SUNRISE, SKYLIGHT POLARIZATION, AND THE EARLY MORNING ORIENTATION OF NIGHT-MIGRATING WARBLERS[1]

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Abstract. Field observations reveal that night-migrating passerines sometimes fly during early morning hours. Functional consideration of daytime flights have overshadowed proximate questions regarding the sensory basis of daytime orientation. I conducted a series of early morning cage-orientation experiments in spring with four species of migrating warblers (Parulinae) on the north coast of the Gulf of Mexico. Whereas birds were poorly oriented on overcast mornings, the headings for three species were oriented in a seasonally appropriate direction when individuals were tested on clear mornings with the horizon glow from the rising sun visible. Moreover, the direction of activity was influenced in a predictable way by manipulating the pattern of skylight polarization. Skylight at sunrise appears to function as a source of directional information for morning flights of migrating warblers. This interpretation is consistent with field observations of the orientation behavior of free-flying migrants, and reinforces speculation that solar-related information is involved in the orientation of ongoing migratory flight, or redetermined orientation following nighttime displacements. In any case, the responsiveness of several species in a cage situation may allow controlled experiments on the question of course correction and redetermined migratory flight.

Key words: Migration; orientation; sunlight; polarization; trans-Gulf migrants; morning activity.

INTRODUCTION

Passerines that typically migrate at night are also observed migrating by day, often during the morning hours shortly after sunrise (e.g., Rabøl 1967, 1969; Rabøl and Hindsbo 1972; Gauthreaux 1978; Bingman 1980; Hall and Bell 1981). The functional significance of morning flight has received considerably more attention than the sensory basis largely because the phenomenon is sometimes associated with cases of apparent displacement (e.g., Baird and Nisbet 1960; Myres 1964; Rabøl and Hindsbo 1972; DeSante 1973, 1983; Murray 1976; Able 1977; Gauthreaux 1978; Richardson 1978a). For example, some of the morning flights that are common along coasts probably represent efforts to regain land following offshore drift the preceding night (e.g., Myres 1964), whereas others occur in response to winds unfavorable for continued flight (e.g., Richardson 1978a). Gauthreaux (1978) suggests that the morning movements at inland localities may function to correct for wind drift sustained during nocturnal migration, and he refers to such flights as redetermined migrations (sensu Lack and Williamson 1959). Other early morning movements of nocturnal migrants may simply represent ongoing migration (Bingman 1980). For example, nocturnal migrants that cross ecological barriers, such as the Gulf of Mexico, initiate flight at night but of necessity complete

their flight in daytime (Lowery 1951, Gauthreaux 1971, Wood 1982).

I conducted cage experiments with several species of migratory warblers (subfamily Parulinae) to address three questions about the sensory basis of daytime orientation of typically night-migrating passerines. First, do night-migrating birds orient their morning cage activity in a seasonally appropriate direction? Whether the movement of nocturnal migrants during early morning hours represents ongoing migratory activity (e.g., Bingman 1980), redetermined migration (e.g., Gauthreaux 1978), or both, the observed flights are typically well oriented. The same cannot be said of cage activity recorded at this time. Wiltschko and Hock (1972) reported seasonally appropriate directionality among captive European Robins (*Erithacus rubecula*) tested in the morning, but only if the birds showed nocturnal restlessness the night before a morning test. Orientation of morning activity following nights without nocturnal restlessness was unrelated to the bird's migratory direction. When Able (1977) tested several species of migrants on Block Island, off the northeastern Atlantic coast, oriented cage activity was interpreted as a positive phototactic response to the rising sun.

Second, if migrants are found to be well oriented, does the sunrise position function as a reference in the selection of a direction? Wiltschko and Hock (1972) concluded that selection of a migratory direction was dependent upon the earth's magnetic field after monitoring the orientation behavior of European Rob-

ins during daylight hours following nights of migratory activity. They added that orientation behavior may also be influenced by a bird's sun compass. Gauthreaux's (1978) description of the initiation of morning flights by nocturnal migrants implicates the role of solar cues in the orientation of free-flying birds:

> On overcast mornings migrants frequently circled, called, changed direction abruptly, and often landed after a brief period of flight. On those mornings when solid cloud cover was present for the first hour or two of a watch, the number of migrants was greatly reduced, but when cloud cover dissipated and the sun was visible, the number of migrants showing redetermined flights increased dramatically.

If the sun provides compass information at this time, orientation might deteriorate when the sun's position is not visible (Sunrise Visible Experiment).

Third, if a migrant (re)determines a migratory directon around the time of sunrise, does the bird take advantage of the pattern of skylight polarization, an especially prominent directional reference at sunrise (Polarization Experiment)? Evidence from cage-orientation experiments conducted during the sunset period with White-throated Sparrows (*Zonotrichia albicollis*) is consistent with the hypothesis that migrants are able to orient their activity with respect to the pattern of skylight polarization (Able 1982). Experiments with homing pigeons also point to the significance of skylight polarization for compass orientation (Phillips and Waldvogel 1982). If the pattern of skylight polarization influences morning orientation, a shift in the pattern of polarization would effect a corresponding shift in activity.

METHODS

Cage-orientation experiments were conducted in April 1984 and 1985 using migrating warblers that had stopped in an isolated woodland (29°45'N, 93°33'W), along the north coast of the Gulf of Mexico following a trans-Gulf crossing. Narrow coastal woodlands ("cheniers") that lie scattered along the southwest coast of Louisiana are important staging and stopover sites for trans-Gulf migration. This habitat supports a luxuriant vegetation that provides a place to rest and replenish energy reserves following a long (18 to 24 hr) flight of approximately 1,000 km over the Gulf of Mexico. Birds were mist-netted either late the afternoon before a morning test or prior to civil twilight the morning of a test. The Sunrise-Visible Experiment compared the orientation of birds tested on mornings when the horizon

glow from the rising sun was clearly visible (approximate azimuth = 80°) with the orientation of birds tested under overcast morning skies. Behavior was examined by placing individuals in funnel shaped Emlen Orientation Cages (Emlen and Emlen 1966) near the beginning of civil twilight and activity recorded for 90 min. During the last 30 min of a test the bird could see the disc of the sun if they clung, for instance, to the wire mesh top at the opposite (west) side of the cage.

The Polarization Experiment was performed under clear skies before the sun's disc was visible to the caged migrants (approximately 60 min). The top of each orientation cage was completely covered with a linear polarizer (*Edmund Scientific*) that oriented the E-vector the same in all parts of the sky, polarized light from all parts of the sky almost 100%, and reduced transmission to 25% of ambient. Individuals were assigned randomly to one of two groups: (1) polarizer E-vector oriented 45° counterclockwise from the azimuth of sunrise and (2) polarizer E-vector oriented 45° clockwise from the azimuth of the sunrise. The two groups were thus exposed to skies of identical color and light intensity patterns, but had E-vectors that differed from each other by 90° and from the natural zenith sky E-vector by ±45°.

Activity records from Emlen funnels were divided into 16 22.5° sectors and quantified according to a density scale. The mean direction of activity and the concentration of activity were calculated according to vector analysis. The headings were pooled for each species according to experimental situation and subjected to analysis (see Batschelet 1981). All vector mean headings were included regardless of the length (r) of the vector. Analysis of the relationship between vector length and vector direction suggests that meaningful orientation is not dependent upon the concentration of activity (see Wiltschko and Wiltschko 1978).

RESULTS

SUNRISE VISIBLE EXPERIMENT

Only the orientation behavior of species for which there were sufficient data to draw inferences is presented (see Fig. 1). When tested on clear mornings (horizon glow from the rising sun visible), trans-Gulf migrants displayed early morning cage activity that was oriented in a seasonally appropriate direction. Two species, the Ovenbird (*Seiurus aurocapillus*) and the Northern Waterthrush (*S. noveboracensis*), show northerly orientation, though the distribution of headings for the latter is bimodal along a North-South axis (Fig. 1). The distribution of headings for the Kentucky
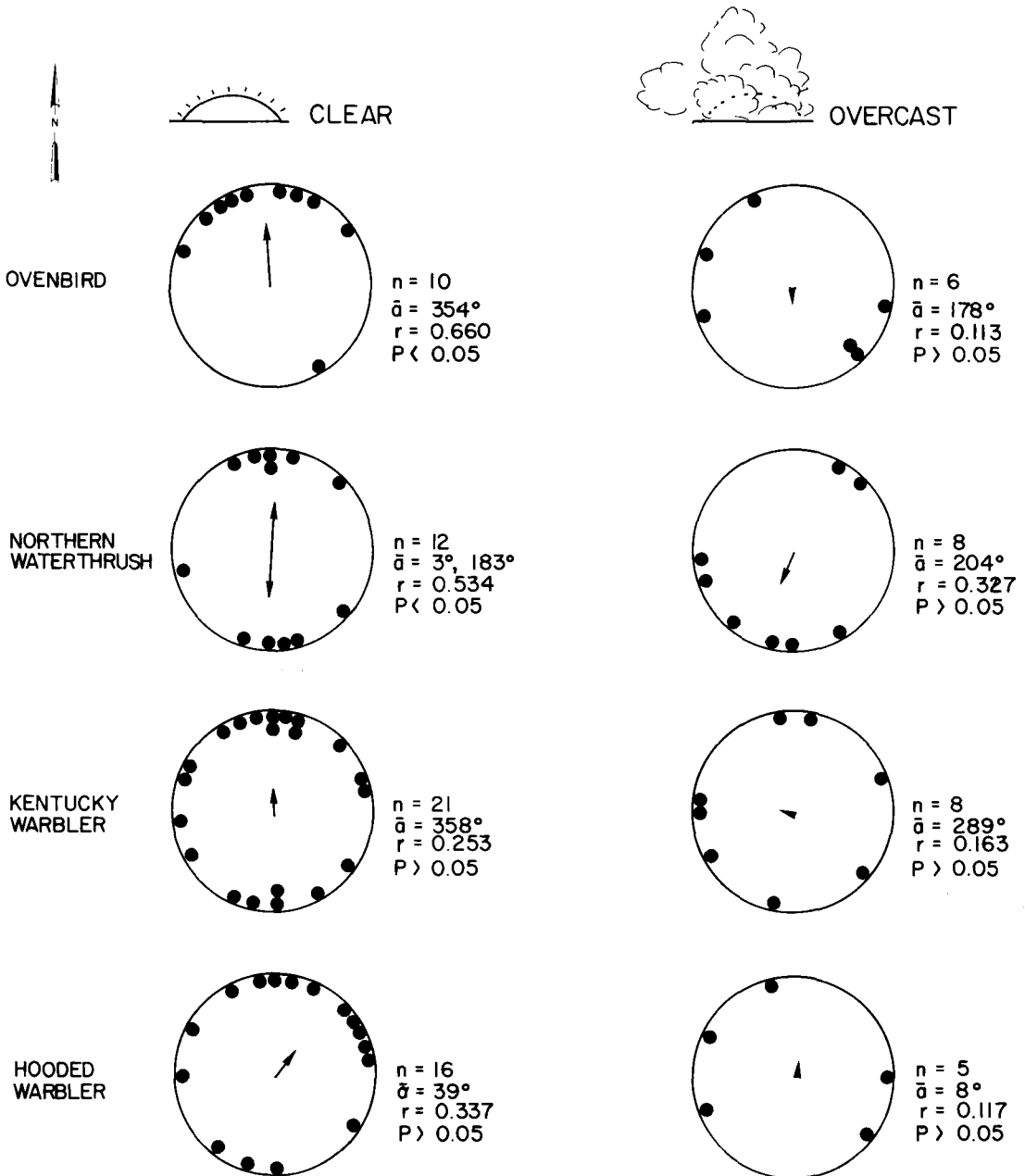
FIGURE 1. Orientation of migrants tested under clear early morning skies (sunrise visible) and under overcast morning skies (sunrise not visible). Individual mean headings are shown as dots along the circumference. The mean vector (ā) of a sample is represented as an arrow whose length (r) is drawn relative to the radius of the circle = 1. The distribution of headings for the Northern Waterthrush under clear conditions is statistically bimodal (see Batschelet 1981) and the two modes are shown. The P value refers to the likelihood that a distribution of headings is statistically uniform. Geographic north is to the top.

(*Oporornis formosus*) and Hooded (*Wilsonia citrina*) Warblers under the "Clear Sky" test are statistically uniform though inspection reveals a northerly bias in both patterns. If all individuals ($n = 59$) regardless of species are pooled the distribution is oriented northward (mean $= 4°$, $r = 0.265$, $P < 0.05$). When different individuals of the same four species were tested on overcast mornings, their activity was statistically less well oriented in each case (Fig. 1). Thus, the position of the sun in the early

morning influences the daytime orientation of night migrants and appears to be a source of compass information.

POLARIZATION EXPERIMENT

Results of tests with polarizing material placed over the test cages indicates that the orientation of early morning cage activity is influenced in a predictable way by manipulation of the pattern of skylight polarization. I pooled the mean vectors according to test condition
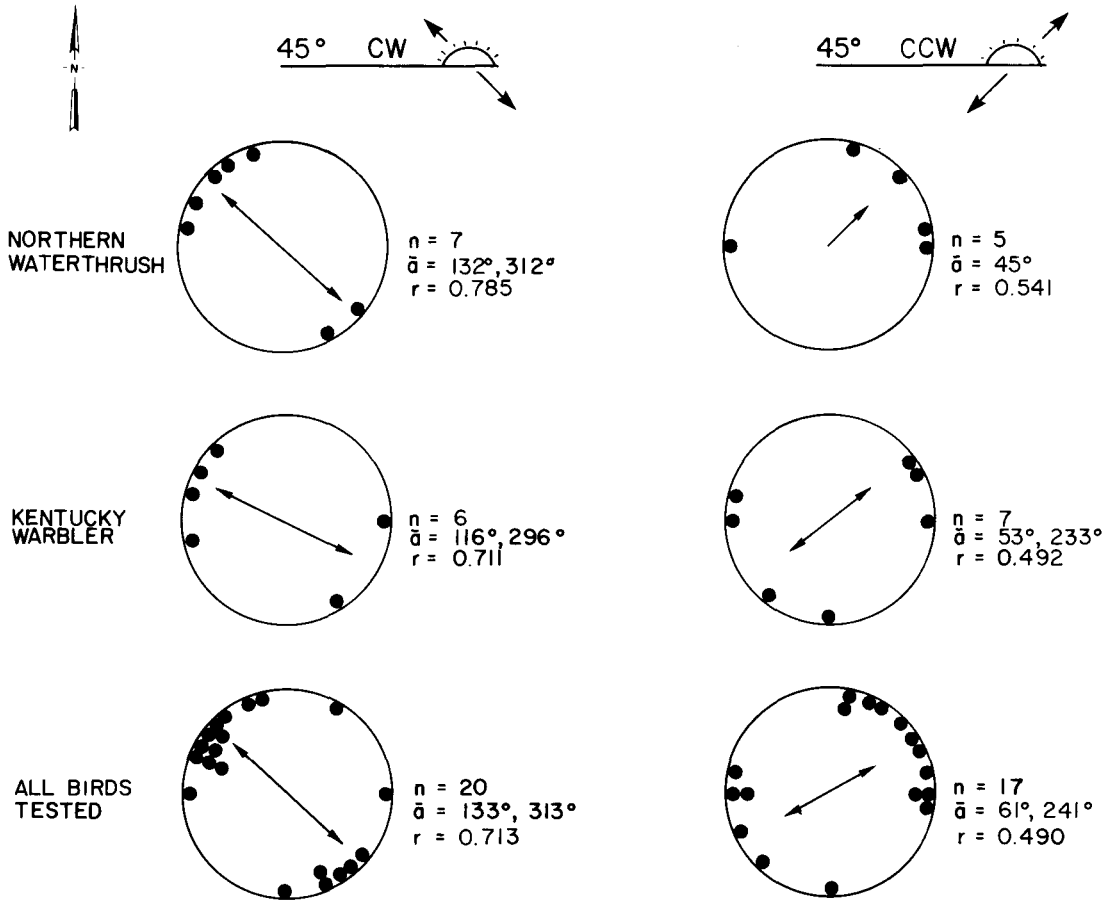
FIGURE 2.   The orientation of Northern Waterthrushes and Kentucky Warblers tested early in the morning with the E-vector of imposed polarized light oriented 45° clockwise (CW) and 45° counterclockwise (CCW) of the azimuth of sunrise. The dots represent mean headings. The distributions of the pooled headings are bimodal in all but one case. Also shown are the distributions for all warblers tested under the two conditions.

for the two species with sufficient sample sizes for analysis, Northern Waterthrush and Kentucky Warbler (Fig. 2). The resultant means for the two test conditions are oriented roughly parallel to the E-vector of polarization and perpendicular to each other in terms of geographic direction. When the means for all birds tested under the two conditions are pooled, the pattern becomes more evident and is obviously bimodal (see also Able 1982).

DISCUSSION

Individuals of at least four species display what appears to be migratory orientation when cage-tested in the early morning. Occasionally, activity was oriented toward or 180° away from the horizon glow of the sunrise in what might be a phototactic response, but the pattern of mean headings is northward and appropriate for spring migration. Although I cannot say how the early morning activity of these migrants compares with their migratory orientation at night (see Wiltschko and Hock 1972), the northerly orientation of the cage activity

is consistent with direct visual observations of the nightly initiation of migration from Gulf coastal habitat similar to my study site (Hebrard 1972). Moreover, the orientation of the cage activity is consistent with observations of migrants that fly northward from stopover sites along the northern Gulf coast shortly after arrival at midday (see Gauthreaux 1971, Moore pers. observ.). Because our knowledge of migratory orientation depends heavily upon the results of cage-experiments with nocturnal migrants (see Schmidt-Koenig 1979, Baker 1984), it is essential that results such as those reported here are interpreted in light of field observations of migratory behavior.

Second, the migrants involved in my early morning experiments appear to use the sun in some way as a reference for compass orientation. Although migratory birds are capable of deriving compass information from a wide array of environmental references (Schmidt-Koenig 1979, Keeton 1981, Baker 1984), the support for that conclusion depends on experiments with migrants conducted shortly before

or soon after their nightly departure. Of course, there is no a priori reason to believe that daytime orientation is less complex. Cage orientation studies with typically diurnal migrants, though few in number (e.g., Gluck 1982, Holmes 1982), suggest integration of information from different sources. For example, Gluck (1982) reported oriented activity for European Goldfinches (*Carduelis carduelis*) held in orientation cages without a view of sun, implicating magnetic cues, but the direction of activity was seasonally inappropriate in both fall and spring. He speculated that these diurnal migrants required a view of sun to establish their migratory direction.

Third, migrants respond to the imposed pattern of skylight polarization by orienting their activity parallel to the E-vector. This response implicates the axis of skylight polarization as a source of information for the orientation of morning as well as early evening ('dusk') migratory activity (see Brines and Gould 1982, Able 1982). On the one hand, a migrant could use the relationship between the polarization direction of polarized skylight (E-vector) and the sun's azimuth to locate the position of sun when it is below the horizon or otherwise obscured. Alternatively, the characteristic band of maximum polarization might be used independently of sunrise to determine geographic direction. It should not be concluded on the basis of these experiments or Able's (1982) work with White-throated Sparrows that the orientational value of directional information obtained at sunrise (or sunset) is dependent upon polarization patterns visible at the time. The critical experiment that would separate the influence of sun position itself (whether at sunset or sunrise) from the pattern of skylight polarization remains to be conducted.

Bimodal orientation characterized the behavior of Northern Waterthrushes in both the Sunrise and the Polarization Experiments. Although it is not readily apparent why this species or any of the species tested, for that matter, would display a bimodal pattern under the Sunrise Experiment test conditions, the pattern might suggest some ambiguity in the orientation process. Based on the bimodality found in both experiments it might be tempting to infer that migrants are using the pattern of skylight polarization to orient their early morning activity. However, the bimodality evident in the Polarization Experiment distributions probably reflects ambiguity associated with the experimental treatment; the two 'ends' of the E-vector cannot be distinguished in the type of polarization patterns presented to the caged birds (see also Able 1982). Hence, unambiguous compass directions are not provided. Migrants using polarization patterns under natural skylight (Sunrise Experiment) should be able to distinguish unambiguously a geographic direction (see Brines and Gould 1982).

Fourth, the cage-orientation results reported here are consistent with speculation that early morning activity may be involved in the redetermination of migratory orientation following nighttime displacements. If night migrating birds select a direction prior to their nightly departure and then try to maintain that direction while aloft, when do they adjust for the orientational errors and displacements that occur while en route? Of course, how well migrants maintain a preferred heading is difficult to evaluate. Once aloft migrants are seldom observed to be disoriented, though flight in seasonally inappropriate directions is not an uncommon observation (Griffin 1973; Richardson 1978b; Able 1980, 1982). Orientation errors do occur (Herbert 1970), especially among younger, less experienced migrants (e.g., Ralph 1978, Gauthreaux 1982, DeSante 1983) not to mention the likelihood that many migrants are occasionally wind drifted. Although it is possible that migrants "correct" while aloft, it is more likely they redetermine direction on the ground either soon after landing or shortly before their next departure. Based upon direct visual observations, Gauthreaux has advanced the intriguing hypothesis that early morning flights are a corrective measure for displacement experienced during a night's migration (but see Bingman 1980). The morning following displacement would be a reasonable time to reorient (Able 1977). In any case, the responsiveness of several species to a cage paradigm may allow controlled experimental work on the question of error correction and redetermined migratory flight.

ACKNOWLEDGMENTS

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