GONADAL AND FAT RESPONSE TO A 5:1 RATIO OF LIGHT TO DARKNESS IN THE WHITE-THROATED SPARROW

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In the course of experiments in which the premigratory physiological state was induced in winter in juncos, White-throated Sparrows, and other fringillids, a few individuals were subjected suddenly to constant, long day lengths. When compared with birds receiving gradual increases in day length, it was noted that these individuals responded sooner. On the basis of this observation it seemed possible that the amount of light which a bird received each day, or the total amount within a given period of time, might determine the time of response. Hence, it was postulated that summation of day lengths or the daily dose of light, rather than increasing day lengths as such, might be the critical environmental factor in determining the time of migration and the time of breeding. If this were true, the constant day lengths or decreasing day lengths to which equatorial and transequatorial migrants are subjected might play a role in the timing of the stimulus for spring migration. Summation of day lengths could also explain the timing of breeding in the tropics.

To test these postulates several series of experiments were performed and the pertinent observations of other investigators were studied critically. The results, which were reported briefly (Wolfson, 1952*a*) indicated that the rate of response was related to the length of day. None of the experiments, however, was designed to differentiate between duration of light, duration of darkness, or proportion of light to darkness as the effective stimulus. The purpose of this paper is to report the first of a series of experiments which were designed to determine the role of each of these factors.

If the effective stimulus is the amount of light which a bird receives in a given period of time, or the ratio of light to darkness, then birds receiving 20 hours of light per day in one dose, or in four equal doses of 5 hours, should respond equally well. In both cases they would receive the same ratio of light to darkness (5 to 1) and the same total amount of light (20 hours) and darkness (4 hours) per 24-hour period. A basic difference, however, would be the length of each cycle; in one case it would be 24 hours, in the other only 6 hours.

Several experiments had already been performed in our laboratory in which birds were exposed to 20 hours of light per day at various times of the year. They showed that White-throated Sparrows and juncos respond well to such a light schedule. Some of these data have been published (Wolfson, 1952*b*).

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MATERIALS AND METHODS

At the time the present experiment was conceived only a small group of birds remained in our aviaries. Included were 9 White-throated Sparrows (*Zonotrichia albicollis*) and one Slate-colored Junco (*Junco hyemalis*). These birds had been trapped in October in fall migration and had been held under natural conditions of day length until the experiment began. They were prepared for the experiment on January 18 at which time they were weighed, banded, and their fat deposition and cloacal condition recorded. The experiment began on January 25 and was terminated on April 5, 1952, 71 days later.

The birds were housed in three Hendryx flight cages (24″ × 15″ × 19″) which were placed in a light proof aviary (7′ long × 5′ wide × 8′ high). Lighting was provided by two 40-watt white fluorescent bulbs (Sylvania) and controlled automatically as follows: (1) on at 9:00 a.m., off at 2 p.m.; (2) on at 3 p.m., off at 8 p.m.; (3) on at 9:00 p.m., off at 2:00 a.m.; (4) on at 3:00 a.m., off at 8 a.m. Intensity within the cages varied from 20-foot candles at the bottom of the cage to 50-foot candles at the perches nearest the lights. Temperature was practically constant at 74°F., but it occasionally fell to 72°F. or increased to 75°F.

Food consisted of unmixed canary seed supplemented at regular intervals with millet seed and Gaines dog meal. Food and water were available at all times.

Observations were made on fat deposition, body weight, gonads, accessory sex organs, and occurrence of song. Presence of sperm and sperm motility were determined

Table 1

Gonadal and Fat Response in Birds Exposed to a 5:1 Ratio of Light to Darkness in 6-hour Cycles

No., sex, plumage	Body weight and fat deposition				Reproductive organs			
	Initial weight and fat	Fat response	Response weight and fat	Per cent change	Autopsy date	Gonadal response	Measurements	Activity
736 ♂ int.	27.0 L	+	31.9 H	+18.2 +27.1	Feb. 22 (28)	+	7.3×4.3— 70.67 5.2×4.7— 60.15	Moderate. Stage 4.
771 ♂ int.	28.2 L	—	24.8 N	—12.1	Apr. 5 (71)	+	3.1×2.6— 10.97 8.7×7.1—229.63	Moderate. Non-motile sperm. Stage 5.
773 ♂ im.	31.8 H	+	34.6 H	+ 8.8 +12.3	Mar. 22 (57)	+	6.5×4.9— 81.72 6.0×5.5— 95.03	Submaximum. Motile sperm. Stage 5.
717 ♀ im.	25.3 L	+	34.4 H	+36.0 +45.8	Apr. 5 (71)	+	Ovar. — 51.2 Ovid. — 37.2	Maximum. L. foll. — 2.0
721 ♀ im.	25.5 L	+	35.8 H	+40.4 +50.4	Apr. 5 (71)	+	Ovar. — 17.0 Ovid. — 24.6	Moderate. Follicles .4—.6
725 ♀ im.	26.8 L	+	28.9 H	+ 7.8 +25.1	Apr. 5 (71)	+	Ovar. — 62.4 Ovid. — 33.4	Maximum. L. foll. — 1.0
735 ♀ int.	26.9 L	+	29.8 H	+10.8 +28.5	Mar. 22 (57)	+	Ovar. — 796.4 Ovid. —1606.6	Ready to ovulate. L. foll. — 9.0. Three other foll. 3.8 — 8.0
744 ♀ im.	24.3 N	+	28.9 H	+18.9 +23.5	Apr. 5 (71)	+	Ovar. — 22.0 Ovid. — 13.2	Moderate. L. foll. — .9
775 ♀ im.	27.3 L	+	33.0 H	+20.9 +32.5	Mar. 22 (57)	+	Ovar. — 52.8 Ovid. — 50.2	Maximum. L. foll. — 2.0
419 ♀ (Junco)	18.5 L	+	23.9 H	+29.2 +36.6	Apr. 5 (71)	+	Ovar. — 38.8 Ovid. — 20.8	Maximum. L. foll. — 2.0

Body weight and fat deposition: Initial weight is the body weight in grams at the start of the experiment. Fat classes are abbreviated as follows: N—none, L—little, M—medium, H—heavy. Fat response is given as positive or negative. Response weight is the highest body weight reached if there was a fat response, or the lowest body weight when the response was loss of weight. The per cent change is given first in terms of the initial weight; under this is the per cent change in terms of the lowest body weight, which occurred on February 1 or February 8. The figure in parenthesis under the autopsy date is the number of days of experimental treatment.

Reproductive organs: The long and short axes (in mm.) of the left testis are given first for each individual. This is followed by the volume ($mm.^3$). Measurements for the right testis are given under those of the left. For the females, weights of ovaries and oviducts are given in milligrams. Measurements of follicles are the diameter (mm.) of the largest follicle, or when one is not differentiated, the diameter of the follicles in general. The terms moderate, submaximum, and maximum summarize the activity of the testis, as indicated by spermatogenesis and development of the glomus (seminal vesicle), and the activity of the ovary, as indicated by the size of the follicles and the condition of the oviduct.

by means of the method described recently (Wolfson, 1952*c*). Fat deposits were classified as little, medium, heavy, or none, based on their amount and distribution (Wolfson, 1942). Body weight was determined by regular weighings. These occurred at approximately weekly intervals during the first half of the experiment in order to follow the rate of response. The fat condition was recorded with each record of body weight. Weighing was facilitated by mild etherization of the birds. During each handling observations were made also on the cloaca, which changes in relation to gonadal activity. The type of crown and head plumage was classified as immature, intermediate, or adult, but the type of plumage is not known to be directly related to the age of the bird.

At the time of autopsy the lower part of the back with its reproductive organs was preserved in Bouin's fixative. After transfer to 80 per cent alcohol the length and width of the testes were measured as they lay on the dorsal body wall; their volume was calculated by using the formula for the volume of an ellipsoid. The diameter of the follicles in the intact ovary were measured, and observations and measurements were made on the oviduct. The inactive oviduct is a relatively thin and straight tube. As the oviduct grows its walls become thicker and convoluted. The ovary and oviduct were weighed after transfer to 80 per cent alcohol on a Roller-Smith torsion balance. The testes were studied histologically. The stages used to indicate degree of spermatogenesis are those of Wolfson (1942), where stage 1 is minimum and stage 5 is the breeding condition.

RESULTS

The results are presented in table 1 and figure 1.

Fat deposition and body weight.—All the birds, with one exception, showed a strong fat response. In some individuals large amounts of fat were deposited and with great rapidity. The average of the per cent increase in body weight in the White-throats was 22.8 per cent, when the initial weight is used as the starting point. However, when the lowest weights of February 1 and 8 are used, the average of the per cent increase is 33.7 per cent. Number 771 is omitted in these calculations since it did not show a fat response. Number 773 is also omitted since it was initially fat, but in figure 1 it is interesting to see that in spite of this initial condition it showed the same pattern of changes in body weight. The comparable figures for the Slate-colored Junco in the experiment are 29.2 per cent and 36.6 per cent, respectively.

In figure 1 the body weight and fat deposition are plotted against time to show the rate of response. In general there was one pattern of response: a decrease in body weight, reaching a minimum in one to two weeks after the start of the experiment, followed by an increase in body weight which reached its peak in about three weeks, and, finally, a loss in weight during the last half of the experiment. Increases and decreases in fat deposition accompanied these changes in body weight, as shown in the figure. The lapse of time from the start of the experiment until the fat response began was 11 days ± 3 for nos. 419 and 744, 18 days ± 3 for nos. 717, 725, 735, 736, 25 days ± 3 days for no. 721, and sometime after 35 days for no. 775. For the 7 birds where the onset is known within 3 days the average time of onset was approximately 16 days (± 3) after the start of the experiment. The lapse of time from the onset of fat deposition until a medium or heavy deposit was reached for the first time in these same 7 birds was 7 days (± 3). The individual curves are presented in the figure rather than the average for all of the birds in order to emphasize the variations in amount and time of response. Those on the right side of the graph were more or less similar in rate of response, but those in the upper part did not respond as well quantitatively. Those on the left side of the graph differed from the others in being a little slower in responding (no. 744), much slower in responding (no. 775), or showing a heavy deposition of fat throughout the experiment (no. 773).

One especially noteworthy response was that of no. 721. For two weeks its weight had been fairly constant at about 24.0 grams. It began to respond sometime during the week following February 15, and on February 22 it had increased its weight to 26.4 grams (an increase of 10.9 per cent from its weight on February 15). Its fat deposition changed also from none to medium. One week later, on February 22, it weighed 35.8 grams, an increase of 9.4 grams or 50.4 per cent, and showed a very heavy fat deposition! For this period of 7 days this bird was adding weight on the average of 1.33 grams per day, a truly remarkable rate.

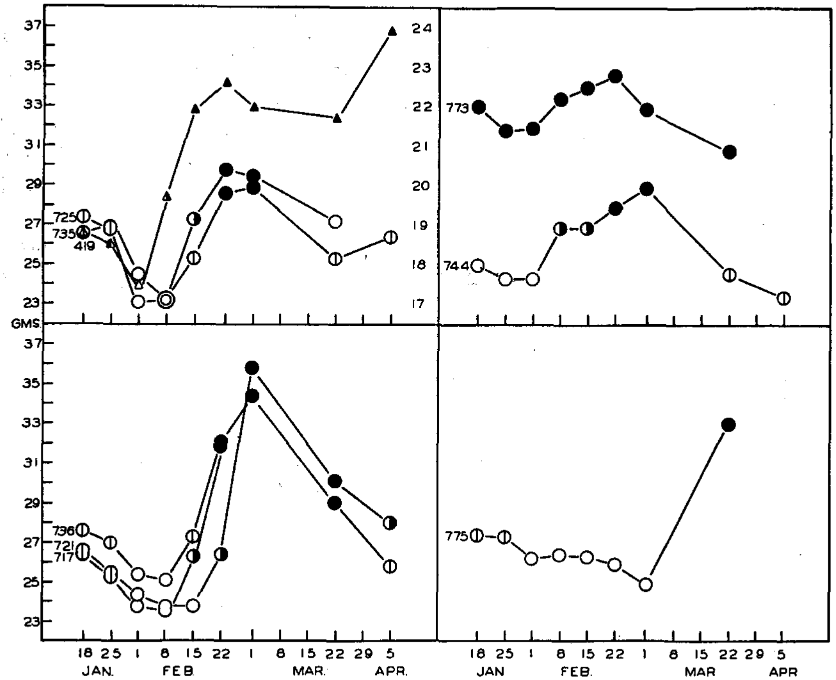

Fig. 1. Changes in body weight and fat deposition of birds showing response. Circles, White-throated Sparrows; triangles, Slate-colored Junco; scale for body weight of junco on right side of upper left graph. Fat deposition indicated: open symbol, no fat; line through symbol, little fat; half solid symbol, medium fat; solid symbol, heavy fat. Experiment began on January 25.

Gonads and accessory reproductive organs.—All the birds showed a strong gonadal response with concomitant development of the accessory reproductive organs. The most unusual response, however, was that of female no. 735 which was ready to ovulate after 57 days of experimental treatment. The largest follicle was 9.0 mm. in diameter, and three additional large follicles ranged from 3.8 to 8.0 mm. The oviduct was fully developed. This is the most advanced stage of ovarian and oviducal development we have ever seen in our laboratory. Ordinarily the females do not respond well to additional lighting. Whether this bird would have ovulated is impossible to say. In view of the strong response of this female, the responses of the other females were compared with birds which responded to 20-hour days when exposed at various times of the year, and with birds with naturally enlarged reproductive organs (spring and summer). These comparative data are presented in table 2. Also given in table 2 are the data for birds that have inactive ovaries and oviducts. The numbers of individuals are much too small for statistical analysis, but it is interesting to see that the average weights of the ovaries and oviducts of the birds in the present experiment (exclusive of no. 735) are considerably larger than the average weights for birds with active reproductive organs. The only other highly developed female condition we have seen in our laboratory was in a Whitethroat which was captured in spring migration and exposed to 24 hours of light per day beginning May 23. When autopsied on July 2 its ovary weighed 91.6 milligrams and its largest follicles ranged from 2.2 to 3.7 mm.; its oviduct weighed 217.8 milligrams.

The rapid development of the testes is shown by no. 736 which showed sperm formation and moderately developed seminal vesicles after only 28 days. In no. 773 the cloacal protuberance reached submaximum size and motile sperm were obtained for the first time on March 2, 37 days after the start of the experiment; sperm production continued until autopsy on March 22. The marked asymmetry of the testes in no. 771 was also reflected in the seminal vesicles. The left one weighed 7.6 mg. and contained no sperm; the right one weighed 11.8 mg. and contained sperm. Despite its small size the left testis

Table 2

Weights of Ovaries and Oviducts in White-throated Sparrows under Various Conditions

	Treatment or condition	Ovary Mean wt. (mgs.)	Ovary Range	Oviduct Mean wt. (mgs.)	Oviduct Range
A	5:1 ratio of light to darkness in a 6-hour cycle.	166.9 (6)[1]	17.0–796.4	294.2 (6)	13.2–1606.6
		41.1[2] (5)	17.0– 62.4	31.7[2] (5)	13.2– 50.2
B	20-hours light per day from Jan. 4 to Feb. 21.	22.1 (6)	18.8– 26.4	11.3 (6)	6.2– 22.8
C	24-hours light per day from May 23 to July 2.	41.3[3] (3)	10.4– 91.6	81.7[3] (3)	12.8– 217.8
D	Natural day lengths (from the wild and captivity). (a) May and June	34.1 (6)	29.4– 39.6	14.4 (6)	9.6– 23.6
	(b) July	18.3 (3)	15.6–23.4	5.5 (3)	4.8– 6.8
E	Inactive (from the wild and captivity).	5.4 (13)	2.0– 7.0	2.3 (13)	1.0– 4.2
F	Active (from the wild and experiments).	27.6[4] (13)	18.8– 39.6	13.0[4] (13)	6.2– 23.6

[1] Number of birds in the group.
[2] These means calculated without using the data from no. 735.
[3] These figures include data from one highly developed bird, no. 497 (ovary, 91.6; oviduct, 217.8).
[4] The data from no. 735 and no. 497 were not included in calculating these means; also omitted were the data from the 6-hour cycle experiment.

had reached stage 5. In both testes some tubules showed signs of regression. Non-motile sperm were obtained on March 1 and again on March 22 in this bird.

The first signs of cloacal change were seen in nos. 773 and 717 on February 15. On February 22, 8 out of the 10 birds showed a cloacal response, and by March 1 all of the birds had responded.

Song.—Singing was heard for the first time on February 2, but it was weak, occasionally incomplete, and infrequent until February 11. On that date it became normal in volume and length and occurred frequently until the end of the experiment.

DISCUSSION AND CONCLUSIONS

Despite the small number of birds involved, the results indicate clearly that birds on a 6-hour cycle with 5 hours of light and 1 hour of darkness showed a strong fat and gonadal response. The extent and rapidity of response is similar to that in birds which are exposed to 20 hours of light per day. However, two possible differences may exist. In a 6-hour cycle the females show a tendency toward a greater reproductive response and the fat response of the group as a whole tends to be greater. The fat response must be interpreted with caution, however, since many White-throats (in captivity and under natural conditions) show increases in body weight and fat deposition in winter (Wolfson, unpublished data, and Odum, 1949).

The results are interpreted as supporting the thesis that the daily dose of light regulates the rate of the response. It must be borne in mind, however, that the proportion of light to darkness per 24 hours and per cycle was the same. Therefore, the possibility remains that the proportion of light to darkness in a given cycle, rather than the daily dose of light, is the critical factor in determining the rate of response.

In contrast to our results it has been shown recently in Bobwhite Quail (Kirkpatrick and Leopold, 1952) and in the White-throated Sparrow and Slate-colored Junco (Jenner and Engels, 1952) that the same dose of light per 24 hours does not give the same response. When the daily amount of light was given in one dose no gonadal response occurred. However, when the dark period was interrupted for a short time with a period of light, the birds showed a gonadal response. The conclusion of these authors is that the duration of the period of darkness is a major controlling factor in the photoperiodic response. This is certainly one possible interpretation of some of the results which have been reported so far, but the exact roles of light and darkness and their relation to each other still remain to be determined. Moreover, species differences and seasonal differences in physiological state must be taken into account. For example, in the late summer and fall short days or increased amounts of darkness are necessary to prepare juncos for subsequent response to light (Wolfson, 1952*b*). Finally, the possible stimulus of the proportion of light to darkness in a given cycle must not be overlooked.

LITERATURE CITED

Jenner, C. E., and Engels, W. L.

1952. The significance of the dark period in the photoperiodic response of male juncos and white-throated sparrows. Biol. Bull., 103:345-355.

Kirkpatrick, C. M., and Leopold, A. C.

1952. The role of darkness in sexual activity of the quail. Science, 116:280-281.

Odum, E.

1949. Weight variations in wintering white-throated sparrows in relation to temperature and migration. Wilson Bull., 61:3-14.

Wolfson, A.

1942. Regulation of spring migration in juncos. Condor, 44:237-263.

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.

1952*c*. The cloacal protuberance—a means for determining breeding condition in live male passerines. Bird-Banding, 23:159-165.

Department of Biological Sciences, Northwestern University, Evanston, Illinois, February 10, 1953.