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Skylight polarization as perceived by desert ants and measured by video polarimetry

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Abstract North African desert ants belonging to different genera and inhabiting different areas (sand dunes, salt pans, inundation flats and gravel plains) exhibit different ways of skylight navigation: some rely especially on the polarized light in the sky, others depend more effectively on the position of the sun. Are these differences due to species- or genus-specific idiosyncrasies of the ant's skylight compass, or are they caused by differences in the overall degree of polarization prevailing in the celestial hemisphere that vaults the different kinds of habitat? Theoretically, such differences are to be expected, as various parameters known to influence the degree of polarization in the Earth's atmosphere – such as the albedo of the ground and the content of water vapour, dust and haze in the airlayers above the ground – do vary between the different types of habitat mentioned above. The first wide-field, videopolarimetric study of skylight polarization presented here clearly shows that at any particular locality the temporal (day-to-day) variations of the degree of skylight polarization are much more pronounced than the differences recorded at the same local time at different localities. In contrast, the angle of polarization is unaffected by atmospheric disturbances and accords well with the predictions of Rayleigh scattering. Consequently, differences in behavioural performances of navigating North African desert ants are due to interspecific and intergeneric differences in the ants' navigational systems rather than to general differences in the skylight stimuli experienced by the ants during navigation.

Key words Navigation · Polarized light · Video polarimetry · Ants · Skylight parameters

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Introduction

In his seminal paper on skylight navigation in insects, especially in ants, Santschi (1923) wondered why certain genera and species used the sun as a compass, while others relied predominantly on the sun-free parts of the sky. In his lifetime, it was not known yet that the decisive aspect of light perceived by insects in the "circumsolar" celestial hemisphere was the distribution of E-vectors of linearly polarized light – later discovered in bees (von Frisch 1949), and now extensively studied in desert ants of the genus *Cataglyphis* (for a review see Wehner 1994).

The differences, however, that Santschi had observed among different genera and species are still a riddle. Are they really due to differences among different taxonomic groups of ants, or are they caused by characteristics of the habitats occupied by the different species? As the habitats of the *Aphenogaster*, *Messor*, *Monomorium* and *Cataglyphis* species are rather varied and include desert regions in mountains, sand-dune areas, salt pans or coastal inundation plains, several parameters such as water content, haze, frequency of clouds and the turbidity of the atmosphere vary accordingly. All these factors have strong influences on various optical aspects of scattered skylight (Coulson 1988 pp 350, 423). One can imagine, for example, that due to the lower level of aerosols and haze in totally arid, vegetation-free desert mountain areas, the degree of skylight polarization is higher there than in coastal regions, where haze commonly occurs. The atmosphere above salt pans, even if covered by hard, dried-out soil, can contain large amounts of water vapour due to the evaporation of water from the moist underground. How much do these differences in the structure of the ants' habitats influence the degree of polarization in the sky? This is an important question, because the degree of polarization largely influences the accuracy of navigation (Wehner 1982; Edrich and von Helversen 1987). Furthermore, to what extent does the degree of polarization depend on the spectral composition of skylight? The *Cataglyphis* retina is equipped with short-wavelength (ultraviolet) and long-wavelength (green) photoreceptors, but only the former are used in E-vector navigation. Do the atmospheric factors mentioned above influence the degree of polarization more strongly in the short- than in the long-wavelength region of the spectrum, or vice versa? In order to answer these questions, we have recorded different parameters of polarized light (degree of polarization, angle of polarization, radiant intensity, and the spectral dependencies of these parameters) within large areas of skylight in three different North African habitats: desert highlands, salt pans, and coastal inundation plains.

Apart from the polarimeters of Prosch et al. (1983) and North and Duggin (1997), all polarimeters currently employed in atmospheric optics (see Coulson 1988 pp 533–571) have very small apertures (diameter 1–4°). This is not the method of choice to record large-field distributions of spatial and temporal variations within patterns of scattered skylight. Therefore, in the present account we use wide-field polarimeters, and hence are able to provide the first video-polarimetric imaging study of the spatial distribution of the degree and angle of polarization across the celestial hemisphere.

Materials and methods

Recording techniques

A highly sensitive tube camera (Hamamatsu Beam Finder III) was used to film wide-field skylight windows through a linearly polarizing filter (H'NPB polarizer, Polaroid Company, characterized by good polarization characteristics also in the ultraviolet range of the spectrum) and through one of two colour filters (green filter: B + W 061, transmission maximum at $\lambda = 530$ nm; UV filter: A5194-01 wide-band Hamamatsu filter with a transmission maximum at $\lambda = 330$ nm and transmission less than 3% for $\lambda > 400$ nm) in front of the objective lens. For details of the video-polarimetric technique see Horváth and Varjú (1997). The camera (spectral sensitivity ranging from $\lambda = 200$ nm to $\lambda = 750$ nm) was set on a tripod where it could be accurately adjusted with respect to both azimuth and elevation. It was connected to a portable video recorder (Sony 8-mm video Walkman GV-S50E). Within a few seconds, recordings were taken with the polarizer aligned in the 0° (vertical), 45°, and 90° (horizontal) direction. This set of measurements was made independently in the green and ultraviolet range of the spectrum. All technical details were spoken into a microphone and recorded as an audio signal by the video Walkman.

The recorded scenes were then digitized frame by frame using a frame grabber (Screen Machine II, FAST Multimedia AG, Munich). The personal computer (Pentium 133) was connected to a stop-frame video recorder (Sony EV-C500E Hi8). The three digitized video pictures taken from a particular skylight window (when the polarizer had been aligned consecutively in the three directions mentioned above, i.e. $\varphi = 0°$, 45°, and 90°), yielded the modulation of the three parameters intensity I, degree of polarization δ, and angle of polarization χ. The latter is defined as the angle between the local meridian and the E-vector, i.e. $\chi = 0°$ represents vertical E-vectors. A sinusoid $[I = A\sin(\varphi + \chi) + B]$ was fitted to the intensity modulation for each pixel of the picture in order to determine I_{max}, I_{min}, and the angular position χ of I_{max}. From these data we calculated the mean light intensity, $I = (I_{max} + I_{min})/2$, and the degree of polarization, $\delta = (I_{max} - I_{min})/(I_{max} + I_{min})$, for each pixel within the skylight window. To obtain intensity data that are proportional to the real radiant intensities in the ultraviolet and green range of the spectrum, the spectral transmission characteristics of polarization filters, spectral filters and camera optics as well as the spectral sensitivity of the camera sensor were taken into account. The maximum intensity value ($I = 100\%$) obtained this way in a given spectral range corresponds to the intensity of skylight emanating from the brightest region of the celestial hemisphere (the area in the immediate vicinity of the sun). Finally, we

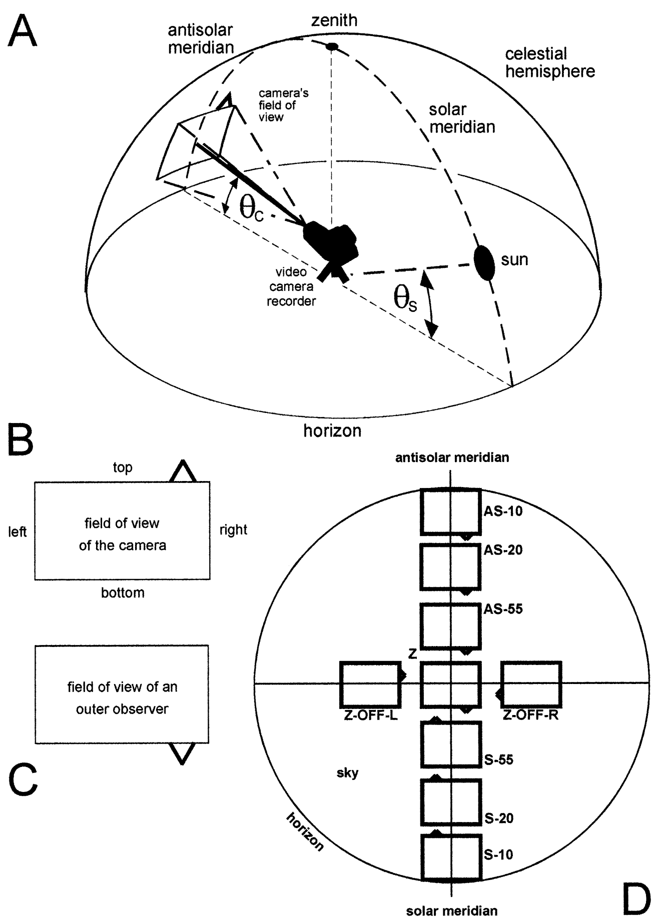


Fig. 1 A The geometry of the video-polarimetric recordings of skylight polarization. The elevation of the video camera and the sun is Θ_c and Θ_s, respectively. **B** The camera's field of view. The *small triangle* indicates the top right. **C** The field of view of an outside observer looking at the celestial atmosphere from above ("astronaut's view" used in Fig. 2). **D** The positions of the skylight windows within which video-polarimetric data were obtained. When the camera was oriented towards the antisolar and solar meridian, the rectangular window representing the field of view of the camera is designated by "*AS-*" and "*S-*", respectively. The *numbers* following these designations indicate the elevation of the camera (degrees). The window "*Z*" means that the camera recorded the region around the zenith. In the case of the window "*Z-OFF*" the camera was first rotated by 90° from the solar meridian then elevated by 45° in the plane perpendicular to the solar meridian (*R*, right; *L*, left). The field of view of the camera, i.e. the size of the skylight windows, is 50° × 40° (horizontal and vertical extent, respectively)

produced two-dimensional false-colour maps of I, δ, and χ on the computer screen with pixel resolution.

The Hamamatsu camera used in the recordings mentioned above had a field of view of 20° in the horizontal and 15° in the vertical direction. In order to obtain a larger field of view, we used in addition a Sony Hi8 CCD-VX1E video-camera recorder equipped with a rotating linearly polarizing filter (Hama, mounted dichroic sheet polarizer). Using this camera, we recorded the polarization patterns of the sky in the green range of the spectrum ($\lambda_{max} = 550$ nm) with a field of view of 50° in the horizontal and 40° in the vertical direction.

The geometrical arrangement of the skylight windows, from which measurements were taken, is shown in Fig. 1. At any particular habitat and time of day a total of maximally eight different skylight windows was selected for recording: three windows along the antisolar meridian at elevations of 10°, 20° and 55° above the horizon (AS-10, AS-20, AS-55), three windows along the solar meridian at elevations of 10°, 20° and 55° (S-10, S-20, S-55), one window at the zenith (Z), and one window at the meridian oriented at right angles to the solar and antisolar meridian, and centred at an elevation of 45° above the horizon (Z-OFF). Of course, no recordings were taken of skylight windows, in which the sun happened to appear at a particular time of day. Due to the relatively low levels of radiant intensity at sunrise and sunset and because of the relatively low ultraviolet transmission characteristics of the polarizers and ultraviolet filters, we could not take ultraviolet recordings with the Hamamatsu camera when the sun was at the horizon.

In Fig. 1 small triangles in the upper right corners of the skylight windows indicate the orientation of the field of view of the camera. The skylight patterns shown in Fig. 2 are designed as if an "outer observer" looked at the celestial hemisphere ("astronaut's view"). Figure 1B, C indicates how the conversion from the camera's view to the austronaut's view is performed.

Habitats

Recordings were taken under clear-sky conditions in three North African (Tunisian) habitats occupied by different species of desert ants (genera *Cataglyphis*, *Messor*, *Aphenogaster*, *Monomorium*): (1) within the vast expanses of salt-pan area of the Chott el Djerid (site "Tozeur", east of El Mahassen; 33.9°N, 8.5°E), (2) in the extremely arid and vegetation-free highland area of the south-eastern parts of the North African Dorsale (close to the Tunisian/Algerian border; site "Metlaoui", halfway between Metlaoui and Moulares; 34.3°N, 8.2°E), and (3) in the coastal inundation plains of the Tunisian Sahel zone (site "Maharès", 34.6°N, 10.5°E).

Results

Figure 2 provides false-colour images of radiant intensity (I), degree (δ) and angle (χ) of polarization (E-vector orientation), as measured through the green channel of the video polarimeter. In Fig. 3 histograms are given for these three skylight parameters, calculated for the patterns shown in Fig. 2.

These figures, given as examples, yield some important results. The spatial distribution of the angles of polarization conforms rather well with what one would expect from an ideal atmosphere characterized by only primary scattering. The degree of polarization, however, is highly reduced even in the cloudless sky vaulting a North African subtropical habitat. As to be expected, the degree of polarization gradually increases and the radiant intensity gradually decreases with increasing angular distance from the sun. The radiant intensity is the smallest and the degree of polarization is the highest at about 90° from the sun. For larger angular distances than 90° measured from the sun the radiant intensity gradually increases, and the degree of polarization decreases again towards the antisolar point of the sky. Note that in Fig. 3 (left figure) the measured radiant intensity along the solar meridian is slightly smaller (patterns S-10, S-20, and S-55) than that along the antisolar meridian (patterns AS-10, AS-20, and AS-55). This asymmetry is caused by the fact that taking the recordings from the whole set of skylight windows lasted for about 15 min, and that the procedures started at the antisolar meridian. During this period of time the radiant intensity within the sunset sky decreased rapidly.

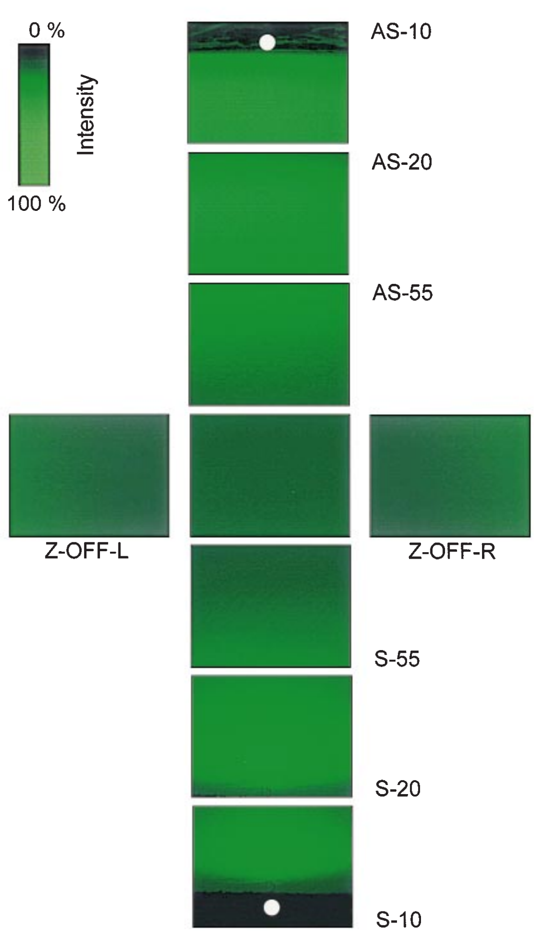
The dark zone passing through the zenith at right angles to the solar/antisolar meridian (Fig. 2, left figure: Z-OFF-L, Z, Z-OFF-R) is of particular interest. As revealed by the middle panel of Fig. 2, it is within this band-like zone of scattered skylight that the degree of polarization reaches its maximum. However, as the corresponding histograms of Fig. 3 (middle panel) show, this maximum does not amount to the theoretically possible value of $\delta = 100\%$ for an ideal Rayleigh atmosphere, but to only about 60%.

The parameter that deviates substantially from the predictions based on a theoretical (Rayleigh) atmosphere is the degree rather than the angle of polarization. In Table 1 the degree of polarization is given in the long- and short-wavelength range of the spectrum for two different elevations of the sun ($\theta_s = 35°$ and $\theta_s = 70°$) at three different types of habitat. None of the three study sites exhibits significantly higher or lower degrees of polarization than any of the other sites. Whenever we had performed two measurements at the same site on two subsequent days, the degree of polarization differed, sometimes remarkably, from one day to another. For example, at the *Maharès* site the green channel pointing at AS-20 exhibited values of $\delta = 20.1\%$ and 29.9% ($P < 0.001$) on August 8 and 10, 1996, respectively, even though the human observer could not detect any obvious differences in the appearance of the celestial hemisphere. The same statistically significant differences ($P < 0.001$) hold for all measurements made on two separate days in the same region of the sky; with the only exception of skylight window Z, at Maharès, for sun elevation 70° (see Table 1). In conclusion, the temporal (day-to-day) variations at one particular site always exceeded the variations that are due to the spatial (geographical) location of that site. Finally, in all skylight windows the degree of polarization was always higher in the green than in the ultraviolet range of the spectrum. This is in accord with what one would expect to occur in an ideal (Rayleigh) atmosphere.

Discussion

The starting point of the present investigation was the question whether different types of habitat occupied by

Fig. 2 Skylight parameters within the celestial windows shown in Fig. 1D. The recordings were taken at sunset on 9 August 1996 at the shore of Maharès. The sun and antisun are indicated by *white dots*. Because of the wide field of view of the camera there is a certain overlap between adjacent skylight windows.
Skylight parameters: radiant intensity, *I* (*left panel*; inset: *I* scale, for definition see text); degree of polarization, δ (*middle panel*; inset: δ scale, for definition see text); E-vector orientation (angle of polarization), χ (*right panel*; inset: colour code of χ; the angles χ are measured relative to the local meridian). All data in this figure refer to the green channel of the polarimeter; for UV data see Table 1



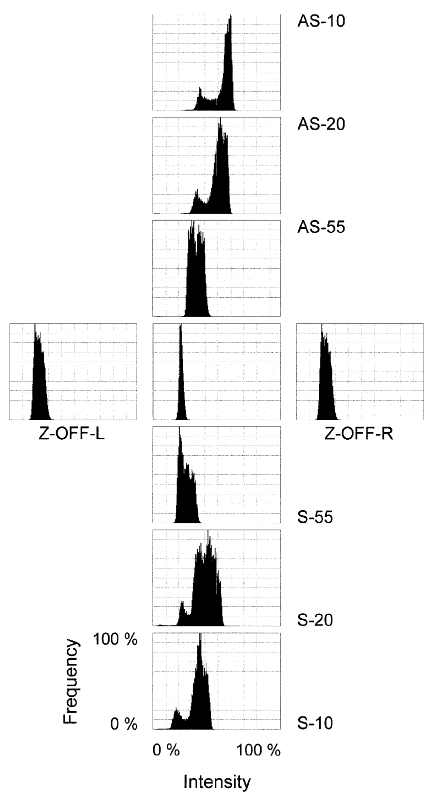
different insect navigators varied in one or another optical aspect of skylight polarization. Such conjectures are not unwarranted. Water vapour and aerosols, which cause absorption and multiple scattering events, might occur in the atmosphere more frequently above one type of habitat than above another. Furthermore, differential reflections from the ground are known to influence the optical properties of skylight patterns as well.

The general result emerging from our measurements is that the question posed above cannot be answered in the affirmative. The degree of polarization, which is much more affected by atmospheric disturbances and surface reflections than is the angle of polarization, does not vary systematically among the different types of desert habitat. The day-to-day fluctuations of the degree of polarization are much larger than the habitat-based variations. Hence, Santschi's (1923) early observation that for navigation some species of ants inhabiting particular geographical regions relied more on scattered skylight than direct sunlight, cannot be explained on the basis of the distinctness of skylight cues available to the ants in these different habitats. Instead, the interspecific differences must be caused by peculiarities of the ants' species-specific navigational systems.

Apart from this main result, there is a number of important aspects of the real sky that can be deduced from the first wide-field polarimetric study of the sky presented here. Most importantly, even in the cloudless sky vaulting a subtropical desert landscape the degree of polarization within medium-sized (40° × 50°) skylight windows never exceeded mean values of δ = 60% (and 75% in individual pixels of sky). Behavioural experiments performed in bees show that the orientation of the E-vector cannot be inferred from pixels of sky within which the degree of polarization is lower than δ = 10% (von Frisch 1967; Edrich and von Helversen 1987). Polarization-sensitive interneurones in crickets exhibit threshold values of δ = 5% (Labhart 1996).

Another important finding is that in accord with Rayleigh theory the degree of polarization in the long-

Fig. 3 Histograms of radiant intensity, *I* (*left panel*), degree of polarization, δ (*middle panel*), and angle of polarization, χ (*right panel*). All data refer to the green channel of the polarimeter and are shown, as false-colour images, in Fig. 2



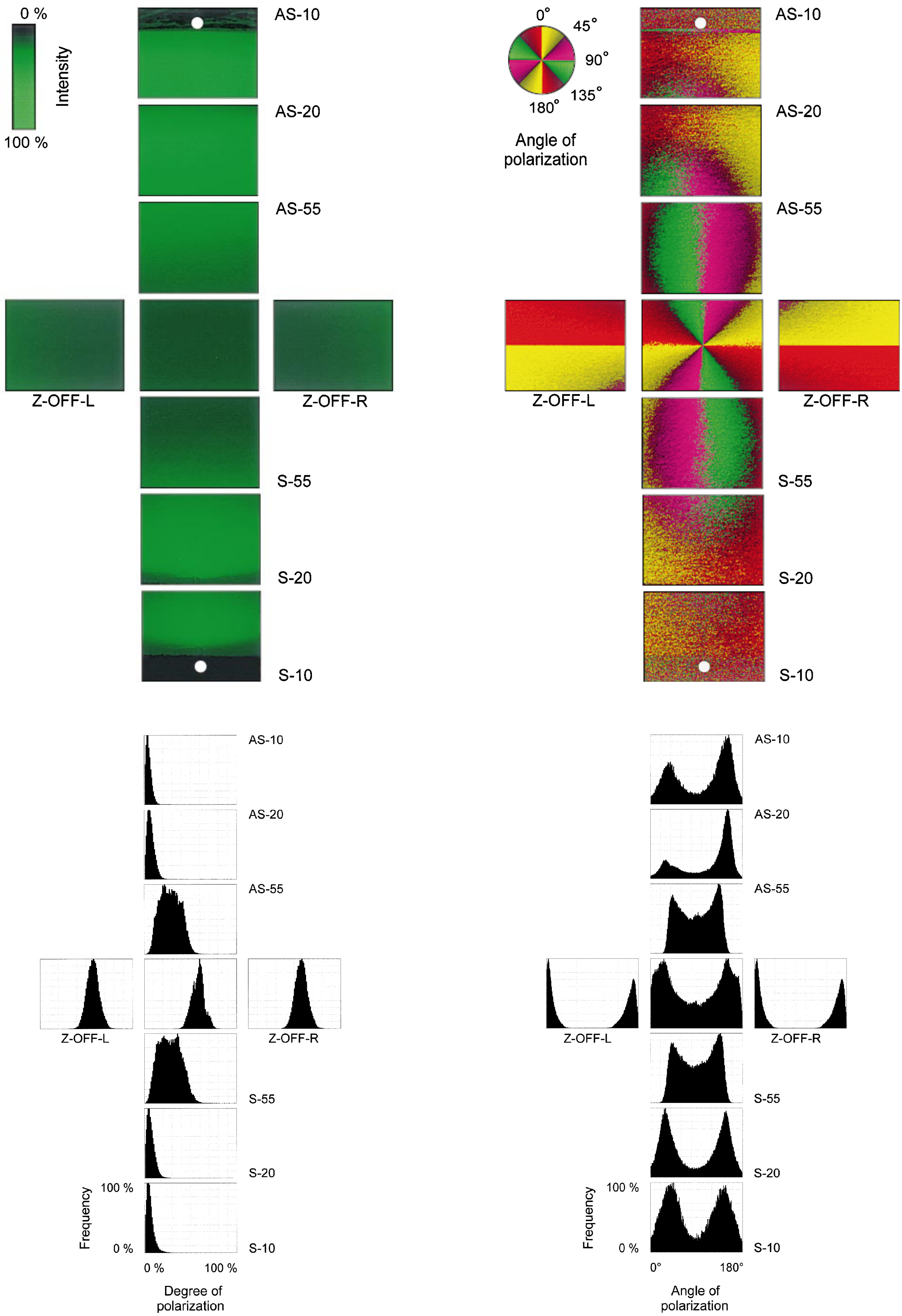

0 %
Intensity
100 %
AS-10
AS-20
AS-55
Z-OFF-L
Z-OFF-R
S-55
S-20
S-10
0°
45°
90°
135°
180°
Angle of polarization
AS-10
AS-20
AS-55
Z-OFF-L
Z-OFF-R
S-55
S-20
S-10
AS-10
AS-20
AS-55
Z-OFF-L
Z-OFF-R
S-55
S-20
S-10
Frequency
100 %
0 %
0 %
100 %
Degree of polarization
AS-10
AS-20
AS-55
Z-OFF-L
Z-OFF-R
S-55
S-20
S-10
Frequency
100 %
0 %
0°
180°
Angle of polarization

Table 1 Degree of polarization of skylight (in %) measured by video polarimetry in the ultraviolet (UV) and green (G) spectral range (window size 20° × 15°) at three different Tunisian study sites (Tozeur: chott, 04.08.1996; Metlaoui: mountains, 05.08.1996 and 06.08.1996; Maharès: coastal area, 08.08.1996 and 10.08.1996). Sun elevation: 70°, local time 1400 hours; sun elevation: 35°, local time 1630 hours. Mean values ± standard deviations. For conventions of direction of view see Fig. 1

Direction of view	Spectral range	Sun elevation Θ_s					
		35°			70°		
		Tozeur	Metlaoui	Maharès	Tozeur	Metlaoui	Maharès
AS-20	UV	8.2 ± 3.9	11.6 ± 4.3	10.9 ± 3.2	20.4 ± 3.6	22.0 ± 4.1	19.1 ± 3.2
			10.3 ± 4.3			22.4 ± 4.1	23.8 ± 3.5
AS-20	G	13.1 ± 5.9	16.1 ± 6.6	14.9 ± 6.3	26.2 ± 4.5	28.6 ± 3.4	20.1 ± 5.1
			14.2 ± 6.0			25.1 ± 3.7	29.9 ± 7.6
AS-55	UV	17.3 ± 5.1	14.4 ± 4.7	20.3 ± 3.8	16.5 ± 3.6	16.5 ± 3.7	17.5 ± 2.9
			18.7 ± 5.2			16.5 ± 4.2	19.1 ± 3.2
AS-55	G	30.4 ± 6.2	36.7 ± 5.7	38.9 ± 7.1	24.1 ± 4.6	25.4 ± 5.7	23.5 ± 3.9
			32.7 ± 6.0			23.7 ± 5.3	31.5 ± 6.8
Z	UV	11.4 ± 3.9	10.6 ± 4.2	13.0 ± 3.3	4.9 ± 2.5	5.1 ± 2.9	4.8 ± 2.1
			12.3 ± 4.4			5.1 ± 2.9	4.8 ± 2.1
Z	G	24.2 ± 6.9	26.2 ± 7.9	29.8 ± 9.0	8.1 ± 3.9	7.5 ± 3.9	7.6 ± 3.7
			24.8 ± 7.6			7.7 ± 4.0	9.5 ± 4.8
Z-OFF	UV	16.9 ± 3.9	17.8 ± 3.9	19.9 ± 2.6	13.2 ± 3.7	14.2 ± 4.7	14.9 ± 6.3
			17.3 ± 3.5			13.3 ± 4.4	17.1 ± 3.2
Z-OFF	G	27.9 ± 6.2	29.0 ± 6.9	34.0 ± 7.2	18.2 ± 6.5	16.0 ± 6.9	24.3 ± 3.2
			27.9 ± 6.5			16.3 ± 6.6	22.2 ± 8.8
S-55	UV	3.8 ± 2.1	5.1 ± 3.1	4.8 ± 2.4			
S-55	G	6.0 ± 4.1	6.3 ± 3.5	7.5 ± 4.2			

wavelength range of the spectrum exceeds that in the short-wavelength range (see also Brines and Gould 1982; Coulson 1988). This effect is due to the greater amount of multiple (secondary- and higher-order) scattering occurring at short wavelengths. Multiple scattering increases negative polarization (Chandrasekhar 1950) and, hence, decreases the degree of polarization – and does so particularly in the short-wavelength spectral range.

Why, then, have ants (Duelli and Wehner 1973) and bees (von Helversen and Edrich 1974) equipped their E-vector-detecting systems with ultraviolet rather than green receptors? Brines and Gould (1982) assumed that the necessary selection pressures had been provided by light scattering beneath the clouds. These small-range scattering events produce E-vector patterns with the same E-vector orientation seen in a clear atmosphere, and are strongest in the ultraviolet. The degree of polarization, however, that is exhibited by these beneath-cloud patterns is very low, especially if the clouds are bright, and usually do not reach the ant's E-vector detection threshold. Instead, as hypothesized by Wehner (1994), ultraviolet receptors might have evolved originally as skylight detectors and might have been incorporated into the E-vector-detecting system only later. Bees, for example, take an ultraviolet but unpolarized beam of light for the sky, particularly for a point lying within the antisolar half of the sky. In contrast, an unpolarized green beam of light is taken for the sun (Brines and Gould 1979; Edrich et al. 1979; Rossel and Wehner 1984). Furthermore, phototactic escape responses as they are exhibited by many species of insect show their sensitivity maxima in the ultraviolet (Wehner 1981).

Due to the high polarization sensitivity of the E-vector-detecting system, desert ants are certainly able to deduce sufficient compass information from polarized short-wavelength skylight. However, it has not been measured in open-field experiments, either in ants or in bees, what the exact relationship between degree of polarization and accuracy of navigation actually looks like. This leads to the most important experiment stimulated by the skylight measurements described in this account.

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