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Calibration of the sun compass by sunset polarized light patterns in a migratory bird

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Summary. Migrating birds derive compass information from the sun, stars, geomagnetic field and polarized light, but relatively little is known about how these multiple sources of directional information are integrated into a functional orientation system. We found that migratory warblers exposed to a rotated polarized light pattern at sunset oriented at a constant angle to the axis of polarization. When polarized light cues were eliminated, this shifted orientation was maintained relative to the setting sun. Polarized light patterns, thus, appear to provide a calibration reference for the sun compass in nocturnal migrants, and may also play a role in calibrating other compass systems.

Introduction

Night migrating birds use a diverse array of directional cues to select and maintain an appropriate migratory direction (Able 1980; Wiltschko 1983; Wiltschko and Wiltschko 1990), including the sun and polarized skylight at sunset when migration is initiated and the stars and/or geomagnetic field after dark (Moore 1987). This high degree of redundancy in the compass systems used for nocturnal migration attests to the strong selection for accurate migratory orientation (Alerstam 1990), and raises the question of how these multiple sources of directional information are calibrated and integrated into a functional orientation system (Able 1980; Wiltschko 1983; Wiltschko and Wiltschko 1990).

The sun compass, the star compass and, possibly, the polarized-light compass are learned during ontogeny and may be periodically recalibrated in adult birds (Able 1980; Wiltschko 1983; Schmidt-Koenig 1990). Thus, each of these compass systems must be referenced either directly or indirectly to an innately determined directional cue in order to encode accurately the appropriate migratory direction. Recent studies have also suggested that the magnetic compass, although having an innate component, may also be recalibrated when placed in conflict with celestial light cues (Able 1980; Able and Bingman 1987).

During ontogeny, rotation of the night sky plays a primary role in the calibration of star patterns in nocturnal migrants (Emlen 1970). In adult birds, however, the star compass appears to be calibrated with respect to the earth's magnetic field (Wiltschko and Wiltschko 1990) and/or to celestial cues present at sunset (Moore 1987). Recently, Able and Able (1990a) have shown that the magnetic compass of young savannah sparrows *Passerculus sandwichensis* can be recalibrated with respect to "rotational north" of an artificial star pattern, suggesting that celestial rotation may provide a primary reference during ontogeny not only for the star compass (Emlen 1970), but for the magnetic compass as well. Evidence that celestial rotation provides the primary reference for calibrating the magnetic compass under natural conditions, however, is more equivocal (Able and Able 1990b; and see Discussion).

Sunset is an important time for the integration of directional information used by many night-migrating birds. Orientation cage studies, as well as observations of free-flying migrants, suggest that celestial light cues present at sunset play a critical role in determining migratory direction (Moore 1987; Sandberg 1991) and that the directional heading established at sunset may be "transferred" to other compass systems to maintain the directional heading during nocturnal migration (Moore 1987). Interestingly, however, when a view of the sky immediately above the horizon was obscured during cage tests nocturnal migrants oriented poorly or in an inappropriate direction (Ottosson et al. 1990; Sandberg 1991). Thus, the region of sky immediately above the horizon appears to be crucial for determining migratory direction.

A number of recent studies of nocturnal migrants have demonstrated that polarized light patterns present at sunset are used by adult birds in preference to other cues (e.g., the setting sun and the earth's magnetic field)

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when the region of sky immediately above the horizon is visible to birds during testing (Able 1982; Helbig and Wiltschko 1989; Helbig 1990). The experiments reported here were carried out to determine whether sunset polarized light patterns provide the primary reference system used by adult nocturnal migrants to calibrate other compass systems, as suggested by Brines (1980; see also Phillips and Waldvogel 1982, 1988).

Materials and methods

Experimental subjects. Yellow-rumped warblers *Dendroica coronata* were studied during the spring migratory season. Birds were mist-netted during the first week in January near Hattiesburg, Mississippi and housed singly in activity cages (40 cm on a side) under the local geomagnetic field. They were fed a diet of commercial monkey biscuits (Zupreem) and mealworms supplemented with vitamins and minerals. Cages were equipped with movable perches attached to microswitches so that activity could be monitored. In 1989, one group of birds was exposed to artificially prolonged day lengths (LD 16:8) which induced migratory disposition, including body mass increase, subcutaneous fat deposition and migratory activity. By inducing migratory disposition early in this group, we were able to conduct orientation tests in late February and March, prior to spring migration. A second group of birds in 1989 was exposed to natural day lengths and tested during the normal period of spring migration.

Orientation cages. Orientation cages used in these experiments were designed to present the birds with an artificial polarized light pattern originating from the region of sky immediately above the horizon while simultaneously giving them access to other compass cues (i.e., the sun and magnetic field). The cage has been described in detail elsewhere (Moore and Phillips 1988), and consisted of an Emlen funnel (Emlen and Emlen 1966) which prevented a view of surrounding landmarks and was centered within a hexagonal enclosure consisting of six 32 cm × 26 cm windows and covered by a top of 3/8″ plywood ((Fig. 1a). The hexagonal enclosure was aligned so that one pair of windows located 180° apart faced north and south along the N-S geomagnetic axis. Windows were constructed so that light first passed through a depolarizer (Moore and Phillips 1988) and then through a Polaroid filter which transmitted wavelengths greater than 400 nm (Edmund Scientific Company). The polarizer was aligned to produce either a vertical or horizontal E-vector. Depolarization of the incoming light prevented changes in light intensity from occurring when the polarization axes of the filters were rotated.

An artificial polarization axis was produced by aligning the polaroid filters in two windows located 180° apart to produce a vertical E-vector (Fig. 1a) simulating the vertical alignment of the E-vector within the band of maximum polarization (BMP) on the horizon at sunset (Brines 1980; Phillips and Waldvogel 1982, 1988). The remaining windows had polaroid filters aligned to produce a horizontal E-vector so that the effect of the depolarizers and polaroid filters on the relative intensity and spectral content of light was the same in all directions.

Testing procedures. Five orientation cages were used on each day of testing to record migratory activity for approximately 2 h during the sunset period. Sky conditions were clear on the horizon ($\leq 3/10$ths cloud cover). Activity records were divided into sixteen 22.5° sectors and quantified according to a density scale (Moore 1980). Birds that failed to reach a criterion of 40 hops/night were excluded from analysis (Moore 1980). Directional bearings were pooled by experimental treatment and analyzed according to standard procedures for circular distributions (Batschelet 1981). In conditions where a bimodal distribution of bearings was expected due to the symmetry of the artificial polarized light pattern, bearings were doubled prior to analysis (Batschelet 1981).

Conditions under which birds were tested are indicated by the diagrams within the circular distributions in Fig. 1. Birds were initially tested in a control condition to determine the direction of migration prior to any manipulation (Fig. 1b). In 1988, control tests were conducted without depolarizers or polaroid filters covering the orientation cage windows, permitting an unaltered view of the natural sky (Fig. 1, solid symbols). In 1989, control tests were conducted with polaroid filters aligned to produce a vertical E-vector in all directions, i.e., with directional polarized light cues eliminated (Fig. 1, open symbols).

After the initial test, birds in both years were randomly divided into two groups which were tested on three nights under a shifted polarization axis. One group was exposed to a polarization axis rotated 60° clockwise from the N-S axis, and the other to a polarization axis 60° counterclockwise (Fig. 1c). After three nights of exposure to an altered polarization axis, the birds were tested with the polaroid filters on the six windows aligned to produce a vertical E-vector in all directions so that directional polarized light information was eliminated (Fig. 1d). In 1988, birds remained in migratory condition long enough to be tested under a fourth condition. Mirrors were attached at a 45° angle from the cage windows to rotate the apparent position of the setting sun 90° counterclockwise with directional polarized light cues absent.

Results

In both years, the distribution of bearings obtained under the control condition was oriented in a northward direction. These control data are consistent with the spring migratory orientation observed in previous studies of this species (Moore and Phillips 1988) and roughly coincided with the northern end of the natural polarized light axis for the time of year when the experiments were conducted. When warblers were exposed to shifted polarization axes (Fig. 1c), the distributions of bearings were bimodally distributed along the new polarization axes. These data confirmed the results of the earlier study (Moore and Phillips 1988) indicating that yellow-rumped warblers orient with respect to an artificial polarized light pattern in preference to the position of the setting sun and the alignment of the geomagnetic field.

When birds exposed to artificial polarization axes for three nights were subsequently tested without directional polarized light cues (Fig. 1d), the two groups continued to exhibit bimodal orientation coinciding with the former polarization axes. These results indicate that exposure to a shifted polarization axis resulted in recalibration of one or more of the other compass systems used by yellow-rumped warblers for migratory orientation.

Our previous study suggested that warblers tested without access to polarized light information rely on the sun compass (Moore and Phillips 1988). In 1988, we were able to confirm this conclusion using birds that had been exposed to artificial polarization axes by carrying out tests with directional polarized light cues eliminated and sunset position rotated approximately 90° counterclockwise (Fig. 2). When the position of sunset was rotated, the birds' orientation shifted to maintain the same angle relative to the setting sun.

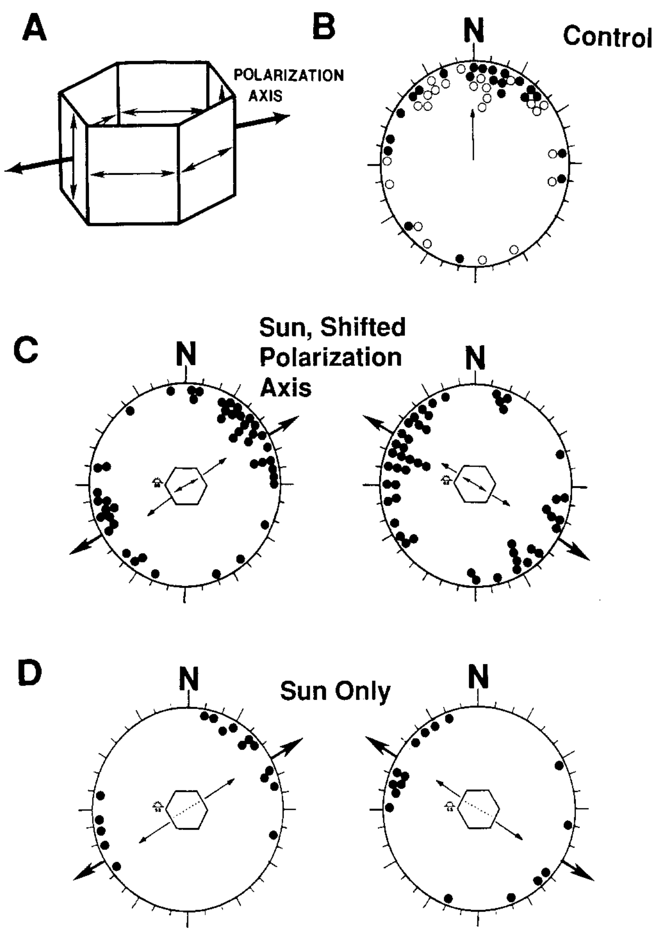

Fig. 1. **A** Hexagonal enclosure used to produce artificial *polarization axis* (see text). **B** In the control condition, the mean bearing in 1988 (*solid symbols*) was 3° ($n=22$, $r=0.57$, $P<0.001$) and in 1989 (*open symbols*) was 354° ($n=24$, $r=0.42$, $P<0.02$). Distributions in the two years did not differ ($P>0.50$, Watson U^{c}) and yielded a combined mean bearing of 359° ($n=46$, $r=0.49$, $P<0.001$, Rayleigh test). **C** Individual birds were tested on three nights in the sun, shifted polarization axis condition. Although all of the bearings are plotted, statistical analyses were carried out using a mean axis of orientation for each bird calculated from its nightly bearings. Birds exposed to a polarization axis rotated 60° clockwise oriented along an axis of 53–233° ($n=16$, $r=0.67$, $P<0.001$). Birds exposed to a polarization axis rotated 60° counterclockwise oriented along an axis of 119–299° ($n=17$, $r=0.59$, $P<0.002$). The two distributions differed significantly ($U^{\mathrm{c}}=0.475$, $P<0.001$), and the 95% confidence intervals for both groups contained the expected polarization axis. **D** In the "sun only" condition, the group that had been exposed to an E-vector axis rotated 60° clockwise oriented along an axis of 57–237° ($n=16$, $r=0.67$, $P<0.001$). The group that had been exposed to an E-vector axis rotated 60° counterclockwise oriented along an axis of 122–302° ($n=17$, $r=0.59$, $P<0.002$). The two distributions differed significantly ($U^{\mathrm{c}}=0.39$, $P<0.001$) and 95% confidence intervals for each distribution contained the *former* polarization axis

Discussion

Yellow-rumped warblers clearly gave precedence to directional information from the artificial polarized light pattern used in these experiments over other available compass cues (e.g., the sun and geomagnetic field; Fig. 1c). This finding is consistent with a number of previous studies of adult nocturnal migrants (e.g., Able 1982; Helbig and Wiltschko 1989; Helbig 1990), with the only exceptions being studies in which the region of sky near the horizon was at least partially obscured (Bingman and Wiltschko 1988, and Bingman pers. commun.; Sandberg 1988). These exceptions, therefore, are likely to result from differences in experimental design, rather than species-specific differences in the use of polarized light cues (see Helbig 1991).

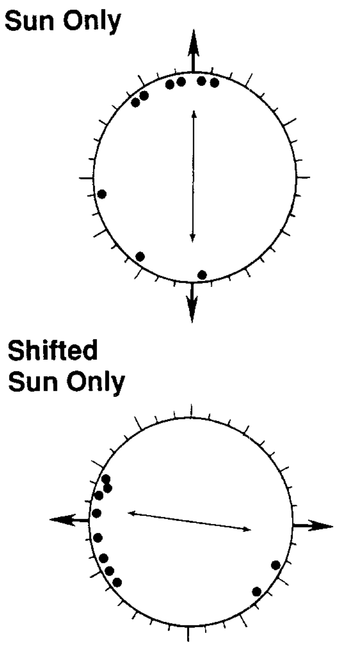

Fig. 2. In 1988, birds were tested in both the "sun only" condition (*upper distribution*, data included in Fig. 1d) and the "sun only, shifted 90°" condition (*lower distribution*). Because of small sample sizes, data from the two groups were pooled with respect to the polarization axis to which the birds had been exposed in the "sun, shifted polarization axis" condition (Fig. 1c). Bearings obtained with the natural sun position (*upper diagram*) coincided with the former axes of polarization (0–180°, $n=9$, $r=0.63$, $P<0.03$), while the bearings obtained with the position of the setting sun rotated 90° were shifted by a comparable amount (97–277°, $n=10$, $r=0.60$, $P<0.03$). The two distributions were significantly different ($U^{\mathrm{c}}=0.30$, $P<0.005$), and the 95% confidence intervals for both distributions included the former position of the polarization axes in relationship to the setting sun. *Arrows* at the outer edge of each distribution indicate the expected axis of orientation if sun position was calibrated with respected to the artificial polarization axes

Nocturnal migrants exhibit seasonally appropriate migratory orientation when the region of sky near the horizon is visible, even when a large area of sky centered on the zenith is blocked from view (Moore 1980; Moore and Phillips 1988; and see Fig. 1a), but do not exhibit appropriate migratory orientation when given a view of the sky that is restricted to a region within 45° of the zenith (Ottosson et al. 1990; Sandberg 1991). Taken as a whole, these data suggest that celestial light cues, and, in particular, polarized light cues, from the region of sky near the horizon play an important role in establishing the migratory direction of adult nocturnal passerines.

In contrast to the present study, a consistent finding of previous orientation cage studies that have used artificial polarized light patterns has been that the distributions of bearings showed a bias toward the bright region of sky around the setting sun (Able 1982, 1989; Sandberg 1988; Helbig and Wiltschko 1989; Able and Able 1990c). The absence of a phototactic response to the setting sun in our data (Fig. 1) suggests that the artificial polarized light patterns used in this study more closely approximated critical features of the natural polarized pattern used by nocturnal migrants to determine migratory direction.

In the present study, the polarization filters did not transmit wavelengths below 400 nm. However, the absence of near-ultraviolet light does not rule out the possibility that yellow-rumped warblers use an ultraviolet-sensitive photoreceptor for polarized light detection, as proposed by Phillips and Waldvogel (1982, 1988) for the homing pigeon *Columba livia*. Due to the broad-band absorption spectra of vertebrate photopigments, the ultraviolet photoreceptor in birds (maximum spectral sensitivity around 370 nm; Chen et al. 1984) would be able to detect short-wavelength visible light in the range of 400–450 nm.

In addition to demonstrating the use of polarized light as an orientation cue, our data indicate that exposure to an altered polarization axis at sunset caused yellow-rumped warblers to recalibrate one of their other compass systems, most likely the sun compass. Several nights of exposure to the altered polarization axis appeared to be necessary for this recalibration to occur. In a previous study of yellow-rumped warblers (Moore and Phillips 1988), a single night of exposure to a new alignment of the polarization axis produced no evidence for the use of polarized light cues to calibrate other compass systems. A similar pattern has been found in some species that use the geomagnetic field to calibrate the star compass (Wiltschko and Wiltschko 1976; Beason 1989), i.e., several days of exposure to an altered alignment of the magnetic field appeared to be required to "update" the calibration of the star compass.

Are polarized light cues involved in the calibration of other compass systems? In nocturnal migrants, the magnetic compass appears to be calibrated with respect to an as yet unidentified celestial reference system (Able and Bingman 1987). Able and Bingman's findings suggest, furthermore, that in species where the star compass is calibrated with respect to the magnetic field (e.g., Wiltschko and Wiltschko 1976; Beason 1989), the star compass may ultimately be calibrated with respect to this unidentified celestial reference system as well.

Able and Able (1990 b) concluded that in the savannah sparrow, the reference system used to calibrate the magnetic compass is derived from the axis of celestial rotation. An alternative proposed by Phillips and Waldvogel (1988) is that celestial polarized light patterns are used to calibrate both the sun compass and the magnetic compass. Although Phillips and Waldvogel's proposal was based on studies of the homing pigeon *Columba livia*, a nonmigratory species, our current findings from yellow-rumped warblers (Figs. 1 and 2) indicate that celestial polarized light patterns also provide an important calibration reference in a nocturnal migrant, at least for the sun compass. Whether or not celestial polarized patterns also play a role in calibrating the magnetic compass in nocturnal migrants remains a question for future research. We should emphasize, however, that reference systems derived from rotation of the celestial sphere and from celestial polarized light patterns are not necessarily mutually exclusive, since the axis of celestial rotation may be detected by means of polarized light cues (Brines 1980).

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