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*CAPACITY FOR PHOTOPERIODIC RESPONSE AND ENDOGENOUS FACTORS IN THE REPRODUCTIVE CYCLES OF AN EQUATORIAL SPARROW**

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In previous reports[1, 2] on the reproductive cycles of an equatorial population of the Andean sparrow, *Zonotrichia capensis*, I have shown that males in their natural environment, where significant seasonal changes in photoperiod are not encountered, undergo cycles of regression and recrudescence that reflect an innate rhythmic attribute. Such males normally show 4 months of sustained reproductive capacity followed by regression and regrowth of the testes, which events together occupy 2 months. Therefore, two complete cycles normally occur in a 12-month period. The cycles of different individuals are imperfectly coordinated by environmental factors so that some males may be found to be reproductively active in the population at all periods of the year. In females, which control the culminative stage of breeding, nest building and ovulation may occur throughout the year in the population, but egg laying shows two peaks at 5- and 7-month intervals. These peaks are correlated with the rainfall cycle and probably are mediated by the molt cycle, which is influenced particularly by the dry periods.[2, 3]

The question arises, then, whether this equatorial race of *Zonotrichia capensis* has the mechanism to respond to seasonal photoperiodism as do its north-temperate relatives, *Zonotrichia leucophrys*,[4] *Z. atricapilla*,[5] and *Z. albicollis*.[6] Is it positively stimulated by long days and inhibited by short days and does it possess the post-breeding refractory period of its northern relatives which adaptively blocks[7] late summer and autumnal breeding?

Methods.—Birds from the study area in the Western Andes of Colombia were brought to Berkeley, California, in 1959 and maintained in aviaries until early 1965. The sparrows were housed in units approximately 8 × 8 × 7 feet, with outdoor exposure. From 1960 on, they were isolated by pairs. The initial six birds were augmented by three young, hand-raised in 1960. The birds nested frequently, repeat nestings occurring at short intervals after eggs or young were lost or taken. The cumulative reproductive record, spanning $5^1/_2$ years, shows 76 clutches of eggs laid. The repetition of events and the extent of this record are regarded as sufficient evidence for certain conclusions about cycles even though the total number of individuals involved is small.

The sparrows were subjected to the photoperiods of latitude 38° in which the natural light, extending from a little before sunrise to a little after sunset, ranges from 10 hr on December 22 to $15^1/_4$ hr on June 22; in Colombia they experience a virtually constant $12^1/_2$-hr day.

The nesting record of the captives shows the fertility period of the males either by the presence of embryos or young in the cage or on occasion by testis measurement through laparotomy or by examining the cloacal protuberance, which if enlarged to a diameter of more than 5 mm is a sure indication of full reproductive state. Since replacement nestings usually ensued at intervals of 3 or 4 weeks, it was not possible for a male to go through a regression and recrudescence in this short period. Successive production of fertile eggs or maintenance of the cloacal protuberance was therefore judged to show sustained reproductive state.

The birds were maintained on a diet of canary seed and ground dog food (Walter Kendall Burger Bits) with irregular increments of live insects that dropped into the cages or which were at times provided in efforts to raise the young.

Results.—Males attained or retained full reproductive capacity in the period of short days. The cumulative record shows seven instances in which by laparotomy the testis was proved to be fully developed or the cloacal protuberance was at breeding size on or about December 22 (±2 weeks). This involved four different individuals, as shown in Table 1.

There were four instances in which these same males were not at breeding level on or about the winter solstice and one instance in 1964 (bird 1) when breeding condition was attained in mid-January within a few days of this period. In three cases, as shown in the table, regression in the autumn had preceded the winter breeding condition; the record on this point for the others is incomplete.

The data show that the reproductive state in the males is not inhibited by the short photoperiods of latitude 38°. Evidently the endogenous rhythmic factor in these males returns them to breeding condition regardless of day length, at least day lengths of 10 hr or greater. The time when this state is attained is irregular and apparently dependent on when the preceding regression occurred, for the innate timing mechanism is obviously rather inexact.

A modification of the male cycle was evident as a prolongation of the period of

TABLE 1

MIDWINTER DATES FOR FULL REPRODUCTIVE STATE

Individual	Date determined*	Prior history
Male 1	December 20, 1959	
	January 2, 1961	Autumnal regression
	January 6, 1963	Autumnal regression
Male 2	December 20, 1959	
	December 20, 1962	Autumnal regression
Male 3	December 20, 1959	Autumnal breeding condition
Male 4	January 2, 1961	

* No determinations were attempted in midwinter of 1961–1962.

breeding capability. Males near the equator sustain capacity normally for 4 months and in no instance known for more than 6 months. In the captives at latitude 38° records of continued breeding state in seven instances were of 5, 7, 7, 9, 9, 9, and 10 months' duration and the three shorter of these were records incomplete at one end of the period or the other and may well have been 1 or 2 months longer than indicated (Fig. 1). This extension of the reproductive period occurs through the long-day segment of the year. Once reproductive level is attained in the winter or early spring, it would appear that the stimulus of long days from the spring equinox to the fall equinox maintains it, and that any tendency to rhythmic regression is overridden by this stimulus. This form of sparrow does not, then, have a refractoriness expressed as an obligatory regression following sustained breeding and prolonged exposure to long days such as is manifest in starlings.[8] Moreover, the sparrows recrudesce so promptly following a regression, both in the wild and in the laboratory, in a matter of 6 to 12 weeks, that refractoriness in the sense of quiescence prolonged beyond the point of time necessary for regrowth apparently does not exist. I have earlier shown[7] that immature refractoriness to light stimulus is in effect absent in *Zonotrichia capensis*. This was further substantiated by a young male raised in captivity in 1960, which on the long days of late summer attained full reproductive level at an age of 3 months.

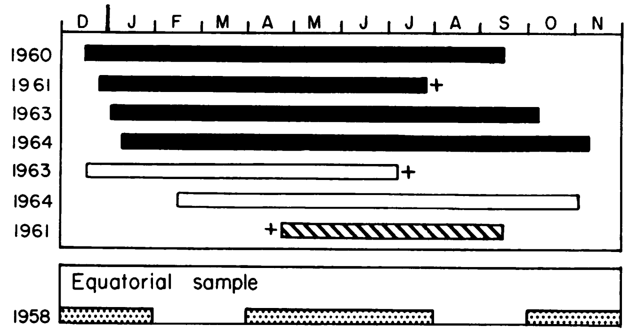

FIG. 1.—Records of continuous reproductive capacity in males of *Zonotrichia capensis*. Upper section shows experimental males under photoperiods of latitude 38°. Lengths of bars indicate span of reproductive capacity in terms of months for the years indicated and involving the preceding December; plus marks reflect probability of unrecorded extension of the period. Solid black bar, male 1; white bar, male 2; diagonally marked bar, male 5. Lower section shows sample case history normal for birds in equatorial area. (The seemingly orderly shift of the span for male 1 is probably an accident of the sampling periods chosen in different years.)

In the $5^1/_2$-year interval, females confined their egg laying to the period of the year when day length was 11 hr or greater. No nests were initiated or eggs laid in December, January, or early February when day lengths were less than 11 hr. This resulted, therefore, in one long breeding period each year collectively for the group, as shown in Figure 2. This period was principally from March to October. This span of reproductive activity was virtually the same in each year and the two females which contributed the best records continued to lay without cessation during this interval; eggs or young lost by them were followed by a new laying usually within 1 or 2 weeks of the loss. The losses may have had some part in stimulating continued nesting, but they did not do so as days became short in October. More-

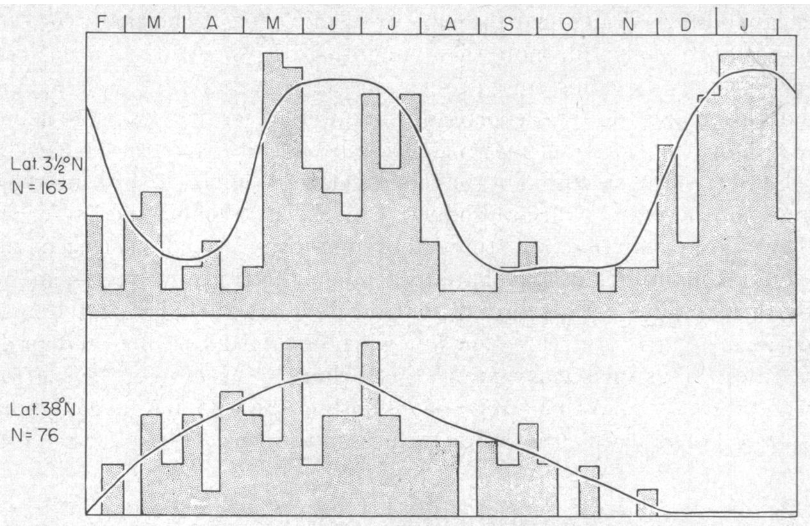

FIG. 2.—Frequency of occurrence of nestings under contrasting photoperiod regimes grouped by 10-day intervals. *Above:* composite record for all females for the year 1958–1959 [adapted from Miller, 1962 (ref. 2)] for the equatorial area. *Below:* composite record for $5^1/_2$ years of 5 females at latitude 38°N. Curves represent approximations fitted by eye.

over, in the field in Colombia females did not long continue replacement nesting in this way.

The prolonged unimodal nesting season of the captives under north-temperate photoperiodism was not influenced by wet or dry periods which were of much greater contrast than were those that have some coercive influence in the natural environment. For example, the annual dry season at Berkeley in which no rain falls from mid-May to late September did not inhibit nesting as the moderately low rainfall periods did at the Andean station. This inhibition in Colombia apparently is effected by the induction of molt. No general molt occurred in the captives until the end of the breeding period, which usually was in the fall.

Temperatures at Berkeley in the period of laying ranged from freezing in some years in March and April, and thus as cold as any condition in December and January, to summer temperatures in the 90-degree range for a number of days in succession. Neither of these extremes interrupted or slowed down the nesting efforts.

The evidence indicates, therefore, that the female reproductive cycle expressed in the culminative phase of laying is inhibited by short days (10–11 hr) unlike the situation in males. But like the response in males, activity in females is stimulated by long days. The response mechanism in this sparrow to the dry periods of its equatorial environment, which eventually represses laying, appears to be overridden by the stimulating effect of long days.

Summary.—Andean sparrows, *Zonotrichia capensis*, from an equatorial area were subjected to a seasonal photoperiod regime at latitude 38°N at Berkeley, California. The male reproductive cycle is not inhibited by short days (10–11 hr), and recrudescence of the testes occurs under these conditions as a reflection of the endogenous rhythm demonstrable in populations near the equator. Long days, up to $15^1/_4$ hr, stimulate abnormal extension of the reproductive period from 4 months to 7–10 months. There is no regression triggered by prolonged exposure to long days.

In females ovulation is repressed by short days of 10–11 hr, but it is stimulated and extended by long days. Photostimulation overrides influences of rainfall or drought which in the natural environment have been shown to have some effect.

There is no mechanism in this sparrow for effectively blocking late summer and autumnal breeding such as does exist adaptively in its congeneric relatives of the temperate region.

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*TRANSPLANTATION OF THE NUCLEI OF PRIMORDIAL GERM CELLS INTO ENUCLEATED EGGS OF RANA PIPIENS**

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Recently, it has been clearly demonstrated that the primordial germ cells in amphibians are set aside from the presumptive somatic cells very early in embryonic development, and in all probability later give rise to all of the definitive gametes.[1, 2] This early segregation of germ cells from somatic cells appears to depend, in anurans at least, on a distinctively staining,[3–5] UV-sensitive[6, 7] cytoplasm, originally localized in the vegetal cortical region of the fertilized egg. This distinctive cytoplasm is later incorporated into a limited number of cells in the presumptive endoderm—the primordial germ cells. The germ cells remain in the endoderm, surrounded by differentiating endoderm cells until late in embryonic development when they migrate dorsally and laterally into the genital ridges. This brief history of the primordial germ cells poses some interesting and important problems. Here we will be concerned with one of these, having to do with the "developmental capacity" of the nuclei of primordial germ cells relative to that of the adjacent somatic endoderm cells.

Previous studies in *Rana pipiens* have shown that, during embryonic development, the somatic endoderm nuclei become progressively restricted in their capacity to promote development when transplanted into enucleated eggs.[8, 9] Heretofore, there has been no such test of the developmental capacity of germ cell nuclei. The germ cells by definition must exhibit unrestricted developmental capabilities