.	129.9	178.0	10.3	19.9	15.1	22.5	7.5

the mean monthly maxima and minima, but the changes are slightly antagonistic and tend to cancel each other. There are few or no periods of the year when frost is an important factor.

The hillsides on which the birds were collected varied from a predominantly western exposure south of Vara Blanca on the leeward slope of Volcán Barba to an easterly exposure along the road from Vara Blanca to the summit of Volcán Poás. Vara Blanca lies in a saddle between the two volcanoes. The eastern exposure receives the full impact of weather coming from the Caribbean lowlands. In the early morning there usually is a cloud bank hanging over the eastern slopes of Poás while the western side of Barba tends to be relatively free of such clouds until later in the day.

RESULTS

GENERAL SUMMARY OF OBSERVATIONS IN THE COLLECTING AREA

The following observations were made in 1967.

January. In early January most birds were in groups of more than two and apparently were not paired. Some pairs may have been beginning to desert the feeding flocks. By the end of January, pairs were encountered around Vara Blanca, but at Poasito (1875 m) we found a group of five to eight birds, and at 2200 m there was a flock of 30 or more birds.

February. By 25 February the birds were paired except at the 2200 m site where I again found a flock of about 50.

March. By the end of March even the flock at 2200 m had dispersed and the spaced, territorial males were singing on all sides.

April. In late April I first encountered family groups, but no flocks of adults. The oldest young collected were nearly full grown and probably had hatched from eggs laid in early March or late February (see Miller 1961 for estimate of time for development).

May. On 21 May males still were spaced and singing, but it was extremely difficult to find members of a pair together, and it was very difficult to collect females, many of which were probably incubating. There were many family groups, but no flock of adults.

June. On the last visit in 1967, during four hours in the morning of 25 June, I heard only two short songs from one male at 10:05. Adults usually were seen either in pairs or in family groups. We encountered a flock of more than 20 birds which included some adults, but mostly juveniles.

August. D. R. Paulson (pers. comm.) noted birds in small flocks, in pairs, or alone.

November. Dr. G. H. Lowery, Jr. (pers. comm.) reported no evidence (song, young) of breeding in *Zonotrichia* around Vara Blanca in mid-November.

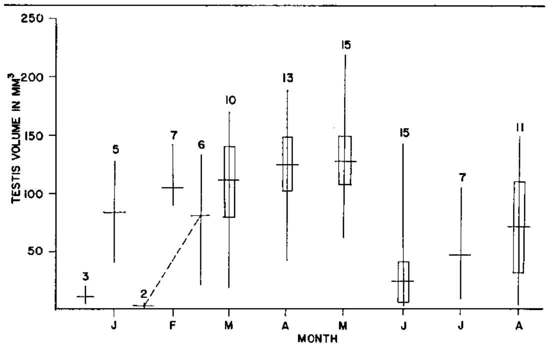

FIGURE 1. Cycle of changes in testis volume of *Zonotrichia capensis* from early January to late August. The July records are from 1966; June and August data combine 1966 and 1967 samples; January to May data are from 1967 only. All collections, except three males in early January, were made in the last third of each month. The two mean values connected by a dotted line are birds from 2200 m. The vertical line denotes range; the horizontal line is the mean; the rectangle equals $\pm$ 2 standard errors of the mean; the numbers refer to sample size.

In 1966 no concerted attempt was made to cover large areas so the data are not strictly comparable to those of 1967. In June, I found groups of adults and young scattered about the hillsides, but no obvious pairs. In July, most of the birds were taken from a group of more than 20. On this visit I heard only two whisper songs. By August the birds occurred singly, or in a few family groups, and at least some of the birds were reforming pairs after the short summer period in flocks. Song was at a low level compared to the spring breeding period of 1967.

TESTIS CYCLE

The data for testis volume in 1966 and 1967 are shown in figure 1. Although there are no data from the last months of the year, the major aspects of the cycle for birds below 2200 m can be discerned. There was an increase in testis size from early January to a plateau from February through May, followed by a decline in average and maximum size. There was a short period in July and August when the birds showed a second increase in testis size. This was followed by another decline which probably was not reversed until sometime in December. Gonads of early January birds from below 2200 m were already above resting levels reported for this species (Miller 1959). At 2200 m the cycle was delayed by about one month.

DATA FROM FEMALES

January. In the late January sample from near Vara Blanca, no females had enlarged follicles or other evidence of current breeding activity.

February. Of the four females taken around Vara Blanca in February, two had edematous brood patches and undoubtedly were involved in the breeding effort (Selander and Kuich 1963). The other two, and two from 2200 m, had not developed brood patches.

March. In the March sample, two of seven females from around Vara Blanca had brood patches while the other five had follicles of various sizes up to 6 mm. In part this may reflect a difference in ease of collecting females which are not involved in nesting as opposed to those that are incubating.

April. Of nine females taken in April, six had brood patches. Most of them were not new, probably indicating that the birds were feeding young. Three females did not have brood patches and none of the three had ovarian follicles larger than 2 mm. These three females were molting or had recently molted and may have been first-year birds hatched the previous fall which were undergoing their first complete molt without participating in the spring breeding period. One female collected while feeding fledglings had two enlarged follicles (to 8.5 mm) and probably would have started a second brood in the near future.

May. Of nine females in the May sample the only one that had not developed a brood patch had follicles to 1.5 mm long, a nonbreeding level (Miller 1962). A slight amount of body molt on this bird probably was the start of the complete adult molt prior to a first breeding period. This bird had only about one-half of the skull ossified and probably was hatched the previous fall.

June. All four June females were in a nonbreeding state (ova 1 mm or less).

July. In July one female had an inactive ovary and one had three recently ruptured follicles. The latter bird was in very fresh plumage and probably was starting another breeding period following the postnuptial molt in May and June.

August. The August sample contained seven females, all with inactive ovaries; one appeared to be recrudescing.

NESTS AND YOUNG

The only nests found in the study area were located on 23 April. One contained three eggs and the other held one egg and one young.

Data also are available for young which were seen or collected during the study period. On the assumption that the growth rate of individuals in this population approximates that reported by Miller (1961) for Colombian birds, one can estimate the approximate date on which the egg was laid which produced each young. The calculated egg dates have been grouped by months (table 2) to reduce error from differential growth rates or timing of the postjuvenal molt in the two populations. These records, plus the July female with recently ruptured follicles, extend the nesting season from my own records from late February or early March into the summer months and nearly parallel the season reported by Skutch (1967).

TABLE 2. Presence of eggs in nests of *Zonotrichia capensis* as determined by estimation of age of hatching of young in the population.

	Number of nestings		
Month	Wolf	Skutch[a]	Panamá and Costa Rica[b]
January	0	0	8
February	2	3	1
March	4	3	4
April	8	1	10
May	3	0	5
June	0	1	1
July	1[c]	3	2
August	–	1	2
September	–	–	5
October	–	–	1
November	–	–	0
December	–	–	3
Totals	18	12	42

[a] The data from Skutch (1967) are for nests actually found and the date of laying has been estimated from the date of hatching.
[b] Data from museum specimens of young taken throughout the range of *Z. c. costaricensis* without regard to locality.
[c] Female with recently ruptured follicles.

AGE OF BREEDING BIRDS

The degree of wear of the plumage of these sparrows by early January precludes any attempts at aging individuals on feather characteristics as they approach the February-to-May breeding period, and degree of skull ossification is the only criterion available for determining the age of birds after January. In most passerine birds the skull ossifies during the first six to ten months of life. In Colombia, *Zonotrichia capensis* requires eight to ten months from the day on which the egg was laid to achieve full ossification (Miller 1961). The degree of skull ossification of adult-plumaged birds in this study is presented in table 3. Prior to the spring nesting season several specimens in the sample had the skull incompletely ossified. Only in March did all specimens show fully granular skulls. After March there was another increase in the number of adult-plumaged birds that had incompletely ossified skulls. Throughout the remainder of the sample period the percentage

TABLE 3. Numbers of adult-plumaged individuals of *Zonotrichia capensis* with completely ossified and incompletely ossified skulls.

Month	Sex	Incompletely ossified[a]	Completely ossified[b]	% of total incompletely ossified
January	M	2 (5, 5)	8	20
	F	1 (5)	11	8
February	M	1 (4)	13	7
	F	0	7	0
March	M	0	10	0
	F	0	9	0
April	M	2 (4–5, 6)	12	14
	F	1 (4–5)	9	10
May	M	3 (4, 5, 6)	14	18
	F	4 (3, 4, 4–5, 5)	6	40
June	M	2 (4–5, 5)	12	14
	F	0	14	0
July	M	1 (5)	6	14
	F	0	2	0
August	M	1 (5–6)	3	25
	F	0	4	0

[a] Numbers in parentheses refer to stage of skull ossification ranging from 1 (completely single layer) to 7 (fully ossified).
[b] Refers to number of individuals with skulls completely ossified.

remained about the same. However, the samples for some months were very small and may not have been representative of the population. The decline in percentage as the breeding season approached was indicative of the age of the territorial birds. Those individuals hatched the previous spring should have had either fully ossified skulls or should have been approaching the fully ossified condition by January and February. After that, birds with portions of the skull still single layered are probably from the fall breeding period of the previous year. Examination of the birds gave no reason to suspect that the course of ossification was irregular or abnormal in which case deviations should have occurred in the timing of ossification and/or as pattern abnormalities (Nero 1951).

In the samples from early 1967 there were no juveniles, only a few birds with unossified skulls, and no molting adults. Within the limits of the sampling procedure this suggests that there is only limited breeding in the fall. The absence of young in the samples also suggests that the fall breeding period does not extend into November.

To summarize, most adults in the breeding population in February and March were either one year old or older. In later samples the percentage of birds with partly unossified skulls increased, providing evidence for some successful fall nesting. The young produced probably normally do not enter the spring breeding population or do so only late in the breeding period. There is no evidence that

TABLE 4. Degree of prenuptial molt in the sample population* of *Zonotrichia capensis*.

Plumage molted	Male ($N = 21$)		Female ($N = 13$)		
	N	%	N	%	% (M + F)
Body	17	81	12	92	85
Wing	10	48	8	61	53
Tail	5	24	1	8	18

* Only months of March and April included.

fall breeding extends into November and December.

MOLT

Prenuptial molt. Although Miller (1961) reported no prenuptial molt in the Colombian population there was a definite, but only partial, prenuptial molt, at least of body plumage, in some individuals in the Vara Blanca population. Fewer birds molted small numbers of remiges, usually one or two inner secondaries. I found no evidence of a prenuptial primary molt. Less than one-fourth of the specimens showed any tail molt, usually limited to the inner pair of rectrices, occasionally more (table 4). Body molt occurred in the same sequence as in the postnuptial molt and the degree of completeness probably reflected the amount of time in which the bird was engaged in the molt. The main period of prenuptial molt is January to March (fig. 2). In part this overlaps the onset of breeding. There are insufficient data to analyze possible rela-

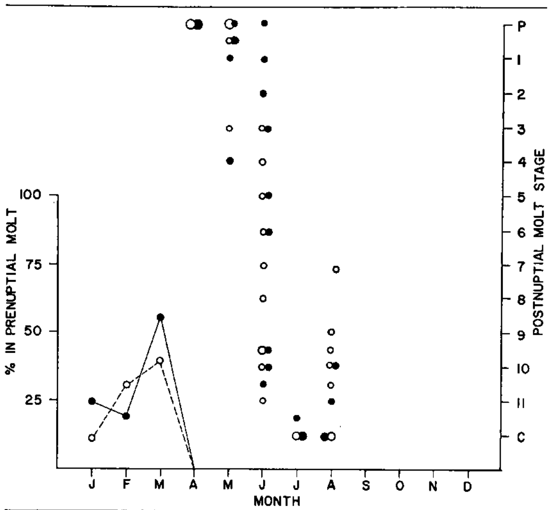

FIGURE 2. Timing of prenuptial and postnuptial molt in *Zonotrichia capensis*. Prenuptial molt is from January to March; postnuptial molt is from May to August. Stages of the postnuptial molt follow Miller (1961). Circle indicates males; dot indicates females. For postnuptial molt, small symbols = 1–2 individuals; intermediate symbols = 3–4 individuals; large symbols = 9 or more individuals. There were no stages containing between 4 and 9 individuals.

TABLE 5. Relation between reproductive capacity and molt in *Zonotrichia capensis.*

Molt stage	Testis size (in mm)											
	1	2	3	4	5	6	7	8	9	10	11	$\bar{X}$
Premolt							3	10	1			7.9
1												–
2												–
3								1	1			8.5
4		1										2.0
5				1		1						5.0
6		1										2.0
7			2	1								3.3
8			1	1								3.5
9		2		2	1			1				4.2
10			2						1			5.0
11						1	1					6.5
Complete			3		1	1	4	2				5.8

tionships between completeness of molt and time of reaching full breeding condition.

Postnuptial molt. The postnuptial molt differs in no significant way from that reported by Miller (1961) for Colombian birds. This complete molt is positioned in the annual cycle after the spring breeding period. I have used the stages that Miller erected to plot timing of this molt in the Vara Blanca birds (fig. 2). The molt, on a populational basis, extends from May to August or September, while for an individual it is probably about two months, equalling that reported by Miller for Colombian birds.

At present, it is not known whether the birds which breed in the fall undergo a second complete molt following fall breeding. The occurrence of a prenuptial molt and the worn condition of some of the individuals in early January suggests that if a complete fall molt does occur, it is not widespread in the population. Among north temperate species which have a fall breeding period there apparently is no complete molt following fall breeding (Payne MS; Selander and Nicholson 1962).

Relation between reproductive capacity and molt. There is limited evidence (table 5) that males in intermediate stages of the postnuptial molt have smaller testes on the average than males early and late in the molt. Perhaps more importantly, no male in molt stages 6–8 had testes over 4 mm, while several birds in late stages of molt had much larger testes which morphologically appeared to be newly enlarging. This suggests that there is a rapid recrudescence near the end of the molt preparatory to fall breeding.

DISCUSSION

The preceding data combine to give the following presumed breeding periodicity for this population: a well-documented peak of breeding from February into May, and sometimes June; a second peak starting in late July or August, of unknown duration and probably of much reduced magnitude, following the postnuptial molt. At the end of the year there is no breeding activity until December when the gonads of the males begin to enlarge.

This seasonality of breeding corresponds to periods of reduced rainfall, although the August rainfall still is above 200 mm. Breeding in September would fall in a period of maximum rainfall. Average monthly temperatures during spring breeding are slightly below the annual average, but the absolute minima for the year occur during these early months. The spring breeding period begins before the vernal equinox and ends while day length still is increasing. Fall breeding is during the period of shortening photoperiods, but probably is completed before the autumnal equinox.

It seems to me that for bird species, such as this sparrow, in which breeding can occur in many months of the year, it is proper to consider different breeding seasons during the year only if they are separated by a nonbreeding period in the individuals participating in the peaks. If the peaks represent consecutive nestings by the same individuals without reduced gonadal activity they are simply multiple clutches. The following studies of breeding seasons of other populations of the Andean Sparrow offer information pertinent to this consideration.

Skutch (1967) reported nests in all months from February to August, except May, in two localities near Vara Blanca. He concluded that the birds had two breeding seasons, although there was no evidence for a molt or period of reduced gonadal activity between the two periods. Skutch noted that there was sufficient time for a complete molt.

Blake (1958), reporting on a collection of birds from the slopes of Volcán Chiriquí in Panamá, noted that *Z. c. costaricensis* had a breeding season with peaks in May and August. He thought that this represented two broods, but did not distinguish whether they were in the same nesting season or in two different seasons.

Baepler (1962) reported a two-peaked breeding period near the northern limit of the range of the Andean Sparrow in Guatemala. He thought that the bulk of the population bred in the fall during the heaviest rains of the year, with lesser activity in the spring. He did not document whether this was a single season with several clutches or two seasons.

Miller (1959, 1962) reported two nesting

TABLE 6. Stomach contents of specimens of *Zonotrichia capensis* from vicinity of Vara Blanca in 1967.

Month	No. with seeds[a]	No. with insects[a]
February	16	1
March	17	11
April	17	22
May	17[b]	30
June	23	27

[a] One specimen may be recorded in both categories.
[b] Mostly < 20% of total volume.

seasons of about equal magnitude at intervals of five and seven months in Colombia. Each nesting period was followed by a complete molt and a non-reproductive condition in the majority of the population. Some individuals could be found nesting at all seasons of the year.

On the basis of these studies it should be possible to estimate the influence of various environmental parameters in regulating the breeding cycles of these populations. It will be well to keep in mind the basic differences between proximate and ultimate factors controlling the breeding seasons. Ultimate factors are those which evolutionarily determine timing of breeding while proximate factors are the cues used to time breeding each year.

The ultimate factor which has received the most attention in the literature is the availability of food to provide sufficient surplus energy for the female to form eggs and/or the parents to rear offspring (Lack 1966). Although no data were collected on food availability, there is a definite change in diet of the Vara Blanca population from seeds before the spring breeding period to insects during reproduction and a lesser change back to seeds during the molt (table 6). Most or all of the nestlings and fledglings were fed insects; independent young ate mostly seeds. It probably is safe to assume that the birds, to some extent, are timing their breeding to correspond to availability of adequate supplies of insects.

Miller (1962) after noting that "food sources . . . were always present in abundance" concluded that the factor controlling female breeding potential in Colombia was competition between breeding and molt for the available energy resources and that timing of molt coerced timing of breeding. Similarly Snow and Snow (1964) stated that "the annual cycle from year to year must depend on the birds' response to some recurring environmental factor or factors whose effect is to induce the onset of molt." This tentative conclusion was derived from evidence that in many species the timing of the annual molt was more rigid and tended to be more coincident than the diverse and variable breeding seasons. In the Vara Blanca area a similar precision in timing of molt was evident. I feel that molt is relegated, evolutionarily, to periods that are unfavorable for breeding. In some tropical areas, these periods could be very short. The presence of the molt between the two breeding peaks rather than late in the year suggests that the second breeding period is added to the first only under favorable circumstances or that the latter part of the year is poor for either molting or breeding.

On the assumption that the ultimate factor(s) somehow is correlated with timing of breeding rather than molt we can consider possible proximate factors in terms of their predictive power in relation to the environmental conditions which make certain times of the year more favorable for breeding than others. Day length changes about 38 min greater and less than 12 hr during the course of the year. Although Miller (1960:521) stated that "at latitude 10° photoperiodic influences are clearly felt and probably these prevail weakly even to latitude 5°," his conclusion was derived mostly from general breeding data for entire avifaunas. While there is a peak of breeding activity from April to June near 10° north latitude (Skutch 1950; Snow and Snow 1964), it is not so for all species. As is probably true for the Vara Blanca population, Snow and Snow (1964) concluded that the correlation of the peak of breeding with photoperiod is mediated through other climatic factors, which tend to vary in tandem with photoperiod at this latitude. In fact photoperiod probably has relatively little coercive effect even at this latitude. For the study population of *Zonotrichia* at 2200 m the photoperiod was identical to that at Vara Blanca. However, the birds came into breeding condition about one month later than the Vara Blanca individuals. This would suggest that photoperiod alone is unable to coerce the breeding cycle even to within relatively narrow limits as it does in the north temperate zone. Another argument against the importance of photoperiod, even at this latitude, is the presence of young *Z. c. costaricensis* from nestings distributed almost throughout the year (table 2), even when day lengths are less than 12 hr and, possibly in late December, when they are the shortest of the year. Many of these individuals were from essentially the same latitude as the population at Vara Blanca.

Rainfall is an important climatic parameter which Miller (1962) thought controlled the timing of molt and, through this, breeding in females. He postulated that the period of molting somehow was regulated through factors associated with drying out and increased sun exposure in the dry season. Rainfall could also influence the availability and the amount of food required for the young and/or adults, but Miller thought that food was always present in abundance. The bulk of breeding of the Colombian birds came during the late part of the rainy seasons and the first part of the dry seasons. Around Vara Blanca breeding occurred in periods of heavy rainfall and during the dry season. Baepler (1962) thought that more of the Guatemalan birds were breeding in the rainiest months of the year. It is interesting that the monthly rainfall in Colombia never approached the maximum amounts recorded in any of several months at the Vara Blanca site.

The temperature regime should be influenced to some extent by the rainfall cycle. In Colombia the birds bred at the lowest and highest temperatures of the year (Miller 1962). In Costa Rica nearly the same result was noted. The birds bred when the mean minimum temperatures were either low or high, but the maximum temperatures were generally high. However, there is remarkably little temperature variation throughout the year as measured by the maximum and minimum averages. Perhaps most important are the times of absolute minima which come during the first four months of the year when the major breeding period is at its peak. Thus, there is little evidence for a monofactorial control of breeding by temperature.

At this time it is probably more profitable to consider the regulating devices in terms of a series of factors, very likely different ones in various populations, rather than a single factor. It does seem clear that we will not reach an understanding of the several levels of control of breeding in the tropics until we can establish the evolutionary factor(s) which determines the time of breeding. With these data one can then approach the problem of which environmental parameters can modify the timing of the ultimate factors and hence would be most successfully used to predict periods of maximum reproductive success. At the proximate level a fruitful approach now will be in detailed laboratory studies of the responses of several populations to varying climatic regimes.

SUMMARY

Breeding in a population of the Andean Sparrow (*Zonotrichia capensis costaricensis*) in the highlands of Costa Rica occurred from February to May or June and again in July or August, but the duration and magnitude of this second season were not documented. The annual molt took place between the spring and fall breeding periods and there was a partial prenuptial molt prior to spring reproduction.

It is argued that ultimate control of cycling is related to timing of reproduction and not to timing of molt as suggested by Miller. Comparison with other breeding seasons in the neotropics, especially in the same species, lead to the conclusion that no monofactorial, proximate control of breeding is operating and probably the several factors are different among populations.

ACKNOWLEDGMENTS

Portions of this study were carried out while I was a faculty member in a course sponsored by the Organization for Tropical Studies in Costa Rica. The work in 1967 was supported by an Elsie Binger Naumberg fellowship from the American Museum of Natural History. For help in the field I am indebted to Richard D. Sage, Dr. and Mrs. Dennis R. Paulson, Donald Viers, and my wife, Janet. I must express my sincere appreciation to members of the Organization for Tropical Studies, especially Stephen Preston, Jorge Campabadal, and Liliana Escheverría, for administrative and logistic support in Costa Rica. The authorities of the Secretaría de Agricultura y Ganadería provided permits to collect specimens in Costa Rica.

John Davis, Robert B. Payne, Robert W. Storer, and Harrison B. Tordoff kindly offered comments on the manuscript.

Finally, I thank the following museums and their curators either for allowing me to view specimens in their care or for sending materials on loan: American Museum of Natural History (Dean Amadon and Wesley E. Lanyon); Museum of Comparative Zoology (Raymond A. Paynter, Jr.); U. S. National Museum (Richard Zusi and Paul Slud); Louisiana State University Museum of Natural History (George H. Lowery, Jr.); University of Michigan Museum of Zoology (Robert W. Storer and Harrison B. Tordoff); Los Angeles County Museum (Kenneth E. Stager); Chicago Natural History Museum (Emmet R. Blake); and the Museum of Vertebrate Zoology, University of California, Berkeley (Ned K. Johnson). Alexander Wetmore kindly made available his recently collected material from Panamá.

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