

SKYLIGHT POLARIZATION PATTERNS AND THE ORIENTATION OF MIGRATORY BIRDS

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Summary

Patterns of polarized light present in the clear dusk sky provide directional information relevant to the orientation behaviour of migratory birds. Experiments performed with white-throated sparrows (*Zonotrichia albicollis*) and American tree sparrows (*Spizella arborea*), North American night migrants, examined migratory orientation between the time of sunset and the first appearance of stars under several manipulations of skylight polarization patterns. Under clear skies, birds tested in Emlen funnel orientation cages oriented their hopping basically parallel to the E-vector of polarized light, with a bias towards the brightest part of the sky (sunset direction). Under solid, thick overcast conditions (no polarized light from the natural sky), birds showed axially bimodal hopping orientation parallel to an imposed E-vector. When birds were tested in cages covered with depolarizing material under a clear sky, their hopping orientation was seasonally appropriate and indistinguishable from controls viewing an unaltered clear sky. Skylight polarization patterns are not necessary for the occurrence of migratory orientation, but birds respond strongly to manipulations of the E-vector direction. The results reported here support the hypothesis that the relevant stimulus is the E-vector orientation rather than other parameters of skylight, e.g. intensity or colour patterns, degree of polarization. It appears that these night migrants are using skylight polarization at dusk as one of a set of multiple compass capabilities. Because of the necessarily artificial nature of the polarized light stimuli used in the experimental manipulations, it has not been possible to establish the relationship between this orientation cue and other known mechanisms (magnetic, sun and star compasses).

Introduction

The orientation behaviour of migratory birds is based on complex mechanisms involving a variety of environmental sources of directional information: the sun, stars, geomagnetic field, skylight polarization patterns and wind direction (see Able, 1980; Able & Cherry, 1985; Wiltschko, 1983; Baker, 1984; Moore, 1987, for reviews). The relative importance of the various cues and their modes of interaction remain poorly understood, despite a considerable amount of recent research. This is probably a result of variation from at least two sources: (1)

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different species may employ different mechanisms or may at least weight cues differently; and (2) interactions among directional cues may vary within species geographically (Able, 1982a) or as a function of age (Able & Bingman, 1987; Wiltshko *et al.* 1987). In choosing the migratory direction on a day-to-day basis, a number of North American bunting species (Passeriformes: Emberizinae) rely primarily on information obtained around the time of sunset (see Moore, 1987, and references cited therein).

Experiments with Savannah sparrows (*Passerculus sandwichensis*) have shown that migratory orientation at dusk is based on visual information from the clear sky and that the visual cues take precedence over magnetic directions, at least in the short term (Moore, 1985). The directional information used by this species can be shifted with mirrors (Moore, 1982). White-throated sparrows (*Zonotrichia albicollis*) subjected to a 3-h fast clock shift and tested under clear skies between sunset and the first appearance of stars showed shifts in orientation consistent with a time-compensated sun compass mechanism (Able & Cherry, 1986). These data are consistent with the hypothesis that the birds are utilizing the sun's disc at sunset or the post-sunset horizon glow as the orientation cue. However, the discovery that homing pigeons in controlled laboratory situations could be conditioned to discriminate rotating from stationary polarized light and between widely separated stationary E-vectors raised the possibility that birds might use polarized skylight as an orientation cue (Kreithen & Keeton, 1974; Delius *et al.* 1974; Burkhalter & Wang, 1979).

Honeybees (*Apis mellifera*) and at least five aquatic vertebrates have been shown to perform oriented movement based on the E-vector of linearly polarized light (Waterman, 1979). Light from clear blue sky is polarized, and both the degree of polarization and the orientation of the E-vector axis are related directly to the position of the sun (Rozenberg, 1966; Coulson, 1974; Brines & Gould, 1982). Thus, skylight polarization patterns could be used as an extension of sun compass orientation as shown by von Frisch (1949, 1967) for honeybees, as the primary celestial compass as in *Cataglyphis bicolor* (Duelli & Wehner, 1973), as an indicator of the sun's azimuth at or shortly after sunset, or even as a means of estimating true north, as described by Brines (1980). Skylight polarization is particularly conspicuous at dawn and dusk when the maximum degree of polarization (typically 70–80 % in clear, blue sky) occurs near the zenith.

During the period between sunset and darkness, many nocturnal migrant birds initiate migratory flight. Spring tests with white-throated sparrows in orientation cages during this dusk period showed that their orientation was strongly influenced by manipulations of the polarized light patterns they observed in the sky overhead (Able, 1982b). Similar effects have been obtained by Moore (1986) and Moore & Phillips (1988) working with several species of New World warblers (Parulinae), but not with the European robin (*Erithacus rubecula*) (Sandberg, 1988). Here I report the results of a variety of experiments designed to assess the behaviour of night-migrating birds in response to skylight polarization patterns and their role in migratory orientation.

Materials and methods

Subjects and general test conditions

The birds used in these experiments were white-throated sparrows and American tree sparrows (*Spizella arborea*) captured in mist nets or traps while on migration through the Albany, New York, area. White-throated sparrows captured early in autumn migration were individuals born during the previous summer (and thus 2–4 months old) on their first migration and adults that had made at least one previous round trip. Birds used in spring tests had completed at least one autumn migration and part of the spring return. American tree sparrows overwinter in the Albany area and were used only in spring experiments.

Birds were housed in individual box cages constructed of wood and aluminium screening in a wood-frame garage in which the magnetic field was normal. They were maintained on natural photoperiod and provided with food *ad libitum* (chick starter supplemented with mixed seed) and water. Orientation tests were performed at two open-field sites near Berne, Albany County, New York. The ambient magnetic field at these sites (measured with a Develco model 9210 triaxial fluxgate magnetometer) was normal (total intensity = 5.6×10^4 nT, inclination = 71°).

All orientation tests were performed in Emlen funnel cages (Emlen & Emlen, 1966), modified with respect to the top covers, as described below for each treatment. No shields were used, so birds could see the sky nearly to the horizon, but no objects on the ground were visible. Birds were placed in the cages just after the sun had disappeared below the local horizon and the tests were terminated immediately before the appearance of the first stars (a period of about 50 min). The hopping records of the birds were analysed as described by Cherry & Able (1986) and the data were subjected to the standard procedures of circular statistics (Batschelet, 1981).

Control tests

These tests involved no manipulation of cues. The funnel cages were covered with one of two types of screening: (1) aluminium window screening sprayed matt black or (2) black vinyl crop-protection netting with 15 mm mesh.

Tests with polaroids

Orientation cages were entirely covered with sheet polaroids (HN-38, Polaroid Corp.) laminated between Plexiglas. This material is a linear dichroic polarizer with the following characteristics: principal transmittances at 500 nm, $k_1 = 0.86$, $k_2 = 0.005$; percent transmission essentially flat between 500 and 700 nm, dropping off sharply to near zero below 400 nm and above 800 nm; leakage was no more than 0.005 % of unpolarized light.

Tests of birds in cages covered with polaroids were performed under two conditions: (1) completely clear sky with low humidity; and (2) solid, thick overcast conditions sufficient to obscure completely the sun's position to a human

observer. Under clear skies, two types of manipulations of polarization patterns were performed. (1) In the first type, polaroids on top of the cages were oriented with their transmission axes either 45° clockwise from the azimuth direction of local sunset (45°CW group) or 45° counterclockwise from sunset azimuth (45°CCW group). (2) In the second set of tests, polaroids on top of the cages were oriented with their transmission axes either 90° from the sunset azimuth ($\text{SS} + 90^\circ$) or parallel to the sunset azimuth ($\text{SS} + 0^\circ$). For each test, birds were assigned randomly to test groups.

Under solid, thick overcast conditions, natural skylight is essentially unpolarized (Brines & Gould, 1982). By covering the orientation cages with polaroids, I was thus able to impose polarized light without being concerned about the interaction between the polarizer and the pattern of polarized light present in clear sky. In these tests, polaroids on top of the orientation cages were oriented, at 20° intervals, in all compass directions and birds were assigned randomly to cages.

Tests under 'depolarized' skylight

Eliminating all polarized light from a clear sky while still enabling the birds an unobstructed view is technically impossible. The best one can do is 'pseudodepolarization', in which linear wave retarders are employed to produce such a mixture of polarization forms that the overall effect is, for practical purposes, the same as if the light were depolarized (Shurcliff, 1962). I accomplished this by covering each orientation cage with two sheets of high-order polyester wave-retarding material, Melinix (Polaroid Corp.), positioned with their fast axes at 45° to one another (each sheet had 15–17 cycles of retardance at 500 nm; N. W. Schuler, personal communication). These covers were placed on top of the cages in an orientation with respect to the sunset azimuth that produced maximal depolarization.

Results

Polarized light manipulations under a clear sky

The typical natural skylight polarization pattern at sunset is shown in Fig. 1A (constructed from data in Brines, 1978; Brines & Gould, 1982). At all times, the percentage of polarized light from a given portion of the sky is related directly to the position of the sun. The degree of polarization is maximal at 90° from the sun and decreases monotonically in both the solar and anti-solar directions. At dusk, the band of maximum polarization (BMP) is at the zenith and aligned north–south when the sun sets in the west. The direction of vibration of the polarized light (E-vector orientation) is also a function of the sun's position such that it is everywhere perpendicular to the plane containing the sun, the point in the sky being observed, and the observer. The pattern of light intensity is also obvious, being brightest towards the sun, but note that there is also a brighter region in the anti-solar direction. Related as they are to the sun's position, these patterns could in themselves provide some of the compass information available from the sun.

The birds tested in cages covered with polarizers aligned 45°CW and 45°CCW re

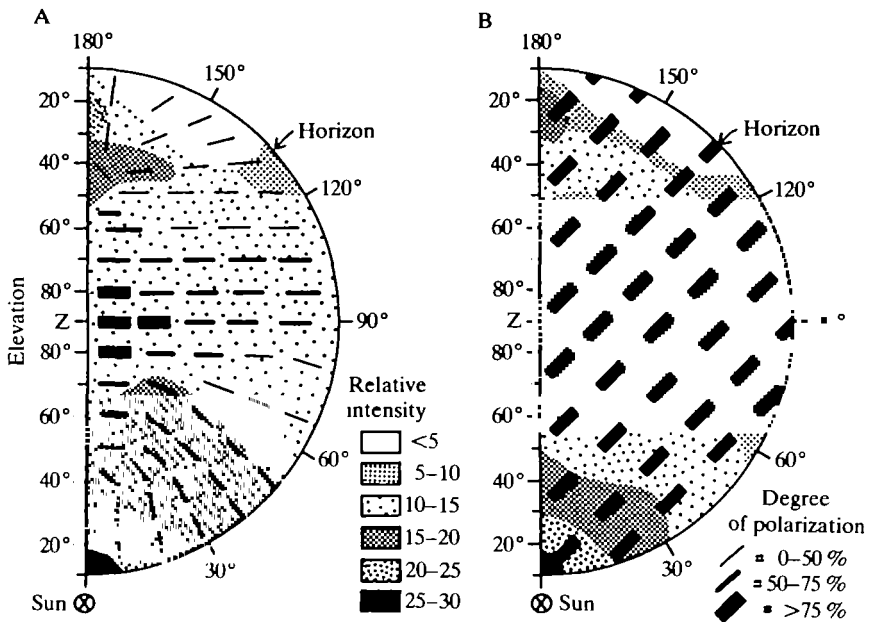


Fig. 1. Diagrammatic representations of E-vector orientation, percentage polarization and light intensity in the natural clear sky at sunset (A) and as viewed by the test birds through the polaroids placed on top of the orientation cages (B). Each hemisphere represents half of a fish-eye lens view of the sky when the sun is 4–5° above the horizon. (A) Typical sunset pattern constructed from measurements at 500 nm (data in Brines, 1978; Brines & Gould, 1982). (B) Pattern viewed through HN-38 laminated sheet polaroid aligned 45°CW from the azimuth of sunset. *Relative intensities*, indicated by stippling, were dependent upon the angle between the transmission axis of the polaroid and the E-vector axis and relative light intensity in the natural sky as shown in A, and were computed from Mueller matrices. The thickness of the E-vector bars indicates the degree of polarization in that part of the sky.

sunset azimuth were exposed to a sky pattern that differed in several respects from the natural one (Fig. 1B). Because the polarizer allows virtually no unpolarized light to pass, light from all parts of the sky was nearly 100% polarized. In addition, the E-vector orientation was the same everywhere. Thus the imposed pattern of polarized light was somewhat less complex than that in the natural sky. The calculated light intensity pattern in this configuration paralleled the natural one, but was overall slightly darker because the transmission axis of the polarizer was not parallel to the ambient E-vector in most parts of the sky. The two treatment groups (45°CW and 45°CCW), however, were exposed to sky views that differed only in E-vector orientation; patterns of intensity, colour and degree of polarization were identical. This symmetrical design thus provided a strong test for response to E-vector alignment *per se*.

The orientation of hopping activity of white-throated sparrows under these two test conditions in spring 1981 is shown in Fig. 2. There was obviously a strong tendency for the birds to orient their activity parallel to the E-vector axis, with a

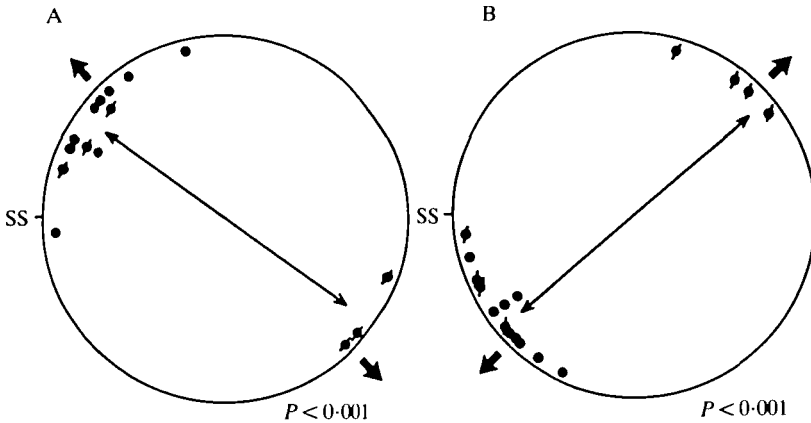


Fig. 2. Orientation of hopping activity of white-throated sparrows during the period between sunset and the first appearance of stars in cages covered by polaroids. (A) Orientation of 11 birds when tested under polaroids aligned 45°CW from sunset azimuth (SS) (modes = 125° and 305°; $r = 0.818$). (B) Orientation of 13 birds when tested under polaroids aligned 45°CCW from sunset azimuth (modes = 50° and 230°; $r = 0.839$). Points represent the mean of the modal directions for each individual, pooled over all its tests under each condition (see Materials and methods). In cases where the distribution of a bird's pooled modes was significantly bimodal, those two modes are shown as dots with a slash mark. Arrows outside the circle indicate the E-vector axis. Arrows within the circles indicate the mean vector of the distribution and P -values refer to the Rayleigh test. North is approximately at the top of each circle, varying slightly as sunset direction changed over the season.

bias towards the end of the E-vector axis nearest the sunset azimuth. Both distributions were significantly oriented and they differed from one another ($P < 0.001$, Watson's U^2 test). Because the two treatments differed only in the fact that the E-vector axes were orthogonal, I conclude that the apparent orientation of the axis of skylight polarization had a major effect on the directional hopping of these birds.

During the 1983 spring migration season, identical experiments were performed with 14 American tree sparrows. In the 45°CW treatment, with the E-vector aligned at 335–155°, the mean of the modes for each bird was 313° ($r = 0.801$; Rayleigh $P < 0.001$); in the 45°CCW treatment (E-vector aligned at 245–65°), the mean of the modes was 270° ($r = 0.733$; Rayleigh $P < 0.001$). These two distributions are significantly different ($P < 0.001$, Watson's U^2 test). The response of the American tree sparrows was nearly identical to that of the white-throated sparrows, except that they showed almost no tendency towards bimodality and in both treatments exhibited a stronger bias from the E-vector axis towards the sunset azimuth.

Experiments in cages covered with polaroids aligned parallel to (SS + 0° group) and perpendicular to (SS + 90° group) the solar–antisolar meridian were performed with white-throated sparrows in spring and autumn 1980. As in the tests

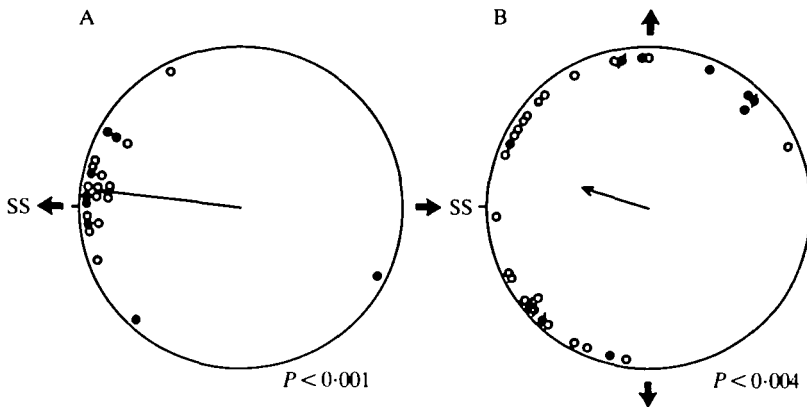


Fig. 3. Orientation of hopping activity of white-throated sparrows during the period between sunset and the first appearance of stars in cages covered by polaroids. (A) Orientation of 22 birds when tested under polaroids aligned in the solar-antisolar direction ($SS + 0^\circ$). (B) Orientation of 29 birds when tested under polaroids aligned 90° from sunset azimuth ($SS + 90^\circ$). Solid circles are spring tests, open circles refer to autumn tests. Other symbols as in Fig. 2.

described above, birds observing the sky in these two treatments were exposed to orthogonal E-vector axes. In addition, the sky viewed through these polaroids differed in other ways between the two treatments. Because in the $SS + 0^\circ$ treatment the transmission axis of the polaroid was orthogonal to the predominant ambient E-vector in the zenith sky where polarization is greatest, light from that part of the sky was disproportionately filtered out, producing the familiar dark band across the sky corresponding to the BMP (see Wehner, 1976, for illustrations). This band was not present in the $SS + 90^\circ$ treatment. Thus the two groups of birds viewed sky patterns that differed not only in E-vector alignment, but also in light intensity and colour patterns.

The orientation of the birds under these two test conditions was also dramatically different (Fig. 3). In the $SS + 0^\circ$ tests, orientation was strongly towards the sunset direction (mean of modes = 277° , with sunset normalized to 270° ; $r = 0.851$; Rayleigh $P < 0.001$). In the $SS + 90^\circ$ tests, the distribution showed a non-significant tendency towards bimodality and great angular spread (mean of modes = 287° ; $r = 0.427$; Rayleigh $P < 0.004$). The two distributions differed in dispersion ($P < 0.01$, Watson's U^2 test). Again, there was a tendency for the birds to hop parallel to the E-vector axis with a strong bias towards the brighter western portion of the sky.

Polarized light manipulations under solid overcast conditions

Without some other source of directional information (e.g. light intensity or colour pattern differences, or an independent compass), polarization patterns of the type presented to the birds in these experiments do not provide unambiguous compass directions: the two 'ends' of the E-vector axis cannot be distinguished.

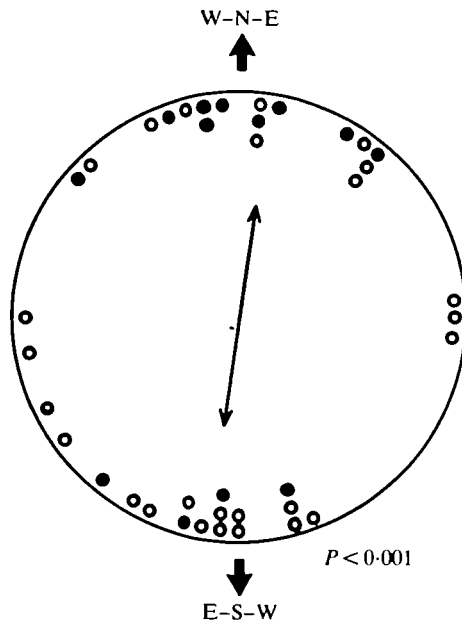


Fig. 4. Orientation of hopping activity of 39 white-throated sparrows tested under solid overcast skies at dusk. Cages were covered by sheet polaroids aligned, at 20° intervals, in all possible compass axes. Birds were assigned randomly to cages. The data are plotted normalized with respect to the E-vector axis. Symbols as in Figs 2 and 3.

Experiments under solid overcast skies allow a test of whether the departures from axial bimodality parallel to the E-vector in the clear sky experiments were due to visual cues such as intensity differences. By imposing polarization patterns under a uniform overcast sky, other factors being equal, we could predict axially bimodal orientation.

During the spring of 1984 and the autumn of 1983 and 1984, I performed tests with white-throated sparrows assigned randomly to orientation cages covered with polaroids aligned, at 20° intervals, in all possible axial directions. The orientation of the hopping activity of these birds is shown in Fig. 4. The orientation of the birds in these tests was axially bimodal (with angles doubled, $r = 0.483$; Rayleigh $P < 0.001$) and aligned with the E-vector axis. The distribution of E-vector axes that yielded the data comprising these tests did not differ from random ($r = 0.134$) and, plotted with respect to absolute compass directions, the birds' activity was not oriented (spring tests, $r = 0.181$; autumn tests, $r = 0.130$). Combining the data from the two seasons indicated a trend (Rayleigh $P < 0.10$) towards bimodal orientation with modes at 303° and 123° . This suggests that there might be some underlying, perhaps magnetic, orientation. However, it seems clear that the observed orientation was primarily a response to the imposed polarization pattern. As in the tests performed under clear skies, the birds oriented parallel to the

E-vector axis, but with equal likelihood of hopping in each of the two axial directions.

A test for reflection artefacts

Polarized light striking reflective surfaces is differentially scattered as a function of the angular relationship between the E-vector and the reflective surface viewed by the subject. Specifically, the intensity of reflected light generated by primary scattering of the incident polarized light is proportional to $\sin^2\theta$, where θ is the angle between the E-vector and the line of sight of the subject. In practice, for animals confined within a circular surround, maximal reflection and therefore brightness should come from those surfaces perpendicular to the E-vector. If responding to brightness patterns only, we would expect a positively phototactic animal to orient perpendicular to the E-vector, a negatively phototactic one to orient parallel to the E-vector.

The blotter material from which Emlen funnels are made is porous and not highly reflective. In addition, the sides of the funnel slope up and away from the bird so that it cannot view light reflected perpendicular to the funnel surface. These factors mitigate against the likelihood of brightness differences being responsible for the observed orientation. In addition, nocturnal migrants are notorious for exhibiting positive phototaxis in orientation cages, leading one to predict orientation perpendicular to the E-vector. Nonetheless, I thought it important to attempt a test for orientation to horizontal intensity differences.

The Emlen funnels were divided into eight equal sectors and alternate sectors were covered with grey blotter (Munsell N4/). Birds were tested under clear skies with polaroids aligned at 45°CW and 45°CCW covering the tops of the cages. During a given test, half the subjects were placed in funnels with dark sectors parallel to the E-vector axis, half in funnels with white sectors in those positions (Fig. 5). Statistically significant bimodal orientation was observed in both treatments, both sets showed orientation parallel to the E-vector axis as observed in standard white funnels, and the two treatments did not differ from one another. These data indicate that the birds were not responding to intensity differences in reflected light and are consistent with the hypothesis that the relevant environmental stimulus is the E-vector.

Orientation under 'depolarized' skylight

White-throated sparrows were tested during the period between sunset and the first appearance of stars in cages covered with pseudodepolarizers. Other individuals (controls) were tested at the same time in cages with screen or netting tops. In both spring and autumn, orientation was unimodal. In spring, sparrows tested with depolarizers oriented towards 306° ($r = 0.744$; Rayleigh $P < 0.001$), a direction very similar to that of the controls (309°; $r = 0.637$; $P < 0.001$) (Fig. 6A,B). In autumn, birds of both groups hopped towards WSW (depolarizer birds, 259°, $r = 0.784$, $P < 0.001$; controls, 249°, $r = 0.455$, $P < 0.001$). In neither

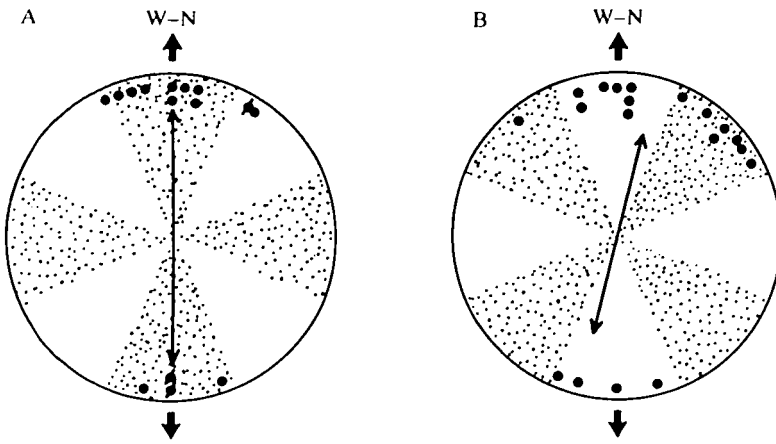


Fig. 5. Orientation of hopping activity of white-throated sparrows tested as in Fig. 1, but in orientation funnels dividing into eight equal sectors alternating white and grey. (A) Tests in which dark sectors were aligned parallel with the imposed E-vector. (B) Tests in which white sectors were aligned parallel with the imposed E-vector. Other symbols as in Figs 2 and 3.

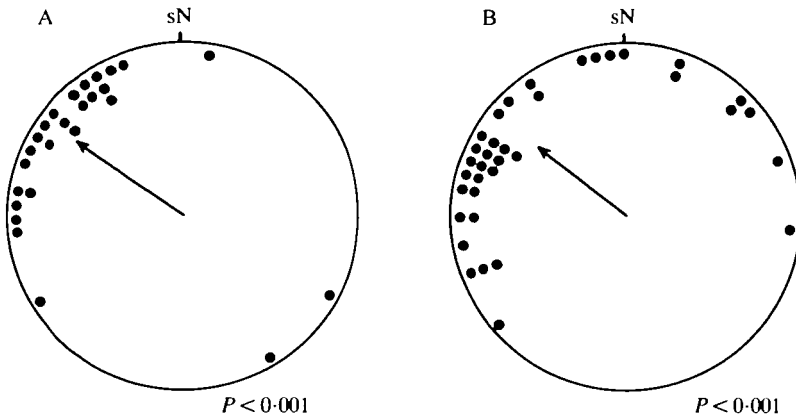


Fig. 6. Spring tests of white-throated sparrows under pseudodepolarizers (see Materials and methods). (A) Orientation of hopping activity of 26 birds tested once each in cages covered with depolarizing material. (B) Orientation of hopping activity of 36 birds tested simultaneously with those in A in cages covered with screen tops (controls). Tests were conducted on six dates. sN, geographic north. Other symbols as in Figs 2 and 3.

season was there any difference in orientation between birds tested under depolarizers and controls exposed to the unaltered dusk sky.

Discussion

The experiments described here demonstrate that skylight polarization at dusk

can influence the orientation of two species of night-migrating birds. The behaviour observed was orientation parallel to the E-vector axis. Under clear skies, orientation tended to be directed towards the end of the E-vector axis nearest the sunset azimuth (i.e. the brightest part of the sky). There was usually a tendency towards bimodal orientation, even under clear skies, and when polarized light was imposed upon the birds under solid overcast skies, axial bimodality parallel to the E-vector was observed. However, the orientation of the birds under depolarized skylight was similar to that of untreated controls. These results raise several questions. What specific cues from polarized skylight do the birds use in orientation? How do they resolve the inherent ambiguity in the E-vector axis to derive a single orientation direction? What is the relevance of skylight polarization to migratory orientation and how does it relate to other known orientation cues?

As shown in Fig. 1, the polarized light patterns visible to the birds under the various experimental manipulations differed from the natural sky pattern in several ways. Yet the birds seemed able to orient their hopping remarkably well even under this altered sky pattern. This suggests that the birds were using some aspect of the cue environment that is both unaltered by the introduction of polaroids and varied by the experimental treatments (e.g. CW vs CCW configurations). Only the E-vector orientation pattern in the solar-antisolar meridian and in the orthogonal meridian passing through the zenith fits these constraints. E-vector patterns in other parts of the sky were altered by the polaroids (compare Fig. 1A and 1B), and other potential directional cues such as colour or light intensity patterns did not differ between the 45°CW and 45°CCW treatment groups. The tests under solid overcast skies also point to the conclusion that the birds' orientation was to the E-vector axis itself. Under these conditions, the brightest parts of the sky usually did not correspond to the sunset direction and the colour patterns differed dramatically from those in clear sky. Yet the birds still showed orientation parallel to the E-vector axis.

Intuitively, it makes sense that animals attempting to use skylight polarization patterns for orientation should rely on the E-vector itself. Measurements by Brines (1978) and Brines & Gould (1982) showed that the radiance and spectral distributions, as well as the pattern of degree of polarization in clear sky, were more variable and conformed less well to the predictions of primary Rayleigh scattering theory. E-vector orientation was relatively insensitive to disturbing atmospheric factors, especially in highly polarized parts of the sky. At sunset, the BMP is directly overhead and it is in this region of the sky that the E-vector stimulus is strongest and provides the most reliable information about sun position (Brines & Gould, 1982). It is thus not surprising that in insect species (Brines & Gould, 1982), amphibians (Taylor & Adler, 1973; Adler & Taylor, 1973; Taylor & Auburn, 1978; Auburn & Taylor, 1979), reptiles (Adler & Phillips, 1985) and birds, E-vector orientation is the primary parameter of polarized skylight affecting orientation.

If animals employed only E-vectors as orientation cues, then under the simplified patterns presented in these experiments, bimodal orientation would be

predicted. In the natural sky (see Fig. 1A) there is no ambiguity, and even under the polaroids used here there exist numerous asymmetries that could be used to resolve any ambiguity in the E-vectors and produce a unimodal orientation. In the natural sky several cues are available: colour differences (sky whiter near the sun, bluer farther away; sunset glow colours); intensity differences (brightest near the sun); degree of polarization; angular change in E-vector over a small patch of sky. In theory, an animal could use any of these variables to discriminate the two directions of an E-vector axis. Under the polaroids used in these tests, the degree of polarization was 100% throughout and the alignment of E-vectors was everywhere the same, so under these conditions the birds must have relied on intensity and/or colour cues when tested under clear skies. In all the clear sky tests under polaroids there was a tendency towards bimodality, but there was always a very strong bias towards that end of the E-vector axis nearest the sunset azimuth. In the 45°CW and 45°CCW configurations, the mean directions were always biased slightly towards the sunset azimuth and in the SS + 0° and SS + 90° treatments this was reflected in the very tight, unimodal orientation directly towards sunset in the former group, and the enormous spread and asymmetrical bimodality in the latter. These experiments were not designed to isolate this supplementary stimulus, but the data are consistent with orientation based on the E-vector axis, biased by a positive phototactic response towards the brightest area of the sky (the sunset direction). Although in no case except the SS + 0° treatment did birds hop towards the brightest direction, phototactic effects are well known in birds hopping in orientation cages.

Honeybees and desert ants (*Cataglyphis*) use only polarized light of ultraviolet wavelengths for orientation (von Frisch, 1967; Duelli & Wehner, 1973; von Helverson & Edrich, 1974; Wehner, 1976; Brines & Gould, 1979). No systematic studies have been reported on terrestrial vertebrates. To my knowledge, all experiments involving birds have employed stimuli restricted to the human visible range (e.g. Delius *et al.* 1974; Kreithen & Keeton, 1974; Able, 1982*b*; Moore, 1986; Moore & Phillips, 1988), although it has been known for some time that several species of birds can see ultraviolet light (Kreithen & Eisner, 1978; Emmerton & Delius, 1980; Goldsmith, 1980; Parrish *et al.* 1981, 1984; Chen *et al.* 1984). Most workers have used HN-38 polaroid filters which have nearly zero transmission at wavelengths <400 nm. Thus, whereas we cannot say that birds do not respond to polarized light stimuli in the ultraviolet, the behavioural data from my experiments and those cited above show that they are responsive to polarized light within the human visible spectrum.

Honeybees seem to employ skylight polarization patterns primarily as a back-up means of estimating the position of the sun when it is obscured by a partly cloudy sky (von Frisch, 1967). In *Cataglyphis*, polarized light patterns in the ultraviolet apparently provide the primary compass information (Duelli & Wehner, 1973). As Brines & Gould (1982) showed, ultraviolet wavelengths are the least reliable for performing these tasks, so why insects use only those wavelengths for polarized light orientation is puzzling in itself. They proposed that, under special conditions

(e.g. partial cloud cover or under extensive vegetation), there may be advantages in relying on patterns in the ultraviolet. It may be that birds employ polarized light to solve orientation problems that are quite different from those faced by insects and may therefore have no need to rely exclusively, if at all, on short wavelengths. We need to know exactly how birds are using polarized light in orientation and how that information relates to other directional cues. The sensory mechanism of retinal polarized light perception in vertebrates is unknown (but see Young & Martin, 1984, for a model), but probably fundamentally different from that of the arthropod compound eye.

In my experiments as well as in more recent tests by Moore (1986) and Moore & Phillips (1988), night migrants showed a strong tendency to orient parallel to the imposed E-vector at dusk and dawn. During the spring and autumn migration seasons the E-vector in the BMP is aligned more or less north-south at sunrise and sunset and thus corresponds generally with the direction of migration flow. Orientation parallel with the E-vector could be a reflection of the use of polarized light patterns directly as a compass. However, the results from the clear sky tests are not entirely consistent with this interpretation. In the 45°CW configuration, the birds did indeed hop predominantly towards the NW, a seasonally appropriate direction. But in the 45°CCW configuration the birds hopped towards the SW end of the imposed E-vector rather than the expected NE. It appears that the orientation re the imposed polarized light coupled with a positive phototaxis overrides whatever other cues might normally be used to derive a seasonally appropriate, unimodal direction.

Many species of night-migrating birds probably possess multiple compass capabilities, e.g. sun, magnetic and star compasses. The clear sky and solid overcast tests described here involved the creation of unnatural directional relationships between skylight polarization patterns and the sun and magnetic field, i.e. they can be interpreted as cue conflict experiments. My results and those obtained by Moore (1986) and Moore & Phillips (1988) show clearly that under these circumstances birds orient with respect to the E-vector even when consultation of either the sun or the magnetic compass would have revealed that they were sometimes hopping in a seasonally inappropriate direction. A simple interpretation of this sort of result would be that polarized light cues override the other directional stimuli. Moore & Phillips (1988) manipulated both the E-vector axis and the sunset direction (with mirrors). Their results with yellow-rumped warblers (*Dendroica coronata*) also suggested that polarized light cues override stimuli from the sun's disc. I am sceptical of this interpretation because it has not been possible to manipulate skylight polarization patterns independently of the other relevant directional cues without also presenting the birds with polarized light stimuli that differ markedly, both qualitatively and quantitatively, from the natural sky patterns. The artificial patterns are both much simpler (E-vector axis everywhere the same) and stronger (light from all parts of the sky nearly 100% polarized). In the natural sky the degree of polarization is very rarely greater than 80% and high values are found in only a small region of the sky. I think it likely

that some aspect of the artificial stimulus situation may elicit a stronger orientation response than that exhibited in response to the natural patterns. One prominent feature of bird orientation under polaroids is the increase in bimodality compared with tests under the natural sky or under depolarizers. This cannot be attributed to the presence of an axial polarized light cue because an E-vector axis is present in both the clear natural sky and that viewed through the polaroid. The greater incidence of bimodality must be due to the salience of the stimuli produced by the polaroid. That kind of difference precludes any strong conclusions about the relative importance under natural conditions of polarized light to other modes of orientation.

Tests under depolarized skylight indicated that polarized light cues are not necessary for the expression of migratory orientation. That is not surprising: there is much evidence that the orientation system of migratory birds is replete with back-up mechanisms (see, for example, Wiltschko, 1983). Yet birds do respond strongly to manipulations of skylight polarization patterns at times and in contexts that suggest relevance to nocturnal migratory orientation. Exposing birds to altered relationships between the E-vector axis and sunset position produces effects on orientation that persist, in the absence of any polarized light, in *Zugunruhe* throughout the subsequent night (K. P. Able, unpublished data). Certainly there is considerable useful information available in skylight polarization for an animal that can use it. Not only does the static relationship between the sun and polarized light patterns provide a basis for compass orientation, but the dynamic properties of skylight polarization can provide true (geographic) compass directions, latitude, and true local sun time (Brines, 1980). There is thus the potential for polarized skylight to provide not only another source of compass information but also information that might be used to calibrate other orientation cues (Phillips & Waldvogel, 1988) or act as part of a true navigation system (Brines, 1980). Clever experiments will be required to delineate the specific ways in which birds are using the information available in skylight polarization patterns.

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References

- ABLE, K. P. (1980). Mechanisms of orientation, navigation, and homing. In *Animal Migration, Orientation and Navigation* (ed. S. A. Gauthreaux, Jr), pp. 283-373. New York: Academic Press.

- ABLE, K. P. (1982a). Field studies of avian nocturnal migratory orientation. I. Interaction of sun, wind and stars as directional cues. *Anim. Behav.* **30**, 761–767.
- ABLE, K. P. (1982b). Skylight polarization patterns at dusk influence the migratory orientation of birds. *Nature, Lond.* **299**, 550–551.
- ABLE, K. P. & BINGMAN, V. P. (1987). The development of orientation and navigation behavior in birds. *Q. Rev. Biol.* **62**, 1–29.
- ABLE, K. P. & CHERRY, J. D. (1985). Laboratory and field studies of avian migratory orientation. In *Migration: Mechanisms and Adaptive Significance* (ed. M. A. Rankin), pp. 516–525. Port Aransas, Texas: Contrib. Marine Sci. Suppl., vol. 27, Marine Science Institute, University of Texas.
- ABLE, K. P. & CHERRY, J. D. (1986). Mechanisms of dusk orientation in white-throated sparrows (*Zonotrichia albicollis*): clock shift experiments. *J. comp. Physiol.* **159**, 107–114.
- ADLER, K. & PHILLIPS, J. B. (1985). Orientation in a desert lizard (*Uma notata*): time-compensated compass movement and polarotaxis. *J. comp. Physiol.* **156**, 547–552.
- ADLER, K. & TAYLOR, D. R. (1973). Extraocular perception of polarized light by orienting salamanders. *J. comp. Physiol.* **87**, 203–212.
- AUBURN, J. S. & TAYLOR, D. H. (1979). Polarized light perception and orientation in larval bullfrogs *Rana catesbeiana*. *Anim. Behav.* **27**, 658–668.
- BAKER, R. R. (1984). *Bird Navigation: The Solution of a Mystery?* London: Holmes & Meier.
- BATSCHLET, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- BRINES, M. L. (1978). Skylight polarization patterns as cues for honey bee orientation: physical measurements and behavioural experiments. Ph.D. thesis. The Rockefeller University, New York.
- BRINES, M. L. (1980). Dynamic patterns of skylight polarization as clock and compass. *J. theor. Biol.* **86**, 507–512.
- BRINES, M. L. & GOULD, J. L. (1979). Bees have rules. *Science* **206**, 571–573.
- BRINES, M. L. & GOULD, J. L. (1982). Skylight polarization patterns and animal orientation. *J. exp. Biol.* **96**, 69–91.
- BURKHALTER, A. & WANG, S. J. (1979). Discrimination of polarized light by the pigeon. *Experientia* **35**, 917.
- CHEN, D. M., COLLINS, J. S. & GOLDSMITH, T. H. (1985). The ultraviolet receptor of bird retinas. *Science* **225**, 337–340.
- CHERRY, J. D. & ABLE, K. P. (1986). An alternative method for the analysis of Emlen funnel data. *Auk* **103**, 225–227.
- COULSON, K. L. (1974). The polarization of light in the environment. In *Planets, Stars, and Nebulae* (ed. T. Gehrels), pp. 444–471. Tucson, AZ: University of Arizona Press.
- DELIUS, J. D., PERCHARD, R. & EMMERTON, J. (1974). Polarized light detection and an electrophysiological correlate. *J. comp. Physiol.* **90**, 560–571.
- DUELLI, P. & WEHNER, R. (1973). The spectral sensitivity of polarized light orientation in *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. comp. Physiol.* **86**, 37–53.
- EMLEN, S. T. & EMLEN, J. T. (1966). A technique for recording migratory orientation of captive birds. *Auk* **83**, 361–365.
- EMMERTON, J. & DELIUS, J. D. (1980). Wavelength discrimination in the 'visible' and ultraviolet spectrum by pigeons. *J. comp. Physiol.* **141**, 47–52.
- GOLDSMITH, T. H. (1980). Hummingbirds see near ultraviolet light. *Science* **207**, 786–788.
- KREITHEN, M. L. & EISNER, T. (1978). Ultraviolet light detection by the homing pigeon. *Nature, Lond.* **272**, 347–348.
- KREITHEN, M. L. & KEETON, W. T. (1974). Detection of polarized light by the homing pigeon, *Columba livia*. *J. comp. Physiol.* **89**, 83–92.
- MOORE, F. R. (1982). Sunset and the orientation of a nocturnal bird migrant: a mirror experiment. *Behav. Ecol. Sociobiol.* **10**, 153–155.
- MOORE, F. R. (1985). Integration of environmental stimuli in the migratory orientation of the Savannah sparrow, *Passerculus sandwichensis*. *Anim. Behav.* **33**, 657–663.
- MOORE, F. R. (1986). Sunrise, skylight polarization, and the early morning orientation of night-migrating warblers. *Condor* **88**, 493–498.
- MOORE, F. R. (1987). Sunset and the orientation behaviour of migrating birds. *Biol. Rev.* **62**, 65–86.

- MOORE, F. R. & PHILLIPS, J. B. (1988). Sunset, skylight polarization and the migratory orientation of yellow-rumped warblers (*Dendroica coronata*). *Anim. Behav.* (in press).
- PARRISH, J., BENJAMIN, R. & SMITH, R. (1981). Near-ultraviolet light reception in the mallard. *Auk* **98**, 627–628.
- PARRISH, J., PTACEK, J. A. & WILL, K. L. (1984). The detection of near-ultraviolet light by nonmigratory and migratory birds. *Auk* **101**, 53–58.
- PHILLIPS, J. B. & WALDVOGEL, J. A. (1988). Celestial polarized light patterns as a calibration reference for the sun-compass of homing pigeons. *J. theor. Biol.* **131**, 55–67.
- ROZENBERG, G. V. (1966). *Twilight. A Study in Atmospheric Optics*. New York: Plenum Press.
- SANDBERG, R. (1988). Skylight polarization does not affect the migratory orientation of European robins. *Condor* **90**, 267–270.
- SHURCLIFF, W. A. (1962). *Polarized Light: Production and Use*. Cambridge, MA: Harvard University Press.
- TAYLOR, D. H. & ADLER, K. (1973). Spatial orientation by salamanders using plane polarized light. *Science* **181**, 285–287.
- TAYLOR, D. H. & AUBURN, J. S. (1978). Orientation of amphibians by linearly polarized light. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 334–346. Berlin: Springer-Verlag.
- VON FRISCH, K. (1949). Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzen der Bienen. *Experientia* **5**, 142–148.
- VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, MA: Harvard University Press.
- VON HELVERSON, O. & EDRIK, W. (1974). Der Polarisationsempfänger im Bienenauge: Ultraviolett-rezeptor. *J. comp. Physiol.* **94**, 33–47.
- WATERMAN, T. H. (1979). Polarization sensitivity. In *Handbook of Sensory Physiology*, vol. VII/6 (ed. H. Autrum). Berlin: Springer-Verlag.
- WEHNER, R. (1976). Polarized light navigation by insects. *Scient. Am.* **235**, 106–115.
- WILTSCHKO, W. (1983). Compasses used by birds. *Comp. Biochem. Physiol.* **76A**, 709–717.
- WILTSCHKO, W., DAUM, P., FERGENBAUER-KIMMEL, A. & WILTSCHKO, R. (1987). The development of the star compass in garden warblers, *Sylvia borin*. *Ethology* **74**, 285–292.
- YOUNG, S. R. & MARTIN, G. R. (1984). Optics of retinal oil droplets: a model of light collection and polarization detection in the avian retina. *Vision Res.* **24**, 129–137.