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The effects of an altered photoperiod upon the migratory orientation in the White-throated Sparrow (Zonoirichia albicollis)

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THE EFFECTS OF AN ALTERED PHOTOPERIOD UPON THE MIGRATORY ORIENTATION IN THE WHITE-THROATED SPARROW, *ZONOTRICHIA ALBICOLLIS*

INTRODUCTION

A variety of cues are available that a nocturnal migratory bird might use to orient during its journey. Perhaps the best established is their use of the information available in the celestial sky. But how much information do they gain? Experiments have shown that the apparent nightly movement of the stars caused by the earth's rotation aids in providing the bird a north-south axis or compass information (Emlen, 1967b; Gauthreaux, 1969). In addition, certain constellations in the northern circumpolar region are crucial for this axis determination (Emlen, 1967b). The celestial sky also changes in a regular manner with the seasons. Although the configuration of the constellations remains the same, their location appears to change throughout the year due to the earth's revolution around the sun. Does this seasonal shift contribute to the major reversals of direction taken each year by migratory birds?

In a planetarium, if the sky is advanced twelve hours from a particular migratory season, it produces the celestial equivalent of the opposite migratory season while location and time of day remain the same. Sauer and Sauer (1960) used this technique to test the aforementioned hypothesis with two species of European warblers, one Garden Warbler *(Sylvia atricapilla)* and three Blackcaps *(Sylvia borin)*. Their results appeared inconclusive as these birds oriented both to the north and south. Emlen (1967b) performed a similar experiment using Indigo Buntings *(Passerina cyanea)*. When a planetarium sky simulating a fall migratory season was shown to these birds in the spring, they continued to orient in a northerly direction. Thus there seems little support for the hypothesis that changing star patterns contribute to the seasonal reversals in orientation.

These results raised the possibility that changes in a bird's physiological condition during the year influenced its orientation as well as the periodic occurrence of fat stores, feather molt, and gonadal growth. Emlen (1969a) tested the orientation of two groups of Indigo Buntings in opposite migratory conditions simultaneously in a planetarium. The birds viewed a celestial sky appropriate for the spring season. Therefore, the control group consisted of birds in a spring physiological condition and the experimental group of birds, in a fall migratory condition. The results indicated that the birds prepared for a fall migration did orient to the south even when allowed to view a sky appropriate for spring migration. Emlen concluded that annual changes in the physiological condition, and not environmental cues, contributed to the major reversals in migratory orientation.

The purpose of this study was to further test this conclusion with the White-throated Sparrow *(Zonotrichia albicollis)* under a natural celestial sky instead of a planetarium. In addition, to see if there were not merely a specific seasonal effect in Emlen's results, all tests in the present study were conducted during the fall migratory season instead of the spring.

METHODS

Two groups of White-throated Sparrows were brought into spring and autumn migratory condition simultaneously by means of photoperiod manipulation. The annual cycle in the experimental group was manipulated so that their physiological condition (spring) 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. At that time they were moved to an environmental chamber and maintained on a short daylength of nine hours light, fifteen hours dark (LD 9:15) until the period of testing in September 1975. On 21 September 1975, 15 days prior to the first test, this group was 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 the birds 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 ten days for weight, fat deposits, and molt status. Nocturnal activity was monitored continuously by keeping all birds in activity cages and recording gross locomotor activity on Esterline-Angus event recorders.

As a result of the extended winter photoperiod, birds in the experimental group did not attain the spring migratory or breeding condition until September

1975 when the photoperiod was increased to 15 hours. At the same time, the control group was experiencing a normal fall migratory condition. Thus both groups were available for testing in September 1975: the experimentals were physiologically prepared for a spring flight and the controls for an autumn journey.

Orientation was tested by means of the 'footprint' technique (Emlen and Emlen, 1966). 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 which is located approximately 30 miles north of Milwaukee, Wisconsin. At this distance, the potential visual and acoustic biases from the city are negligible. Each test was three and one-half hours long and ran from 21:00 -00:30 hours EST. Birds were not removed from their living cages until after sunset and were returned each morning before the following sunrise. All tests were conducted under clear celestial skies.

Analysis of data. Intensity of footprints was quantified by comparison with an arbitrary scale similar to that described by Emlen and Emlen (1966). The activity of a single bird was totaled over all nights tested and subjected to Rayleigh's test of randomness for circular distributions. Application of this test has been described by Batschelet (1965, 1972). The null hypothesis states that the data have a uniform distribution. If the bird's activity deviated from random, then the distribution of its marks would be non-uniform, i.e. they would fall in a preferred direction. This direction is the mean angle from all nights of activity.

Determination of Rayleigh's test statistic (z) depends upon N. Using the footprint technique, N is a measure of the total activity of the bird. N was calculated as described by Emlen (1969b, appendix 5) with the following modifications. First, we estimated 1.4 hops per activity unit instead of 2.8 that Emlen used. Second, for statistical purposes, it is important to insure that each hop a bird makes is independent of the one preceding it. Emlen stated that 'this independence level (I.L.) is approached at four and definitely reached at eight hops. However, the data he presents shows that values from four onward give essentially the same result. The value selected is of some importance as it can significantly alter the final value of N. This in turn, could influence whether or not a bird showed statistically significant orientation. Consequently, in this paper, N values for each level (N8 and N4) are employed and a mean angle and mean angular deviation calculated if either produced a definite orientation ($p \leqslant 0.05$).

RESULTS

Of the eight experimental birds that were active, only one (773) showed definite orientation directed towards the north. Two other birds, 620 and 562 were oriented only for nightly mean headings and N(4) I.L. respectively. This orientation likewise was directed towards the north. The activity for the rest did not deviate significantly from random. The individual orientation of the control birds in fall migratory condition was little better than the experimentals. Only two birds, 608 and 503 showed any directional preference. Both oriented in a southwesterly manner.

If the nightly mean headings for all birds in each of the two experimental groups are pooled, then both groups are highly significant at all levels tested. The mean direction of all birds in a spring migratory condition was slightly east of north. Birds in an autumnal migratory condition were oriented almost WSW. Fig. 1 illustrates the distribution of total activity and nightly mean headings for each group.

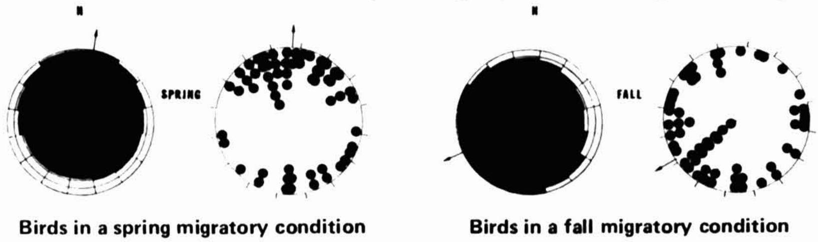

Fig. 1 Orientation of two groups of White-throated Sparrows in opposite migratory conditions. (Left) Vector diagrams represent the total activity for all birds in each group. (Right) Total mean nightly headings.

DISCUSSION

There are probably at least two explanations possible for the increased significance of the pooled data. 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 the subject of some controversy and has been discussed recently by Emlen (1975). One could argue whether there is real biological significance with this kind of statistical significance. Nonetheless, the calculation made in this study shows not just marginal significance, but with p values mostly well under 0.01. This suggests that each group displayed a definite tendency to select a direction, and that this direction was determined by its physiological condition, and not by the seasonal information that may be contained in celestial cues.

Support for an internal control of migratory orientation has come from the work of Martin and Meier (1973) with the White-throated Sparrow *(Z. albicollis)*. They induced either spring or fall migratory physiological condition and its appropriate orientation by altering the temporal administration of two hormones, prolactin and corticosterone. North or south orientation was also achieved by injections of exogenous prolactin at specific intervals after the suspected endogenous daily rise in corticosterone levels. They concluded that a bird's orientational preference each migratory season was due to the annual change in the circadian release of these two hormones. These results could provide an important link in our understanding of how orientation is initiated each season. Since photoperiodic changes are an important cue for timing the annual cycle, there may be good reason to suspect that this stimulates an annual hormone response such as described above. More evidence is needed which would link the natural change in seasonal photoperiod with an endogenous change in the physiological-hormonal condition. Even more important and inherently more difficult is to acquire evidence regarding the mechanism linking the physiological-hormonal condition with the overt change in locomotor orientation.

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