# THE EXPRESSION OF INNATE REPRODUCTIVE RHYTHM UNDER CONDITIONS OF WINTER LIGHTING

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EXPERIMENTS on the effect of photic stimulation on the reproductive cycle of birds have been particularly extensive in the passerine genera *Zonotrichia, Junco, Sturnus,* and *Passer.* Recent reviews and summarizations (Wolfson, 1952; Burger, 1953; Miller, 1954) have made it evident (1) that positive light stimulation in these genera will induce gonad recrudescence at rates dependent largely on the daily length of exposure, (2) that prolonged or excessive stimulation will induce and maintain a resting or refractory state, and (3) that the innate rhythmic tendency which these photic stimuli mold into expression consists of required alternation of processes of (a) activation and growth and (b) regression and reorganization. What has not been adequately shown is whether or not the innate rhythmic tendency can reach full expression on a short-day regime. Specifically, will this tendency to resume activity after a normal rest period proceed under a constant light dosage characteristic of the wintertime experience of the species? Some evidence indicates that this will occur, but it is not wholly satisfactory.

Bartholomew (1949) found that in the House Sparrow (*Passer domesticus*) the males would attain full reproductive state on a constant 10-hour day, but the experiment was started on January 23, which is later than ideal in relation to the normal annual cycle, and the birds were pretreated with an 8-hour day, the exact effects of which are uncertain. Moreover the 10-hour period is slightly longer than the effective mid-winter day length at the latitude where the birds were taken. Burger (1953) found that males of the Common Starling (*Sturnus vulgaris*) attained full reproductive state after 16 weeks of constant 9½-hour days, but again this experiment was begun after the winter solstice, on February 2. Burger goes on to comment (p. 2) that it "does seem necessary to demonstrate experimentally for many more species whether or not short days permit a normal reproductive periodicity. . . . It remains . . . to be seen whether or not starlings reared and kept for several years under short days might develop a self-regulating cycle of an annual or non-annual character."

The experiment herein reported on Golden-crowned Sparrows (*Zonotrichia coronata*[1]) was designed to show the capability to re-

[1] The name for this species is properly *atricapilla,* but to avoid confusion in the physiologic literature, the more familiar *coronata* is employed.

crudesce in males in the absence of photic stimulation greater than that normally received on December 21. The housing and care of the birds at Berkeley, California, was similar to that in previous experiments on this species (Miller, 1948, 1954) except that the experimental cage was darkened with plywood panels and roofing paper and was provided with a light-tight ventilating system. The temperatures in the experimental and adjoining control cages, both situated out-of-doors, differed no more than 4° C on warm days and normally not this much. There was of course greater daily fluctuation in temperature and wind sweep in the control cage. The experimental cage was totally dark except when the lights were on for a 10-hour period each day. During this 10-hour period on alternate days the door panel was opened several hours to permit entry of natural light. The 10-hour regime was set to coincide with the normal interval between awakening and quiet roosting in a local flock of wild Golden-crowned Sparrows on December 21, 1953. The experiment was begun on this date following a normal fall rest period experienced either entirely in the wild or partly in outdoor cages.

The experimental procedure was maintained until the last autopsy on September 20, 1954. Data on the condition of the testes were extended by laparotomy of some individuals. This operation on experimentals and controls had no detectable influence on the health or gonad response of the birds. Laparotomy permitted measurement of the testis and approximate calculation of its volume. Nine records on six experimental birds were obtained from May 1 to September 4. Six control readings were combined with those of previous years derived from the same cage to show the normal cycle of testis increase and subsequent regression (fig. 1).

The helpful assistance of Robert I. Bowman in the conduct of the experiment is gratefully acknowledged.

*Results.*—The testes in the experimental birds quite evidently never attained functional condition. The curve for size of the testis shows a partial enlargement, slightly but significantly above that of minimum winter condition and above that of birds of previous years experimentally maintained in a refractory condition (Miller, 1954, fig. 1). This slight enlargement prevailed somewhat erratically from May through August, but it was most evident in June and July when volumes of 4.05 mm.$^3$ were recorded. These however are to be compared (fig. 1) with volumes of 191.65 and 222.52 mm.$^3$ in controls in these same months and 1.00 mm.$^3$ or less at winter minimum.

The maximum histologic development reached was stage 5 of Blanchard (1941) in which primary spermatocytes in synapsis are

abundant, but the manifestation of stage 5 was atypical in that Leydig cells in the spaces between tubules were noticeably less in numbers than normal for this stage. In any one interstice up to three enlarged Leydig cells could be seen whereas normally many of the interstices contain two or three times this many. Such a testis in an experimental bird was examined from an autopsy of May 1. On June 12 a testis that had apparently reached this same condition was regressing; there were degenerating synaptic primary

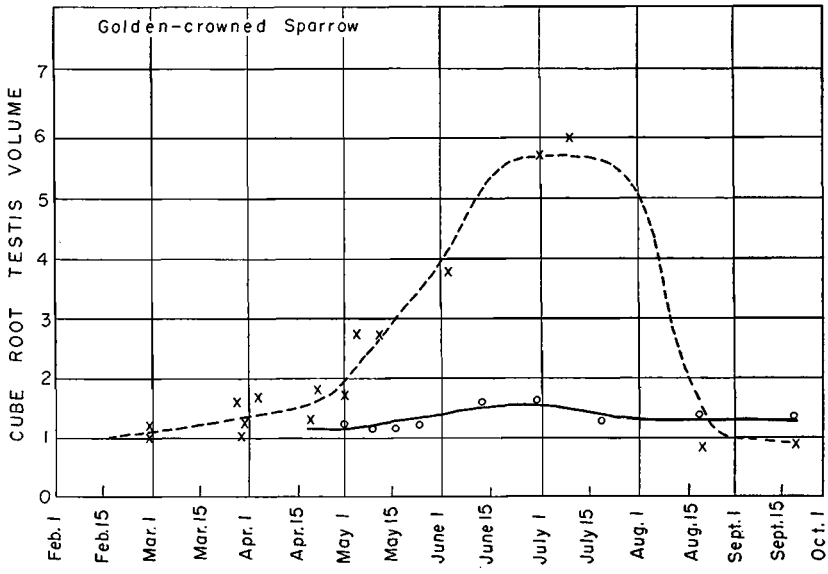


FIGURE 1. Testis volume, in millimeters, of Golden-crowned Sparrows. Broken line and X's represent controls from several years. Solid line and circles represent experimentals held in 10-hour cage from December 21, 1954, to dates of autopsy.

spermatocytes, still with dense chromosome clusters, in the lumina of the tubules and no sign of later stages such as spermatids and sperm; active Leydig cells were absent. On June 30 a testis that had attained stage 4 or 5 was just beginning to regress by break down of synaptic primary spermatocytes; Leydig cells were present in limited numbers as in the bird of May 1. Histologic samples of July 20 and September 20 were in stage 2 with no sign of sex cells advanced beyond the spermatogonia; there were occasional rather small Leydig cells such as may be seen in an inactive testis. Presumably these two had regressed from partly activated conditions like those just described. The controls in June and July were of

course in stage 7, but those of late April and early May were in stages 4 and 5.

Experimentals showed large deposits of subcutaneous fat from June 12 to September 20, but not in May. Controls showed conspicuous fat in May correlated with testis stages 4 and 5 but only moderate fat while in stage 7. Experimentals underwent prenuptial molt in early May but no annual molt (one individual remaining) in August and September. A control underwent annual molt in August.

Included in the experimental cage were three examples of the local, permanently resident race *nuttalli* of the White-crowned Sparrow (*Zonotrichia leucophrys*). This form normally reaches stage 5 by mid-February (Blanchard, 1941) when effective day-lengths for the birds are about 12 hours. Stage 7 is reached by mid-March when days are about 13 hours. The experimental sample is too small to yield conclusive data on *nuttalli*, but on May 1 and 2 these three birds in the 10-hour cage had attained histologic stages 6, 7, and 7, with volumes of 18.39, 134.42, and 167.60 mm.$^3$, respectively. Thus their recrudescence had carried to completion, but whether or not it was on normal schedule is uncertain. The manifestation of stage 6 on May 2 suggests that a very considerable lag may occur under the 10-hour regime.

*Conclusions.*—In *Zonotrichia coronata* light stimuli above the amounts normal in mid-winter are necessary for the pituitary-gonad mechanism of the male to attain reproductive state. An innate tendency to recrudesce, more or less on schedule, is evident from the partial development achieved. This innate process falls short at the level of stage 5 of the testis, the primary spermatocytes reaching synapsis but failing to proceed with the maturation divisions. Subsequent regression to a resting state occurs while still on a constant 10-hour day. At stage 5 in these experimental birds the number of Leydig cells is abnormally low, which situation probably reflects a low level of the gonadotropins from the pituitary. Inadequate amounts of gonadotropins may also be the factor that stops the maturation processes in the sex cells. Burger (1953: 231) also reports that recrudescence in *Sturnus* on an 8½-hour day proceeds to but not beyond the primary spermatocyte stage.

Preliminary results for *Zonotrichia leucophrys nuttalli* suggest but do not yet prove that mid-winter light suffices in this form for full gonad development although this is probably not achieved with such light on normal schedule.

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*Museum of Vertebrate Zoology, University of California, Berkeley, California, November 14, 1954.*