7-1983

Effects of Temperature on Testicular Photosensitivity in the White-Throated Sparrow (Zonotrichia Albicollis)

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1983

EFFECTS OF TEMPERATURE ON TESTICULAR PHOTOSENSITIVITY IN THE WHITE-THROATED SPARROW (*ZONOTRICHIA ALBICOLLIS*)

A Thesis

Presented to

the Faculty of the Department of Biology

Western Kentucky University

Bowling Green, Kentucky

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Laurel Prinz Matthews

July 1983

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EFFECTS OF TEMPERATURE ON TESTICULAR PHOTOSENSITIVITY IN THE WHITE-THROATED SPARROW (ZONOTRICHIA ALBICOLLIS)

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ACKNOWLEDGEMENTS

I wish to express sincere thanks to my major professor, Dr. Blaine Ferrell, for suggestion of this topic and his patience and guidance throughout the project. Thanks are also due to the other members of my committee, Drs. Gary E. Dillard and Joe E. Winstead for their instruction and reviewing of this paper. Contributions made by Ms. Yvonne Stifel, Ms. Bobbi Dowden, and Mr. Rodney McCurry are also greatly appreciated.

I would like to dedicate this manuscript to my husband, Terry L. Matthews, whose love, encouragement, and technical assistance contributed directly to the completion of this work.

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Laurel Prinz Matthews July 1983 34 pages

Directed by: Drs. Blaine R. Ferrell, Gary E. Dillard, and Joe E. Winstead

Department of Biology Western Kentucky University

It has been shown in studies involving many temperate-zone avian species that annual variation in day length is a major environmental factor influencing the timing of seasonal events such as gonadal development, molt, fat deposition, and migration. The mechanism whereby these birds measure day length involves a circadian rhythm of photosensitivity which is entrained by the daily photoperiod. If light occurs such that it coincides with the photosensitive phase of this rhythm, an event such as gonadal recrudescence is induced. This study was carried out in photosensitive White-throated Sparrows in winter and spring of 1982 to explore the possibility that temperature might modify the expression of the circadian rhythm of testicular photosensitivity. Upon treatment with interrupted-night photoperiods, birds held on LD 9:15 at temperatures averaging 27.6 C exhibited a daily rhythm in testicular photosensitivity, whereas birds held on LD 9:15 at temperatures averaging 3.7 C did not show such a daily rhythm. These results support the hypothesis that temperature modifies the timing of certain seasonal events in the White-throated Sparrow by

influencing the expression of a circadian rhythm of photosensitivity.

INTRODUCTION

During the past several decades, much research has been done in regard to understanding the mechanisms by which photoperiodic organisms measure day length. It is now generally accepted that length of the daily period of light and its seasonal changes play a fundamental role in the regulation of the annual cycles of many plants and animals. It has been shown in numerous studies involving different avian species of temperate zones that day length is important in synchronizing the reproductive cycle with the environmental cycle such that reproduction occurs at a time of year when breeding success is most likely (Meier and Ferrell 1978). Seasonal variation in day length is a major factor influencing the timing of events such as gonadal development, molt, migratory fat deposition, and migratory behavior in birds. Photoperiodic control of the annual reproductive cycle has been known since the seventeenth century when Dutch bird netters produced singing decoys in autumn in order to net migrants by holding males on reduced light in spring and summer (Hoos 1937 in Farner 1964). A correlation between increase in gonad size and the lengthening days of spring had been frequently observed (Etzold 1891, Loisel 1900-1902 in Allender 1936); however, formal experimentation in this area was not initiated until 1925 when it was discovered that premature spermatogenesis and vernal migration could be

induced out of season in male Dark-eyed Juncos (Junco hyemalis) by adding several hours of artificial illumination to natural winter day lengths (Rowan 1925, 1926). Bissonnette (1930), working with Sturnus vulgaris, confirmed Rowan's report (Rowan 1938; Bissonnette 1937). It has been demonstrated using different avian species that regulation of testicular growth involves a circadian rhythm of photosensitivity (Hamner 1963, 1964; Farner 1964, 1965; Menaker and Eskin 1967; Follett and Sharp 1969; Turek 1974; Meier 1976; Meier and Ferrell 1978; Kumar and Tewary 1982). Elliot et al. (1972) demonstrated this mechanism in mammals. Bünning (1936, 1960) was the first to propose a mechanism based on circadian rhythms to explain photoperiodism in plants and animals. According to this hypothesis, light has a dual action in photoperiodic systems. The onset of light entrains or sets the timing of a rhythm of photosensitivity to the inductive effects of light. If the daily photoperiod is of sufficient length, light will occur coincident with the photosensitive (photoinducible) phase of the photosensitivity rhythm and will induce a physiological process such as gonadal development, a response normally produced only by long day lengths. Light coinciding with any other phase of the rhythm of photosensitivity will not affect the gonads. As first shown by Hamner (1963) and supported by numerous studies (Farner 1964, 1965; Menaker and Eskin 1967; Follett and Sharp 1969; Turek 1974; Meier 1976; Meier and Ferrell 1978; Kumar and Tewary 1982), induction does not depend on

the length of the photoperiod but rather on the time at which light occurs.

Few investigations have been directed toward studying proximate factors other than light which might influence the timing of events annually. Prior to the classical experiments of Rowan (1938), it was assumed that reproduction in temperate latitudes was regulated by the warming temperatures of spring (Marshall 1959). After Rowan's work showing the significance of light, the importance of other factors such as temperature was discounted by many. Some of Rowan's original work showing recrudescence in Dark-eyed Juncos at temperatures of -47 C seemed to indicate the relative unimportance of temperature in the avian reproductive cycle. Spermatogenesis was induced independently of rising temperatures. Likewise, Kendeigh (1941) reported that in English Sparrow (Passer domesticus), exposure to fluctuating outdoor temperatures did not inhibit gonadal development under a lengthened photoperiod. Results of other studies, however, have indicated that temperature is an important proximate factor involved in timing of reproduction. Results of one experiment wherein the stage of gametogenesis in feral birds was examined at exactly the same time of year and locality during two successive winters, one unusually cold and the other extremely mild, demonstrated the inhibiting effect of cold temperature and the accelerating effect of mild temperature (Marshall 1959). Burger (1948) found that under favorable photoperiodic conditions, recrudescence in Starlings proceded at a faster rate when

birds were subjected to constant high temperatures (32-35 C or 38-40 C) than when birds were subjected to fluctuating moderate temperatures (11-24 C). Farner and Mewaldt (1952) demonstrated with White-crowned Sparrows that if length of photoperiod and light intensity were sufficient to induce premature gonadal development, the rate of development could be accelerated by exposure to higher temperatures. Warm temperatures by themselves did not induce gonadal development.

The data from previous investigations seem to be in agreement in regard to the effect of temperature on the rate of gonadal development induced by long day lengths. Ambient temperatures higher than normal during the natural period of reproductive development accelerate this development. However, there is little information regarding the effect of colder than normal temperatures. It seemed likely that temperature has a modifying effect on photoperiodism. Therefore, the following experiments were designed to determine whether or not cold temperatures modify the photoperiodic effect on the expression of the seasonal events related to avian reproduction and, if so, by what mechanism.

MATERIALS AND METHODS

The White-throated Sparrow, Zonotrichia albicollis, a small migratory, passerine species was used in the present investigation. Birds, captured during January and February 1982, in Bowling Green, Kentucky, using chicken wire traps, were held in a large indoor aviary until experimental treatments were initiated. During this time they were maintained under natural photoperiod conditions (i.e., approximately LD 9:15). This day length is reportedly not sufficient to stimulate reproductive development (Wolfson 1959; Farner et al. 1953). The gonads are no longer refractory to light stimulation at this time of year and can be photostimulated with increased day lengths (Shank 1959).

Once a sufficient number of birds was captured, they were laparotomized to determine sex. Measures of certain physiological and behavioral parameters used in previous studies (Eyster 1954; Weise 1956) were chosen to monitor seasonality. They included left testis width, body weight, subcutaneous fat stores, and daily locomotor activity. Males were preferred because gonadal growth is easily monitored in situ. Females were released. However, several females were mistakenly included in the group of birds used in Experiment I. Data from female birds were not included in statistical analyses.

The birds were divided into two groups of 18 birds

each. One group was exposed to warm temperatures throughout the experiment,and the other group was exposed to cold temperatures for the duration of the experiment. The two temperature treatment groups were each subdivided into three photoperiodic treatment groups. Birds in each of these groups were held under a basic LD 9:15 schedule. The light period of this schedule will subsequently be referred to as the daily photoperiod. In addition to this daily photoperiod, birds in each group received one additional hour of light during a particular phase of the dark period. Birds of groups 1, 2, and 3 received this additional hour of light at 12, 16, and 20 hours after the onset of the daily photoperiod, respectively. Therefore, each bird was exposed to ten hours of light daily which is not sufficient to stimulate rapid testicular growth in White-throated Sparrows (Wolfson 1959; Farner et al. 1953). These treatment groups will subsequently be designated by W-12, W-16, W-20, C-12, C-16, and C-20. C or W represent the temperature treatment and 12, 16, and 20 represent the time of onset of the additional hour of light. All birds received food and water ad libitum.

The birds were housed individually in cages within photoperiod chambers. These light-tight, ventilated compartments were equipped with 15-watt fluorescent lights that provided an intensity of light at perch height of 340 lux in cages in warm-temperature chambers and 410 lux in cages in cold-temperature chambers. Light onset was operated automatically by timers. A Taylor maximum-minimum thermometer

was placed inside each photoperiod chamber and the high and low temperatures were recorded daily.

In addition, one of the two perches in each cage rested on a microswitch attached to the cage externally and these in turn were wired to an Esterline-Angus event recorder. Activity (perch hopping) of the birds was continuously recorded during the last two weeks of each experiment. Each time the bird hopped onto the perch, an electrical circuit was completed and the movement was recorded as a dash on a continuously moving paper chart. The paper chart was subdivided into 10-minute increments. Locomotor activity during these 10-minute intervals was assigned a value of 0.0, 0.3, 0.6, or 1.0 activity units representing increasing degrees of activity. The sum of these six 10-minute values represented the total amount of activity which occurred during a given hour. Hourly activity was therefore assigned a value ranging from 0 representing no activity to 6 representing continuous activity. Six days of activity were averaged together and graphed to form a representative daily activity pattern.

Experimental treatments were carried out between 7 February and 28 February 1982 (Experiment I). They were repeated between 8 March and 6 May 1982 (Experiment II). During Experiment I, the photoperiod chambers containing groups W-12, W-16 and W-20 were placed indoors where temperatures ranged from 18.9 C to 31.1 C and averaged 25.1±2 C. Temperatures inside chambers containing groups C-12, C-16

and C-20, placed out-of-doors under a shelter, fluctuated between -15.6 C and 10.6 C and averaged 5.7±2 C. During Experiment II, the W groups were similarly placed indoors where the average temperature was 27.6±2 C. Due to warming weather, the C groups were placed inside a walk-in cooler where the temperature was maintained at 3.8±2 C throughout the test period.

After three weeks of exposure to the experimental conditions, the birds were laparotomized. Left testis widths were measured in situ to the nearest 0.1 mm. Body weights were measured to the nearest 0.01 gm and visual observations of subcutaneous fat deposition were made. The fat deposition index used was a subjective measurement of observable subcutaneous fat similar to the index used by McCabe (1943), Blanchard (1941), and Wolfson (1945). This system of five classes provided an index of subcutaneous fat in which 0 represented no visible fat in the furcular depression or on the abdomen. Classes 1, 2, and 3 represented successively increasing increments of fat and class 4 represented maximum fat deposition in both furcular depression and abdominal regions.

Results of Experiment II indicated that there was not a dramatic response to the photoperiod treatments by either W or C groups after three weeks. Therefore, treatments were continued for an additional three weeks. The locations and conditions of the experiment remained the same. This additional three week period of treatments will be considered as part

of Experiment II.

Data of both Experiments I and II were analyzed statistically by one way analysis of variance using an SPSS computer program (Nie et al. 1975). The responses of the three photoperiodic treatment groups were compared within each temperature treatment group. Student-Newman-Keuls multiple range test was used to identify significant differences among the three photoperiodic treatment groups within each temperature treatment group. Differences were considered significant at the 95% confidence level ($p \leq 0.05$).

RESULTS

Experiment I was carried out as a pilot study during the month of February 1982 to determine if a daily rhythm of testicular photosensitivity is involved in photoperiodism in the White-throated Sparrow and, if so, whether its expression is influenced by temperature. Results are presented in Table 1 and Figures 1 and 2. The experiment was begun with a fairly homogeneous group of birds. Fully regressed gonads with the testis width measuring 1.1±0.1 mm were observed during the preliminary laparotomies. Body weights were similar initially (i.e., average weight of 27.90±0.73 gm) and subcutaneous fat stores were low. At the conclusion of three weeks of treatment (Figure 1), the average testis width (i.e., 1.1±0.3 mm) of birds in the cold treatment groups was similar to the initial testis width. There were essentially no differences in testicular growth among the three photoperiodic treatment groups at this temperature (Figure 1). There was a slight change overall in the left testis width (i.e., 0.6±0.2 mm) in birds held at W (Table 1). Birds of group W-16 showed the greatest response with an average change of 0.8±0.1 mm in testis width. However, this change in width was not statistically different from the change in testicular width observed in birds of groups W-12 and W-20. All birds lost body weight during the experiment. The average amount lost among the cold and warm acclimating

TABLE 1. Changes in testicular widths, body weights, and fat stores in White-throated Sparrows maintained under LD 9:15 at either W (25.1±2 C) or C (5.7±2 C) in response to interrupted-night photoperiod treatments. Experiment I was carried out between 7 February and 27 February 1982.

Treatment	N[1]	Change in testis width (mm)	Change in body weight (gm)[2]	Fat stores[2] initial	final
C - 12[3]	4	0.0±0.0[4]	-1.66±0.58	1.6	1.4
W - 12	4	0.5±0.1	-2.15±0.29	1.3	1.1
C - 16	4	0.0±0.0	-1.80±0.74	1.3	1.1
W - 16	4	0.8±0.1	-1.58±0.49	1.5	1.6
C - 20	4	0.0±0.0	-1.61±0.47	1.0	1.5
W - 20	2	0.5±0.3	-3.80±0.34	1.5	0.3
ANOVA[5] - C		N.S.			
ANOVA - W		N.S.			

[1]The number of birds in each group at the end of the experiment.

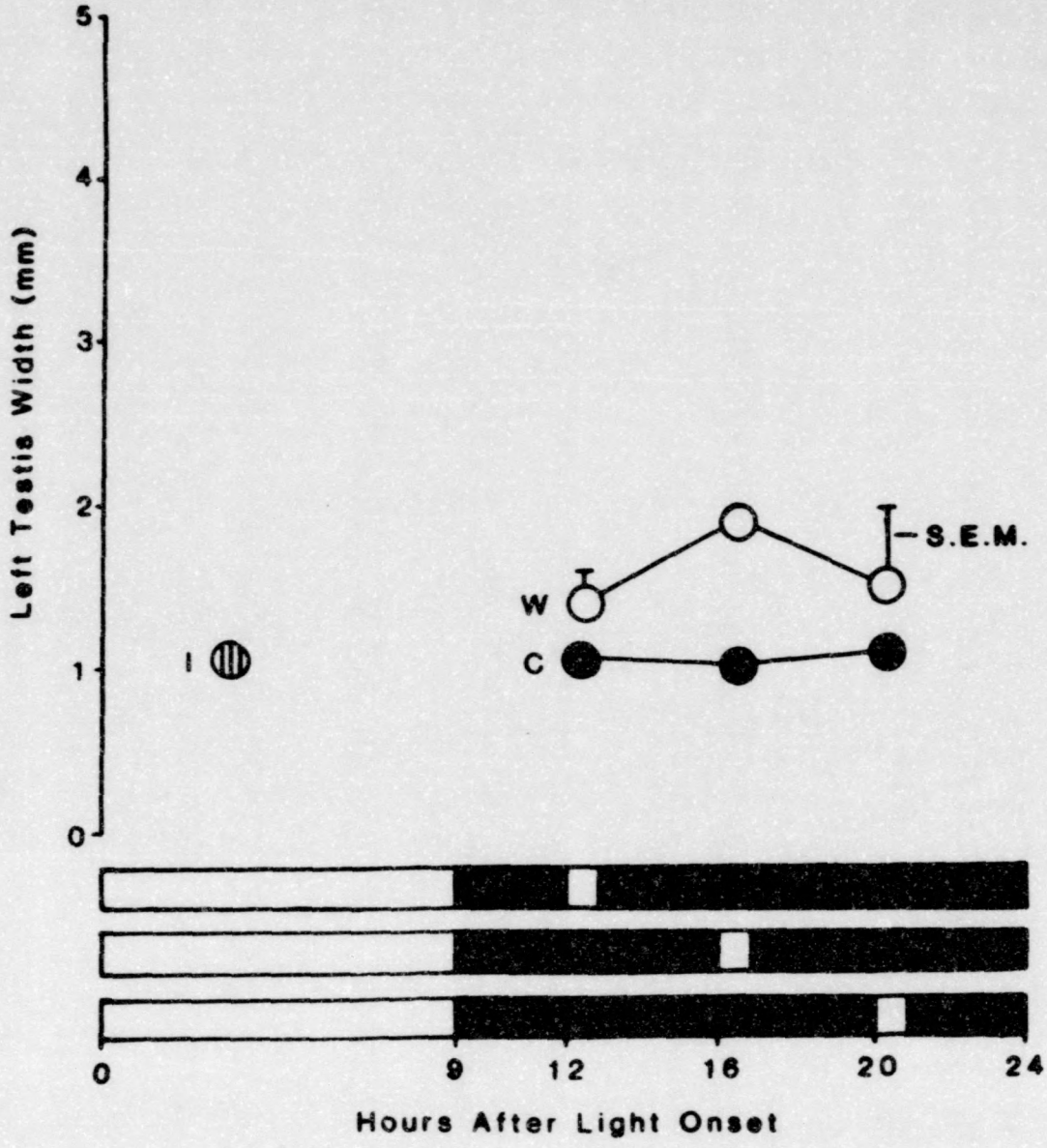
[2]Only males were included in the means.

[3]Cold (C) or warm (W) acclimating birds exposed to an additional hour of light during the indicated hour after the onset of the daily light period.

[4]Mean ± one standard error about the mean.

[5]Analysis of variance among photoperiodic treatment groups within W or C treatment groups.

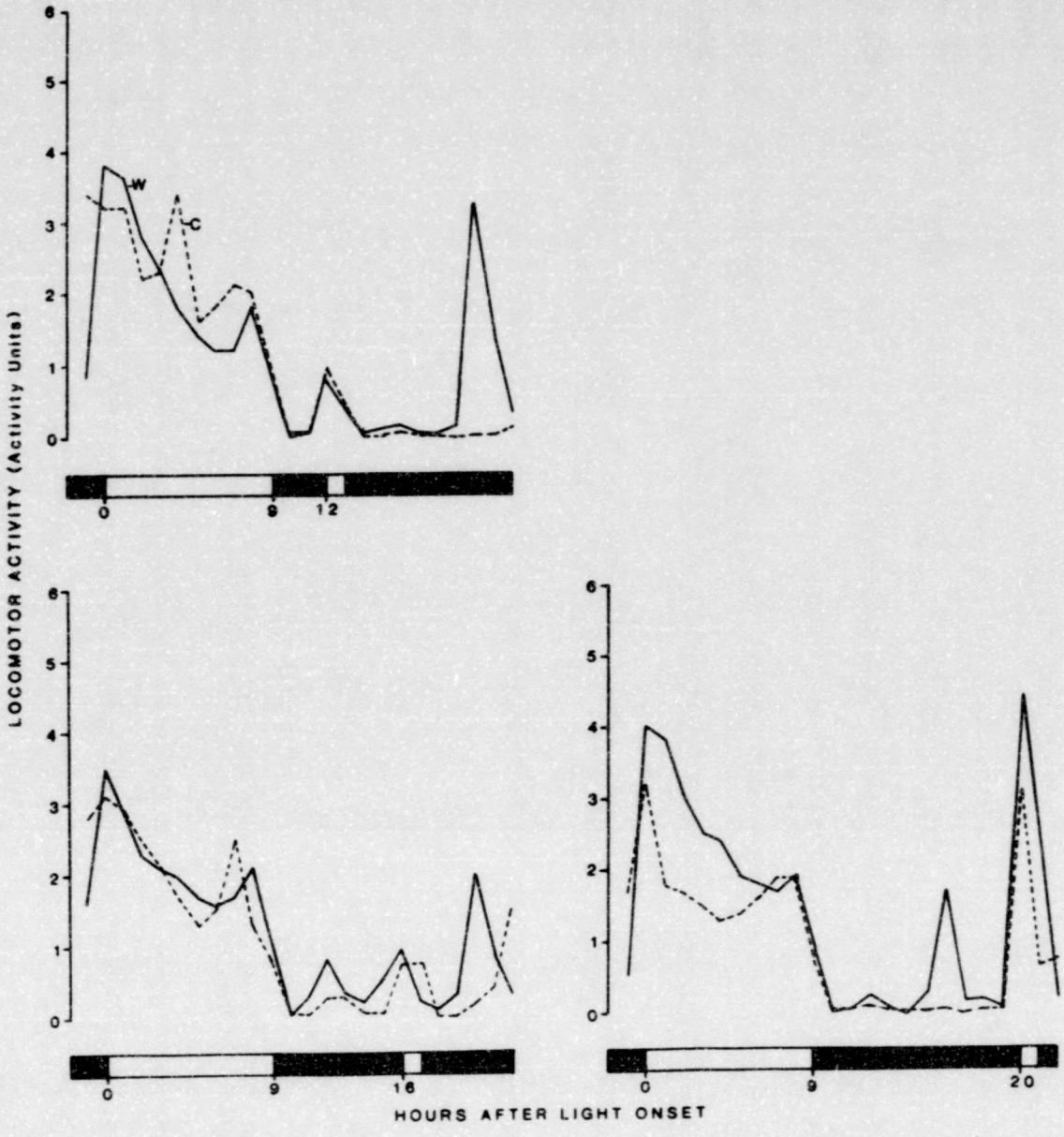
Figure 1. Left testis width in sparrows of Experiment I held under photoperiodic schedules represented by unshaded (light) and shaded (dark) areas in the lower horizontal bars. Testicular responses to photoperiodic treatments are depicted above the interrupted-night photoperiod representation. The hatched circle represents mean initial testis width, open circles represent mean testis widths of birds held at warm temperatures (25.1±2 C) after three weeks of treatment, and dark circles represent mean testis widths of birds held in cold conditions (5.7±2 C) after three weeks of treatment. Treatments were initiated 7 February 1982. Vertical lines represent one standard error about the mean (S.E.M.).


Left Testis Width (mm)
5
4
3
2
1
0
I
W
C
S.E.M.
0
9
12
16
20
24
Hours After Light Onset

birds was 1.69±0.60 gm and 2.57±0.37 gm, respectively. In general, fat store changes reflected body weight changes.

The locomotor activity patterns of all birds were similar throughout the treatment period regardless of the temperature and photoperiod treatment. An obvious daily rhythm characterized by a sharp rise of locomotor activity in the morning was evident. Peak levels of locomotor activity occurred coincident with the onset of the daily light period. Some anticipation of onset of light was exhibited as indicated by onset of activity occurring one to two hours before actual onset of the light period. Locomotor activity steadily declined during the light period until late afternoon at which time a smaller peak of activity occurred at approximately one hour before the offset of the daily light period. The activity then proceeded to decline until a low point was reached usually one hour after the daily light period. From this point, activity began to increase again in anticipation of the hour of additional light. Definite responses to the light interruptions are indicated by the corresponding peaks of activity. The recordings suggest further that the birds also anticipated the light interruptions of the other treatment groups in that the onset of activity preceded the onset of these interruptions. Although birds not receiving light also responded during other interruption times, a light meter reading indicated that there was no leakage of light between compartments of the chambers. Therefore, it is suggested that the noise of the perches and

Figure 2. Daily locomotor activity patterns of the three photoperiodic treatment groups of sparrows of Experiment I held at C (dashed line) and W (solid line) during three weeks of treatment. Bars beneath each group represent the light (unshaded) - dark (shaded) cycles.


LOCOMOTOR ACTIVITY (Activity Units)
HW
C
0
9
12
16
20
HOURS AFTER LIGHT ONSET

microswitches produced as the birds hopped and chipping noises elicited by the birds receiving light probably acted as a general disturbance for all other birds.

Experiment II was conducted to explore further the possibility that temperature might influence the expression of a daily rhythm of testicular responsiveness to light. Results presented in Table 2 and Figures 3, 4, and 5 will be discussed in terms of results obtained at the end of three weeks and at the end of six weeks of treatment. Changes in testis width and body weight after three and six weeks of treatment refer to the differences between initial measurements and measurements after three and six weeks. As in Experiment I, at the end of three weeks of exposure to experimental conditions, there was an insignificant change (0.2 ± 0.1 mm) in the testis widths of those birds exposed to cold regardless of photoperiodic treatment. Testicular growth was slightly greater in birds maintained in warm conditions compared with growth in birds at C. However, widths at three weeks were not significantly different from initial widths. In that results from both temperature treatment groups after three weeks were similar to results at the end of Experiment 1, it is suggested that, as with birds in the first experiment, birds of Experiment II were not fully acclimated to cage conditions at the start of the treatment period. Consequently, responses to treatments were not maximal. Therefore, the experimental conditions were continued for an additional three weeks. At the end of

TABLE 2. Changes in testicular widths, body weights, and fat stores in White-throated Sparrows maintained under LD 9:15 at either W (27.6 2 C) or C (3.8 2 C) in response to interrupted-night photoperiod treatments. Experiment II was carried out between 8 March and 6 May 1982.

Treatment	N[1]	Change in left testis width (mm)		Change in body weight (gm)		Fat stores	
		3 weeks	6 weeks	3 weeks	6 weeks	initial	final
C - 12[2]	6	0.2±0.1[3]	1.3±0.3$_{x5}$	-1.89±0.61	-0.08±1.37	2.3	1.9
W - 12	6	0.8±0.1	2.0±0.1^{x5}	-1.99±0.51	3.57±0.68	1.7	3.0
C - 16	6	0.1±0.0	1.2±0.2$_{x}$	-1.32±0.39	-0.45±1.06	1.8	1.5
W - 16	6	0.7±0.1	1.3±0.2^{x}	-0.52±0.76	3.81±0.87	1.7	3.6
C - 20	6	0.2±0.1	1.5±0.2$_{y}$	-1.30±0.95	2.79±1.30	1.9	3.2
W - 20	6	0.9±0.1	3.2±0.4^{y}	1.31±0.66	5.33±0.94	1.6	3.8
ANOVA[4] - C		N.S.	N.S.				
ANOVA - W		N.S.	$p \leq 0.05$				

[1]The number of birds in each group at the end of the experiment.

[2]Cold (C) or warm (W) acclimating birds exposed to an additional hour of light during the indicated hour after the onset of the daily light period.

[3]Mean ± one standard error about the mean.

[4]Analysis of variance among photoperiodic treatment groups within W or C treatment groups.

[5]Ranking of treatment means according to the Student-Newman-Keuls procedure. Means without a letter in common are statistically different at the 95% confidence level.

Figure 3. Left testis width in sparrows of Experiment II held under photoperiodic schedules represented by unshaded (light) and shaded (dark) areas in the lower horizontal bars. Testicular responses to photoperiodic treatments are depicted above the interrupted-night photoperiod representation. The hatched circle represents mean initial testis width, open circles represent mean testis widths of birds held at warm temperatures (27.6±2 C) after three weeks of treatment, dark circles represent mean testis widths of birds held in cold conditions (3.8±2 C) after three weeks of treatment, open squares represent mean testis widths of birds held in warm conditions (27.6±2 C) after six weeks of treatment, and dark squares represent mean testis widths of birds held in cold conditions (3.8±2 C) after six weeks of treatment. Experiment II was initiated 8 March 1982. Vertical lines represent one standard error about the mean (S.E.M.).

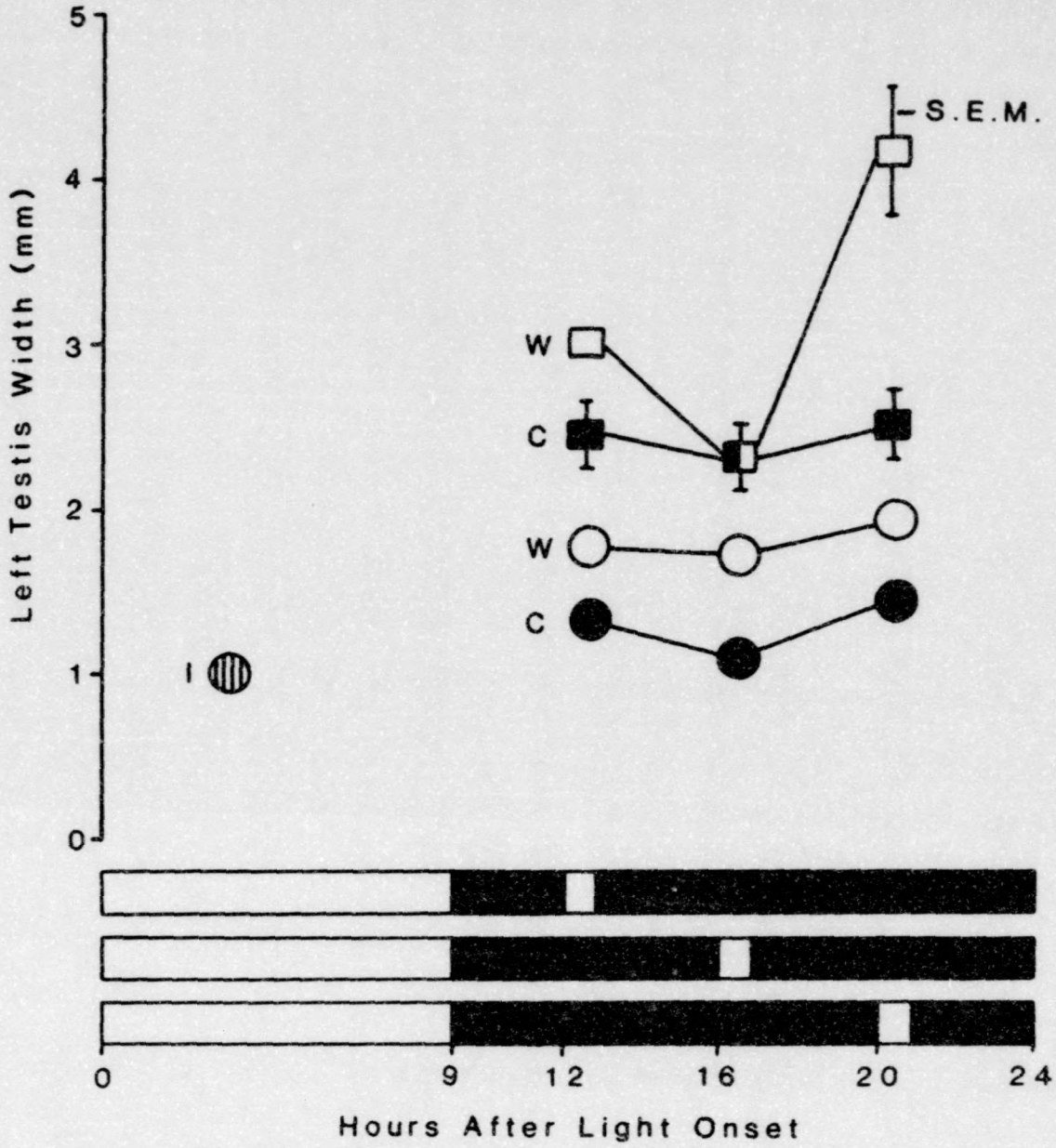

Left Testis Width (mm)
5
4
3
2
1
0
S.E.M.
W
C
W
C
I
0
9
12
16
20
24
Hours After Light Onset

Figure 4. Daily locomotor activity patterns of the three photoperiodic treatment groups of sparrows of Experiment II held at C (dashed line) and W (solid line) during the first three weeks of treatment. Bars beneath each group represent the light (unshaded) - dark (shaded) cycles.

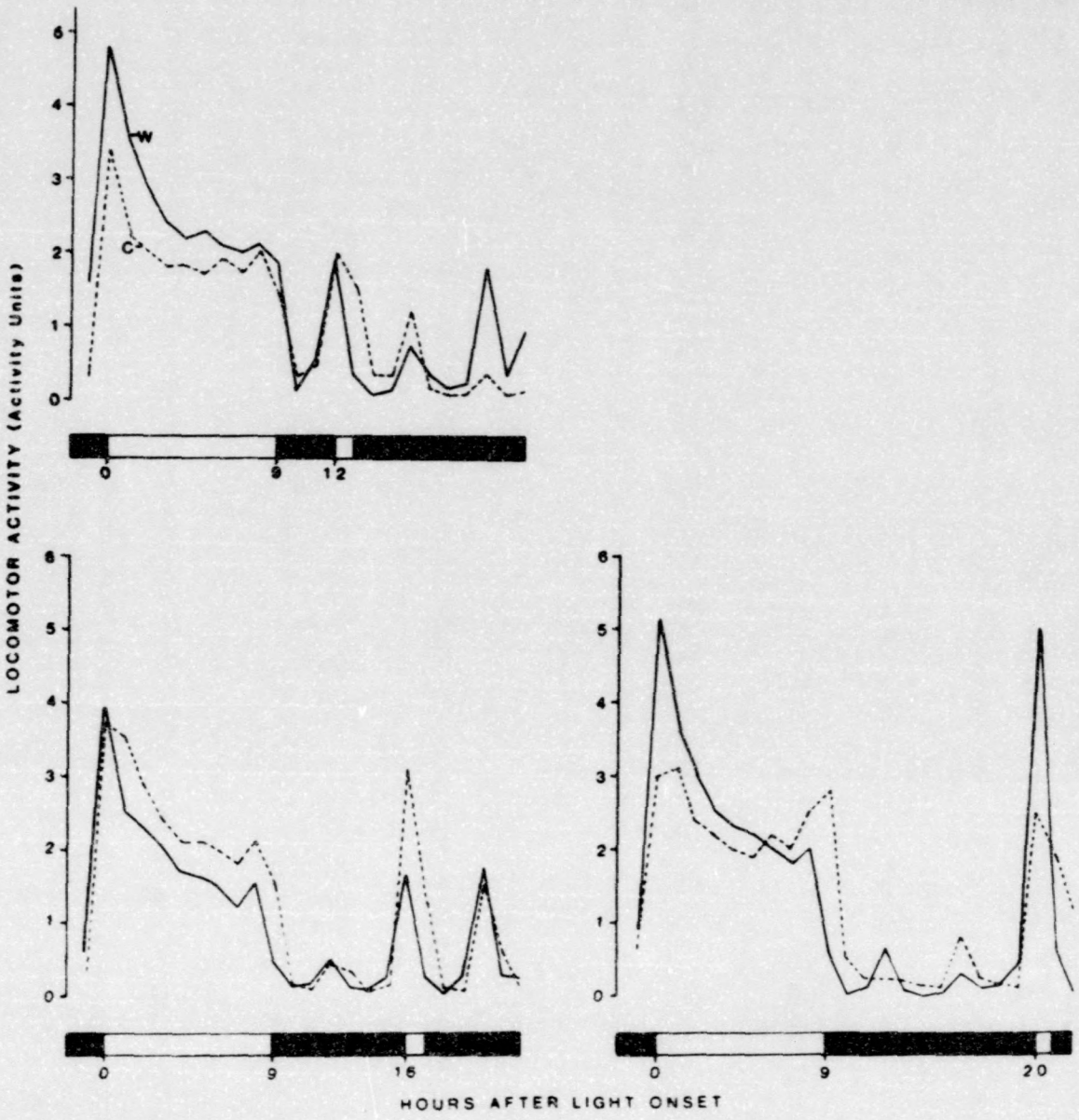
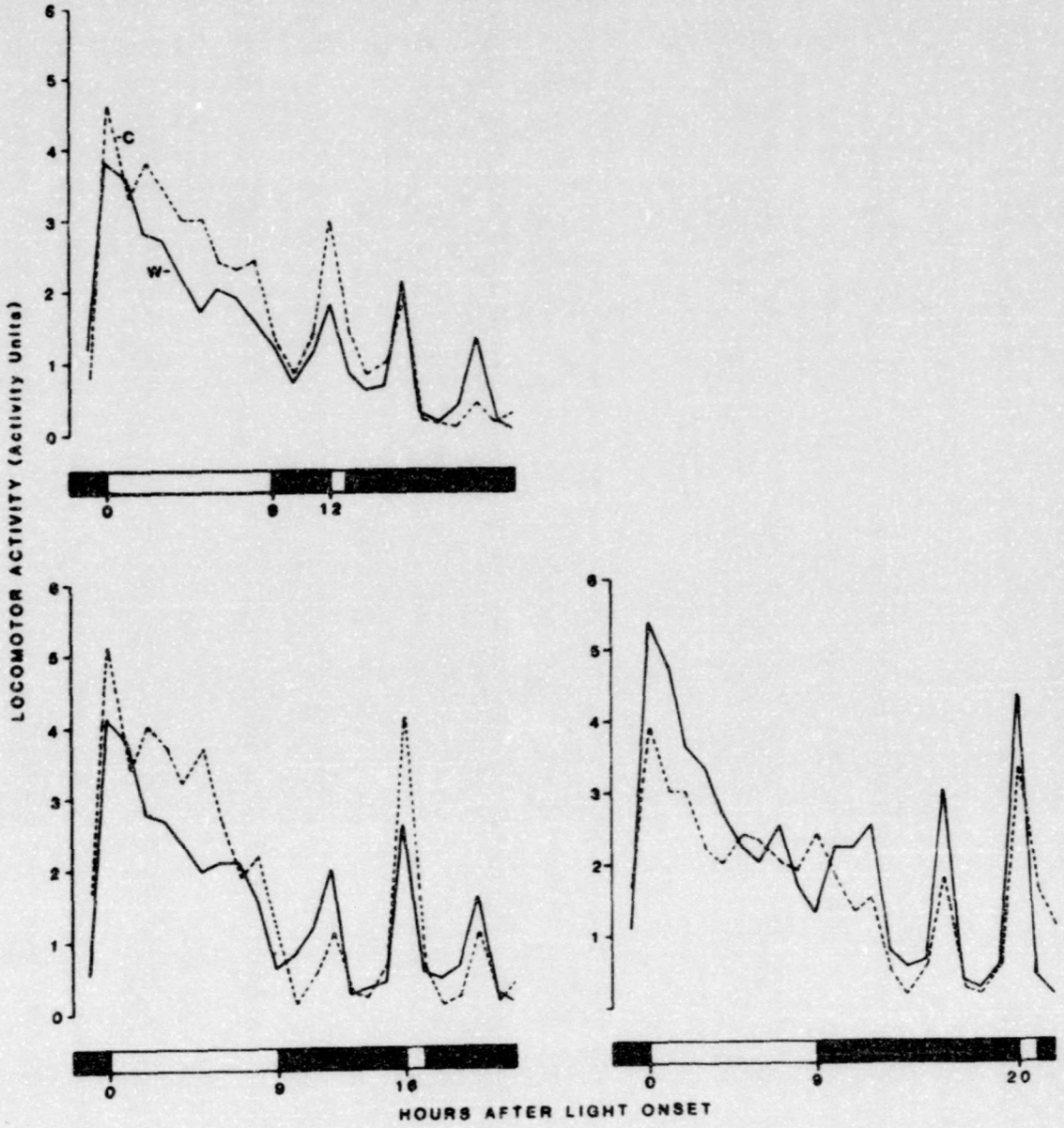

LOCOMOTOR ACTIVITY (Activity Units)
W
C
0
9
12
0
9
16
0
9
20
HOURS AFTER LIGHT ONSET

Figure 5. Daily locomotor activity patterns of the three photoperiodic treatment groups of sparrows of Experiment II held at C (dashed line) and W (solid line) during the second three weeks of treatment. Bars beneath each group represent the light (unshaded) - dark (shaded) cycles.


LOCOMOTOR ACTIVITY (Activity Units)
C
W-
0
9
12
16
20
HOURS AFTER LIGHT ONSET

this time, measurements indicated that recrudescence had continued to progress in all birds of both tmperature treatment groups but at different rates. There was variation among the three photoperiod treatment groups in birds kept at W after six weeks. Birds of group W-20 had testis widths significantly greater than the testis widths of birds in groups W-12 and W-16 (ANOVA: Table 2). The testicular growth responses of birds at C to the three photoperiodic treatments were not significantly different. It should be noted that cold temperature did not totally inhibit recrudescence.

Results of Experiment II indicate that during the first three weeks of treatment, birds of cold temperature treatment groups and two of the three warm temperature treatment groups lost weight (Table 2). This loss supports the idea that birds were not fully acclimated to cage conditions at the start of the experiment. A comparison of changes in body weight during the second three weeks of the experiment indicates that birds generally gained more weight than they had lost during the first three weeks of treatment. The C-16 birds constituted the only group that did not fully regain their weight. The initial and final body weights of group C-12 were essentially the same and their fat stores decreased slightly. Final body weights and fat stores of birds of group C-20 did not differ significantly from those of birds in C-12 and C-16. Birds of W-20 were the only ones that did not initially lose weight and they gained the most weight

comparatively during the second three weeks of treatment. This group also acquired the greatest amount of fat.

The daily activity rhythms of the birds during the six weeks of Experiment II are characterized by a sharp peak of activity in the morning, a gradual decline in activity in the afternoon and then a brief burst of activity just prior to the offset of light. Again there were definite responses to light occurring during the dark period indicated by the well-defined peaks of activity occurring coincident with the additional hours of light. As in Experiment I, all of the birds became active during the light interruptions due to the general disturbance made by those receiving light. The activity rhythms of birds during the second three weeks of Experiment II are similar to those during the first three weeks with the exception of those exhibited by birds of group W-20 which had the greatest testicular development. In comparison to birds of other W groups, birds in this group exhibited greater diurnal activity but, more importantly, the activity level did not decline radically in the late afternoon and did not diminish after the offset of the daily light period. There was a short period of rest in the late afternoon; however, activity increased quickly just prior to the completion of the daily light period. It leveled off for a time, rose again to peak three hours after offset of the daily photoperiod, and then immediately decreased as the birds entered a period of rest. This pattern of nocturnal unrest is similar to that found by Weise (1956) in

photostimulated White-throated Sparrows.

DISCUSSION

Similar to findings in other studies, results of this investigation indicate that photoperiodism in White-throated Sparrows involves circadian mechanisms. Seasonal physiological and behavioral events are regulated in part by endogenous (photosensitivity) rhythms which are circadian in nature and synchronized by entraining agents such as the daily light period. Despite the fact that birds of this study were held under non-stimulatory photoperiodic schedules in regard to total amount of light per day (i.e., less than ten hours), certain physiological and behavioral events (i.e., gonadal growth, subcutaneous fat deposition, and nocturnal unrest) were induced in those birds held at W that received light 20 hours after the onset of the daily photoperiod. Light occurring at this time apparently coincided with the photosensitive (photoinducible) phase of the testicular photosensitivity rhythm in these birds. Its effect was additive during the experimental period thus resulting in observable gonadal growth. Light occurring 12 or 16 hours after onset of the daily photoperiod did not coincide with the photosensitive phase and consequently did not induce recrudescence. These results are in accordance with those from studies carried out in other avian species (Hamner 1963; Farner 1964,1965; Menaker and Eskin 1967; Follett and Sharp 1969; Turek 1974; Meier 1976; Meier and Ferrell 1978;

Kumar and Tewary 1982) in which circadian mechanisms were found to be involved in photoperiodism.

Results of these experiments indicate that environmental temperature is also an important factor influencing the timing of certain stages of the avian reproductive cycle. Cool temperatures slowed gonadal growth in birds in all three photoperiodic treatment groups. The results of the second three weeks of Experiment II dramatically illustrate this point. Although Experiment I and the first three weeks of Experiment II did not produce significant results, growth of gonads of birds exposed to cold was not as progressed as those of birds held at W (Figures 1 and 2). Temperature appears to be a secondary influence on the timing of testicular growth within the seasonal cycle. These results are in accordance with results of previous investigations by Engels and Jenner (1956) which indicated that while temperature is an important factor affecting the initiation of seasonal gonadal development in birds, photoperiod is the primary factor. Engels and Jenner reported that after six weeks of treatment, testes of Juncos exposed to a LD 12:12 and warm (24-29 C) conditions were approximately four times as large as testes of birds maintained under a LD 12:12 and either constant cold (4-8 C) conditions or cold dark periods and warm light periods. In addition, testes of Juncos in the LD 11:13 warm group were almost as large as those in a LD 12:12 cold group, and testes of birds in the LD 11:13 cold group were significantly larger than those held in warm temperatures and LD 10:14.

Therefore, the length of the daily light period or the time of day at which light occurs seems to be a greater limiting factor than temperature in regard to the rate of recrudescence. The rate at which testicular growth occurs is directly related to the daily photoperiod but modifiable by the environmental temperature.

Mode of action of temperature in modifying photoperiodism cannot be determined from results of this investigation. However, one possibility consistant with results of this study is that temperature might simply retard the expression of the daily rhythm of photosensitivity. White-throated Sparrows exposed to cold temperatures (3.8±2 C) did not exhibit a daily rhythm of testicular growth responsiveness to light, whereas birds exposed to warm temperatures (27.6± 2 C) did exhibit such a rhythm. Supporting this idea is the fact that cold temperatures did not totally inhibit the testicular response to light but simply caused it to occur at a retarded rate. However, these results also support the possibility that cold temperatures might inhibit induction in that induction did not occur in response to C-20 as it did in W-20. It is apparent from results of this study that temperature does influence circadian mechanisms involved in photoperiodism,and these possible modes of action need to be explored further.

Changes in fat stores and body weights observed during the second three weeks of Experiment II support the findings concerning gonadal development. In the seasonal cycle of the

White-throated Sparrow, gonadal development begins as day length increases in spring. This gonadal development is associated with the occurrance of prenuptial molt, fattening, and migration to the breeding grounds. According to Weise (1963) and Helms (1968), a pronounced increase in fat stores and body weight occurs in White-throated Sparrows concommitant with development of reproductive organs and a peak is reached just prior to vernal migration. The extra fat stored in the spring serves as an energy reserve for use during migration (Farner et al. 1957, 1961). Although the actual initiation of fat depostion and body weight gain was not timed in relation to the stage of gonadal recrudescence in the present investigation, an overall increase in fat deposition and body weight that coincided with development of gonads was observed. Birds in all three warm temperature treatment groups showed a net gain in body weight and fat stores during the second three weeks of Experiment II. Birds of groups C-12 and C-16 showed no net gain in weight and a loss of stored fat. Birds in the latter group exhibited the least testicular growth during the test period. Absence of gain in weight and fat deposit s might be due to the fat that lower temperatures demanded a higher rate of metabolism for thermoregulation. Thermoregulation, however, does not account entirely for these results in that birds of group C-20 gained weight and fat stores increased. All birds had the same amount of time per day to feed, however, the time of day at which they fed might also partially account for the

difference between groups C-12, C-16 and group C-20.

The observations made concerning Experiment I and the first three weeks of Experiment II indicate that the birds were not fully acclimated to cage conditions at the start of the experimental period. There were no significant differences among the warm or cold temperature treatment groups for any of the physiological or behavioral parameters tested. A daily rhythm of testicular photosensitivity was not yet present at the end of either of these experimental periods. Losses of body weight and fat stores during Experiment I and the first three weeks of Experiment II support the idea that birds were inadequately acclimated to cage conditions. Changes in body weight and fat stores were not found to be different among either temperature treatment group. There were no major conclusions drawn from the results of these two treatment periods concerning the effect of temperature on testicular responsiveness to light. The only conclusion made was that the experimental conditions were not continued long enough to allow for adaptation to cages and testicular response to interrupted-night photoperiods.

The daily locomotor activity patterns of the birds in this study were similar throughout both experimental periods regardless of the temperature at which they were held. Nocturnal activity, indicative of migratory disposition, was not present during Experiment I or the first three weeks of Experiment II. This fact is not surprising in that body weight, subcutaneous fat deposition and gonadal development

had changed little among these birds. Locomotor activity does not appear to affect gonadal development, an effect similar to that noted in previous studies (Farner and Mewaldt 1955; Bissonnette 1931; Wolfson 1949). Nocturnal activity, characterized by a second peak of activity shortly after the offset of lights, was exhibited by individuals of group W-20. Nocturnal activity did not exceed the diurnal rate, a result similar to findings reported by Eyster (1954) in a study of White-throated Sparrows. He also reported that although the morning peak remained the same, there was some reduction in diurnal activity during the height of spring migration. In the present study, not only was the morning peak higher, but diurnal activity was also higher in birds exhibiting nocturnal unrest. Eyster also found that the White-throated Sparrow usually has a rest period of one-half to two hours following the completion of the daily light period before the onset of nocturnal unrest. In the present investigation, this period of rest lasted from two to three hours. In the majority of birds at warm temperature, the afternoon peak occurred one hour prior to the offset of light at which time activity decreased to a low point one hour after offset of light. The activity of group W-20 was different in that the afternoon peak was reached earlier at three hours prior to the completion of the daily photoperiod and the low point occurred at the time of offset of light. The period of rest shifted two hours in those birds exhibiting nocturnal unrest. While activity did not totally cease

during these rests, there was a period of about three hours during which it was declining. The locomotor activity patterns as well as the fat stores and body weights of the birds of group W-20 indicate that these birds were in the seasonal condition of spring migration whereas the birds exposed to W-12, W-16 or to cold temperatures did not appear to be in this conditon.

In conclusion, results of this investigation indicate that the timing of reproduction, migration, and fattening in White-throated Sparrows is regulated by photoperiod. This effect of light involves circadian mechanisms that can be modified by temperature -- thereby fine tuning the timing of the expression of seasonal events such as gonadal growth, subcutaneous fat deposition, and body weight. A daily rhythm of testicular growth responsiveness to interrupted-night photoperiods was evident in birds maintained on a LD 9:15 schedule at 27.6±2 C, whereas birds maintained on a LD 9:15 schedule at 3.8±2 C did not show such a rhythm. This responsiveness to temperature would be ecologically advantageous. If the timing of migration, nesting, and reproduction is rigidly controlled by photoperiod length, these events might in certain years be induced when temperatures are not favorable. In years when cool temperatures coincide with increasing day length, the cool temperatures might reduce food availability and require increased energy expenditure for incubation and feeding of young. If cool temperatures inhibited testicular responsiveness to increased day lengths,

loss of young would be avoided. Possible modes of action of temperature on photoperiodism need further investigation.

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