THE NATURAL TERMINATION OF THE REFRACTORY PERIOD IN THE SLATE-COLORED JUNCO AND IN THE WHITE-THROATED SPARROW

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It has been demonstrated that birds of several passerine species show gonadal recrudescence within six or seven weeks, when given sufficient artificial increases in day length in late fall or in winter. Birds treated in late summer or early fall, however, do not respond. The period between regression of the gonad, normally at the end of the breeding season, and the time the gonad responds to photostimulation, has been designated the refractory period.

The experiments reported here were undertaken to determine by systematic study when the refractory period ends in the Slate-colored Junco *(Junco hyemalis)* and in the White-throated Sparrow *(Zonotrichia albicollis)*—species in which the natural termination of the refractory period had not been investigated. Secondarily, the effect of treatment with short days in the fall on the duration of the refractory period in these species was studied.

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INTRODUCTION

Rowan (1929) observed in his pioneering experiments that Slate-colored Juncos *(Junco hyemalis)* exposed to stimulating photoperiods begun before November 1 at Edmonton, Alberta, exhibited an "irregular and slow recrudescence" of the gonads. Juncos given gradual increases in day length after November 1 showed a "regular and extremely uniform recrudescence." Although Rowan's experiments did not deal with gonadal refractoriness directly, these results indicated that a refractory period occurs in this species. Wolfson (1952a) has reported on the dissipation of the refractory period in the Slate-colored Junco. A systematic study was not undertaken, but responses of groups exposed to stimulating photoperiods between August 27 and November 8 compared with responses of other groups placed in 20-hour day lengths on December 4 led to the conclusion that the end of the period occurs between November 8 and December 4 in Evanston, Illinois.

Approximate dates for the termination of the refractory period in other species have been reported. Miller (1948) found that the end of the refractory period at Berkeley, California, occurred between November 5 and 20 for both adult and immature Golden-crowned Sparrows *(Zonotrichia atricapilla).* More recently Miller (1954) has confirmed this and has shown that in at least two races of the White-crowned Sparrow *(Z. leucophrys),* termination occurs in the last week of October. His conclusions were based on responses of groups used over a period of years in a number of widely differing experiments. Wolfson (1945), also at Berkeley, obtained a response to supplementary light begun October 18 in a few White-crowned Sparrows. Oregon Juncos *(Junco oreganus)* treated at the same time did not respond. Farner and Mewaldt (1955), working with male White-crowned Sparrows *(Z. l. gambelii)* concluded that the refractory period ends, with individual variations, during the last two weeks of October and the first week of November at Pullman, Washington. All members of the groups exposed to 15-hour day lengths on November 8 and January 1 exhibited a significant gonadal response. Kendeigh (1941) found that in the House Sparrow *(Passer domesticus)* both sexes responded to gradually increased day lengths begun November 2 at Urbana, Illinois. The age of the birds was not given. Riley (1936), working at Iowa City, Iowa, found that when male House Sparrows were exposed to stimulating photoperiods begun September 30, immature birds responded, but adults did not. Davis (1953) reported the development of the gonads of immature House Sparrows in late spring, but Vaugien (1952) found refractoriness in immature House Sparrows in summer. Burger (1949) states that the refractory period probably ends in the Starling *(Sturnus vulgaris)* by mid-November at Hartford, Connecticut, but no data are given.

Regulation of the reproductive cycle by alternation of treatment with short days and treatment with long days has been demonstrated in a number of species and indicates the regulatory role of the environment in the termination of the refractory period. Wolfson (1954a) produced five cycles in the Slate-colored Junco and four in the White-crowned Sparrow in a year. Rowan (1929) obtained two cycles within a few months in the Slate-colored Junco. Miyazaki (1934) induced two cycles in the Mejiro *(Zosterops palpebrosa)* and Damsté (1947) produced three cycles in the Greenfinch *(Chloris chloris).* The results of Wolfson (1954a) and Burger (1947) showed that short days regulate the dissipation of the refractory period in the Slate-colored Junco and in the Starling, respectively.

METHODS

Slate-colored Juncos and White-throated Sparrows were trapped on the campus of Northwestern University during the fall migration of 1951. Evanston lies within the winter range of the Slate-colored Junco, and is in the path of migration for both species. The birds were kept in a large indoor aviary until the start of the experiments. Experimental birds and controls were housed in Hendryx flight cages (24″ x 15″ x 19″), with a maximum of seven birds per cage. The experimental rooms and conditions and feeding were identical to those described by Wolfson (1954a) and need not be repeated here.

In order to determine when the refractory period ends for the population as a whole, several groups were exposed to highly stimulating 20-hour photoperiods beginning on successive dates. Four groups of each species were transferred at two-week intervals. The initiation and duration of treatment for each group was as follows:

Group 1—November 3—49 days (autopsied December 22)
Group 2—November 18—48 days (autopsied January 5)
Group 3—December 2—49 days (autopsied January 20)
Group 4—December 16—46 days (autopsied January 31)

Three groups were pretreated with short days before being subjected to 20-hour day lengths to study the effects of such treatment on the subsequent response. A group of twelve juncos was treated with 9-hour day lengths beginning October 3. Thirty-one days later, November 3, they were transferred to the 20-hour room and treated for forty-eight days. They were autopsied December 21. Group 1 served as controls. Two groups of White-throated Sparrows were treated in the following manner. The first group was placed in the 9-hour room on October 2. Thirty-one days later, November 2, the birds were transferred to the 20-hour room and treated for forty-nine days. They were autopsied December 21. The second group was placed in the 12-hour room on October 1. Thirty-four days later, November 4, the birds were transferred to the 20-hour room and treated for forty-nine days. They were autopsied December 23.

Data were obtained on body weight, fat deposition, and reproductive activity. Weighing was done at two-week intervals. At each weighing birds were examined for fat deposits, which were recorded as little, medium, heavy or none (Wolfson, 1942). Fat deposition occurs as a response to increasing photoperiods in some species (Wolfson, 1952b). Judgments of lipid deposits were subjective, but differences between the classes were marked. Cloacal size was noted, and sperm smears were made from males whose cloacas were enlarged (Wolfson, 1952c). Gonads were fixed in Bouin's fluid. Testes were measured and prepared for histological study. Testicular volumes were computed from the measurements of the axes, using the formula for the volume of an ellipsoid. Stages of spermatogenesis were determined, using those described by Wolfson (1942), in which Stage 1 is minimum and Stage 5 the breeding condition. Ovaries were weighed, after treatment with 80% ethyl alcohol, on a Roller-Smith torsion balance with a sensitivity of 0.2 milligram. Ovarian follicles were measured. Degree of reproductive activity was estimated by observations on the gonads and the accessory reproductive organs. As activity increases, each ductus deferens and its seminal vesicle becomes enlarged and filled with sperm; a few large follicles differentiate in the ovary, the oviduct becomes convoluted, and its walls thicken.

Age was determined by examination of the skull at the time of autopsy. By December 20 many immature birds have skulls that are completely ossified. Since all birds were killed after that date, only those with incomplete ossification were recorded as immature.

RESULTS

Fat responses are given in Table 1. Gonadal responses are given in Table 2. These summaries mask the individual variation, which was marked in some cases as will be pointed out, but they exhibit well the differences between the groups.

Fat Responses—Slate-colored Junco—Eleven birds of group 1 showed an increase in fat. The one that did not respond, #414, lost 5.5% of its initial weight. The range of weight change was from —8.0% to +29.0%. The two males of group 2 that showed no response lost 1.1% and 3.8% of their initial body weight. The others gained from 1.2% to 26.4%. Body weight gain in group 3 was marked, ranging from 12.9% to 23.0%. In group 4 the increase was not quite so great as a whole. Individual variations, however, were greater, ranging from +6.3 per cent to +24.8 per cent. The controls showed changes ranging from —5.3 per cent to +14.0%. The latter bird, an immature female, was not as heavy as the others, both at the beginning and at the end. The birds pretreated with 9-hour days also showed great individual variation, ranging from —1.2 per cent to +25.7 percent.

Fat Responses—White-throated Sparrow.—Of the two birds of group 1 which showed increased fat, one increased in body weight 5.0 per cent. The other lost 13.5 per cent. The other birds lost from 8.1 per cent to 25.0 per cent of their initial weight. In group 2, the bird that increased its fat gained 0.4 per cent. The others ranged from a 4.6 per cent gain to a 5.3 per cent loss. Only one of the 5 birds in group 3 that showed increased fat gained weight. The gain was 2.9 per cent. The others lost from 1.2 per cent to 4.5 per cent. The two birds that did not show a fat response lost 3.6 per cent and 7.4 per cent of their

TABLE 1

FAT RESPONSES OF SLATE-COLORED JUNCOS AND WHITE-THROATED SPARROWS

Slate-Colored Juncos						White-Throated Sparrows					
Group	*Composition*	*Periods of Treatment*	*Fat Re-sponse* +	*Fat Re-sponse* —	*Average % change in body weight*	*Group*	*Composition*	*Periods of Treatment*	*Fat Re-sponse* +	*Fat Re-sponse* —	*Average % change inbody weight*
1	6♂♂, 6♀♀	Nov. 3–Dec. 22 (49)	11	1	+ 6.5	1	11♂♂, 1♀	Nov. 3–Dec. 22 (49)	2	10	—11.3
2	4♂♂, 3♀♀	Nov. 18–Jan. 5 (48)	5	2	+ 9.7	2	2♂♂, 2♀♀	Nov. 18–Jan. 5 (48)	1	3	— 0.6
3	4♂♂, 3♀♀	Dec. 2–Jan. 20 (49)	7	0	+17.1	3	3♂♂, 4♀♀	Dec. 2–Jan. 20 (49)	5	2	— 2.3
4	4♂♂, 3♀♀	Dec. 16–Jan. 31 (46)	7	0	+14.0	4	6♂♂, 1♀	Dec. 16–Jan. 31 (46)	0	7	—11.5
Controls	5♂♂, 2♀♀	Nov. –Jan. 31	4	3	+ 0.2	Controls	4♂♂, 2♀♀	Nov. –Jan. 31	4	3	+ 5.2
BIRDS PRETREATED WITH SHORT DAYS											
Birds pretreated with 9-hour days (31 days)	3♂♂, 9♀♀	Nov. 3–Dec. 21 (48)	9	3	+12.0	Birds pretreated with 9-hour days (31 days)	8♂♂, 4♀♀	Nov. 2–Dec. 21 (49)	4	8	— 8.8
						Birds pretreated with 12-hours days (34 days)	9♂♂, 4♀♀	Nov. 4–Dec. 23 (49)	1	12	—13.8

Total number of days of treatment appear in parentheses following date of autopsy. Number shown under (+) indicates birds that moved into a higher fat class. Birds shown under (—) moved into a lower class or remained the same.

TABLE 2

GONADAL RESPONSES OF SLATE-COLORED JUNCOS AND WHITE-THROATED SPARROWS

SLATE-COLORED JUNCOS							WHITE-THROATED SPARROWS						
Group	*Total No. of birds*		*Response and measurements (means)* +		−		*Group*	*Total No. of birds*		*Response and measurements (means)* +		−	
1	12	♂♂	3	36.1	3	1.0	1	12	♂♂	2	11.2	9	0.7
		♀♀	4	12.7	2	2.2			♀♀	1	6.6		
2	7	♂♂	4	65.5			2	4	♂♂	1	82.3	1	0.8
		♀♀	2	19.7	1	2.6			♀♀			2	5.1
3	7	♂♂	4	111.9			3	7	♂♂	3	117.7		
		♀♀	3	16.7					♀♀	2	13.8	2	6.6
4	7	♂♂	4	112.5			4	7	♂♂	6	130.4		
		♀♀	3	26.5					♀♀	1	13.8		
Controls	7	♂♂			5	0.4	Controls	6	♂♂			4	1.0
		♀♀			2	1.7			♀♀			2	3.4
BIRDS PRETREATED WITH SHORT DAYS													
Birds pretreated with 9-hour days	12	♂♂	3	87.2			Birds pretreated with 9-hour days	12	♂♂	3	73.0	5	0.5
		♀♀	8	14.1	1	2.2			♀♀	2	18.8	2	5.9
							Birds pretreated with 12-hour days	13	♂♂			9	0.6
									♀♀			4	5.8

Testis volumes in cubic millimeters are given following number of males responding (+) or not responding (−). Ovarian weights (in milligrams) are given following number of females responding or not responding.

initial weight. Loss in group 4 ranged from 2.5 per cent to 26.2 per cent. The latter bird was dead in the cage on the morning of autopsy, although it had been alive the evening before. The controls showed changes ranging from —1.3 per cent to +13.6 per cent. The two birds that did not show increased fat also lost weight. The birds pretreated with 9-hour photoperiods lost from 0.9 per cent to 17.7 per cent. Again, there was no correlation between increased fat and degree of change in body weight. Those pretreated with 12-hour photoperiods lost from 6.5 per cent to 23.2 per cent of the initial body weight.

Gonadal Responses—Slate-colored Junco.—Individual responses varied considerably in group 1. Two of the males exhibited maximum activity. Histological observation showed that they had reached stage 5. Testis volumes ranged from 49.4 to 61.5 mm^3. In a third bird, the volume was 5.7 mm^3 for the left testis and 8.0 mm^3 for the right. In males that did not respond the testicular volumes ranged from 0.5 to 1.36 mm^3. In responding females, the activity ranged from moderate to maximum, with ovarian weights from 10.0 to 17.6 mg. Activity was not strictly correlated with ovarian weight. In the bird showing maximum activity the ovary weighed 11.4 mg. Several large follicles were present. The oviduct weighed 18.2 mg. The ovaries of the females that did not respond weighed 2.0 and 2.4 mg. The activity of the responding males in group 2 ranged from little to maximum. Testicular volumes ranged from 2.5 to 134.4 mm^3. Two males were at stage 5; one was at stage 4; the fourth was at stage 2. One female showed minimum activity, with an ovarian weight of 2.6 mg. One showed little activity, with an ovarian weight of 11.8 mg. The third ovary weighed 27.6 mg. and activity was submaximum. In group 3 all the males were at maximum; testicular volumes ranged from 22.0 to 205.3 mm^3. Two females exhibited submaximum activity, with ovarian weights of 9.6 and 16.6 mg. The third was at maximum with an ovarian weight of 23.8 mg. All the males of group 4 showed maximum activity, with testicular volumes ranging from 53.0 to 179.5 mm^3. One female showed submaximum activity, with an ovarian weight of 17.2 mg. The other two were at maximum, with ovarian weights of 26.2 and 36.0 mg. The controls all showed minimum activity, with the exception of one in which the testis was in stage 2. Volumes ranged from 0.2 to 0.7 mm^3. Ovaries weighed 1.2 and 2.2 mg. The last two groups, therefore, showed comparatively uniform responses.

In the group pretreated with 9-hour days, the three males were at maximum, with testicular volumes ranging from 57.1 to 108.9 mm^3. The females that responded ranged from little to maximum activity. Ovarian weights ranged from 7.2 to 22.2 mg., again with no absolute relationship between weight and activity.

Gonadal Responses—White-throated Sparrows.—One responding male of group 1 was at stage 2 and showed little activity, with testicular volumes of 2.0 and 2.1 mm^3. The other was at stage 4, had testicular volumes of 19.1 and 21.6 mm^3, and showed moderate activity. Testicular volumes of males not responding ranged from 0.4 to 1.1 mm^3. The one female showed moderate activity and the ovary weighed 6.6 mg. In group 2 the male that responded exhibited maximum activity, and was at stage 5. Testicular volumes were 86.7 and 77.9 mm^3. The other male showed minimum activity and was at stage 1. The two females showed minimum activity. Ovarian weights were 4.8 and 5.4 mg. The three males of group 3 exhibited maximum activity. Testicular volumes ranged from 68.8 to 187.0 mm^3. One female that responded showed maximum activity, the other little. Ovarian weights were 22.0 and 5.6 mg., respectively. The other two showed minimum activity with ovarian weights of 6.2 and 7.0 mg. In group 4 all the birds showed maximum activity. Testicular volumes ranged from 58.1 to 217.2 mm^3. In the controls the volumes of the testes ranged from 0.4 to 2.4 mm^3. Ovarian weights were 2.0 and 4.8 mg.

In the group pretreated with 9-hour days, the testes of the three males that responded were at stage 5. Two showed submaximum activity, the other maximum. Testicular volumes ranged from 24.8 to 114.0 mm^3. In males that did not respond testicular volumes ranged from 0.3 to 0.8 mm^3. One female that responded showed moderate activity, with an ovary weight of 14.6 mg. The other showed submaximum activity with an ovarian weight of 23.0 mg. Ovarian weights in females that did not respond were 5.2 and 6.6 mg. In the group pretreated with 12-hour photoperiods testicular volumes ranged from 0.3 to 1.2 mm^3. Several were at stage 2, although all exhibited minimum activity. Ovarian weights ranged from 3.6 to 9.2 mg.

Gonadal Responses in Relation to Fat Responses.—Fat responses of juncos in groups 3 and 4 correlate well with gonadal responses. All birds showed gonadal recrudescence and increased fat deposits. Juncos of the other two groups were not as consistent. In group 1 several birds showed fat increases with minimum gonadal activity. In group 2 the only bird that did not exhibit a gonadal response had increased fat deposits and gained slightly in weight. Two other birds lost slightly in weight and showed no fat response, but gonadal response was evident.

The White-throated Sparrows, with few exceptions, lost weight during the course of the experiments. Three males and one female of group 3 showed both fat and gonadal responses, as did one of the males in group 2. No other bird of the first four groups showed both. Group 4 was consistent in showing maximum gonadal activity, no fat response, and considerable weight loss.

The control groups of both species varied in the amount of fat deposits. The only junco that did not show a gonadal response among the group pretreated with 9-hour photoperiods also did not show a fat response and lost 1.2 per cent of its initial weight. The other two birds that did not show fat responses gained a little more than 1 per cent of their initial weight. These changes are not significant. One male and one female of the group of White-throated Sparrows pretreated with 9-hour day lengths showed both fat increases and gonadal increases. Only one bird of the group pretreated with 12-hour day lengths showed a fat increase. It lost 11.5 per cent of its body weight.

No differences in fat or gonadal responses were found between age groups or sexes. The impression was gained, however, that the female juncos did not respond as strongly as the males.

DISCUSSION AND CONCLUSIONS

The Fat Response.—The difference in fat response between the White-throated Sparrow and other species studied, including the Slate-colored Junco, is marked. My results in this junco agree with those in the Oregon Junco and the White-crowned and Golden-crowned Sparrows (Wolfson, 1945; Miller, 1948). The White-throated Sparrow presents a somewhat different problem. The majority of my birds exhibited no fat deposition, and weight loss was almost universal except in the controls. Wolfson (1953) reported heavy fat deposition and a weight increase in eight out of nine White-throated Sparrows placed in stimulating day lengths on January 25. Wolfson (1954b) also reported a less abrupt increase in fat deposition that took place in birds under natural day length conditions in late January and early February. It seems possible that fat deposition and gonadal recrudescence are regulated differently in this species, and that the birds are refractory with respect to fat deposition for a somewhat longer period of time in the fall than with respect to gonadal recrudescence.

Natural Termination of the Refractory Period.—Results of the investigations reported here indicate that most Slate-colored Juncos are able to respond to stimulating photoperiods by November 18, and that probably all are responsive by December 2. The response of juncos exposed to long days on November 18 was not complete, either quantitatively or qualitatively. However, more than half the November 3 group exhibited a gonadal response, and all but one showed fat deposition. In earlier experiments begun December 4 practically all individuals were responsive (Winn, 1950; Wolfson, 1952b). Rowan (1929) obtained a good response in a group of seventy-five juncos given supplemental illumination beginning November 1. Possibly the latitude was a factor in obtaining this early response. Day length at Edmonton, Alberta, is much shorter by November 1 than it is at Evanston, and short days are known to speed the termination of the refractory period, as shown by this study and also by Burger (1949), Wolfson (1952b, 1952c) and Miller (1954).

For the White-throated Sparrow, the refractory period ends in the population at Evanston sometime between December 2 and 16. A few individuals gave a gonadal response when exposed to 20-hour days November 3 or November 18. Most of the December 2 group responded, but the response was not complete. In the December 16 group all individuals attained maximum gonadal activity.

Pretreatment with 9-hour days hastened the end of the refractory period in the Slate-colored Junco. The results of the experiments with the White-throated Sparrows are not as conclusive. The fact that five out of twelve birds pretreated with 9-hour day lengths responded, and responded to a greater degree than group 1, indicates that an effect is present. However, a difference in response to treatment with 9-hour days is evident in these species. Lack of response in White-throated Sparrows pretreated with 12-hour day lengths might seem to indicate that this photoperiod failed to prepare the birds for the subsequent response to long days. A longer duration of treatment with 12-hour photoperiods, from 3-6 months however, has been effective in a few individuals (Wolfson and Shank, unpublished data, and Wolfson, unpublished data).

In both species the rate of gonadal recrudescence for responding individuals in the earlier groups appears to be slower than the rate in later groups. Earlier individuals, although treated for the same length of time, did not show as much activity as later individuals.

SUMMARY

Slate-colored Juncos were transferred from natural conditions of day length to 20-hour day lengths at two-week intervals beginning November 3. Both gonadal and fat responses showed that the refractory period ends in the population at Evanston, Illinois, between November 18 and December 2, although some individuals respond earlier.

Gonadal responses in a similar experiment with White-throated Sparrows indicate that the refractory period ends in this species some time between December 2 and 16. Fat responses were not obtained.

Juncos that were pretreated with thirty-one 9-hour days before transfer to 20-hour day length on November 3 showed both a fat and a gonadal response after forty-eight days of photostimulation. Compared with the controls, the treatment with 9-hour days accelerated the dissipation of the refractory period.

Five out of twelve White-throated Sparrows pretreated with 9-hour photoperiods for 31 days before stimulation with 20-hour photoperiods showed a gonadal response. White-throated Sparrows pretreated for thirty-four days with 12-hour photoperiods gave no response to subsequent treatment with long days.

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