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SKYLIGHT POLARIZATION PATTERNS AND ANIMAL ORIENTATION

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SUMMARY

1. Although many invertebrate animals orient by means of ultraviolet skylight polarization patterns, existing measurements of these patterns are inadequate for full analysis of the biologically relevant information available from the sky. To fill this gap we have used a precision scanning polarimeter to measure simultaneously the intensity, degree, and direction of vibration (*E*-vector orientation) of polarized light at 5° intervals over the sky. The resulting sky maps were constructed for u.v. (350 nm) and visible wavelengths (500 and 650 nm) under a variety of atmospheric conditions.

2. Our measurements confirmed that the patterns of radiance and degree of polarization of skylight are highly variable and hence unreliable as orientation cues; but patterns of *E*-vector orientation are relatively stable and predictable over most of the sky under all but very hazy or overcast conditions.

3. The observed *E*-vector patterns correspond more closely to predictions based on first order (Rayleigh) scattering at 650 and 500 nm than at 350 nm. This is true both in terms of absolute accuracy and the proportion of the sky with relatively 'correct' information. Yet most insects respond to polarization patterns only at u.v. wavelengths. This apparent paradox can perhaps be resolved by assuming that there is no great selective advantage for any particular wavelength when large areas of blue sky are visible, but that under special and difficult conditions ultraviolet has advantages over longer wavelengths. Measurements under partially cloud-covered sky, for instance, or under extensive vegetation, show that both spuriously polarized and unpolarized light resulting from reflexions present more troublesome interference at longer wavelengths than in the u.v.

4. The accuracy of orientation achieved by dancing honey bees appears to be greater than can readily be accounted for by assuming that they use a strictly geometrical or analytical processing system for their orientation to polarized light.

INTRODUCTION

Honey bees and a host of other animals orient themselves by using the sun as a compass. Since the sun is frequently hidden behind clouds, trees, or the horizon, an ability to infer its position by other means or to replace it altogether with some other compass system is crucial. Von Frisch (1948, 1949, 1967) demonstrated that when the sun is not visible, bees can orient their flights and communication dances by means of the extensive patterns of polarized ultraviolet (u.v.) skylight. For clear sky, these patterns are quite regular and depend so strongly on the position of the sun that it is tempting to speculate that animals come programmed to use them to calculate the sun's location. The biologically relevant parameters of the actual patterns, however, have never been adequately measured. Therefore, we have mapped the appropriate features of the sky under a variety of atmospheric conditions in u.v. (350 nm) and visible (500 and 650 nm) wavelengths. We discuss what bees might actually observe in the sky, and why evolution should have chosen the u.v. wavelength band as the basis of an orientation system.

According to the simplest (Rayleigh) theory (Strutt, 1871), when unpolarized sunlight scatters from molecules in the atmosphere, it becomes partially polarized, depending on the scattering angle – the angle between the incoming (direct solar) and outgoing (skylight) rays. If simple Rayleigh theory were sufficient to describe sky radiation (i.e. if light scattered only once and all atmospheric constituents were small and isotropic), the sky pattern observed would be geometrically simple (Fig. 4A, 5B). Skylight would be partially linearly polarized (p), depending on the scattering angle θ, such that

$$p(\theta) = \frac{\sin^2(\theta)}{1+\cos^2(\theta)}$$

Thus, toward the sun ($\theta = 0°$), the light would be unpolarized ($p = 0$), while the maximum degree of polarization ($p = 1$) would occur for scattering angles of 90° (Fig. 4A). In addition, each partially polarized skylight ray would exhibit a predominant vibration direction (E-vector orientation) perpendicular to the plane of the scattering angle. Together, these parameters would produce a well-defined pattern (Fig. 5A, B). Wavelength is also an important variable, because scattering occurs inversely proportional to the fourth power of the wavelength. Thus, u.v. wavelengths are scattered about 16 times more effectively than red.

Honey bees, as well as many other arthropods, behave as though they can infer the position of the sun from information obtained from the blue sky; they can orient their dances when allowed a view of 15° or more of the sky (von Frisch, 1948, 1949, 1967; Zolotov & Frantsevich, 1973), and under some conditions even smaller areas may be sufficient (Rossel, Wehner & Lindauer, 1978). It is crucial that bees can orient themselves even when only spots of the sky are visible, since they must often fly with most of their view of the sky obscured by vegetation. In addition, they frequently dance outside the hive or on the surface of a swarm cluster from which only restricted patches of the sky may be visible. This is a constant problem for the tropical honey bees (from whom they evolved) which live and dance on exposed limbs in the dense tropical forests (Wilson, 1971, p. 266).

Bees can also use polarized artificial light sources for orientation (von Frisch, 1949, 1967, pp. 395 ff.; Rossel *et al.* 1978) and, under some conditions, even sources subtending less than a degree in visual angle (Edrich & von Helversen, 1976; Brines, 1978; Brines & Gould, 1979) are adequate. The mechanisms by which they accomplish this could be of several types. Because primary Rayleigh scattering produces a pattern which is symmetrical with respect to the sun, it is possible that bees use regularities of this pattern to 'place' the sun with respect to any visible patch of sky. For example, the sun should be located at the intersection of the great circle perpendicular to the E-vector orientation seen at a point in the sky and the horizontal circle defining the solar elevation (Kirschfeld, Lindauer, & Martin, 1975). Obviously, such a geometrical solution of the orientation problem would be practicable only if the Rayleigh predictions (or some other reliable geometrical form) are correct for the natural sky. Similarly, although a number of other theoretical possibilities, some non-geometrical in nature, have been suggested (Kirschfeld *et al.* 1975; van der Glas, 1977; Rossel *et al.*), evaluation of each depends on what information actually exists in the sky. Ideally, this means that the pattern of the entire sky at any given instant must be known under a variety of conditions, in order to determine what information is used by animals. Also, since any biological orientation system presumably reflects a nearly optimal use of the available cues, a detailed knowledge of how various atmospheric and ground conditions affect the sky patterns could provide useful insights about the likely mechanisms of animal orientation.

We already know some of the important biological factors. Von Frisch (1967, pp. 401 ff.), for example, showed that only polarized light which stimulates the ultraviolet receptors (hereafter called u.v.) is important to honey bees, and then only if it is above a certain minimum (about 10%) of percentage polarization. He also demonstrated that E-vector information is the most important parameter for orientation. These observations have been confirmed for bees (Zolotov & Frantsevich, 1973; von Helversen & Edrich, 1974; Brines, 1978), ants (Duelli & Wehner, 1975; reviewed by Wehner, 1976), and probably apply to insects in general. While only u.v. wavelengths have been demonstrated to provide information for polarization orientation in bees, the presence or absence of longer wavelengths often determines *whether* the polarization information is used (Kirschfeld, 1973; van der Glas, 1977; Brines, 1978; Brines & Gould, 1979). Although we do know instances in which u.v. wavelengths do not mediate polarization sensitivity, these generally involve aquatic animals and may be special cases because u.v. wavelengths are strongly attenuated by transmission through water (for review, see Waterman, 1979).

Considering skylight polarization patterns, one important question is whether u.v. sensitivity developed because of physical or biological factors. The important physical variables are total intensity, degree of polarization, and E-vector orientation of each part of the sky as a function of wavelength. However, physical aspects are difficult to evaluate since u.v. wavelengths have been largely ignored in measurements of skylight polarization, and as a result virtually no biologically relevant data exist.

A principal cause for concern is that the pattern in the u.v. should diverge *most* from simple theory because u.v. photons scatter so greatly in the atmosphere. This factor should diminish the extent of sky pattern useful for orientation by reducing the percentage polarization and causing large disturbances in the radiance and spectral distributions. Although in principle these sources of 'noise' are well known and were central factors in von Frisch's conclusion that the honey bee orientation system could not be based on analysis of patterns of percentage polarization or radiance, their precise impact on orientation has not been determined.

Might honey bee u.v. sensitivity be explained by some property of the *E*-vector orientation in this wavelength band? Von Frisch, relying on the suggestions of Sekera (cited by von Frisch, 1967, p. 382) postulated that u.v. polarization patterns might be advantageous as cues for orientation not only because the u.v. *E*-vector orientation ought to approximate simple theory most precisely but also because it might be most *stable* during marginal sky conditions, unlike patterns in longer wavelengths which may be easily disrupted. This idea seems to have become widely accepted in the literature. Although the evidence for this conjecture seems very slim, any strategy which could extend the conditions under which successful orientation is possible would certainly constitute a major selective advantage.

To provide data to evaluate how u.v. sky information might be advantageous for orientation, we designed and built a precision polarimeter which measured quickly and accurately the skylight radiation parameters in narrow and white spectral bands for half of the sky under diverse atmospheric conditions. Our goal was to provide 'snapshots' of the actual sky. Ultimately, we hope to be able to correlate these snapshots with behavioural data gathered simultaneously.

MATERIALS AND METHODS

Polarimeter

At regular points in the sky we recorded the 'Stokes vector', a conveniently succinct description of polarized light which completely specifies a light beam, and also simplifies computation of any effects created by optical devices, such as detector configuration (see Shurcliff, 1962). This is especially important because we do not yet know precisely the form of the biological detector system and thus, in effect, do not know how the sky patterns actually appear to animals.

Our polarimeter was based on the principle that a 'retardation plate' (= 'waveplate') has a net observable effect only on polarized light passing through it. We rotated a half-wave plate which modulated only the polarized component of the analysed light beam and did not affect the unpolarized part. The optical principles of such 'active' polarimeters are described in a general way by Serkowski (1974). Given any partially polarized light beam, our instrument generated a 40 Hz sine wave superimposed on a d.c. component. A Stokes vector completely describing linearly-polarized light could be instantaneously derived from this wave, since the d.c. component was proportional to total intensity, the amplitude of the 40 Hz component to degree of polarization, and the phase-specified *E*-vector orientation. A device described by Sekera (1955, pp. 2 ff., 1957*a*, pp. 311 ff., 1957*b*, pp. 487 ff.) provided the original inspiration for our instrument, although in its final form our polarimeter differed substantially, particularly in how quickly and extensively it could measure the sky.

Skylight first entered a collimator tube 100 mm long (Fig. 1) in which baffles effectively eliminated oblique rays. A linear-iris diaphragm located at the distal end of the tube limited the area of the sky analysed to between 8·5° and 4°, which could be increased to 19° by removing the collimator. Sky measurements reported here always corresponded to about 6° spots of the sky and are approximately equal to the area viewed by a typical honey bee ommatidium (Laughlin & Horridge, 1971; Eheim & Wehner, 1972).

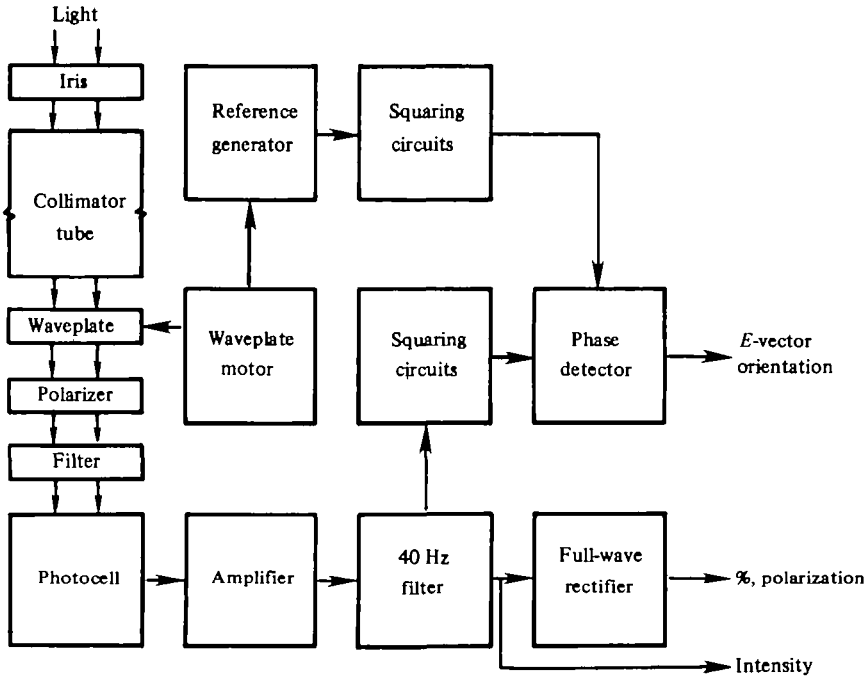


Fig. 1. Principal components of the scanning polarimeter. Operation is described in the Methods section.

The polarization modulator was a high-quality, half-wavelength retardation plate designed to be essentially achromatic, which yielded better than 90% accuracy between 330 and 700 nm. It was constructed from optical quartz and magnesium fluoride by Karl Feuer Optical Associates, Montclair, New Jersey. This waveplate was rotated about its centre at 10 Hz by a precision synchronous motor. Because of the two optic axes, any incident polarization was modulated at 40 Hz, while the unpolarized component remained unaffected.

After the retardation plate, skylight passed through a fixed, u.v.-transmitting linear polarizer (Polaroid Corp., Cambridge, Mass. HNP'B) cemented between two very thin quartz plates with u.v.-transparent optical epoxy (Epotec, Inc., Watertown, Mass., no. 500). Specific wavelengths were analysed by inserting narrow-band interference filters into the beam after the polarizer. Since the polarizer remained fixed with respect to the filters and light detector, errors due to polarization sensitivity of the photocell were eliminated. Wavelength bands could be selected during operation of the machine by three filters accommodated inside the instrument which could easily be moved into the beam. The four spectral ranges used in these measurements were derived either by using very narrow (9 nm half-maximum bandwidth) filters centred on 350 (Karl Feuer Optical Associates), 500 and 650 nm (Ditric Optics, Inc., Marlboro, Mass.) or a Corning Glass Works (Corning, N.Y.) no. 3965 ('white') filter which passed u.v. and visible light but absorbed near-infrared. The white measurements correspond to those generally reported in the literature. Secondary transmission regions of the narrow filters were blocked to a minimum optical density of four and an average optical density of seven. Special care was taken to eliminate near-infrared radiation, to which the photodetector was quite sensitive. The wavelength bands used were selected to provide data representative of the entire visual/u.v. spectrum as well as values specifically for: (1) the behaviourally determined (von Helversen & Edrich, 1973) sensitivity maximum of polarization orientation of honey bees (the 350 nm [u.v.] filter); (2) the approximate, broad maximum of the energy distribution of skylight [the 500 nm [blue/blue-green] filter); and (3) wavelengths closer to the maximum photon flux of daylight (the 650 nm [red] filter). Obviously, actual photon flux as well as information content in each spectral band are important variables in considering various polarization-detection strategies.

The photodetector was a large, u.v.-optimized photovoltaic cell (ECG, Inc., Salem, Mass., no. UV 4000B) which was strictly linear over seven decades of irradiance. Current produced by incident skylight was converted to voltage by a very high-input impedance (FET) operational amplifier and the gain was further increased by other precision amplifiers, which made the polarimeter extremely sensitive. The photovoltaic cell voltage was the electrical analogue of the optically modulated beam of skylight, and was processed by the electronic circuits schematized in Fig. 1. The outputs of these circuits were (1) d.c. level, (2) amplitude of the 40 Hz component, and (3) phase, which correspond to the Stokes parameters of total intensity, degree of polarization, and *E*-vector orientation, respectively.

The polarimeter was enclosed in a light-tight aluminium box coated on the inside with flat black paint, and attached to a modified equatorial telescope mount with principal axes aligned with the zenith and horizon directions. Conventional setting circles on each axis enabled the polarimeter to be directly positioned in the horizontal co-ordinates corresponding to any point of the sky, and precision potentiometers provided easy and accurate electrical specification of position. The two voltages corresponding to the azimuth and zenith distance and the electrical correlates of the Stokes parameters were continuously available to an analogue-to-digital converter of a Digital Equipment Corp., Marlboro, Mass. PDP-11 minicomputer which acquired, stored, and manipulated the data.

Since the daytime quantal flux is enormous for all wavelengths considered here, and since we were mainly interested in the general, wavelength-dependent features of skylight polarization, especially as a function of atmospheric conditions, the sky radiance is expressed in relative units, while the degree of polarization and *E*-vector orientation are in absolute units. Obviously, the relative radiance distribution for any one wavelength is the same as the relative quantal flux. However, corrections are necessary to compare different wavelengths. The largest errors (about 10% too low) involved measurement of the degree of polarization for 500 nm due to the non-ideal achromatic waveplate. Because of the high linearity of the photodetector system, relative radiances show only very small errors over almost the entire sky. (Depending on the prevailing conditions, a small, variable area around the sun was frequently so bright it saturated the amplifiers, and thus prevented determination of percentage polarization and *E*-vector orientation.) *E*-vector orientation was derived by digital methods and was the most accurate of the three Stokes parameters. Phase varied linearly over a 178° *E*-vector orientation change (the final 2° were undefined because of unavoidable electronic time delays). Under most circumstances, this 2° ambiguity was not serious since its position was measured and could be changed at any time. *E-vector* orientation could be accurately determined within 0·25°

Methods

All sky measurements were taken from the roof of a two-storey building, Eno Hall, Princeton University Campus, Princeton, New Jersey. The time of day was selected so that most of the field of view was unobstructed, especially high in the sky. Appropriate notes appear in the figure legends whenever terrestrial features affected the sky measurements.

Except for a few completely overcast days, azimuth 0° of the measurements corresponds to the plane of the solar vertical. When the sun was visible (even through fairly heavy cloud cover), the polarimeter would be oriented accurately by setting a pin-hole viewfinder on the sun's disc. On completely overcast days, the instantaneous azimuth of the sun was calculated by spherical trigonometry, and the polarimeter orientated as precisely as possible using a magnetic compass with the appropriate corrections for local magnetic deviation. Once the reference axes of the instrument were established, azimuth 0° was readjusted before each new series of sky measurements to correct for the sun's movement. Sky conditions were recorded by subjective description, and supplemented by colour photographs taken through a fish-eye lens (about 170° field of view) during each series of measurements. With practice, points at every 5° of elevation and azimuth of an entire half hemisphere of the sky could be measured within 7–8 min, during which the sun moved about 2° along its arc. Although certain unavoidable errors were a consequence of the rapid measurement process (such as solar movement and the slight inaccuracies attendant upon setting the axes of the instrument), they proved too small to affect the interpretation of the measurements. To determine precisely how closely skylight characteristics matched theoretical predictions as a function of wavelength, single points of the sky could be serially analysed within 10 s at different wavelengths and directly compared.

Although specific Stokes vectors were recorded for each sky point, it is difficult to show succinctly how various measured and theoretical values compared for large areas of the sky unless these differences are graphically summarized. Thus, for this paper the theoretical values of *E*-vector orientation expected from *primary* Rayleigh scattering were calculated by spherical trigonometry (Brines, 1978) and the absolute value of the differences between measured and theoretical values are shown in three-dimensional plots of azimuth, elevation, and deviation from theory, as described in each figure.

RESULTS

Radiance and spectral distribution

The radiance distribution of a clear sky possesses three main characteristics (see Fig. 2): (1) the greatest radiances occur at points in the sky close to the sun; (2) radiance decreases steadily until about 90° from the sun and then increases again to the antisolar vertical; and (3) radiance also diminishes as the zenith distance of the point of the sky observed decreases. Although the first two of these features are similar to the predictions of simple Rayleigh theory (Fig. 4A), even under the most favourable atmospheric conditions encountered during these measurements the measured relative radiance never approximated the predictions of Rayleigh theory, especially for points in the sky with large zenith distances.

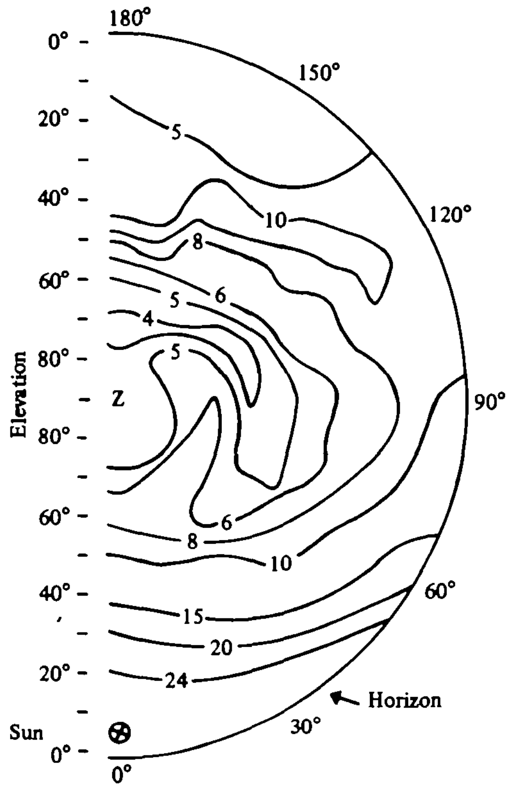


Fig. 2. Relative radiance of a virtually clear sky measured at 500 nm. The measured half-hemisphere of the sky is collapsed on to a plane. The solar elevation is 5°. Isopleths connect points of equal relative radiance. For discussion of this typical example, see text. Z marks the zenith.

The radiance distribution, as expected, was observed to depend strongly on wavelength: the longer the wavelength used for observation, the larger the radiance range observed. That is, the radiance distribution of u.v. light was always much more uniform than that of red. At the same time, the pattern at longer wavelengths more closely approximated the geometrical distributions of radiance predicted by Rayleigh scattering theory. But even in these cases, they did not match well.

Under completely overcast sky, the radiance levels were, of course, much reduced (typically only 5–10% of the radiance of a clear sky) and the radiance distribution was reversed from that of a clear sky: radiance was greatest at the zenith point and least along the horizon. In addition, complete overcast obliterated the wavelength-dependent aspects of sky radiance and the pattern was generally symmetrical around the zenith point. As expected, uneven overcast produced irregular patterns of sky radiance which were difficult to categorize.

For uniformly overcast sky conditions, sky radiance appeared to be independent of solar position, as summarized by the data of Fig. 3A, where the radiance can be seen to be at a minimum at the horizon and at a maximum at the zenith. To determine whether the sun could be located at any wavelength behind complete cloud cover (solar disc not visible to the naked eye or in later analysis of visible light photographs),

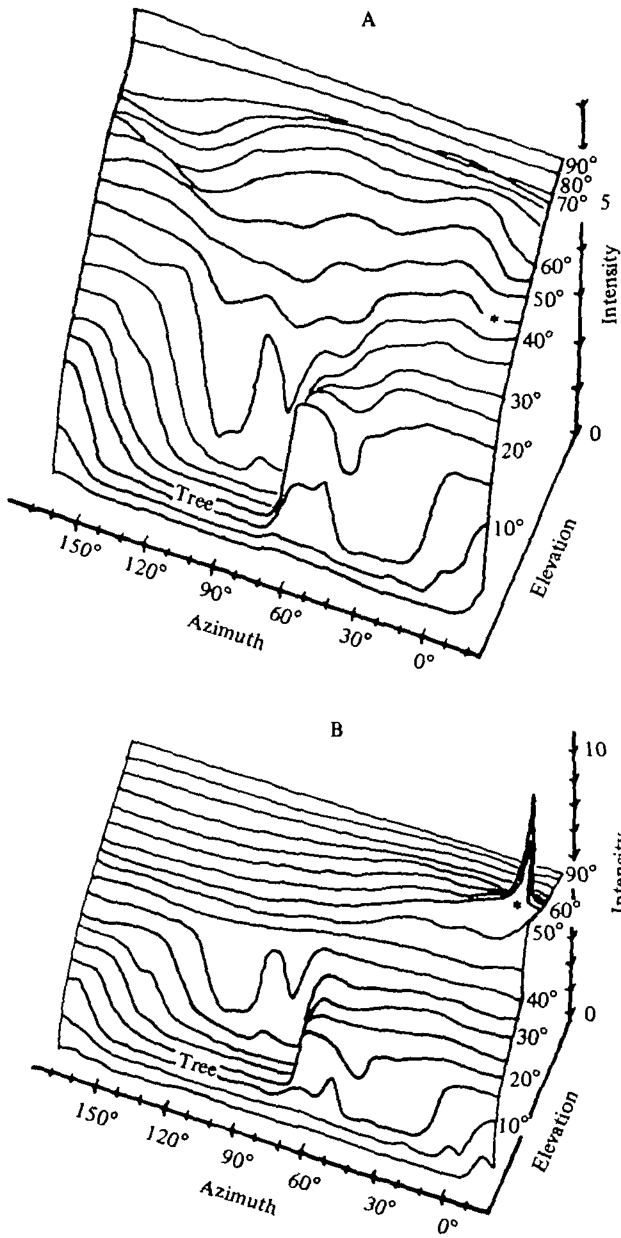


Fig. 3(A) Relative ultraviolet sky radiance for complete overcast measured at 350 nm. A three-dimensional plot of relative u.v. radiance of a quite uniform, dark sky covered with altostratus clouds. Elevation is the ordinate, azimuth the abscissa, and the relative intensity is out of the page. During the measurements, the solar disc was not visible to the naked eye or in a subsequent analysis of photographs. The sun's position behind the clouds (elevation of 45°) is indicated by the asterisk. For discussion, see text. (B) Relative sky radiance for an overcast sky with the solar disc diffusely visible measured at 350 nm. These data were collected later the same day as those shown in Fig. 3A. The solar position is shown clearly by a fairly large aureole.

Table 1. *Quartile distribution of percentage polarization for an exceptionally clear summer day*

(Total of 630 points of the sky.)

Wavelength (nm)	Sun's elevation (deg)	Min 0%	25%	Mean 50%	75%	Max 100%
350	67	0	16	28	33	41
500	60	0	22	45	56	64
650	63	0	18	39	50	58

radiance measurements were taken around the solar vertical. The results of these observations show that, regardless of the wavelength used for analysis, when the sun could not be seen by the naked eye it was not detectable by the polarimeter. Fig. 3A illustrates a typical result for radiance measurements taken at 350 nm in which the asterisk indicates the position of the sun behind unbroken cloud cover. No obvious features in this three-dimensional radiance plot indicate the sun's position. By comparison, when the sun's disc could just be detected by eye, instrumental measurements always showed its presence, as Fig. 3B illustrates for another set of radiance measurements for 350 nm obtained relatively soon after those in Fig. 3A.

Degree of polarization

For clear sky, most measurements of percentage polarization exhibit the general geometrical form predicted by simple Rayleigh theory: very low values are observed toward the sun, and an increase to a relative maximum at scattering angles of about 90°. For scattering angles greater than 90°, the degree of polarization gradually decreases to the plane of the solar vertical. However, the magnitude of percentage polarization is generally quite different from theoretical predictions and is highly dependent on wavelength. Of the four spectral bands used in this study (u.v., blue/blue-green, red, and white), percentage polarization was always smallest in the u.v. and frequently greatest in blue/blue-green. For example, Table 1 gives conventional quartile percentiles for a series of measurements in three narrow wavelength bands gathered on an exceptionally clear summer day within 45 min of each other. The theoretical Rayleigh maximum was rarely approached as closely as in this example. But even for these data, measured patterns only approximated the *entire* range of predicted values. Fig. 4B illustrates that the measured percentage polarization and the geometrical symmetry are generally substantially lower than Rayleigh theory (Fig. 4A) predicts.

When the sky was completely overcast (neither sun nor blue sky visible), the measured degree of polarization was usually less than 1% for most points on the sky vault, especially at small zenith distances. Larger amounts of polarization were frequently measured close to the horizon, but in some cases these could be attributed to the reflexion of skylight from features on the earth's surface.

E-vector orientation

For most parts of the clear sky, the measured *E*-vector orientation corresponded reasonably well to the geometrical predictions of first-order Rayleigh scattering

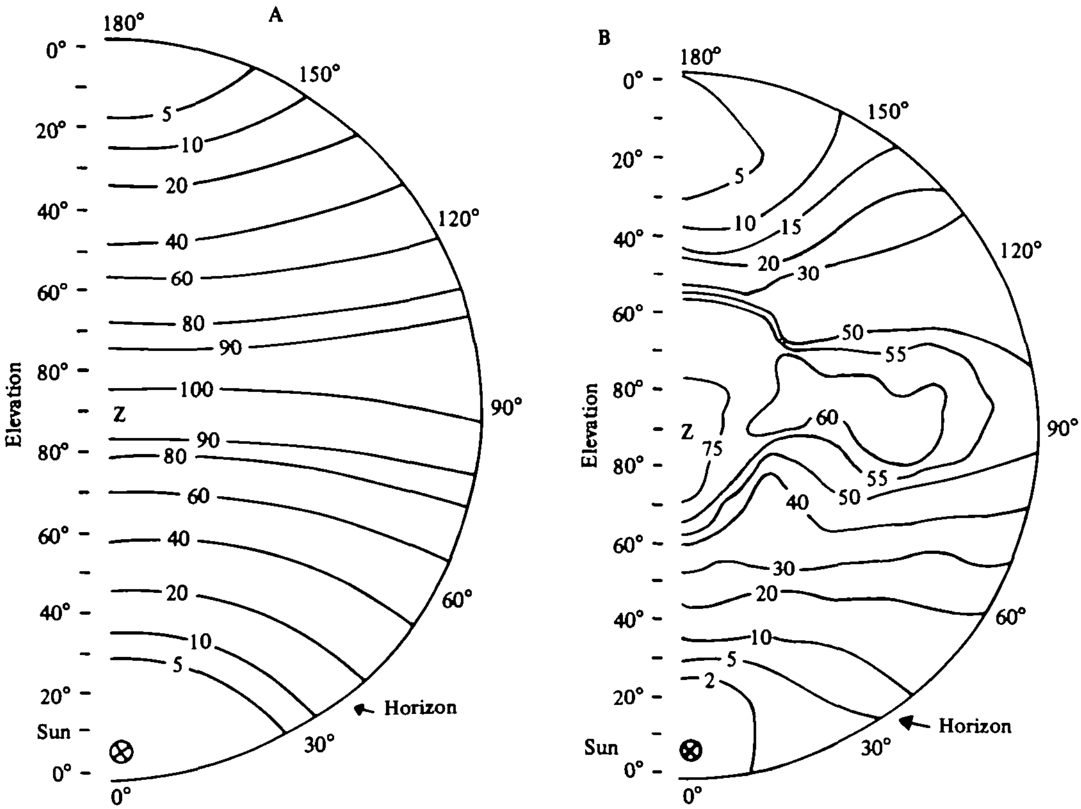


Fig. 4(A) Theoretical distribution of per cent polarization for a solar elevation of 5°. Isopleths connect points in the sky which are expected, on the basis of simple primary scattering, to exhibit equal percentage polarization. This form demonstrates the striking symmetry of the pattern which depends on a single, dominant geometrical parameter: the scattering angle (the angle between the incident direct sunlight and the scattered skylight rays). Minimum (0 %) polarization is expected to be observed toward the sun and antisun, and maximum (100%) along the arc 90° from the sun. (B) Polarization (%) of a clear sky measured at 500 nm. Even under the most favourable atmosphere conditions encountered, both the actual magnitude of degree of polarization and the symmetry of the pattern are generally much worse than theoretical predictions. Solar elevation is 5°, and data were collected simultaneously with those of Fig. 2(A).

Fig. 6 illustrates how closely a typical set of measurements at 350 nm matched the theoretical expectations of Rayleigh scattering. Here, the absolute values of the angular deviation of the observed from the expected are plotted as a function of azimuth and elevation of the point in the sky. It is clear from these data that the only place in the sky where large divergences from theoretical expectations regularly occur is near the solar vertical. (Care was taken to make certain that the amplifier was not saturated, but there was always a small area around the sun itself where this was not practicable. The small deviations at low elevations arose from surface-reflected light.) Of the points measured in the sky, 75% diverged less than 6° from theoretical predictions and most of the large divergences occurred close to the solar vertical. When the sun was low, substantial deviations were also regularly observed near the antisolar point.

For points in the sky far from the sun, small but significant differences were consistently measured in the *E*-vector orientation as a function of wavelength. Generally,

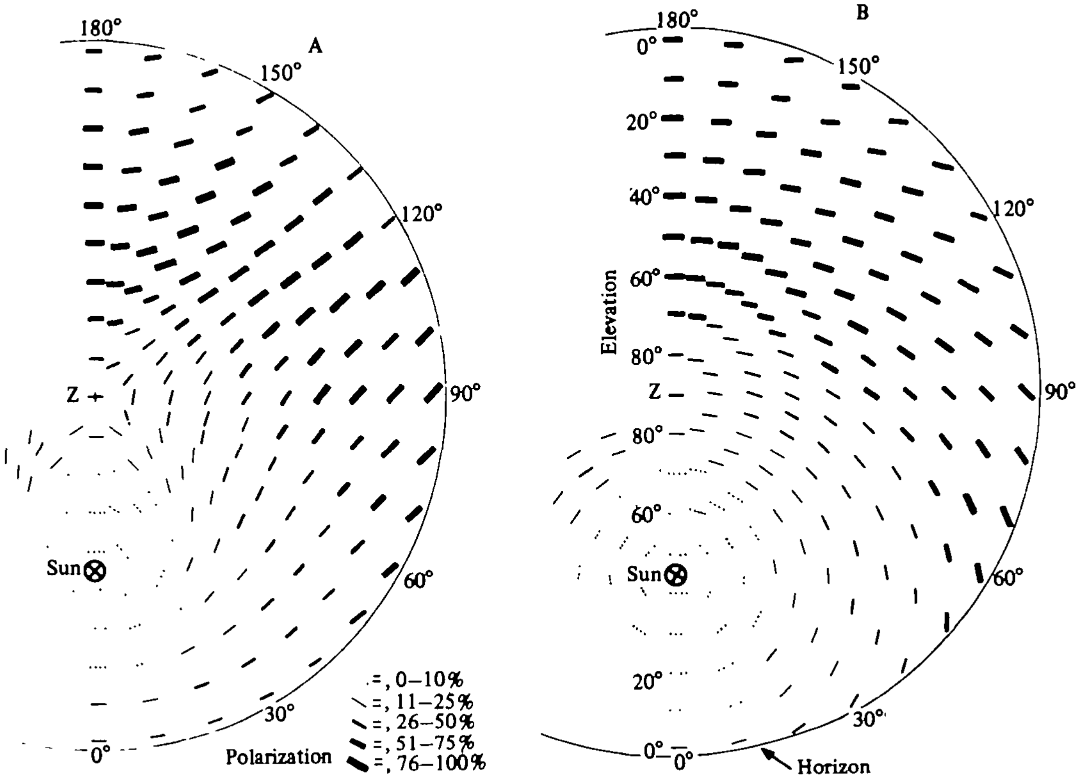
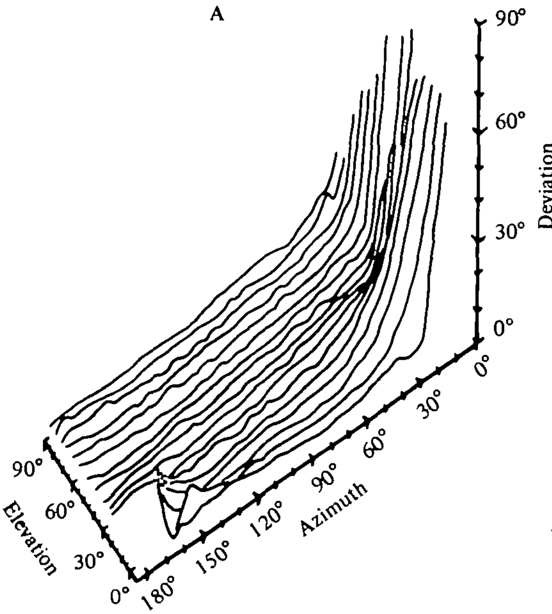


Fig. 5 (A) Theoretical *E*-vector orientation for the sun at 45° elevation. The half-hemisphere of the sky measured is collapsed onto a plane. The solar vertical is toward the bottom of the figure (azimuth 0°) and azimuth increases uniformly counterclockwise 0° to 180°. Only data from 10° intervals are displayed. At each point in the sky shown here, the *E*-vector orientation has the orientation on the page which would be observed in the sky if primary scattering theory were completely appropriate. For example, horizontal *E*-vectors in the sky would be seen as horizontal relative to the bottom of the page in this figure. The thickness of the *E*-vectors indicates qualitatively the degree of polarization. Dotted lines indicate that the polarization is below the known perceptual threshold of honey bees. (B) Theoretical *E*-vector orientation relative to the horizon for the sun at 45° elevation. The same data used for Fig. 5A are plotted here with the *E*-vector orientation drawn relative to the horizon at each azimuth. The result is comparable to a fish-eye view of the pattern and, though less useful for direct calculations, more effectively illustrates the symmetry and dependence of the sky patterns on the position of the sun.

red wavelengths diverged *least* and u.v. *most* from theoretical predictions. Virtually instantaneous analysis carried out on single points of the sky confirmed this observation. Occasionally much larger deviations occurred, and were frequently associated with light haze. For example, for one very clear sky, the *E*-vector orientation of 75% of the measured sky points diverged less than 5°, with practically no differences between u.v. and red. With increasing haze (sky becomes whiter, but no clouds), differences become quite apparent. For one such series of measurements, we found that 75% of the measured sky points diverged less than 10° from theoretical expectations at 650 nm, while measurements at 350 nm (15 min later) exhibited divergences up to 20° for the same portion of the sky. Then a large increase in the sky brightness was observed (within a half-hour) and subsequent measurements in the u.v. showed



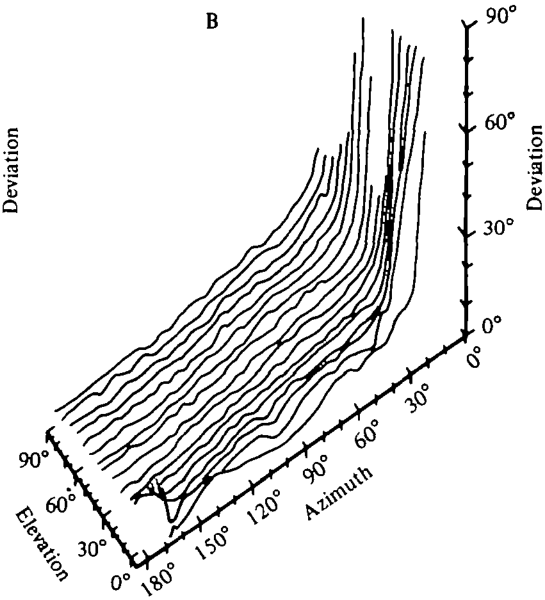


Fig. 6(A) Deviation of *E*-vector orientation from theoretical expectations measured at 350 nm. Magnitude of the differences between the *E*-vector orientation measured in the u.v. for a clear sky and the expectations of primary Rayleigh scattering are plotted. Azimuth, elevation, and deviation from theory form the labelled axes. The solar vertical corresponded to azimuth 0°. The sun's elevation is 4°. Except for points in the sky close to the solar vertical, the measured *E*-vector orientation matched theoretical predictions well. (Of the measured points of the sky, 75% exhibited deviations less than 6°.) The small deviations at low sky elevations arose from light reflected from a building. (B) Deviation of *E*-vector orientation from theoretical expectations measured at 650 nm. These data were collected immediately after the u.v. data shown in Fig. 6(A). Solar elevation was −4°. Like data for u.v. wavelengths, the measured *E*-vector orientation of parts of the sky far from the sun agreed fairly well with theoretical predictions. Notice, however, that the *E*-vector orientation at these long wavelengths is closer to theory over a larger area of the sky: the large deviations extend for a smaller distance out from the plane of the solar vertical. Similar sky measurements at 500 nm produced plots of deviation intermediate in form and magnitude between those for u.v. and for red.

deviations of up to 28° for 3/4 of the sky measured. The dependence of *E*-vector deviation on wavelength was striking under these kinds of atmospheric changes.

The *E*-vector orientation of points in the sky close to the sun always exhibited a strong wavelength dependence, since deviations in the u.v. extended farther from the solar vertical than those at longer wavelengths. For blue/blue-green wavelengths, the circumsolar deviations of *E*-vector orientations extended over an area intermediate in size between those of the shorter and longer wavelengths. These observations were well supported by a comparison of *E*-vector orientation of a wide variety of clear skies.

For light, irregular cloud cover, the measured *E*-vector orientation pattern was quite close to theoretical expectations, and similar to that on clear days. For example, 11 separate measurements in the u.v. showed that 75% of the sky deviated less than 14° from Rayleigh theory compared to clear-sky deviations of less than 10° over 75% of the sky.

For completely overcast skies, no wavelength-dependent differences were ever

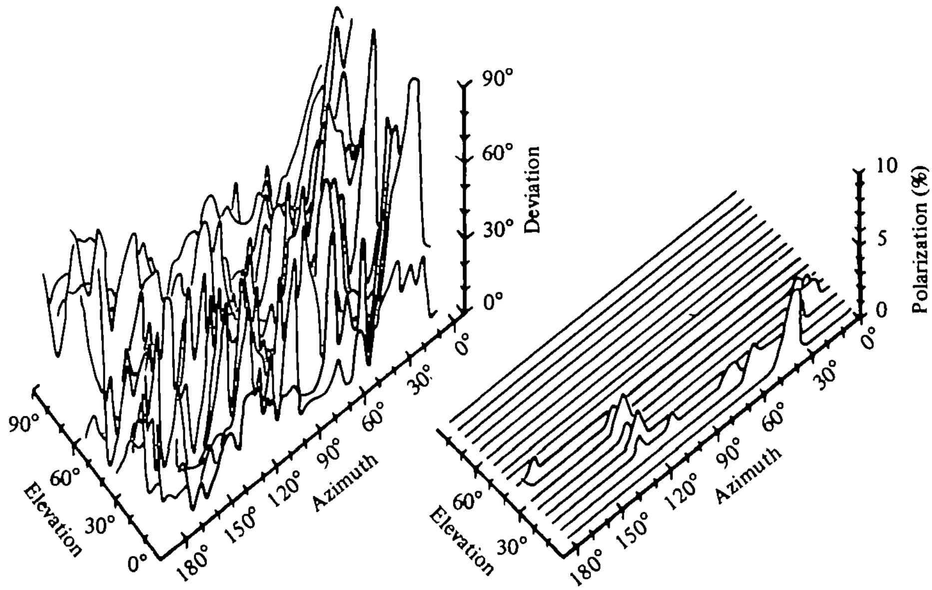


Fig. 7. Absolute percentage polarization and deviation of E-vector orientation for a completely overcast sky measured at 350 nm. As summarized by this representative example, when the sky was completely overcast (sun's disc never visible during measurements), the E-vector orientation diverged greatly from theoretical expectations. The fluctuations are probably not significant everywhere. Large deviations occurred regardless of the wavelengths used for the measurements. At the same time, the measured percentage polarization was virtually zero over the entire sky, as shown in the accompanying plot of absolute percentage polarization as a function of position on the sky vault.

observed: the sky polarization pattern seemed equally poor, irrespective of wavelength. (Measurements were difficult because percentage polarization was usually less than 1%.) Fig. 7 illustrates a typical example for data taken at 350 nm, while the accompanying absolute percentage polarization plot illustrates that the measured degree of polarization was virtually zero over most of the sky, reaching a maximum of only 3%, well below the known 10% threshold for honey bees. However, even under these poor conditions there were some small areas of sky with appropriate E-vector orientation.

For non-uniform overcast, especially when the sun's disc was visible, the E-vector orientation over at least part of the sky was usually quite close to the theoretical predictions of simple Rayleigh theory. Fig. 8 illustrates a representative example of this, again for data from measurements at 350 nm. This example demonstrates especially well that the visibility of the sun is an important factor in whether or not appropriate E-vector orientations exist, by providing data collected under both conditions. When the sun's disc was visible (for data up to 75° in elevation), the deviation of measured E-vector orientation from theory was quite small far from the sun, even though the percentage polarization reached only 12%. When, however, the sun was obscured by heavy clouds during the data collection for elevations 80–85°, the deviations increased tremendously. The agreement of observed E-vector orientation with theoretical expectations can be shown in another way: for overcast conditions, the percentage polarization was measured to be virtually zero, *except* in those parts of the sky which

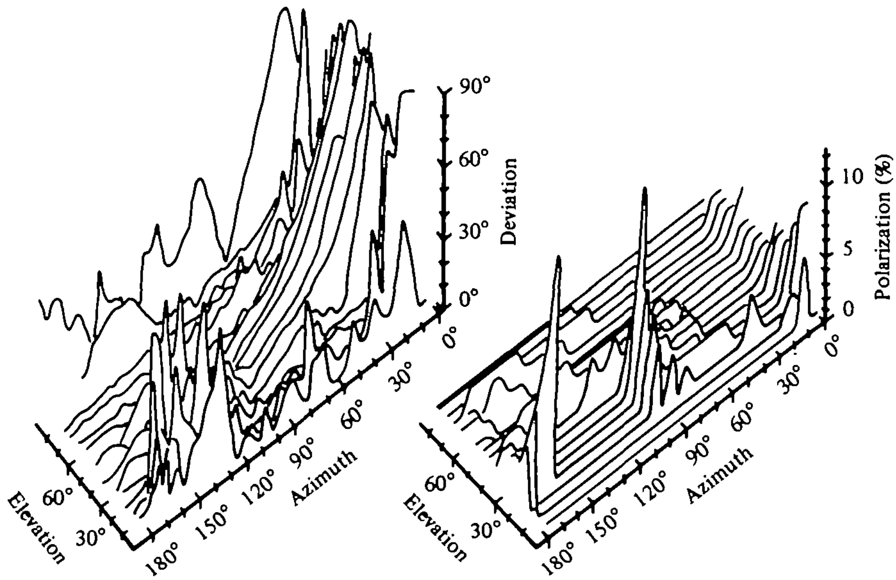


Fig. 8. Absolute percentage polarization and deviation of *E*-vector orientation for an overcast sky with the sun's disc barely visible measured at 350 nm. When the sun's disc was just visible through cloud cover, some appropriate polarization patterns existed, as illustrated by this example. During data collection, the sun's disc was visible until points in the sky with elevation 80–85° were measured. Notice that far from the sun the *E*-vector orientation is close to theoretical expectations. When the sun disappeared behind clouds, the *E*-vector deviation dramatically increased as the percentage polarization decreased.

exhibited *E*-vector orientations fairly close to theoretical predictions. Although all instances of these partial Rayleigh patterns were carefully examined to determine whether the use of any particular wavelength would be advantageous, no clear relationships were apparent. True simultaneous measurements as a function of wavelength were not available, however, and sky conditions changed in various unpredictable ways between measurements. Frequently on such cloudy days, however, the percentage polarization was slightly greater at u.v. wavelengths than at other, longer wavelengths, whereas the reverse was always true for clear days.

DISCUSSION

Our measurements of skylight polarization parameters provide extensive data about those features of skylight radiation which might be used as orientation cues by animals. Sekera (1951, 1955, 1957*a*, *b*), Hansen & Travis (1974), and Coulson (1974) have published comprehensive reviews of many of the physical aspects of skylight polarization, and Brines (1978) has reviewed these in detail in biological terms. Since Waterman (1979) has recently summarized the present state of understanding of many biological aspects of animal polarization sensitivity, we will concentrate here on what information relevant to u.v.-sensitive animals is actually visible in the sky.

Radiance and spectral distribution

Our measurements confirmed earlier work in demonstrating that a chief characteristic of the radiance and spectral distribution of even the clearest sky is *variability*. Therefore, these properties of skylight would provide unreliable orientation cues. The relative relationships of radiance and colour over very large areas of the sky might be useful, since they generally match qualitatively the simple geometry of Rayleigh scattering. But the necessity of using large areas of the sky to make these determinations seems to us to be a rather severe constraint on the general utility of these characteristics as cues, and behavioural experiments clearly show that large areas are not essential for insect orientation.

While the radiance distribution of a cloudy sky is greatly different from the predictions of primary Rayleigh scattering, there is some question whether or not the sun itself is entirely obliterated. Obviously, since the relative position of the sun is a central cue for the orientation of many animals, the answer to this question is important. That the sun may not, in fact, be completely hidden was suggested by von Frisch, Lindauer, & Schmeidler (1960, reviewed von Frisch, 1967, pp. 366 ff.). They concluded that for at least some types of complete overcast (uniform altostratus) honey bees were able to see and orient to the sun's disc through the clouds at u.v. wavelengths. During many of our measurements (exemplified by Fig. 3A), the sun was not detectable as even a 1% brightening in the u.v. or longer wavelengths, but well-orientated dances were still observed in the vertical hive. Either bees are more sensitive to brightness differences than von Frisch concluded, or some non-solar backup system is available on uniformly overcast days.

Degree of polarization

The major conclusion from our percentage polarization data is that while over virtually all environmental conditions the quality and magnitude of the patterns in the natural sky are never very close to theory, they are 'best' at relatively long wavelengths and 'worst' at short ones. That the maximum polarization occurs for intermediate visible wavelengths can be understood by considering the effects of very great multiple scattering in the u.v. and high reflectivity of long red wavelengths by the ground, and especially vegetation. To complicate matters, the magnitude of these parameters often changes dramatically and rapidly, depending on local conditions. As Brines (1978) points out, the major causes of this discrepancy between theory and reality are ones with which bees must have had to deal throughout evolutionary history, and so it comes as no surprise that bees, at least, seem to ignore percentage polarization in orientation except to a minor degree when determining whether what they are seeing is sun or sky (Brines & Gould, 1979).

E-vector orientation

Our repeated observation of the relative insensitivity of *E*-vector orientation to disturbing atmosphere factors is expected from the basic physical characteristics of atmospheric scattering. Since the *E*-vector orientation depends only on the plane of the scattering angle, *any* primary-scattered radiation must possess the appropriate

E-vector orientation. Processes which greatly disturb other Rayleigh parameters – such as multiple scattering and diffuse reflexion – can produce scattering angles of practically all magnitudes and orientations. For highly polarized parts of the sky, multiple scattering is ordinarily of such small radiance that it merely 'dilutes' the simple geometric patterns established by primary scattering, but does not greatly affect the net E-vector orientation. Conversely, as already noted, for those areas of the sky in which the degree of polarization of primary scattering is very small (e.g. close to the sun and antisolar point), the Rayleigh scattering pattern is overpowered and slight amounts of anomalous ('negative') polarization can be observed.

The wavelength dependence of the relatively small E-vector deviations we measured are explained by considering such a multiply scattered component, and our observations that a more pronounced light haze produces greater deviations, especially in the u.v., are not surprising.

The inappropriate patterns observed on completely overcast days are understandable, considering that the great optical density of clouds makes it highly probable that all skylight has been multiply scattered when it emerges.

With respect to orientation, even small E-vector deviations can produce large errors if used in a strictly geometrical way to locate the sun, impairing a forager's ability to return to her hive and causing her to indicate in her dances locations far from the actual goal. Hence, from this point of view, the use of u.v. – the worst wavelength in this regard – is puzzling.

In considering how accurately an animal can orient, we must look also at how extensive usable polarization patterns in the sky are, since bees must often have available only a partial view of the natural sky. In this regard, as discussed above, the sharply increasing proportion of multiply scattered light at shorter wavelengths results in u.v. being the worst wavelength band to use.

How large an area of sky has E-vector patterns which are predicted by primary scattering depends on how much direct sunlight penetrates the clouds or passes through holes and scatters from the air beneath. We expect that only in exceptional circumstances would the polarization patterns produced in the atmosphere above the clouds be transmitted through even relatively thin sections of cloud cover.

Which cues should animals use?

We have found, in common with other workers, that patterns of radiance and degree of polarization are highly variable and would appear to be unreliable cues for orientation. In fact, experiments using artificially-produced polarization stimuli have demonstrated that for honey bees (von Frisch, 1967, pp. 387ff.; von Helversen & Edrich, 1974; Edrich & von Helversen, 1976; Rossel *et al.* 1978; Brines, 1978; Brines & Gould, 1979) and ants (Duelli & Wehner, 1975) the absolute radiation parameters such as radiance, degree of polarization, and spectral distribution are of minor importance over a wide range of magnitudes, and E-vector orientation is the only parameter observed to have a profound effect on animal orientation. The results of our measurements confirm that this skylight parameter is genuinely stable over a wide range of atmospheric conditions and, for large areas of the sky, is relatively close to the predictions of primary Rayleigh scattering theory, and so constitutes a 'best' parameter. One factor to consider is that the largest divergences of the E-vector pattern occur only relatively near the sun and antisun where the degree of polarization is *below* the known perceptual thresholds of animals so far studied. Thus, not only are animals unlikely to be confused by these anomalous patterns since they do not perceive them, but these areas of the sky are often so close to the sun that other cues, such as radiance, would indicate the sun's position reliably. However, the small E-vector deviations measured (which are a function of atmospheric conditions) would impose a limit on the *precision* obtainable by their use. We therefore suspect that bees may not use a strict analytic method for reducing polarization information. In this regard, it is interesting to note that Rossel *et al.* (1978) suggest that their behavioural data could be accounted for by a general, approximate rule for dealing with sky information. However, the dance orientation of bees is often more precise than predicted by this equation, and their supporting data do not completely agree with those reported by Brines & Gould (1979). Further experiments will be necessary to determine the biological details.

Why should animals use the u.v.?

The question of why short u.v. wavelengths are most important for honey bee polarization orientation still remains to be answered. Radiation characteristics of a clear sky cannot be the reason since geometrical information in the u.v. is generally *worse* than in longer wavelengths, especially in terms of degree of polarization, stability of E-vector orientation, and the spatial extent of sky patterns. In fact, considering these factors it seems obvious that detection systems should be limited to *longer* wavelengths. The observation that animals use polarization only in a narrow, short-wavelength spectral band strongly suggests, though, that for some reason longer wavelengths are less useful. One possible factor is that by using u.v. wavelengths, an animal would be fairly sure to analyse the sky and not other polarization patterns, such as those generated by reflexion, which generally are rich in long wavelengths. The problem of determining 'sky' from 'ground' has been speculated upon in some detail by Mazokhin-Porschnyakov (1969) with regard to general insect phototaxis. The results of our behavioural experiments (Brines, 1978; Brines & Gould, 1979) illustrate that the spectral distribution of light can be of great importance in determining how honey bees interpret a polarized light source, and thus give some support to the concept that the differentiation of the source of orientation information is based on wavelength. However, anatomical location of receptors would seem to provide a dependable functional separation of 'sky' and 'ground' and von Frisch (1967) has reviewed the evidence that for honey bees the polarization-sensitive receptors are, in fact, located on the dorsal surface of the compound eyes.

A second possible advantage for a wavelength-sensitive orientation system has been suggested by Wehner (1976). He has postulated that u.v. wavelengths may be used for polarization orientation so that information can be analysed *separately* from motion and form detection which are mediated by longer-wavelength receptors. However, the situation appears to be complex since it has been shown that longer wavelengths can 'mask' the effects of polarized u.v. light for bees if the source is small (Brines & Gould, 1979). Kien & Menzel (1977) have discovered colour-opponent neurones which may be important for this effect. Kirschfeld (1973) has observed similar 'masking' by long wavelengths in optomotor experiments, and Edrich, Neumeyer & von Helversen (1979) and van der Glas (1977) have also shown that longer wavelengths influence orientation. These results demonstrate that u.v. receptors are not always involved *alone* in polarization detection and orientation. Further work will be necessary to determine the physiological basis of these obervations.

Another reason short wavelengths are used for orientation may be that when polarization sensitivity evolved in bees, there *were* great advantages for using u.v. even under clear sky. For example, the atmosphere may have attenuated the u.v. flux to a lesser degree than it does today. Of course, central to such a hypothesis is the idea that present use of u.v. constitutes no liability. Such ideas are hard to evaluate because of the lack of good data about atmospheric conditions and the solar flux of long ago.

While no clear advantage in using u.v. wavelengths for orientation under clear conditions is apparent, we are intrigued by the results of our measurements under overcast skies which do suggest one possible advantage. Ordinarily when the sky was completely covered by heavy clouds, only very small amounts of polarization were detected and the *E*-vector orientations were not correct, while appropriate *E*-vector patterns existed for large parts of the sky when the solar disc was just visible through the clouds. Since the clouds were almost equally opaque over most of the sky under these two conditions, the differences must depend mainly on the presence or absence of direct solar rays. Specifically, if some direct sunlight is incident on the air surrounding the observer, scattering occurs beneath the clouds, producing patterns with the same *E*-vector orientation seen in a clear atmosphere. The radiance, spectral distribution, and degree of polarization, however, are very different from those of a clear sky because a background of virtually unpolarized, diffuse light from the clouds exists, on which the Rayleigh scattered light is superimposed, as well as the diminished depth of atmosphere available for scattering. Under these conditions, the pattern was usually strongest in the u.v.

Unlike clear skies, in which the large volume of air available greatly increases the chance of multiple scattering of short wavelengths, thereby weakening the Rayleigh pattern most in the u.v., on cloudy days *direct* rays from the sun falling on the much smaller volume of air *beneath* the clouds have far fewer opportunities to be scattered even once. Since short wavelengths are much more likely to be scattered, the pattern under these circumstances ought to be strongest in the u.v. However, while this is true, the measured values of polarization under these conditions are typically below the polarization detection threshold of honey bees. Of course, some animals may be more sensitive to polarization and thus be able to detect such weak patterns (and we have reason to suspect that horizontal dance orientation may not reflect the full sensitivity of honey bees). More importantly, as the sky becomes overcast the *E*-vector orientation in the u.v. probably remains stable the longest (even though it approximates theoretical geometry the least). This characteristic may be what Sekera meant in his communication to von Frisch (1967, p. 382) when he claimed that u.v. wavelengths were the least sensitive to 'atmospheric disturbances'.

If our expectation that a very high probability of scattering may differentially establish patterns at short wavelengths is correct, one prediction would be that under

Table 2. *Average percentage polarization measured against 20 different small cumulus clouds at 22–60°, elevation 60–180° from the sun, ratio of cloud radiance to nearby blue sky, and percentage polarization of surrounding blue sky*

(The first three measurements are typical for very hazy summer days (15 clouds), while the last three are representative of relatively clear summer days (5 clouds).)

Wavelength (nm)	Polarization of of cloud (%)	Cloud/sky Radiance	Polarization of nearby blue sky (%)	Sky conditions
350	10	1·2	17	Hazy
500	7	1·7	28	Hazy
600	6	2·7	24	Hazy
350	37	1·2	59	Clear
500	23	1·6	62	Clear
600	17	1·8	39	Clear

the proper geometrical conditions, weak but measurable polarization patterns should exist against clouds when the sky near the sun is relatively clear. Again, if direct solar rays can illuminate at least some air between an observer and the cloud, polarized light geometrically related to the sun's position should be produced by scattering. This possibility was strongly suggested during the course of our measurements, because we were constantly impressed that isolated clouds rarely disturbed the patterns of E-vector orientation.

To test this idea directly and also to obtain measurements of degree of polarization as a function of wavelength for patterns produced by scattering from short optical paths, we pointed our polarimeter at a series of typical summer cumulus clouds.

Representative measurements for both hazy and clear summer skies are summarized in Table 2, in which sky patterns measured against isolated clouds are compared to those from nearby blue sky. Clouds for these data had an elevation of 22–60°, a relative azimuth of 60–180°, and were estimated to be about 2 km distant from the polarimeter. Our results demonstrate several factors clearly: (1) Although the observed cloud radiances were always greater than for clear sky close to the cloud at all wavelengths, the cloud-reflected flux was still wavelength-dependent, and least at short wavelengths. This loss of short wavelengths probably arises in the beam's propagation to and from the cloud, during which it differentially loses its short-wavelength photons by scattering (e.g. Minnaert, 1954, p. 240; Feigl'son, 1966, p. 102). Alternatively if clouds really are more transparent in the u.v. as suggested by von Frisch *et al.* (1960) and discussed above, a smaller proportion of u.v. light would be reflected from clouds towards the observer. Hence, for u.v. wavelengths there would be less background unpolarized light to attenuate the pattern established by scattering of direct sunlight between the cloud and the observer. (2) In all cases, we could measure polarization patterns against the clouds, and the measured E-vector orientation matched the predictions of Rayleigh scattering closely. The degree of polarization of these patterns was *greatest* for u.v., least for red, and moderate for blue/blue-green, which differs greatly from measurements of the cloudless sky where u.v. wavelengths typically exhibit the *smallest* degree of polarization. In the hazy sky measurements, the small levels of polarization measured for adjacent blue sky are indicative of the extent to which multiple scattering degraded the sky patterns. Under better atmospheric conditions, u.v. patterns against clouds exhibited much larger degrees of polarization (Table 2). Whether the atmosphere was clear or hazy, the u.v. was about half again more strongly polarized than blue/blue-green, and twice as polarized as red.

What these results mean for animals (if they could detect polarization at all wavelengths) is that on typical, bright, partly cloudy summer days, there could be large 'blank' spots in the pattern at visible wavelengths resulting from the strong reflectance of unpolarized light from the clouds at those wavelengths, which drive the percentage polarization below the perceptual threshold; while in the u.v. the pattern would tend to be continuous over the sky. Even where the percentage polarization at longer wavelengths is above the $\sim$ 10% threshold measured for 15° segments of the sky (von Frisch, 1967, p. 404), the higher degree of polarization in the u.v. probably allows bees to use smaller patches of sky than would otherwise be necessary. Von Frisch (1967, p. 390), in fact, has commented on the relationship between the degree of polarization and the quality of dance orientation. Hence, in the u.v. virtually any patch of sky which happened to be visible could provide useful orientation information to flying or dancing bees, even if it were covered by an isolated cloud.

While our measurements suggest advantages for the use of short wavelengths under patchy cloud cover, vegetation which obscures parts of the sky may produce an even greater differential enhancement of polarization information in short wavelengths. Such a situation is encountered, of course, very frequently by foraging and dancing honey bees. In these cases, the volume of air available for scattering is *very* short – between tree leaves and a bee, for example – making the scattered flux extraordinarily rich in u.v. photons relative to visible light; while the absorption of u.v. by vegetation would so reduce the unpolarized background that the percentage polarization in the u.v. could be well above threshold. (Of course, the total flux level would be much smaller, and it remains to be determined whether bees' u.v. receptors are sensitive enough.) At the same time, the enormous flux of reflected green and near-infrared photons from vegetation, some of which becomes highly polarized, would tend to change any polarization patterns at visible wavelengths.

In one set of preliminary measurements, for example, we pointed our polarimeter at a shaded tree 7·5 m away, and found that the *E*-vector in the u.v. was less than 5° from the predicted value, while in the blue/blue-green and red the errors were 97° and 92° respectively. Hence, bees flying or dancing under a canopy of vegetation might well be able to see perfectly good patterns of u.v.-polarized light against the leaves overhead. That a pronounced differential reflectance exists is already well known. For example, Krinov's (1960) widely quoted data show a relatively large peak at about 550 nm and huge increases for longer wavelengths. Also, it is interesting to note that measurements by Gehrels (1962) and Gehrels & Teska (1963) show a large decline in the degree of polarization at long wavelengths because of the reflexion of skylight from vegetation surrounding their analysing instrument.

Our sky measurements demonstrate that (1) *E*-vector orientation is the most useful and stable cue in the sky, although it does not generally agree exactly with the predictions of simple theory; (2) any wavelength will serve quite well under clear skies for polarization orientation, although the pattern is slightly better at long wavelengths;

(3) under overcast skies, no wavelength band provides useful polarization information; (4) under partly cloudy skies, the proportion of the sky with reliable polarization information is greatest in the u.v.; (5) under many circumstances, typical and biologically significant Rayleigh scattering patterns may exist against overhead vegetation at u.v. wavelengths. Therefore, we propose that the u.v. sensitivity of animals is at least partly an adaptation for detecting skylight patterns under conditions when useful scattering can occur only relatively close to an animal.

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REFERENCES

BRINES, M. L. (1978). Skylight polarization patterns as cues for honey bee orientation: physical measurements and behavioural experiments. Ph.D Thesis, New York: The Rockefeller University.

BRINES, M. L. & GOULD, J. L. (1979). Bees have rules. *Science, N.Y.* **206**, 571–573.

CHANDRASEKHAR, S. (1950). *Radiative Transfer*. Oxford: Clarendon Press.

CHANDRASEKHAR, S. & ELBERT, D. D. (1954). Illumination and polarization of the sunlit sky on Rayleigh scattering. *Trans. Am. Phil. Soc.* **44**, 643–728.

COULSON, K. L. (1974). The polarization of light in the environment. In: *Planets, Stars, and Nebulae* (ed. T. Gehrels). Tucson, Ariz.,: University of Arizona Press.

COULSON, K. L., WALRAVEN, R. & SOOHOO, L. (1974). Polarization of skylight at an altitude of 3416 m (11200 ft) on Mauna Loa, Hawaii. *Contributions in Atmosphere Sciences* **9**. Davis: University of California.

DUELLI, P. & WEHNER, R. (1973). The spectral sensitivity of polarized light orientation in *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J. comp. Physiol.* **86**, 37–53.

EDRICH, W., NEUMEYER, C. & VON HELVERSEN, O. (1979). Anti-sun orientation of bees with regard to a field of ultraviolet light. *J. comp. Physiol.* **134**, 151–157.

EDRICH, W. & VON HELVERSEN, O. (1976). Polarized light orientation of the honey bee: the minimum visual angle. *J. comp. Physiol.* **109**, 309–314.

EHEIM, W. & WEHNER, R. (1972). Die Sehfelder der zentralen Ommatidien in den Appositions Augen von *Apis mellifera* und *Cataglyphis bicolor* (Apidae, Formicidae, Hymenoptera). *Kybernetick* **10**, 168–179.

FEIGEL'SON, E. M. (1966). *Light and Heat Radiation in Stratus Clouds*. Jerusalem: Israel Program for Scientific Translation.

VON FRISCH, K. (1948). Geloste und ungeloste Ratsel der Bienensprache. *Naturwissenschaften* **35**, 12–23, 38–43.

VON FRISCH, K. (1949). Die Polarisation des Himmelslichtes als orienterener Faktor bei den Tanzen der Bienen. *Experientia (Basel)* **5**, 142–148.

VON FRISCH, K. (1967). *The Dance Language and Orientation of Bees*. Cambridge, Mass.: Harvard University Press.

VON FRISCH, K., LINDAUER, M. & SCHMEIDLER, F. (1960). Wie erkennt die Biene den Sonnestand bei geschlossener Wolkendecke? *Natur. Rundschau*, pp. 169–172.

GEHRELS, T. (1962). Wavelength dependence of the polarization of the sunlit sky. *J. opt. Soc. Am.* **52**, 1164–1173.

GEHRELS, T. & TESKA, T. (1963). The wavelength dependence of polarization. *Appl. Opt.* **2**, 67.

VAN DER GLAS, H. W. (1977). Models for unambiguous *E*-vector navigation in the bee. *J. comp. Physiol.* **113**, 129–159.

HANSEN, J. E. & TRAVIS, L. D. (1974). Light scattering in planetary atmospheres. *Space Sci. Rev.* **16**, 527–610.

VON HELVERSEN, O. & EDRICH, W. (1974). Der Polarisationsempfanger im Bienegauge: ein Ultraviolettrezeptor. *J. comp. Physiol.* **94**, 33–47.

KIEN, J. & MENZEL, R. (1977). Chromatic properties in the optic lobes of the bee, *J. comp. Physiol.* 35–53.

KIRSCHFELD, K. (1973). Optomotorische Reaktionen der Biene auf bewegte 'polarisation-muster'. *Z. Naturf.* **28c**, 329–338.

KIRSHFELD, K., LINDAUER, M. & MARTIN, H. (1975). Problems of menotactic orientation according to polarized light of the sky. *Z. Naturf.* **30** c, 88–90.

KRINOV, P. (1960). In *Handbook of Geophysics*. New York: Macmillan.

LAUGHLIN, S. & HORRIDGE, G. (1971). Angular sensitivity of retinular cells of dark-adapted worker bees. *Z. vergl. Physiol.* **74**, 329–335.

MINNAERT, M. (1954). *The Nature of Light and Color in the Open Air*. New York: Dover.

MOZOKHIN-PORSHNYAKOV, G. A. (1969). *Insect Vision*. New York: Plenum.

ROSSEL, S., WEHNER, R., LINDAUER, M. (1978). *E-vector* orientation in bees. *J. comp. Physiol.* **125**, 1–12.

SEKERA, A. 1951 Polarization of light. In *Compendium of Meterology* (ed. T. F. Malone). Boston: American Meteorological Society.

SEKERA, A. (1955). *Investigations of Polarization of Skylight*. Final Report AF 19(122)239, Department of Meteorology, University of California, Los Angeles.

SEKERA, A. (1957*a*). Polarization of skylight. In *Handb. Phys.* (ed. S. Flugge).

SEKERA, A. (1957*b*). Light scattering in the atmosphere and the polarization of skylight. *J. opt. Soc. Am.* **47**, 484–490.

SERKOWSKI, K. (1974). Polarimeters for optical astronomy. In *Planets, Stars, and Nebulae* (ed. T. Gehrels). Tucson, Ariz.: University of Arizona Press.

SHURCLIFF, W. A. (1962). *Polarized Light: Production and Use*. Cambridge, Mass.: Harvard University Press.

STOCKHAMMER, K. (1956). Die Wahrnehmung der Schwingungsrichtung linear polarisierten Lichtes bei Insekten. *Z. vergl. Physiol.* **38**, 30–83.

STRUTT, J. (Lord Rayleigh). (1871). On the light from the sky, its polarization and colour. *Phil. Mag.* **41**, 107–120, 274–279.

WATERMAN, T. H. (1979). Polarization Sensitivity. In *Handbook of Sensory Physiology*, vol. VII/6 (ed. H. Autrum), pp. 281–469. Berlin: Springer-Verlag.

WEHNER, R. (1976). Polarized light navigation by insects. *Scient. Am.* **235** (7), 106–115.

WILSON, E. O. (1971). *Insect Societies*. Cambridge, Mass.: Harvard University Press.

ZOLOTOV, V. & FRANTSEVICH, L. (1973). Orientation of bees by the polarized light of a limited area of the sky. *J. comp. Physiol.* **85**, 25–36.