AN ANNUAL CYCLE STUDY OF TAN-STRIPED AND WHITE-STRIPED WHITE-THROATED SPARROWS

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THE White-throated Sparrow, *Zonotrichia albicollis*, is a migratory passerine distributed widely in eastern North America. It breeds predominantly in Canada and winters throughout the eastern and southern United States. Lowther (1961) suggested that the species exhibits polymorphism, primarily shown by distinct color differences in the median crown stripe. Evidence supporting the existence of two morphs, a white-striped and a tan-striped includes: 1) a bimodal distribution of the two types of plumages that is independent of both sex and age, 2) selective mating (white-striped birds prefer tan-striped birds), and 3) chromosomal polymorphism (Thorneycroft 1966). Through the study of karyotypes, Thorneycroft (1966) demonstrated that birds with bright nuptial plumage (white-striped) have a single M chromosome and all birds with dull nuptial plumage lack this autosome.

Recently Vardy (1971) presented data conflicting with the theory of polymorphism in White-throated Sparrows. She utilized a six-point classification for rating the median crown stripe that ranged from drab tan (#1) through bright white (#6), and a similar eight-graded system for rating the degree of blackness of the lateral crown stripe. In contrast to Lowther's findings, she detected sex, age, and seasonal differences in plumage. Specifically males in basic plumage (after postnuptial molt) were brighter on the average than females. Birds of both sexes underwent a brightening of crown plumage between the first- and second-winter plumages. Fall migrants, both young and adult, usually had dull crown plumage that brightened during prenuptial molt. She did not obtain a bimodal distribution of the two types of crown plumages within one age class, sex, or season.

We conducted an annual study on caged white-striped and tan-striped White-throated Sparrows to determine if any physiological or behavioral differences could be detected. We monitored body weight, lipid deposits, molt, cloacal protuberance, and nocturnal activity.

MATERIALS AND METHODS

White-throated Sparrows were mist-netted during spring migration near Lewisburg, Northumberland County, Pennsylvania. Birds were housed in an outside aviary and therefore were exposed to local photoperiod changes. In late May sparrows were sexed by cloacal protuberance (Wolfson 1954) and assigned to one of four groups: white-striped males, tan-striped males, white-striped females, or tan-striped females. We then selected the 16 brighest (according to crown plumage)

White-throated Sparrows (8 ♂♂, 8 ♀♀) and the 16 dullest (8 ♂♂, 8 ♀♀) to compose the white-striped and tan-striped groups, respectively. The median crown stripes of male white-stripes were bright white; female white-stripes had grayish-white median crown stripes while those of the tan-striped sparrows were drab tan through tan in color. Birds were not aged as completion of ossification prevents aging spring individuals. The annual cycle experiment began on 11 June and ended on 10 June the following year. All birds were assumed to be at least 1 year old, as most young hatch during the first 2 weeks in June (Lowther and Falls 1968).

All birds were housed individually in activity cages and were isolated optically from one another. Each activity cage (16 (length) × 8½ (width) × 10½ inches (height)) contained two movable perches, each with a microswitch at one end. The microswitches served as activity transducers that activated 6-volt electromechanical digital counters. Total locomotor activity each night was recorded and divided by number of hours of darkness to yield counts/hour. Food ("Layena") and water were available *ad libitum.* Once a week the following variables were recorded: body weight (± 0.1 g), visible fat class (Helms and Drury 1960), molt (see Weise 1956), male cloacal protuberance (Wolfson 1954), and female cloacal projection. The cloacal projection of females undergoes subtle changes throughout the reproductive period compared to the cloacal protuberance of males. At least three stages can be recognized. One is the nonbreeding stage. The projection is convex and small, it tilts forward to make an acute angle with respect to the abdomen, and its cloacal opening is circular. In stage two the projection becomes tilted more caudally and the angle between the cloacal projection and abdomen increases. The cloacal opening is elongated and has a slitlike appearance. Stage three, representing full gonadal development, is characterized by a caudal projection forming an obtuse angle to the abdomen and the opening of the cloaca is markedly elongated.

At the end of the experiment all birds were laparotomized to verify sex.

Data analysis.—Both the timing of events of the annual cycle (onset, peak, termination, and duration) and peak values of these events were compared. Weekly values were used for all data analyses except nocturnal activity for which daily records were utilized. Onset and termination of nocturnal activity characteristic of spring and fall migratory periods were determined by consulting individual bird records and calculating a baseline value for nocturnal activity throughout the stable winter period. When the data consistently deviated above baseline, the first aberrant data point was considered onset while the first data point back to baseline terminated the particular measured event. White-striped sparrows were compared with tan-stripes, and males were compared with females. The Student's *t*-test was used to test the significance of differences in body weight and nocturnal activity. The Mann-Whitney U-test was used for the variables: body fat, molt, and cloacal protuberance. All tests were two-sided.

Results

White-striped versus tan-striped sparrows.—Figures 1 and 2 show nocturnal activity, cloacal protuberance (CLP, ♂♂) or cloacal projection (CLP, ♀♀), fat class, molt, and body weight of white-striped and tan-striped males and females, respectively. The solid lines and stippled areas represent the white-striped birds, the dashed lines and white enclosed areas represent the tan-striped birds. In the first analysis the

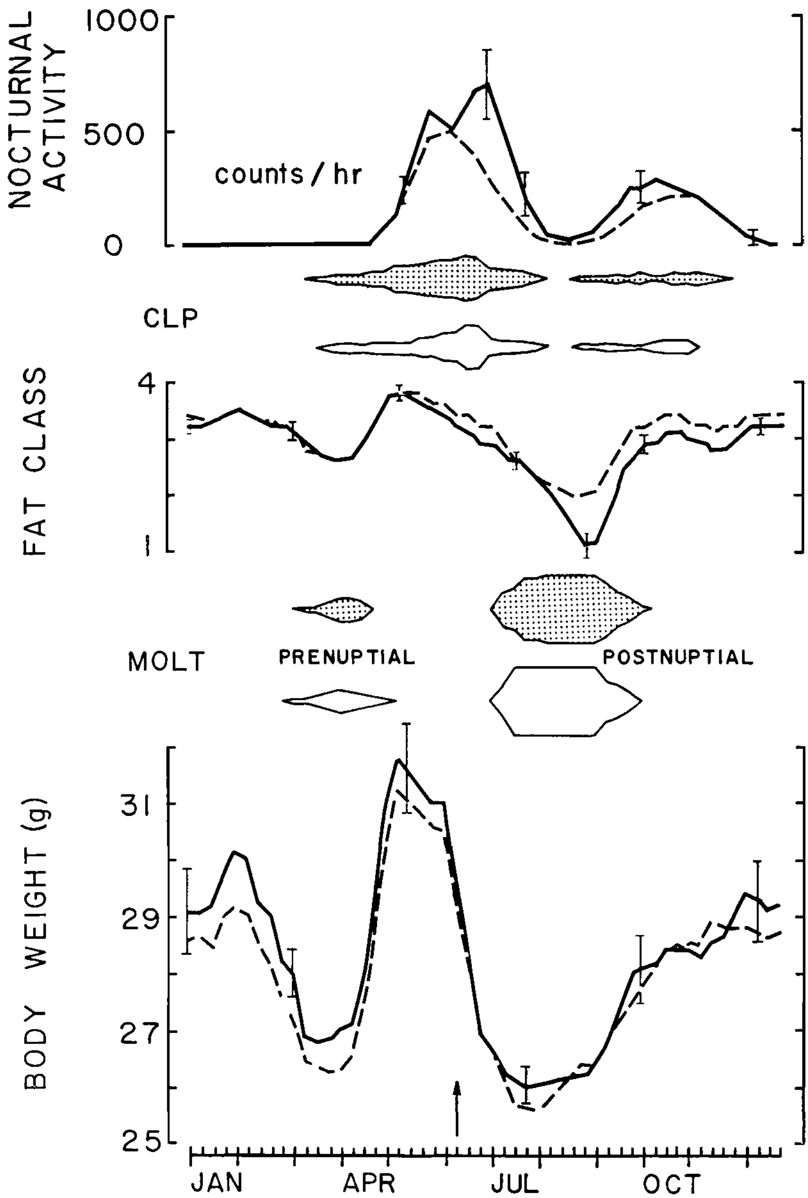

Figure 1. Annual cycle of male White-throated Sparrows. Solid lines and stippling represent white-striped birds, dashed lines and clear spaces indicate tan-striped birds. The arrow marks starting point of experiment. All data shown are 3 value moving averages of weekly means, vertical lines represent 1 SE. CLP = cloacal protuberance.

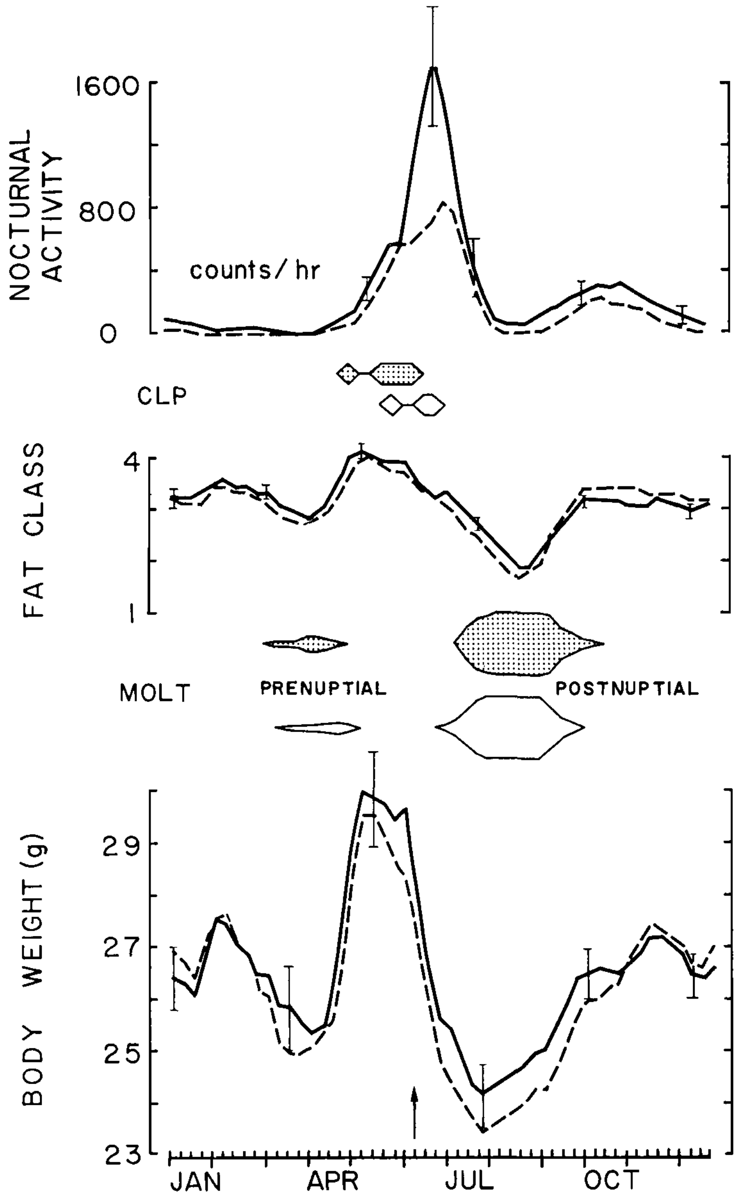

Figure 2. Annual cycle of female White-throated Sparrows. Solid lines and stippling represent white-striped birds, dashed lines and clear spaces indicate tan-striped birds. The arrow marks starting point of experiment. All data shown are 3 value moving averages of weekly means, vertical lines represent 1 SE. CLP = cloacal projection.

TABLE 1
ANNUAL CYCLE EVENTS TESTED BETWEEN WHITE-STRIPED AND TAN-STRIPED WHITE-THROATED SPARROWS

	Onset		Peak		Termination		Duration	
Time of year/event	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Spring								
Body weight[1]	ns	ns	ns	ns	—	—	—	—
Body fat[2]	ns	ns	ns	ns	—	—	—	—
Prenuptial molt[2]	ns	ns	ns	ns	ns	ns	ns	ns
Cloacal protuberance[2]	ns	ns	ns	ns	ns	ns	ns	ns
Nocturnal activity[1]	ns	ns	0.01	ns	ns	0.05	ns	ns
Summer								
Postnuptial molt[2]	ns	ns	ns	ns	ns	ns	ns	ns
Fall								
Cloacal protuberance (♂♂ only)[2]	ns	—	ns	—	ns	—	—	—
Body weight[1]	ns	ns	ns	ns	—	—	—	—
Body fat[2]	ns	ns	ns	ns	—	—	—	—
Nocturnal activity[1]	ns	ns	ns	ns	ns	ns	ns	ns
Winter								
Body weight[1]	—	—	ns	ns	—	—	—	—
Body fat[2]	—	—	ns	ns	—	—	—	—

[1] Student's *t*-test.
[2] Mann-Whitney U-test.

dates of onset, peak, termination, and the duration of physiological and behavioral events shown in Figures 1 and 2 were compared between white-striped and tan-striped White-throated Sparrows. Specifically the timing of the following variables was compared: spring and fall nocturnal activity; spring and fall cloacal protuberance in males; spring cloacal projection in females; spring, fall, and winter body fat and body weight responses; and prenuptial and postnuptial molts. No differences were detected in the timing of any of the events except spring nocturnal activity (see Table 1 for test employed and results). Tan-striped males displayed an earlier peak in *Zugunruhe* than male white-stripes ($P < 0.01$), and tan-striped females terminated *Zugunruhe* before white-striped females ($P < 0.05$).

A second analysis was performed to compare the mean values of physiological and behavioral events, that is, amplitudes of variables were compared at critical periods of the year. Only one significant difference was detected: white-striped males had lower fat class ratings during postnuptial molt than tan-striped males ($P < 0.05$). Two more differences were nearly significant: white-striped females displayed more intense *Zugunruhe* than tan-striped females ($P < 0.1$), and white-striped birds registered more vernal nocturnal activity than tan-stripes ($P < 0.1$).

Males versus females.—In addition to comparing the two proposed morphs, we also compared the two sexes. The following differences in the timing of events were found: tan-striped males attained their peak of spring *Zugunruhe* before tan-striped females ($P < 0.05$, Student's *t*-test); white-striped males terminated fall *Zugunruhe* prior to female white-stripes ($P < 0.05$, Student's *t*-test); tan-striped males began prenuptial molt before tan-striped females ($P < 0.05$, Mann-Whitney U-test); and prenuptial molt of tan-striped males lasted longer than the spring molt of female tan-stripes ($P < 0.01$, Mann-Whitney U-test).

Comparing the intensity of the recorded features of the annual cycle showed the following differences: Females registered more vernal *Zugunruhe* than males ($P < 0.01$, Student's *t*-test). Males averaged approximately 2 g more than females throughout the annual cycle, but males and females showed no significant difference in peak body weights before spring migration. Males were significantly heavier than females prior to fall migration ($P < 0.01$, Student's *t*-test). Cloacal changes of males and females, which reflect gonadal development, were not compared for two reasons: 1) cloacal changes in females are more subtle and hence more difficult to quantify, and 2) optically-isolated females in cages often do not exhibit gonadal development (Helms MS).

Spring versus fall migratory periods.—Body weight and the amounts of body fat and nocturnal activity differed significantly between spring and fall migratory periods in all four groups. Nocturnal activity was 3.7 times greater in spring than in fall ($P < 0.01$, Student's *t*-test). Body weight and body fat values were also significantly higher in spring ($P < 0.05$, Student's *t*-test and Mann-Whitney U-test, respectively).

Discussion

Tan-striped versus white-striped sparrows.—Vardy (1971) presented the first clear evidence disputing the concept of polymorphism in White-throated Sparrows (Lowther 1961). Based upon the five variables measured in our study, no consistent physiological or behavioral differences were detected between white-striped and tan-striped White-throated Sparrows. A total of 63 statistical tests were performed comparing the two proposed morphs in the timing of events composing the annual cycle (see Table 1). Two tests were found significantly different, a number that could be expected through chance alone (1 out of 20). No differences have been noted in the territorial songs of tan-striped and white-striped birds (Falls 1969). Nevertheless a reexamination of the supposed selective mating system of White-throated Sparrows (Lowther 1961) employing the six- and eight-graded rating system for medial and lateral crown stripes (Vardy 1971) seems warranted. In addition, chromosomal studies (see Thorneycroft 1966), including all stages of color variation in the crown from dull tan through bright white, would provide convincing data for or against polymorphism in *Zonotrichia albicollis*.

Spring versus fall migratory periods.—We have shown marked differences between spring and fall periods in caged migrants (see Figures 1 and 2). A greater increase in body weight and body fat occurred during the vernal period. *Zugunruhe* was 3.7 times greater in the spring compared to fall. Overall the vernal period in caged birds can be characterized as more intense.

The most marked difference between spring and fall periods is manifested in nocturnal activity. *Zugunruhe* or nocturnal activity is regarded as the analog of migration in caged individuals or species that normally migrate at night (King and Farner 1965). Gwinner (1972) claims that onset and termination of fall *Zugunruhe* in two Old World warblers, the Willow Warbler (*Phylloscopus trochilus*) and the Chiffchaff (*Phylloscopus collybita*), correspond well with field data on the length of the migratory period. In addition intensity and total quantity of *Zugunruhe* correlate with distance traveled. The correlations are not clear in *Zonotrichia*. A troublesome feature of *Zugunruhe* in White-throated Sparrows is that it lasts considerably longer than actual migration. One possible explanation is that a caged migrant lacks the necessary external stimuli to terminate the motor response. A consummatory act, the attainment of a migratory goal, is not present in the cage environment (Hamilton 1967).

Helms (1963) showed that spring and fall nocturnal activity in *Zonotrichia albicollis* can be divided objectively into motivational and adaptational periods. The division is made arbitrarily at a point in the nocturnal locomotor period where a sudden drop in activity occurs. In most cases a sharp decrease in total counts occurred midway through both the vernal and autumnal periods of nocturnal activity. The motivational period in caged White-throats in eastern Pennsylvania (Table 2) coincides with the following field dates for the spring migratory period in New England: First field movements of White-throated Sparrows are noted about 5 April, the latest around 23 May (length of spring migration equals 49 days) (Helms 1963). Estimates of the spring migratory period determined at Manomet, Massachusetts, when 90% of the species had passed through, extend from about 16 April through 18 May, or 32 days in length (Ralph MS). In caged birds spring motivational *Zugunruhe* averaged 40 to 41 days (see Table 2). Length of the fall migratory period appears more variable. Field dates for New England extend from 5 September through 15 November giving a maximum period of 72

TABLE 2
COMPARISON OF SPRING AND FALL MOTIVATIONAL *ZUGUNRUHE*

	Spring		Fall	
	Massachusetts	Pennsylvania	Massachusetts	Pennsylvania
Sample size	n = 14	n = 32	n = 8	n = 32
Onset of nocturnal activity	10 April	20 April	12 Sept.	4 Sept.
Standard deviation of onset (days)	9.6	7.5	9.6	9.3
Mean duration of activity (days)	40	41 ± 1.3 ($\bar{x}$ ± SE)	40	47 ± 1.6 ($\bar{x}$ ± SE)
Source	Helms (1963)	This study	Helms (1963)	This study

days for fall migration (Helms 1963). The autumn migratory period determined at Ashby, Massachusetts (dates bracket 90% of the total White-throat population migrating through) is estimated at about 38 days, approximately 27 September through 4 November (Ralph MS). Laboratory data showed that fall motivational *Zugunruhe* lasted 40 to 47 days (see Table 2). The greater variability in the fall field data is reflected in laboratory studies. Helms (1963) found no statistical difference between the length of spring and fall motivational *Zugunruhe*. In the present study we found that fall motivational *Zugunruhe* was significantly longer ($P < 0.01$).

Reasonable agreement exists between dates of onset and termination of spring and fall motivational *Zugunruhe* and field data of spring and fall migratory periods in White-throated Sparrows in the northeastern United States. Our data showing a longer duration of fall motivational *Zugunruhe* compared with spring also agree with data from wild populations. Borror (1948) used repeat records of banded White-throats to compare spring and fall migratory periods. He concluded that fall migration lasts longer than spring migration and that birds stay longer at a stopover point in autumn.

Does a threefold difference in intensity of nocturnal activity (see Figures 1 and 2) between spring and fall periods have any biological meaning? A possible interpretation is that fall migration consists of more flights each covering less distance when compared to flight patterns characteristic of spring migration. Lower fat levels in the fall prohibit nonstop flights covering the distances possible in spring. Field data of distance covered per migratory flight are lacking. The difficult task of tracking nocturnal migrants throughout the course of migration should clarify spring-fall migratory strategies.

Fall cloacal protuberance.—A small but consistent cloacal protuberance was recorded in 13 of the 16 male sparrows during the late summer and fall periods. This suggests a slight recrudescence of the gonads following postnuptial molt. Active sexual behavior in autumn is not unusual in resident avian species and fall breeding occurs in some colonies of Tricolored Blackbirds (*Agelaius tricolor*) (Orians 1960). Further evidence for fall gonadal development in White-throated Sparrows is the recurrence of song during September (Falls 1969). Several other bird species have autumnal song and in some species song appears to be a by-product of gonadal activity (Armstrong 1963).

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SUMMARY

We studied the annual cycle in tan-striped and white-striped White-throated Sparrows, *Zonotrichia albicollis*, and monitored the following variables: body weight, body fat, molt, morphological changes in the cloaca, and nocturnal activity. No consistent differences were found between tan-striped and white-striped birds. Differences were observed between fall and spring periods. In spring birds were heavier ($P < 0.05$), had more fat ($P < 0.05$) and displayed more intense *Zugunruhe* ($P < 0.01$). An autumnal cloacal protuberance observed in 13 of the 16 males suggests fall gonadal recrudescence in White-throated Sparrows.

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