RESPONSE TO EXPERIMENTAL LIGHT INCREMENTS BY ANDEAN SPARROWS FROM AN EQUATORIAL AREA

By ALDEN H. MILLER

In the study of breeding cycles of the Andean Sparrow (*Zonotrichia capensis*) in the wild near the equator (3° 30′N) in Colombia, South America, it was discovered that each male undergoes a six-month periodicity (Miller, 1959*a*). The high plateau of breeding potency normally lasts four months and the intervening regression, rest, and recrudescence of the testis occupies two months; two such cycles are passed through each year. Partly correlated with seasonal rainfall, a large proportion of the males in the population are in breeding condition during and just after the latter parts of each of the two annual wetter periods. Yet the control of events by rain, or wetness, however mediated, is incomplete inasmuch as nesting occurs in every month of the year in these sparrows at this location and the cycles of individuals may thus not be coordinate. The two periods of maximum participation in breeding fall close to the summer solstice and the winter solstice, respectively, for latitude 3° 30′N. Therefore, control or coercion by the weak seasonal photoperiodism of this area appears to be ruled out.

The question was posed whether this equatorial representative of the Andean Sparrow has a latent physiologic mechanism for response to light variations of greater magnitude than that which it normally experiences. In other words, does it have the same equipment for response as that possessed by its relatives of the same genus in North America? In planning to test this matter through experimental lighting an immediate difficulty arose of obtaining individuals with known prior history with respect to their reproductive cycles. One could not collect birds at a given time, as is done in the north, and assume that all would be essentially at the same point in the reproductive cycle. The number of individuals for which histories had been traced was small and these free-living birds were needed for completion of the study of natural cycles in the wild. Accordingly, experimentation was directed toward ascertaining the impact of added light on immature individuals whose age could be determined from the persistence of streaked juvenal plumage and/or the stages of the postjuvenal molt.

The problem and the findings need to be viewed against the background of experimental results on the Golden-crowned Sparrow (*Zonotrichia atricapilla* = *Zonotrichia coronata* or earlier nomenclature, see Stresemann, 1949) and the migratory races of the White-crowned Sparrow (*Zonotrichia leucophrys*). In these forms the treatment with an artificial day of 15 to 16 hours' length will stimulate the pituitary-gonad mechanism and lead to the development of the testes to full breeding size in 2½ to 3 months (Miller, 1954). If, however, this treatment is started too soon after the preceding breeding period or too soon after hatching in the case of immature individuals, the autumnal refractory period is encountered and no immediate or delayed response ever ensues. This refractory period terminates about the end of October or the first week of November (Miller, 1954; Farner and Mewaldt, 1955). In other words, under the normally conditioning light regime of the postbreeding period (see Wolfson, 1952), in which day length diminishes, the refractory situation disappears when young birds are 4 to 4½ months old. In this period the day length experienced ranges from 18+ hours down to about 11½ hours, with an average of roughly 14½ hours.

Young of *Zonotrichia capensis* were captured and placed in an outdoor experimental cage at our research station on the Western Andes, west of Cali, where there was a surrounding free-living population of marked birds which served as controls. The cage was 1 × 1 meters square and 2 meters high; it was provided with a 150-watt globe controlled by a time switch so that 4 hours of artificial light was added to a normal daylight period, the aggregate being slightly over 16 hours. To avoid disruptive crowding only six young males were maintained at one time. They were given experimental light starting at ages ranging from 1½ to 4 months. Thus all were by comparison with *Zonotrichia leucophrys* and *Zonotrichia atricapilla* started at a time when they should be refractory.

RESULTS

A total of seven individuals that survived beyond ages of 4 months showed the results detailed in the following table.

Individual	Age at initiation of light dose	Age of attainment of breeding level	Length of light treatment before attainment of breeding level
872	2⅔ months	3⅔ months	1 month
897	2⅚	4⅓	1½
898	2½	6	3½
551	3¼	4½	1¼
552	4	6	2
005	1½	3	1½
881	3 7/12	5⅓	1¾

The age of attainment of breeding level was determined by laparotomies (Miller, 1958). When the testis was less than 7 mm. long but in the range from 3½ to 5 mm. the further recrudescence to be inferred from these sizes was extrapolated from experience with wild birds, wherein it was learned that three weeks is required for enlargement from 3.4 to 7 mm. Most laparotomies showed either full testis size or measurements 4.4 mm. or greater so that estimates to an accuracy of one weeks' time seem indicated. No. 898 is an exceptional case in that laparotomy at 6⅓ months revealed a 5.1 mm. testis, but the bird was then showing evidence of disease from which it succumbed 18 days later. When it died, the testes were again small (2 mm.). But at 5⅙ months a laparotomy had shown (2.9 mm.) that recrudescence was starting and it is probable that the bird attained full development at 6 months from which it was regressing a little later under the influence of disease.

The results, although variable in certain respects, are completely consistent in that all of the seven experimentals showed freedom from refractory reaction normal to northern zonotrichias. Despite the small number of individuals, this consistency makes it permissable to draw conclusions. The fact that some of the sparrows were started on extra light treatment as early as 1½ to 2⅔ months of age and nevertheless showed prompt positive response is furthermore a strong indication that we are not dealing here merely with a slightly shortened refractory period. No. 005, for example, attained a 4.6 mm. testis while still carrying some ventral streaking on the breast and while heavily involved in the postjuvenal molt. It seems clear that the refractory period is either entirely lacking or is radically shorter than in other species of *Zonotrichia*.

In the free-living population of *capensis* young males occasionally attain full reproductive state at 5 months, although normally this is achieved at 6 to 8 months. Certain of the experimentals did not reach breeding level before 5 or 6 months but it should be realized that in these cases the extra light was started long before the date of termination of refractoriness normal for *Zonotrichia leucophrys*; the light did not inhibit recrudescence in the way that it will when thus applied and maintained in *Zonotrichia leucophrys* and *Zonotrichia atricapilla*.

Another aspect of the results is consistent, except for the record of the sick bird no. 898. This feature relates to the promptness of response. Similar light dosages given during non-refractory periods in *leucophrys* and *atricapilla* must be applied for 2½ months at least to bring about full breeding level. In equatorial *capensis* this level is attained in 1 to 2 months. Moreover, all four of the healthy birds that were started early enough on extra light to have made it possible for them to reach full reproductive level before the earliest known age for normal or control attainment of this state did in fact do so. These facts seem to indicate clearly that light has a positive stimulating effect.

DISCUSSION

The species of birds that nest at high latitudes and which generally utilize the stimuli of photoperiodism to perfect the timing of their seasonal activities receive values from the refractory period that follows the breeding season. This period serves to prevent a continued or recurrent gonad enlargement which might otherwise be induced by the days that are still longer than 12 hours in late summer and early fall. I have recently (1959*b*) offered the hypothesis that the postbreeding refractoriness is a positive adaptation for these high latitude species. Those birds that have evolved it conserve the energy that would be utilized in an unnecessary gonad enlargement and the attendant stimulated activities of song, courtship, and territorialism. Moreover, it prevents a reproductive effort that if started at this time would be abortive, wasteful, and dangerous to the adult because of the oncoming winter conditions. In other words, a photoperiod-controlled species must respond positively to light to attain breeding state at the proper time in the spring but it must also have a shut-off system to avoid extended or subsequent stimulation by this light which would be maladaptive.

Young individuals that have no need for recovery from a preceding active breeding state show the same autumnal refractoriness scheduled to extend over the same time (Miller, 1948) as the postbreeding refractoriness of the adults of the species. This circumstance especially points to the positive adaptive value of the refractory reactions, as there is no ready explanation why adults and young, the latter not in need of rest, would so perfectly coincide. Moreover, Wolfson (1955) has shown in Slate-colored Juncos and White-throated Sparrows that the extent of postbreeding refractoriness can be shortened by artificially providing long nights and short days. Thus it appears that refractoriness is a special blocking mechanism with threshholds gauged to the long days and short nights normal to late summer and early fall, a situation that can be upset by manipulation of the photoperiods at that time.

In thus viewing the postbreeding refractoriness as a positive adaptation, we should not confuse this mechanism with the independent tendency in males of all species to alternate regression and recrudescence, an innate tendency that results of itself in a somewhat loosely timed scheduling. This latter situation was especially brought to light in the tracing of individual histories in the wild equatorial population of *Zonotrichia capensis* (Miller, 1959*a*).

The apparent lack of a postjuvenal refractory period in *capensis* could be interpreted in at least two ways. It might be postulated that the period is present but is innately shortened compared to that of its northern relatives. Or it could be assumed that it is present in a form like that of its relatives but becomes diminished in expression by reason of the 12½ hour days and 11½ hour nights experienced from the time of fledging and before onset of artificial lighting. This latter view would not be discordant with results of Wolfson's experimental work (1952) on northern sparrows. Both of these hypotheses have the disadvantage of proposing the existence of a refractory mechanism in *capensis* that would never be important to the organism and would be inoperative in the light regime under which it lives. They would have the merit only of assuming a mechanism similar to that of related species.

Consequently the simplest postulate and therefore the most advisable in the absence of contrary evidence is that a postjuvenal refractoriness does not exist in equatorial *capensis*. It has never developed or it has disappeared as a mechanism because it had no selective advantage. Such a view, conversely, points toward the likelihood that the refractory period has evolved in high latitude species to fit a particular and critical situation in their environment.

SUMMARY

In an equatorial population of the Andean Sparrow (*Zonotrichia capensis*) experiencing, the year around, day lengths of about 12½ hours, normal innate breeding cycles of wild males are of a six-month type, with four months of high reproductive potency and two months of rest and reconstruction of the pituitary-gonad mechanism.

Experimental light treatment of juvenal and immature birds in which they were afforded 16-hour days revealed no sign of a postjuvenal light refractoriness such as that found in high-latitude relatives.

Young males respond positively to light dosages on somewhat variable schedules but with sufficient constancy to conclude that this equatorial population has a latent light-response mechanism leading to stimulation of the gonads. Full reproductive level in males may thereby be reached at 3 to 4½ months of age whereas wild controls attain this rarely at 5 months and normally at 6 to 8 months.

Response to light is more rapid at the same dosages than in the Golden-crowned Sparrow and the migratory races of the White-crowned Sparrow.

It is hypothesized that a postjuvenal refractory period is entirely absent in equatorial representatives of the Andean Sparrow; it would have no meaningful function in such populations. Conversely it is proposed that the postjuvenal and postbreeding refractory mechanisms of high-latitude species are positive adaptations which avoid futile and wasteful late summer and autumnal breeding activity.

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DEDICATION

I take pleasure in dedicating this paper to Erwin Stresemann on the occasion of his 70th birthday in recognition of his contributions to ornithology.

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