THE OCCURRENCE AND MAINTENANCE OF THE REFRACTORY PERIOD IN CROWNED SPARROWS

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The inability to maintain a breeding condition indefinitely has led to the recognition of a state of refractoriness or of a requirement for rest and inactivity before resumption of breeding. Refractoriness has been reported in birds of several species; the phenomenon is fairly well known, for example, in Starlings (Burger, 1949), English Sparrows (Riley, 1936), Slate-colored Juncos (Wolfson, 1952*a*, 1952*b*) and Golden-crowned Sparrows (Miller, 1948). Refractoriness is demonstrated by experimental treatment with light of amounts that under other circumstances would induce gonad development. The failure to stimulate gonad activity has two aspects: (1) the gonads will regress from a breeding state under prolonged treatment with long daily light periods (Burger, 1949; Wolfson, 1952*b*); and (2) inactive birds that have attained the regressed state, naturally or by experimentation, may fail to respond to light stimulation if they have not been inactive long enough. More extended reviews of these matters are to be found in the recent papers just cited.

In the work with Golden-crowned Sparrows (*Zonotrichia coronata*) thus far reported (Miller, 1948, 1949, 1951), it was shown that normal autumnal refractoriness of adults and immatures persists through October and until about November 5. This is true whether gradual light increases or sudden heavy light dosages are given before this date. Once having been put on a long light-day in the refractory period, this species thereafter remains refractory, at least until mid-spring. This sustained refractory condition would seem to be explicable in two ways: (1) the experimental birds become accustomed to long days, or are conditioned to them, during their normal refractory period and require a further increased dose of light to stimulate them to respond; or (2) the birds under constant stimulation prolong a fatigue of the pituitary-gonad mechanism so that response is indefinitely postponed. This second line of explanation was suggested by Burger (1949:223).

To test these alternate hypotheses, an experiment was set up in 1951 designed to rule out or substantiate the first proposition. At the same time it was possible in the seasons of 1951–52, and also in 1950–51, further to document the presence of the normal refractory period and to demonstate even greater experimental prolongation of it into late spring and summer. A further purpose of the experiments in these two years was to develop parallel data on the closely related White-crowned Sparrow (*Zonotrichia leucophrys*) and to determine the histological condition of the testes in the experimental birds and compare it with the normal histological cycle so extensively analyzed in this species by Blanchard (1941) and Blanchard and Erickson (1949).

EXPERIMENTS

As in earlier experiments (Miller, 1948), control and experimental birds were kept in adjoining outdoor screened cages, 8×8×7 feet, at Berkeley, California. The controls were shielded from the experimental cage so that they slept on their roosts while artificial light was being given to the experimentals. The sparrows were trapped in early and mid-October soon after arrival in Berkeley from their northern breeding grounds; a few examples of the locally resident race of White-crowned Sparrow (*Z. l. nuttalli*) were trapped at this time and also were used in the experiments. The type of light added and the water and food supplies were the same as in previous experiments.

1950–51. The experiment in this season was begun on October 24 with a sudden change to a constant 15½ hour light-day. Experimental birds carried through to a point of significant results included 6 male Golden-crowned Sparrows and 10 male White-crowned Sparrows, the latter being of the following racial types: *Z. l. gambelii,* 3; *pugetensis,* 4; *nuttalli,* 1; *pugetensis-nuttalli* intergrades or intermediates, 2. No controls of the Golden-crown were maintained, as data from earlier years were available as adequate control material. Six White-crowns were maintained as controls, consisting of the following races: *gambelii,* 3; *pugetensis,* 2; *nuttalli,* 1. The Golden-crowns were held on the constant light treatment through spring and summer, the birds being sacrificed at intervals from May 24 to August 31, 1951. The White-crowns in the same experimental cage were autopsied from December 31 to May 24; the controls were autopsied from March 4 to May 24.

1951–52. The experiment again was initiated on October 24 with a 15½ hour light-day, but on January 10 the day length was increased to and maintained at 21 hours, thus providing a substantial additional light stimulus to test the hypothesis concerning need of augmented stimulation to overcome refractoriness. At the time of this light increase some birds were moved from the control cage to the experimental cage and thus were switched from normal short winter days to extremely long days after the expected termination of the refractory period. These are referred to subsequently as experimentals of type II contrasted with the initial experimentals, type I. Experimentals of type I maintained to date of autopsy consisted of 4 male Golden-crowned Sparrows and 6 male White-crowned Sparrows of the following races: *pugetensis,* 4; *nuttalli,* 1; *pugetensis-nuttalli,* 1. Experimentals of type II consisted of 3 male Golden-crowns. Controls consisted of 3 male Golden-crowns; no control White-crowns were maintained, as data on controls from the previous year were fairly adequate. The experiment was concluded and most of the birds were autopsied on March 25, except that one experimental type I Golden-crown and one experimental type I White-crown were maintained until July 13, the artificial lighting on them being terminated on March 25 so that they reverted at that time to a normal 13-hour day from 21 hours and experienced a normal gradual increase thereafter to the summer solstice level of about 16 hours of daylight.

RESULTS

In 1951–52, the experimentals of type I that had been started at 15½ hours in the known refractory period, and which were given additional light beginning in January, showed no gonad enlargement on March 25 (see table 1). Three Golden-crowns and 3 White-crowns were autopsied at this time. There was an ample interval since January 10 for the increased light to have stimulated recrudescence. In other words, the refractory state was fully maintained. At the same time the experimentals of type II, 3 Golden-crowns, in the same cage but introduced to the 21-hour day directly from a regime of normal short winter days in January, showed spectacular recrudescence (table 1); one had even attained a testis development approaching that of full breeding condition. Control Golden-crowns on this same date were beginning to show slight but significant advances in line with normal gonad recrudescence (table 1, fig. 1).

The results bearing on extreme prolongation of refractoriness were obtained in the experimentals of 1950–51. Golden-crowns autopsied on June 30, August 1, and August 31 were still at winter minimum gonad size and had remained refractory in the latter instance for essentially a full year from the time the bird must have left its breeding ground in a quiescent condition. In the White-crowns in this same year the refractory period was extended to May 24 when the last were autopsied. The two sacrificed on this date represent the races *nuttalli* and *pugetensis,* both of which races were at the height of breeding condition in the wild at this time. All the experimentals with the exception of one were at winter minimum condition. The exception, a White-crown of the race

Table 1

Data on Experimental and Control Male Crowned Sparrows

Identity	Age at beginning of experiment	Date autopsied	Duration of light treatment in days	Day length in hours and beginning date of treatment	Volume of left testis in mm.^{3}	Fat condition***	Histologic stage****
Z. coronata	?	May 24, 1951	212	15½ (Oct. 24)	0.34	heavy	1–2
Z. coronata	?	June 30, 1951	248	15½ (Oct. 24)	0.50	heavy	2
Z. coronata	?	June 30, 1951	248	15½ (Oct. 24)	0.25	little	2
Z. coronata	?	Aug. 1, 1951	280	15½ (Oct. 24)	0.88	medium	2d
Z. coronata	?	Aug. 1, 1951	280	15½ (Oct. 24)	0.37	little	2
Z. coronata	?	Aug. 31, 1951	310	15½ (Oct. 24)	0.44	none	2
Z. coronata	im.	Mar. 25, 1952	152(I*)	15½–21 (10/24; 1/10)	0.46	none	2
Z. coronata	ad.	Mar. 25, 1952	152(I)	15½–21 (10/24; 1/10)	0.57	none	2
Z. coronata	im.	Mar. 25, 1952	152(I)	15½–21 (10/24; 1/10)	0.58	none	2d
Z. coronata	ad.	July 13, 1952	152(I)	15½–21—normal (10/24; 1/10; 3/25)	0.78	none	2d
Z. coronata	ad.	Mar. 25, 1952	74(II)	21 (Jan. 10)	6.68	none	4
Z. coronata	im.	Mar. 25, 1952	74(II)	21 (Jan. 10)	38.67	medium	5–6
Z. coronata	ad.	Mar. 25, 1952	74(II)	21 (Jan. 10)	85.67	little	6+
Z. coronata	ad.	Mar. 25, 1952	control	normal variable	0.99	little	3
Z. coronata	ad.	Mar. 25, 1952	control	normal variable	3.96	little	3+
Z. coronata	ad.	July 13, 1952	control	normal variable	222.52	medium	7
Z. l. gambelii	im.	Dec. 24, 1945	75	**→15½ (Oct. 10)	0.26	none	?
Z. l.	im.	Mar. 31, 1946	172	→15½ (Oct. 10)	0.28	little	?
Z. l. pugetensis	im.	Jan. 16, 1948	72	→14½ (Nov. 5)	121.89	little	?
Z. l. pugetensis	im.	Feb. 15, 1948	102	→14½ (Nov. 5)	146.15	medium	?
Z. l. pugetensis	ad.	Feb. 15, 1948	102	→14½ (Nov. 5)	150.15	heavy	?
Z. l. pugetensis	im.	Feb. 2, 1950	101	15½ (Oct. 24)	0.40	none	2
Z. l. gambelii	ad.	Dec. 31, 1950	68	15½ (Oct. 24)	0.63	little	1
Z. l. pugetensis	ad.	Dec. 31, 1950	68	15½ (Oct. 24)	0.54	none	2
Z. l. pug.-nutt.	ad.	Mar. 4, 1951	122	15½ (Oct. 24)	0.37	none	2
Z. l. gambelii	ad.	Mar. 4, 1951	122	15½ (Oct. 24)	1.31	little	2
Z. l. gambelii	?	Apr. 18, 1951	167	15½ (Oct. 24)	0.94	medium	1–2
Z. l. pug. nutt.	ad.	Apr. 18, 1951	167	15½ (Oct. 24)	1.05	medium	2
Z. l. pugetensis	ad.	Apr. 18, 1951	167	15½ (Oct. 24)	2.15	none	2d
Z. l. pugetensis	?	Apr. 18, 1951	167	15½ (Oct. 24)	170.81	medium	7
Z. l. pugetensis	?	May 24, 1951	203	15½ (Oct. 24)	0.25	medium	2
Z. l. nuttalli	?	May 24, 1951	203	15½ (Oct. 24)	0.46	little	1–2
Z. l. pugetensis	ad.	Jan. 10, 1952	78	15½ (Oct. 24)	0.47	none	1
Z. l. pugetensis	ad.	Jan. 10, 1952	78	15½ (Oct. 24)	0.50	none	2
Z. l. pugetensis	im.	Mar. 25, 1952	152(I)	15½–21 (10/24; 1/10)	0.73	none	2
Z. l. nuttalli	im.	Mar. 25, 1952	152(I)	15½–21 (10/24; 1/10)	0.82	none	2
Z. l. pugetensis	ad.	Mar. 25, 1952	152(I)	15½–21 (10/24; 1/10)	1.21	none	2
Z. l. pug.-nutt.	im.	July 13, 1952	152(I)	15½–21—normal (10/24; 1/10; 3/25)	158.80	medium	7
Z. l. gambelii	ad.	Mar. 4, 1951	control	normal variable	0.90	little	3
Z. l. pugetensis	ad.	Mar. 4, 1951	control	normal variable	2.81	little	4
Z. l. gambelii	?	Apr. 18, 1951	control	normal variable	6.63	heavy	4
Z. l. pugetensis	?	Apr. 18, 1951	control	normal variable	41.04	heavy	6
Z. l. gambelii	?	May 24, 1951	control	normal variable	180.91	heavy	7
Z. l. nuttalli	?	May 24, 1951	control	normal variable	199.00	heavy	7

* I signifies experimental of type I, see text.
** → signifies day length gradually increased to this figure; date is the beginning of light increase.
*** Fat categories as designated by Wolfson (1945:109).
**** Histologic stages as described and figured by Blanchard (1941) and Blanchard and Erickson (1949); "d" signifies some indication of degenerating spermatogonia.

pugetensis taken on April 18, was in full breeding condition. Two lines of explanation may be offered for such unexpected results. First, the date of ending of the natural refractory period in White-crowns is apparently a little earlier than in Golden-crowns and hence the onset of light treatment on October 24 may have found this individual reactive whereas others were not. Golden-crowns previously were found to be individually variable with respect to refractoriness on November 5. Second, power failures in mid-winter of 2 to 3 day's duration may have broken the light treatment long enough for this exceptional White-crown to react. This second possibility seems rather unlikely, however, as no other experimentals showed effects of such interruption.

Concerning refractoriness in White-crowns in general, it can be stated that experimentals (17 specimens), regardless of race, show refractoriness (see table 1) as in the Golden-crowned Sparrow. In other words, there is a period in the fall when added light does not lead to recrudescence and the refractoriness is maintained under continual light treatment. However, three White-crowns started on gradual light increments on November 5 in 1947 showed no refractoriness in contrast to some Golden-crowns in the same cage. These White-crowns attained full breeding condition by mid-February or earlier, at least three months in advance of the norm for the race *pugetensis* to which they belonged. Wolfson (1945:98) had reported earlier that White-crowns to which he had given light increments beginning on October 18 showed recrudescence. This result contrasts with that for two birds to which I gave similar treatment beginning on October 10 and which showed refractoriness, and with a considerable number that were given suddenly augmented light-days of 15½ hours beginning on October 24 and which also were refractory. Wolfson's birds were receiving only 13 hours by October 24 even though increases started a week earlier. The results therefore seem not inconsistent and point to a termination of refractoriness in this species definitely before November 5, with a variable response to be expected in the last 10 days of October, depending on individual differences and perhaps on the amount of light increment in this transitional period. The exceptional responsive bird referred to earlier fits in with this concept.

The data for all years are reviewed in figure 1. The graphing of gonad size follows the plan used earlier in which the volume of the left testis is plotted as its cube root in order to provide a convenient scale. Detailed tabulation of results on Golden-crowns of earlier years (Miller, 1948, 1951) is not repeated but supplementary data since 1949–50 are given in table 1 as well as all data on White-crowns.

The two individuals, one of each species, that were given special treatment in 1951–52, namely artificial light to March 25 and normal day lengths thereafter, sustained refractoriness until March 25 in so far as all external signs indicated. On July 13 the Golden-crown given this treatment was autopsied and was found still to be at winter minimum state. The shortening of the days to 13 hours in March evidently was not sufficient to break its refractoriness. The White-crown, on the other hand, had by July 13 developed to full breeding condition and was moderately fat. Possibly it had failed to be refractory initially, but more likely the drop from 21 hours to 13 hours of light in March was sufficient to break the refractoriness at that time. On March 25 it had shown no fat and was undergoing a complete molt of body, wing, and tail feathers, almost certainly indications in this species of inactive or regressing gonads. These two birds autopsied in July are inadequate in number to demonstrate the effect of the particular light regime involved, especially since they showed opposite responses. However, the sustained refractoriness of the Golden-crown suggests in conjunction with results on the other experimental groups of this species that there is need for a period of a month or more at 13 hours or less of light daily in order to overcome refractoriness.

The results with respect to subcutaneous fat condition are indicated in the table.

In general, the controls show the normal fat conditions correlated with the gonad cycle in which little or no fat is present in winter when the gonads are small, and in which heavy, or at least medium, amounts of fat appear during recrudescence. At the height of breeding condition in the wild, fat is absent in males, but in captive birds held under conditions where they can not actually breed this may not be true. Refractory birds usually show no large fat deposits even when refractoriness is prolonged. However, some exceptions will be noted in table 1. The results in such experimental individuals are thus

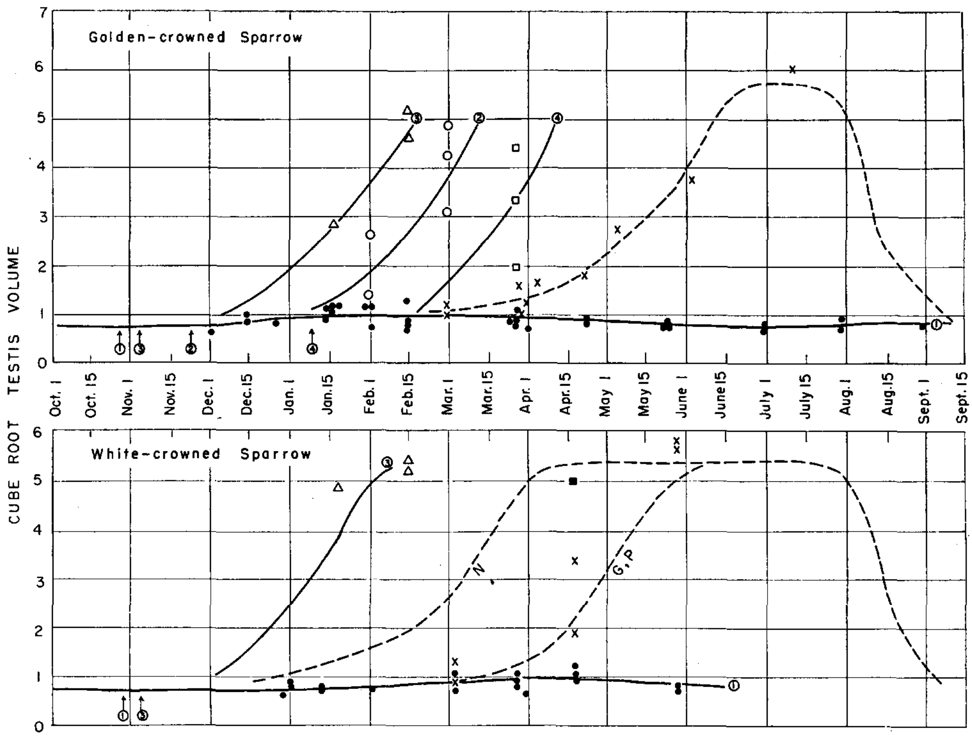

Fig. 1. Testis volume in experimental and control crowned sparrows. Solid dots indicate refractory experimental birds of all years; solid lines marked "1" at right end represent averages for refractory birds. Controls shown by "X's" and by broken lines; lines are drawn partly from general information on normal breeding seasons and from data on *Z. leucophrys* of Blanchard and Erickson; N represents race *Z. l. nuttalli,* G, P, races *gambellii* and *pugetensis*. Triangles and line 3 represent responsive experimentals of 1947–48; open circles and line 2, responsive experimentals of 1946–47; open squares and line 4, experimentals of type II of 1951–52; solid square, single abnormally responsive experimental of 1950–51. Arrows mark onset of light treatment for groups of corresponding number.

more erratic with respect to fat response than Wolfson (1952*b*) reports in experimental State-colored Juncos showing refractoriness. But it should be noted that his birds were kept in indoor cages with little temperature fluctuation whereas mine were experiencing normal daily and seasonal variations in temperature, a situation in which thyroid activity may be influenced in part independently of pituitary control.

The histological condition of the gonads of all experimentals and controls has been checked beginning with the season of 1949–50. The preparations were made from Bouin's fixations, were sectioned at 7 μ and were stained with Harris haematoxylin and eosin B. The material thus is comparable to that analyzed by Blanchard (1941) and Blanchard and Erickson (1949). In the examples of *Zonotrichia coronata* of 1949–50 as in the subsequent material on this species and on *Zonotrichia leucophrys,* all birds showing refractoriness as indicated by persistent small gonad size failed to show histological developments beyond stage 2 of Blanchard. Stage 2 is distinguished from stage 1, the condition of complete quiescence of the autumnal and winter period, by the appearance of a few Leydig cells in the interstitium. Rarely have I found a bird that seemed to have no Leydig cells or at least no partly enlarged and rounded cells in what we suppose is progression toward functional condition. The distinction, then, between stages 1 and 2 is a tenuous one and possibly is not useful as Wolfson (1952*b*) has suggested. However, I can distinguish borderline or doubtful stage 2 gonads with only rare, small Leydig cells as against others with varying numbers of well rounded Leydig cells that clearly qualify as Blanchard's stage 2. In the table, particularly early or dubious examples of stage 2 are indicated as "1–2." Through the technique used I am unable to distinguish differences in the lipoidal content coincident with the enlargement of the Leydig cells from immature or precursor cells as Marshall (1951) has undertaken to do.

The significant histological observations in connection with the experiments are, then, that no refractory bird progresses to stage 3, in which Leydig cells are common and primary spermatocytes appear, and that nearly all such birds do develop some well formed Leydig cells. Thus they just begin the process of recrudescence, if we follow the interpretation of Blanchard and Erickson (1949), but become arrested at this point.

An occasional refractory bird, those marked with a "d" in the table, shows a stage 2 condition but has a noticeable mass of degenerating spermatogonia in the tubule. This suggests that some spermatogonia produced in stage 2 having failed to proceed to the primary spermatocyte stage are being resorbed. These degenerating cells give no sign of having been more advanced types of sex cells; their appearance is quite different from that of the mass of sperm debris and spermatids to be seen in stages of regression following breeding.

The responsive birds (experimentals of type II, especially) and the controls show the expected progress toward the full breeding condition of stage 7 according to date and history of light stimulus.

In the earlier experiments (Miller, 1948) it was shown that prenuptial molt in experimental refractory birds is irregularly manifest and is certainly not fully repressed, although repression might be expected. Some degree of independence of the molt control and the light-pituitary-gonad mechanism was thereby suggested. In the later experiments, molt also has been irregular in amount and timing and hence is not reported in detail. In general the later observations support the earlier suggestion. However, it was noted that some birds of both species autopsied on March 25—individuals that had been and were refractory—were molting more completely than in a prenuptial molt; rectrices and remiges were being replaced as in a postbreeding or annual molt. Such a molt of course occurs normally when the gonads are regressed or in process thereof in a normally occurring refractory period in late summer.

DISCUSSION AND CONCLUSIONS

The prolongation of refractoriness appears to be due to constant fatigue of the response mechanism from light stimulation and not the result of conditioning the birds to a given light program such that further light increments would be needed to break the refractoriness. Apparently Golden-crowned Sparrows and White-crowned Sparrows started on 15½-hour days in the autumn have not had sufficient rest under a short light-day regime to overcome fatigue. They therefore fail initially and subsequently to recover responsiveness. These conclusions are in general agreement with Wolfson's finding (1952*b*) on Slate-colored Juncos and with his interpretations. In the crowned sparrows dealt with by me, the prolongation of refractoriness was extended to 203 days in the White-crown and to 310 days in the Golden-crown. There was no sign that it could not be extended even further beyond the experimentally determined limits. In the Golden-crown, this extension means that refractoriness was prolonged through and beyond the time of normal breeding, to the end of August, when natural populations would have arrived at a second, or subsequent, normal refractory period.

In crowned sparrows of both species, immatures as well as adults show autumnal refractoriness. The immatures display no differences in schedule nor in susceptibility to prolongation of refractoriness compared with the adults. This is significant for the reason that the immatures cannot be in need of rest or recovery from a period of previous gonadal activity, since they have never bred; their maturation of the pituitary-gonad mechanism has not proceeded far enough, apparently, so that they can respond properly, and, once fatigued by premature stimulation, the mechanism fails to respond indefinitely as in the adults. Wolfson (1952*b*) also has found immatures refractory in the State-colored Junco but apparently overlooked (p. 321) the fact that it had been reported earlier in the Golden-crown. The absence or restricted duration of refractoriness in immatures of the English Sparrow (Davis, 1953) constitutes a notably contrasting situation.

In the refractory condition, the gonads show in both species of crowned sparrow a small number of Leydig cells, most individuals thus progressing to histologic stage 2 of Blanchard. At this point, however, recrudescence is stopped. It may be, as suggested earlier (Miller, 1951), that the few Leydig cells of stage 2 indicate a low level of stimulation from gonadotropins from the pituitary and in a sense a capability of the pituitary-gonad machanism to respond. In the light of the later experimental evidence it merely appears that fatigue from overstimulation, presumably of the pituitary (see Miller, 1949), halts a further response. Bailey (1950) has shown experimentally that injection of prolactin of the pituitary is capable of blocking the gonadotropins of the pituitary and thus producing refractoriness to light stimulation. Whether prolactin naturally delivered to the blood stream is actually a factor in regulating and prolonging refractoriness in the birds herewith reported on, is of course unknown. If so, it is not easy to understand why the pituitary should produce excessive amounts of prolactin such as to block its own gonadotropins under the experimental conditions prevailing.

In the experiments conducted in 1950–51 and 1951–52 further data were accumulated to substantiate the time of occurrence of normal refractoriness in the fall. In the Golden-crown this normal period ends about November 5 and at this date shows, as might be expected, some individual variation. It is now shown that the natural termination point in White-crowned Sparrows, of at least two migratory races, comes slightly earlier, in the last week of October.

The experiments with White-crowned Sparrows, in which species the normal cycle has been so fully studied, show that, except for the slight difference in termination date of autumnal refractoriness, the response and the histological conditions are identical with those of the Golden-crown. In both species there is no ability as a consequence of purely inherent forces or rhythms to overcome the effects of an unusual light regime. Apparently internal rhythm in adults in these species in the pituitary-gonad mechanism is to be regarded as in part an inherent need for rest following prolonged activity, such rest to be derived from a period of short light-days as in Slate-colored Juncos. Whether or not an inherent tendency to resume activity after rest would proceed in the absence of normal light-days, that is, on a prolonged regime of winter-length days, is yet to be shown. Certainly resumption is initiated earlier than normal and is accelerated by adding light. As Wolfson (1952*a*:196) has suggested chiefly from work on juncos, internal rhythm is probably only an attribute which requires alternation of processes. The timing of these processes and their amplitude, in their many aspects, seem to be controlled in large measure by day length.

LITERATURE CITED

Bailey, R. E.

1950. Inhibition with prolactin of light-induced gonad increase in white-crowned sparrows. Condor, 52:247-251.

Blanchard, B. D.

1941. The white-crowned sparrows (*Zonotrichia leucophrys*) of the Pacific seaboard: environment and annual cycle. Univ. Calif. Publ. Zool., 46:1-178.

Blanchard, B. D., and Erickson, M. M.

1949. The cycle in the Gambel sparrow. Univ. Calif. Publ. Zool., 47:255-318.

Burger, J. W.

1949. A review of experimental investigations on seasonal reproduction in birds. Wilson Bull., 61:211-230.

Davis, J.

1953. Precocious sexual development in the juvenal English sparrow. Condor, 55:117-120.

Marshall, A. J.

1951. The refractory period of testis rhythm in birds and its possible bearing on breeding and migration. Wilson Bull., 66:238-261.

Miller, A. H.

1948. The refractory period in light-induced reproductive development of golden-crowned sparrows. Jour. Exp. Zool., 109:1-11.

1949. Potentiality for testicular recrudescence during the annual refractory period of the golden-crowned sparrow. Science, 109:546.

1951. Further evidence on the refractory period in the reproductive cycle of the golden-crowned sparrow, *Zonotrichia coronata*. Auk, 68:380-383.

Riley, G. M.

1936. Light regulation of sexual activity in the male sparrow (*Passer domesticus*). Proc. Soc. Exp. Biol. Med., 34:331-332.

Wolfson, A.

1945. The role of the pituitary, fat deposition, and body weight in bird migration. Condor, 47:95-127.

1952*a*. Day length, migration, and breeding cycles in birds. Sci. Monthly, 74:191-200.

1952*b*. The occurrence and regulation of the refractory period in the gonadal and fat cycles of the junco. Jour. Exp. Zool., 121:311-325.

Museum of Vertebrate Zoology, Berkeley, California, June 26, 1953.