

interval between pair formation and first egg laying as occurs in *Z. l. pugetensis* (Lewis 1971). The significant difference in song rates between the last two weeks, 6 July vs. 13 July, was expected as this coincided with the end of the breeding season. The lack of a significant difference in song rates between the first two weeks is another indication of the rapid onset of breeding activities.

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EFFECTS OF ALTERED PHOTOPERIOD ON MIGRATORY ORIENTATION IN WHITE-THROATED SPARROWS (*ZONOTRICHIA ALBICOLLIS*)

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A variety of orientation cues are available to nocturnal migratory birds. Perhaps best established is the use of the information in the celestial sky. Emlen (1967) and Gauthreaux (1969) have shown that the apparent nightly movement of the stars caused by the earth's rotation aids in providing a bird a north-south axis or compass information. Early planetarium experiments (Sauer and Sauer 1960) suggested that the seasonal reversal of directions was due to recognition of changing star patterns during the year. However, subsequent experiments (Emlen 1967) failed to confirm these results and instead suggested that internal rather than external factors were important in initiating migratory orientation.

Rowan's experiments (1929, 1930, 1932) with Dark-eyed Juncos (*Junco hyemalis*) and Common Crows (*Corvus brachyrhynchos*) suggested a physiological basis to orientation. Emlen (1969a) tested the orientation of Indigo Buntings (*Passerina cyanea*) in opposite migratory conditions simultaneously under a "spring" planetarium sky. His results indicated that birds which were prepared for a fall migration did orient to the south even when allowed to view a sky appropriate for spring migration. He concluded that annual changes in the physiological condition, not environmental cues, contributed to the major reversals in migratory orientation. The present study

further tests this conclusion with White-throated Sparrows (*Zonotrichia albicollis*) under a natural celestial sky instead of in a planetarium. In addition, all tests were conducted during the fall migratory season instead of the spring (the latter being when Emlen 1969a carried out his study).

METHODS

Two groups of White-throated Sparrows were brought into spring and autumn migratory condition simultaneously by modifying their photoperiod. The annual cycle in the experimental group was altered so that the physiological condition (spring) of these birds conflicted with the potential seasonal information in the autumn celestial sky. This group was captured with mist nets from migrating flocks in the autumn of 1974. These birds were kept in small individual cages in an outdoor aviary under the natural photoperiod until December 1974. They were then moved to an environmental chamber and maintained on 9 h light and 15 h dark (LD 9:15) until the testing period in September 1975. On 21 September 1975, 15 days before the first test, they were exposed to a spring photoperiod (LD 15:9). Weise (1962) found that White-throated Sparrows could be maintained indefinitely in a winter physiological condition as long as they were kept on short days. Subsequent exposure to long days induced a spring migratory and breeding condition.

A "control" group of birds was captured in May 1975 during spring migration. These birds were kept in individual cages in an outdoor aviary under a natural photoperiod for the entire duration of the experiment. Each bird in both groups was examined approximately every 10 days for weight, fat deposits, and molt status. The results of these measurements are summarized in Figure 1.

Under the extended winter photoperiod, birds in the experimental group did not attain the spring

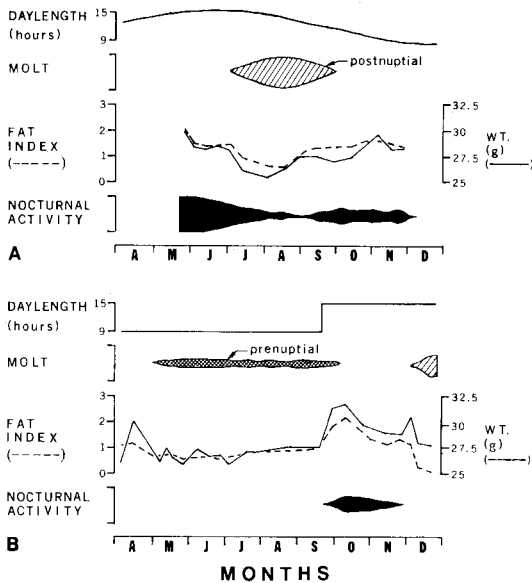


FIGURE 1. The occurrence of molt, fat deposition, weight changes, and nocturnal activity in White-throated Sparrows (*Zonotrichia albicollis*). (A) Control birds on a natural photoperiod and (B) experimental birds exposed to a prolonged short-day photoperiod regime. Subcutaneous fat levels measured according to Weise (1956). Molt measured for 10 body areas.

migratory or breeding condition until September 1975 when the photoperiod was increased to 15 h. At the same time, the control group was experiencing a normal fall migratory condition. Both groups were ready for testing in September 1975: the experimental birds were physiologically prepared for a spring flight and the controls for an autumn journey.

Generally, five birds from each group were tested on a particular night. All experiments were conducted in an open field at the University of Wisconsin-Milwaukee Field Station located 48 km north of Milwaukee, Wisconsin. The potential visual and acoustic biases from the city were negligible. Each test was 3.5 h long and ran from 2100 to 0030. We did not remove birds from their living cages until after sunset and returned them each morning before the following sunrise. All tests were conducted under clear skies.

We measured the intensity of footprints by comparison with an arbitrary scale similar to that described by Emlen and Emlen (1966). The activity of a single bird was totalled over all nights tested and subjected to Rayleigh's test of randomness for circular distributions (Batschelet 1965, 1972). The null hypothesis tested was that the data had a uniform distribution. If a bird's activity was not random, its footprints would be non-uniformly distributed (i.e., they would fall in a preferred direction). This direction is the mean angle determined from all nights of activity.

Determination of Rayleigh's test statistic (z) depends on N . Using the footprint technique, N is a measure of the total activity of a bird. N was calculated as described by Emlen (1969b, appendix 5 with the following modifications). We estimated 1.4

TABLE 1. Orientation of White-throated Sparrows in opposite migratory conditions.

Bird	No. nights active	Total activity ^a	Mean direction ^b
Spring (experimental) group			
1		$N(8) = 279$	7° **
	10	$N(4) = 558$	7° ***
			7° ****
2		$N(8) = 401$	random
	12	$N(4) = 801$	random
			351° **
3		$N(8) = 77$	random
	8	$N(4) = 153$	346° *
			random
TOTAL ^d		$N(8) = 1405$	12° **
	64	$N(4) = 2810$	12° ***
			4° ***
Fall (control) group			
4		$N(8) = 121$	random
	8	$N(4) = 242$	257° *
			243° *
5		$N(8) = 310$	random
	8	$N(4) = 620$	257° *
			243° *
TOTAL ^d		$N(8) = 933$	244° *
	59	$N(4) = 1866$	244° ***
			239° **

^a As calculated by Emlen 1969b; see text for modification.
^b * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.
^c The arithmetic mean of nightly mean headings.
^d Five additional birds in this group showed no significant individual orientation but were included in this total.

hops per activity unit instead of 2.8 as used by Emlen. For statistical purposes, it is important to insure that each hop a bird makes is independent of the one preceding it. Emlen (1969b) stated that this independence level is approached at four and definitely reached at eight hops. However, his data show that values from four onward give essentially the same result. The value selected is of some importance because it can alter the final N and, thus, influence whether or not a bird showed statistically significant orientation. We gave N values for both four and eight hops and calculated a mean angle if either produced a definite orientation ($P \leq 0.05$). In addition, nightly mean headings were recorded for each bird and given the same statistical treatment.

RESULTS

Of the eight experimental birds that were active, only No. 1 showed definite orientation northward (Table 1). Two other birds, Nos. 2 and 3, were oriented only for nightly mean headings and $N(4)$ independence level, respectively. This orientation likewise was directed northward. The activity for five other birds did not deviate significantly from random. The individual orientation of the control birds was no more precise. Only two of seven birds, Nos. 4 and 5, showed any directional preference; both oriented southwestward (Table 1).

When total activity and nightly mean headings for all birds are pooled, it is evident that both groups show a highly significant statistical difference at all

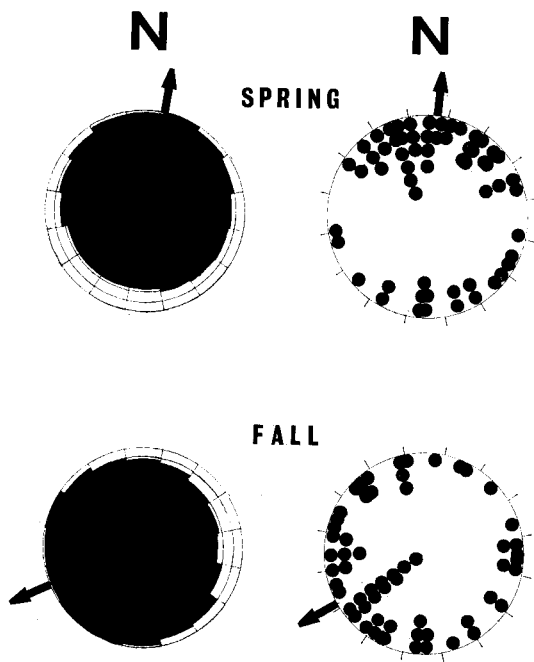


FIGURE 2. Orientation of two groups of White-throated Sparrows in spring (upper) and fall (lower) migratory conditions. Vector diagrams (left) represent the total activity for all birds in each group, and total mean nightly headings are present (right). Vector diagrams are plotted such that the radius equals the greatest number of activity units in any sector totalled for all birds in either group.

levels tested (Fig. 2). The mean direction of the group in spring migratory condition was slightly east of north. Birds in an autumnal migratory condition oriented almost toward west-southwest.

DISCUSSION

At least two explanations are possible for the "statistical improvement" of orientation in both experimental groups. First, individuals that were only marginally (but not significantly) oriented combined to produce a "net" significant orientation. Second, the increased N favors significance with the Rayleigh test.

This second order analysis, in which a mean of means is considered, is subject to controversy (Emlen 1975). One could argue whether there is real biological significance with this kind of statistical significance. Nonetheless, our calculations result in highly significant differences. Each group displayed a definite tendency to select a direction; we conclude that this direction was determined by physiological condition rather than the seasonal information that may be contained in celestial cues.

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