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Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird

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Abstract 1. Young migratory birds enter the world with two representations of the migratory direction, one coded with respect to the magnetic field, the other with respect to celestial rotation. The preferred magnetic direction of migratory orientation is malleable early in life: it may be calibrated by celestial rotation, observed either in daytime or at night.

2. Previous experiments showed that early experience with skylight polarization was necessary for calibration to occur in daytime. In this study, we performed a direct manipulation of patterns of polarized skylight at dawn and dusk.

3. Hand-raised Savannah sparrows (*Passerculus sandwichensis*) were allowed to observe the clear sky for 1 h prior to local sunrise and for one h following local sunset. They never saw the Sun nor stars. The birds observed the sky through bands of polarizing material (HNP'B) aligned with the e-vector axis in one of three orientations with respect of the azimuth of sunrise and sunset: group 1) 90°; group 2) 45° CW; group 3) 45° CCW.

4. Tested indoors in covered cages in both shifted and unshifted magnetic fields, the autumn migratory orientation of the three groups differed significantly. Group 1 oriented magnetic N-S, group 2 oriented magnetic NW-SE, and group 3 oriented magnetic NNE-SSW. These observed orientation directions are very close to those predicted by the manipulations of polarized skylight.

5. These results indicated that a fairly simplified, static polarized light pattern viewed a limited number of times only in dawn and dusk snapshots is sufficient to produce calibration of the preferred magnetic migratory orientation direction.

Key words Migratory orientation · Magnetic orientation · Polarized skylight · Ontogeny · *Passerculus sandwichensis*

Abbreviations CW clockwise · CCW counterclockwise · N north · E east · S south · W west · mN magnetic north

Introduction

The magnetic compass appears to be ubiquitous among migratory birds and of central importance within the suite of orientation mechanisms at their disposal (magnetic, star, polarized light and, perhaps, sun compasses) (Wiltschko and Wiltschko 1991; Able 1994). The development of these orientation capabilities involves complex interactions between genetically-based information and experience guided by innate learning predispositions (Able 1991). Young birds possess two apparently innate representations of the migration direction, one coded with respect to the magnetic field, the other with respect to celestial rotation (Wiltschko and Wiltschko 1991). A functional magnetic orientation capability develops in birds that have never seen the sky (reviews, Able 1991, 1994).

The preferred migration direction based on magnetic information may be modified during at least the first three months of life, however, by exposing naive birds to either the clear daytime or night sky under conditions in which magnetic directions differ substantially from true or geographic directions (Bingman 1983; Bingman et al. 1985; Able and Able 1990a, b, 1993a; Prinz and Wiltschko 1993). Celestial rotation provides information about geographic directions both day and night. At night, a rotating pattern of artificial stars provided a sufficient stimulus to calibrate magnetic

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orientation in young Savannah sparrows (*Passerculus sandwichensis*) (Able and Able 1990b). Experiments in which hand-raised sparrows viewed the clear daytime sky only through depolarizing material showed that experience with skylight polarization was necessary for calibration to occur during daylight (Able and Able 1993a).

Polarized light patterns in the clear daytime sky are a function of the sun's position in the sky and rotate in parallel with its apparent movement. In theory, several parameters of skylight polarization could be used to locate geographic north. Using the dynamic pattern of polarization, a bird might localize the axis of rotation of the celestial sphere by observing the change in polarization patterns as the sun crosses the sky, as suggested by Brines (1980). The pattern of *e*-vectors rotates around the celestial pole point which, like Polaris, indicates true north. A somewhat simpler method involves observation of static patterns of polarized skylight (Phillips and Waldvogel 1982, 1988). When the sun is on the horizon at sunrise and sunset, the area of the sky with maximal polarization (the so-called band of maximum polarization) comprises an arc from horizon to horizon through the zenith. The band itself and the *e*-vector of polarized light within it are aligned orthogonally to the solar-antisolar meridian. At the equinoxes, when the sun rises due E and sets due W, the band and *e*-vector will be aligned geographic N-S and will intersect the horizon vertically only in those two compass directions. Because sunrise and sunset azimuths are symmetrical on any given day, geographic N could be localized at other times of year by determining the azimuth midway between the sunrise and sunset vertical intersection points on the horizon.

In this study we performed a direct manipulation of the patterns of polarized skylight seen by hand-raised Savannah sparrows whose visual experience with the sky was confined to 1 h prior to sunrise and 1 h after sunset. Because it has not been technically possible to simulate the dynamics of rotation of polarized light patterns in the sky, we exposed groups of birds to manipulated static snapshots of the dynamic pattern of polarized skylight. We asked whether exposure to these manipulated patterns of polarized light would be interpreted by the birds as a large magnetic declination and result in predictable differences in the calibration of their subsequent magnetic orientation.

Materials and methods

The Savannah sparrow is a medium-distance nocturnal migrant that nests in grassland, meadow and tundra across North America from the northern United States northwards to 60°–70° N. It migrates to the southern United States southward to northern Central America in winter. We transferred nestling sparrows from nests in the field to a laboratory incubator at 2–5 days post-hatching and hand-raised

them to independence. The birds were fed hourly for 16 h per day on a diet of Nutri-Start (Lafeber Co., Odell, Illinois) administered by syringe. At approximately 2–3 weeks of age, fledglings were weaned gradually onto a diet of Petamine mixed with bits of hard-boiled egg. This diet was slowly replaced with a mixture of turkey starter and white millet and the birds were transferred to individual cages constructed entirely of non-ferrous materials at approximately 3–4 weeks of age.

The birds were housed indoors in a wooden frame garage where they lived in a normal magnetic field and ambient photoperiod provided by incandescent lighting. They had no visual exposure to the outdoors or sky until experiments began. Sixty hand-raised birds from 21 nests were each assigned to one of three experimental groups such that nest mates were, to the greatest extent possible, placed in different groups. On clear or mostly clear mornings and evenings between 13 August and 25 September 1993, birds were placed outdoors in modified Emlen funnel cages (Emlen and Emlen 1966) from which they could view a portion of the sky. Each funnel cage was covered with a 30-cm diameter clear acrylic dome to the outside surface of which was affixed a band of polarizing material (HNP'B, Polariod Corp.) spanning the dome from horizon to horizon and passing through the zenith (Fig. 1A). Light transmission through these two layers of material was essentially flat across the visible spectrum and down to 370 nm in the near UV, below which it dropped off sharply. The remainder of the dome surfaces were covered with Parafilm painted over with melted paraffin to depolarize incoming light (Goddard and Forward 1991). The *e*-vector axis of the polarizing material was aligned parallel to the long axis of the band as shown by the heavy arrows in Fig. 1B.

Birds were given exposure to the clear sky for approximately 1 h prior to local sunrise and 1 h following local sunset. None ever saw the sun nor stars. Each of the three groups experienced a total of 5–6 h of exposure over 3–5 days spread across the treatment period. The three experimental groups were:

- 1) Birds that could view the sky through polarizing material with the *e*-vector axis aligned 90° with respect to the azimuth of sunrise and sunset. This alignment simulates roughly the natural dawn and dusk pattern of polarized light in the part of the sky visible to the birds (Fig. 1B).
- 2) Birds that could view the sky through polarizing material with the *e*-vector axis aligned 45° CW from the azimuth of sunrise or sunset (Fig. 1B).
- 3) Birds that could view the sky through polarizing material with the *e*-vector axis aligned 45° CCW from the azimuth of sunrise or sunset (Fig. 1B).

When the birds came into migratory condition for the first time in late September, their directions of magnetic orientation were recorded in covered Emlen funnel orientation cages during tests conducted indoors in a wooden frame building in normal (5.4×10^4 nT, inclination = 69°) and shifted magnetic fields (total intensity = 5.3×10^4 nT, inclination = 69°, magnetic N = geographic E). The shifted field was produced with a 1.8-m square coil (Merritt et al. 1983; Kirschvink 1992). Birds were prevented from seeing outside the test cages by translucent plastic sheets covering the cages. A dim incandescent light, passing through two diffusers and the translucent cage cover, provided a light of 0.2–0.4 lux in the cages. This variation in light intensity occurred across the array of test cages; light intensity within each cage was uniform. Tests began within 1 h after sunset and lasted for approximately 3 h. Roughly half of the birds were first tested in the normal field condition, the remainder first tested in the shifted field. Thereafter, individuals were assigned randomly to one or the other test condition. The orientation records were analyzed blind with respect to treatment group and test condition according to the methods described in Cherry and Able (1986). Because the directions chosen by the individual birds were the same under the two field conditions (see Fig. 2), the data were pooled for statistical analysis, and to insure independence of data, a single datum was included for each bird. All statistical analyses were as described in Batschelet (1981).

Results

This experiment was designed to test the hypothesis that simple, static patterns of polarized skylight are sufficient to calibrate magnetic orientation. By the hypothesis, the birds of Group 1, which observed the 90° relationship between the e-vector axis and sunrise and sunset azimuth, should take the geographic N-S axis to be 360°–180° (Fig. 1B). Those of Group 2 (45° CW group) should take the geographic N-S axis to be 315°–135°, and the 45° CCW group (Group 3) should take the geographic N-S axis to be 45°–225° (Fig. 1B).

The results of the magnetic orientation tests are shown in Fig. 2. Hand-raised Savannah sparrows typically exhibit axially bimodal migratory orientation when tested over several nights. Individual birds usually orient in a unimodal direction in each test, but often switch to more or less opposite directions on subsequent nights. When raised indoors without exposure to the sky, Savannah sparrows exhibit NW-SE magnetic orientation (Bingman 1983; Able and Able 1990a, 1993b). Birds that have experienced the sky orient similarly if magnetic and geographic directions were approximately coincident (Bingman 1983; Able and Able 1990a, 1993a, b). Group 1 oriented magnetic N-S in both shifted and unshifted fields ($r = 0.591$, modes = 4° and 184°, $P < 0.001$, Rayleigh test, $n = 20$ birds) (Fig. 2A). The 45° CW group (Group 2) oriented magnetic NW-SE ($r = 0.593$, modes = 126° and 306°, $P < 0.001$, Rayleigh test, $n = 18$ birds) (Fig. 2B), whereas the 45° CCW group (Group 3) oriented magnetic NNE-SSW ($r = 0.591$, modes = 32° and 212°, $P < 0.001$, Rayleigh test, $n = 19$ birds) (Fig. 2C).

The observed orientation direction of each group was close to that predicted by the calibration hypothesis. In each case, the predicted direction fell within the 95% confidence interval around the mean orientation direction. The mean directions of the three groups differed (Watson-Williams multisample test, $F_{2, 53} = 7.7$, $P < 0.01$). The mean directions of Groups 2 and 3 differed ($P < 0.001$, Watson's U^2 test), and the angular difference of 86° between them does not differ from the expected and maximum possible difference of 90°, based on 95% confidence intervals about the mean directions. As predicted, the orientation direction of the 90° group (Group 1) fell between the other two, differing by 58° from the 45° CW group and by 28° from the 45° CCW group.

Discussion

In previous experiments on the ontogeny of magnetic orientation in young Savannah sparrows, we showed that visual experience with polarized skylight was

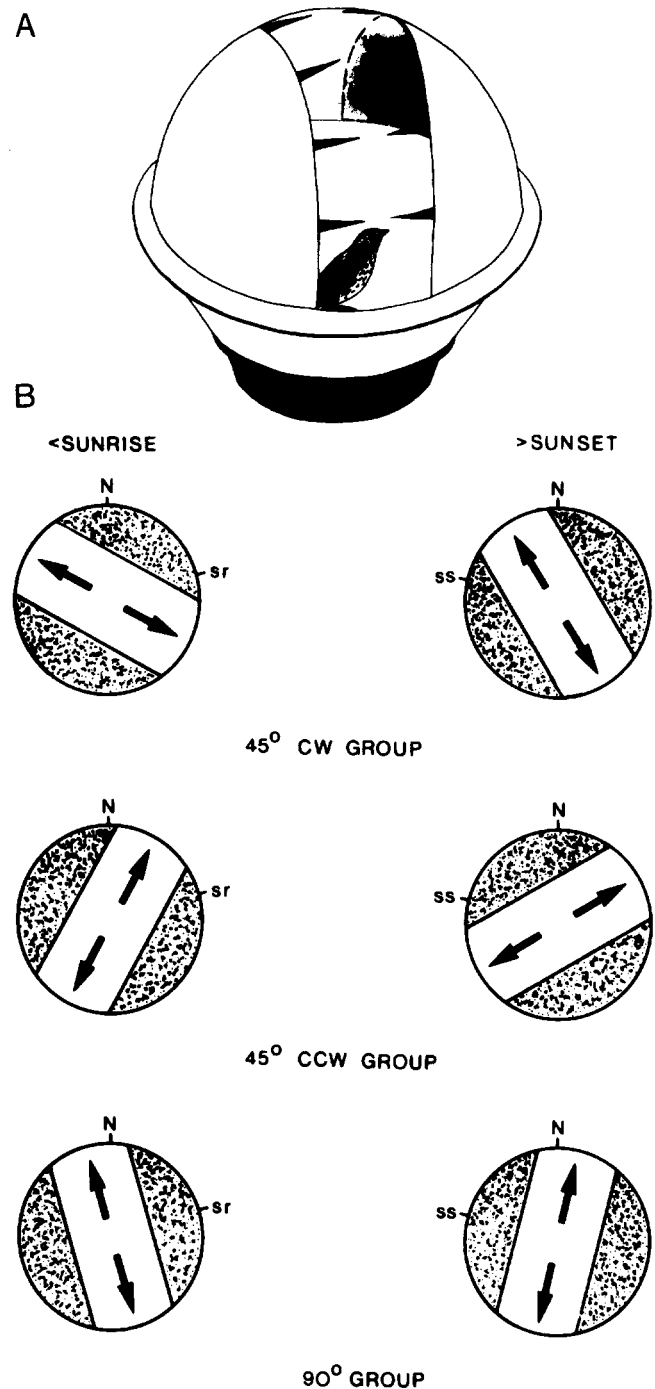


Fig. 1A, B Experimental apparatus and patterns of polarized skylight observed by the three experimental groups. **A** Emlen funnel cage with dome cover. **B** Viewed from above, the e-vector axis of polarized light (heavy arrows) produced by the domes in relation to the directions of sunrise (sr), sunset (ss) and geographic N. The pattern observed by the 90° group roughly simulated the natural condition in the sky. If birds employ these patterns of polarized light to locate geographic N, the 45° CW and 45° CCW treatments should induce large and predictable errors in the calibration of magnetic orientation. For example, if the sun rises at 75°, the polaroids of the 45° CW group would be aligned 120°–300°. On the same day, the sun will set at 285° and at sunset the polaroids were aligned 150°–330°. The birds should behave as if the geographic N-S axis coincides with one of these axes or lies intermediate between the two (135°–315°)

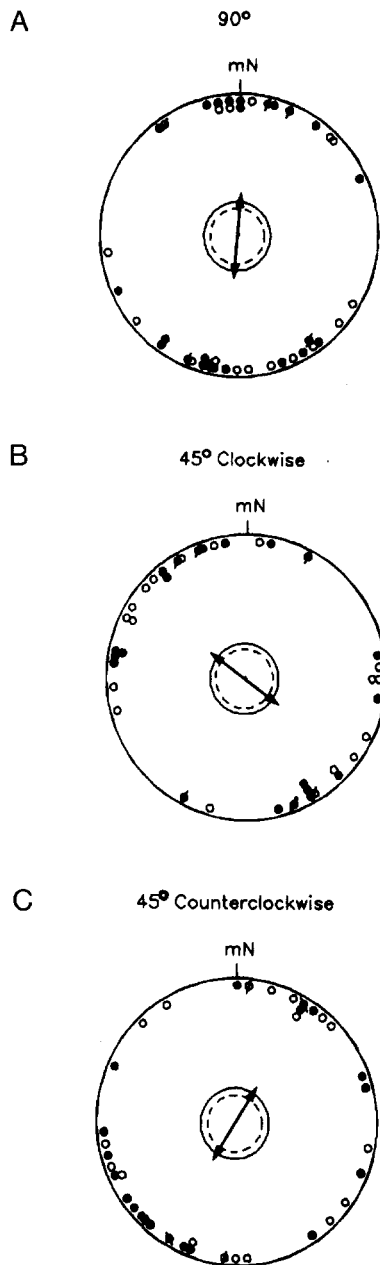


Fig. 2A–C Magnetic orientation of the three groups of birds tested indoors in orientation cages covered with white translucent plastic sheets. Birds were tested in the unshifted magnetic field (*solid dots*) and in a field in which magnetic N was shifted 90° CW (*open dots*). Each *point* represents the mean of the modal orientation directions of each bird under each of the two field conditions. **A** Orientation of the birds exposed to the 90° relationship between the polaroid axis and the azimuth of sunrise or sunset (90° group). **B** orientation of the birds exposed to the 45° CW relationship between the polaroid axis and the azimuth of sunrise or sunset (45° CW group). **C** Orientation of the birds exposed to the 45° CCW relationship between the polaroid axis and the azimuth of sunrise or sunset (45° CCW group). *Points with a slash mark* indicate hopping activity of birds that showed statistically bimodal orientation. The *broken and solid inner circles* represent, respectively, the 5% and 1% significance levels for the Rayleigh test

necessary to produce calibration of the magnetic preference in daytime (Able and Able 1993a). Those birds were also able to see the Sun and no manipulations of polarized light patterns were performed. Therefore, it was not possible to conclude that polarized light was, by itself, also sufficient to effect calibration. In the present study, the nocturnal magnetic migratory orientation of the birds was strongly influenced by the manipulations of polarized skylight to which they were exposed when young. The results also showed that a fairly simplified, static polarized light pattern viewed a limited number of times only in dawn and dusk snapshots is sufficient for this process. Our experiments do not, however, permit further detailed inferences concerning exactly how the birds are using the polarized light information.

Polarized skylight patterns rotate in parallel with the sun's apparent movement across the sky. Birds might locate geographic N by observing the rotation of polarized light patterns in the sky, as described by Brines (1980). Unfortunately, it is not technically feasible to simulate this dynamic pattern and thus Brines' model of its use as a compass is not testable. Empirical evidence from homing pigeons suggested that they employed static patterns of polarization at sunrise and sunset as a reference to geographic compass directions (Phillips and Waldvogel 1982, 1988; Waldvogel and Phillips 1991). Results of experiments with homing pigeons housed in deflector lofts indicated that they paid particular attention to the vertical intersection of the *e*-vector with the horizon and used this reference to identify geographic N and to calibrate their sun and perhaps magnetic compasses (Phillips and Waldvogel 1988; Waldvogel and Phillips 1991).

Our birds could see the sky down to the horizon with which the *e*-vectors of the polarizing material intersected vertically, but they could also observe polarized skylight overhead. Thus whereas the results show that manipulations of the static sunrise and sunset patterns of polarized skylight strongly affect the development of a preferred magnetic direction for migratory orientation, we have no information indicating which part of the sky may be most important in this process. New experiments in which the birds' view of the sky is restricted to small areas will be necessary to answer this question. Likewise, we cannot infer anything about the relative importance of visual experience at sunrise versus sunset. Except at the equinoxes, the sunrise and sunset polarization axes will differ in their orientation. If this angular differences was sufficiently great, one might be able to infer from the orientation of the birds whether they are relying on the sunrise or sunset configuration, or taking the mean of the two as the N-S axis. During our experiment, this angular difference was always $< 35^\circ$; thus the orientation data do not have sufficient precision to answer this question.

In the development of both visual and magnetic orientation mechanisms among migratory birds, celestial rotation has emerged as a factor of central importance. Stellar rotation at night serves as the reference to geographic compass directions underlying the learning of the star compass (Emlen 1970; Wiltschko et al. 1987; review, Able 1991) as well as the calibration of the magnetic preference (Able and Able 1990b). Similar information is available in the daytime sky from two cues, the sun itself and polarized skylight. Data from experiments in which naive Savannah sparrows viewed the clear daytime sky only through depolarizing material showed that the sun is not involved in the daytime calibration of magnetic orientation (Able and Able 1993a). This process appears to depend entirely upon information about celestial rotation inferred from patterns of polarized light. Surprisingly, viewing two simplified static snapshots of the dynamic daily rotation of skylight polarization patterns was sufficient to enable these birds to extract the information necessary to estimate geographic N. This suggests that they possess some rather simple rules for analyzing the complex sky pattern.

The apparent importance of polarized skylight in the development of orientation mechanisms in young birds parallels its role in the day-to-day orientation decision-making of mature migratory birds. Experiments on a number of species of nocturnal migrants have shown that polarized light, viewed at dusk, is the predominant orientation stimulus when placed in conflict with the sun's position or magnetic directions (Able 1982, 1989, review 1993; Moore 1986; Moore and Phillips 1988; Helbig and Wiltschko 1989; Helbig 1990, 1991; Phillips and Moore 1992). Much remains unclear, however, concerning the details of the interaction of polarized light and magnetic orientation in birds that have reached migratory age. We have experiments underway to determine whether the sort of plasticity that characterizes the calibration phenomena we have described in young birds persists in older individuals. The results described by Phillips and Moore (1992) indicate that it may.

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