How Do Water Insects Find Their Aquatic Habitat?

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Celestial Polarization Patterns

Under natural conditions one of the main sources of polarized light is the blue sky, owing to the scattering of sunlight within the earth's atmosphere. The light radiated by the sun is unpolarized (neutral): its electric field vector vibrates in all directions (perpendicularly to the direction of propagation) with the same amplitude. The spatial distribution of the electric field vector of neutral light can be characterized by a polarization circle in a polar-coordinate system, the plane of which is perpendicular to the direction of propagation. Apart from the Arago, Babinet and Brewster neutral points (which are positioned in the vicinity of the solar and anti-solar points), the sky is partially linearly polarized. The spatial distribution of the electric field vector of partially linearly polarized light is characterized by a polarization ellipse. The major and minor axes of this ellipse determine the degree of polarization, and the orientation of the major axis gives the direction of polarization. The electric field vector of maximum amplitude (that is, the half major axis of the polarization ellipse) is called the "E-vector". The square of the electric field vector is proportional to the light intensity.

The skylight polarization was discovered by E. Malus in 1809. The first explanation and mathematical description of the celestial polarization was given by J. W. Strutt alias Lord Rayleigh in 1871, and in 1950 S. Chandrasekhar gave a full modern theory. In the 1970s Z. Sekera developed a computer program to describe both the direction and the degree of polarization for all points in the sky for different atmospheric conditions and for spectral wavelengths, ranging from the infrared to the ultraviolet.

In Rayleigh atmosphere (where only first-order Rayleigh scattering of light is taken into consideration) at any point in the celestial hemisphere, the direction of polarization is always perpendicular to the plane of the triangle formed by the sun, the observer and the point observed. The pattern of polarization shifts around the celestial hemisphere as the sun moves across the sky. The three-dimensional celestial hemisphere can be represented in two dimensions by a polar-coordinate system, where the angular distances from the zenith and the solar meridian are measured radially and tangentially, respectively. In this two-dimensional coordinate system the zenith is at the origin and the horizon corresponds to the outermost circle. **Fig. 1** and **2** show the patterns of the degree and direction of polarization of skylight in clear Rayleigh atmosphere calculated for four zenith distances of the Sun.

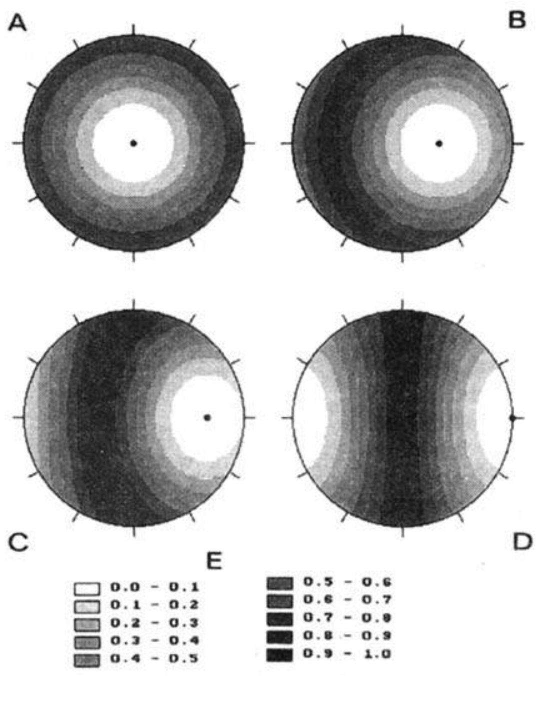


Fig. 1 The pattern of the degree of polarization of skylight as a function of the zenith distance q of the Sun. (A) q = 0° (Sun at the zenith), (B) q = 30°, (C) q = 60°, (D) q = 90° (Sun at the horizon). The Sun is represented by a dot. (E) Colour codes of different intervals of the degree of polarization ranging from 0 (white) to 1 (black) with a step of 0,1

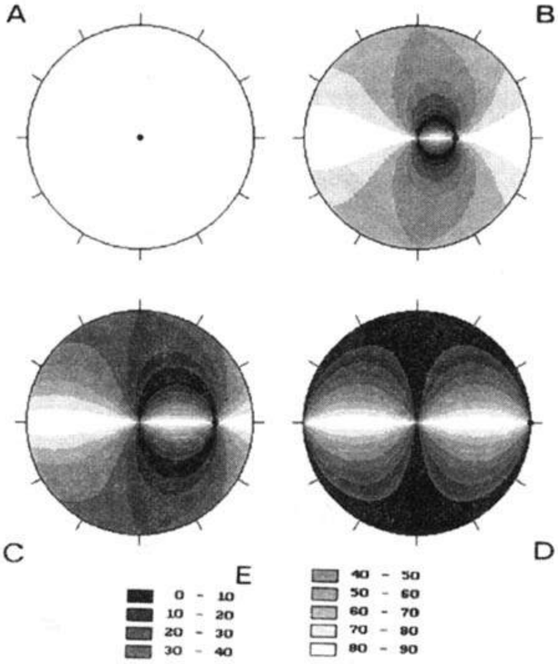
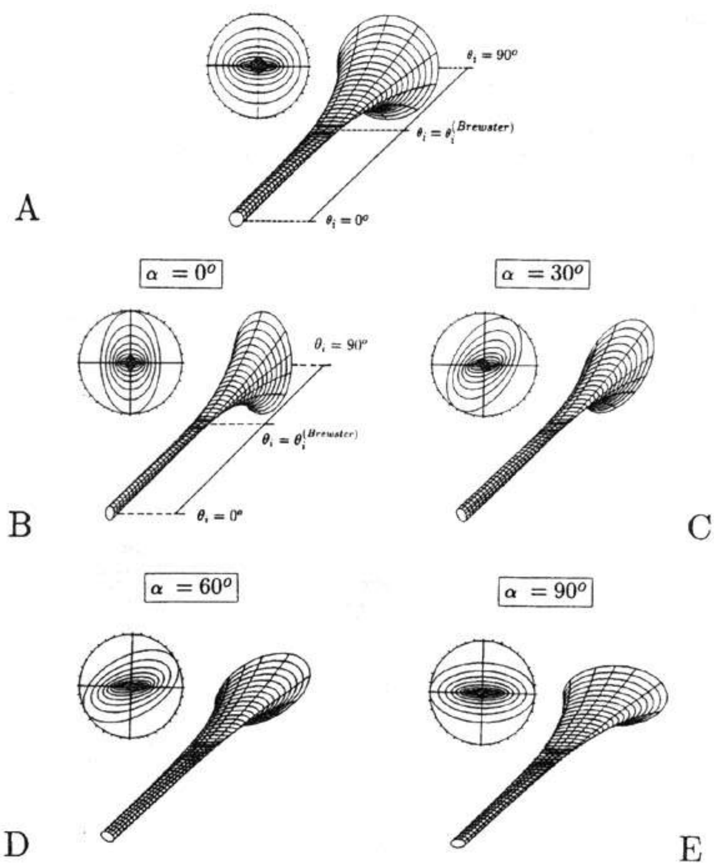


Fig. 2 As Fig. 1 for the direction of polarization (measured from the meridian of the point observed in the celestial hemisphere) of skylight. (E) Colour codes of different intervals of the direction of polarization ranging from 0° (black) to 90° (white) with a step of 10°. Since all the E-vectors of the celestial polarization pattern are horizontal when the Sun is at the zenith, pattern A is homogeneous white

Reflection Polarization of Light at the Water Surface

In nature the other main source of linearly polarized light is the light reflected by shiny surfaces as the water surface or moist substrates. The change of polarization of light due to reflection from the water surface is determined by the Fresnel's formulae. If the incident angle is equal to the Brewster angle (53° from the vertical for the air-water interface), then the reflected light is totally linearly polarized with horizontal E-vector, irrespective of the polarization characteristics of the incident light.



The direct sunlight and the skylight from the Arago, Babinet and Brewster neutral points are unpolarized (its polarization ellipse is circular). After reflection from the water surface, however, the neutral incident light becomes partially linearly polarized. The shape of the polarization ellipse of reflected light depends on the incident angle θi as shown in **Fig. 3A.** The dimension of the reflection-polarization ellipses increases steeply for incident angles larger than the Brewster angle. If the incident light is partially linearly polarized (as the skylight), the characteristics of the reflection-polarization ellipses versus the incident angle are shown in **Fig. 3B–E** for different directions of polarization α and for a given degree of polarization δ = 0.5. One can see that the direction of polarization of reflected light has a sign change at the Brewster angle. This results in that the obliqueness of the reflection-polarization ellipses is contrary for incident angles smaller or larger than the Brewster angle.

Fig. 3 Representation of the shape of the reflection-polarization ellipses as a function of the incident angle qi. (A) The incident light is unpolarized. (B–E) The incident light is partially linearly polarized with degree of polarization d = 0.5 and with different directions of polarization a measured from the vertical plane of incidence

Reflection-Polarization Patterns at Flat Water Surfaces

To represent the reflection polarization pattern of skylight visible at the flat water surface, we use a two-dimensional polar-coordinate system positioned parallel to the air-water interface. This system of coordinates is called the "mirror-system", because it is the mirror image of the corresponding two-dimensional polar-coordinate system of the celestial hemisphere. In the mirror-system the "mirror zenith" (nadir), "mirror sun", "mirror solar meridian" and "mirror anti-solar meridian" correspond to the zenith, sun, solar and anti-solar meridian of the celestial system, respectively. Using Fresnel's formulae, the reflection-polarization pattern of skylight at the flat water surface can be determined and represented by means of a computer. The computed reflection-polarization patterns of the degree and direction of polarization are shown in **Fig. 4A–D** and **5A–D** for four zenith distances of the sun. These patterns correspond to the celestial polarizations patterns in Fig. 1 and 2. **Fig. 4F** shows the reflection-polarization pattern of the degree of polarization calculated for unpolarized incident light from an overcast sky.

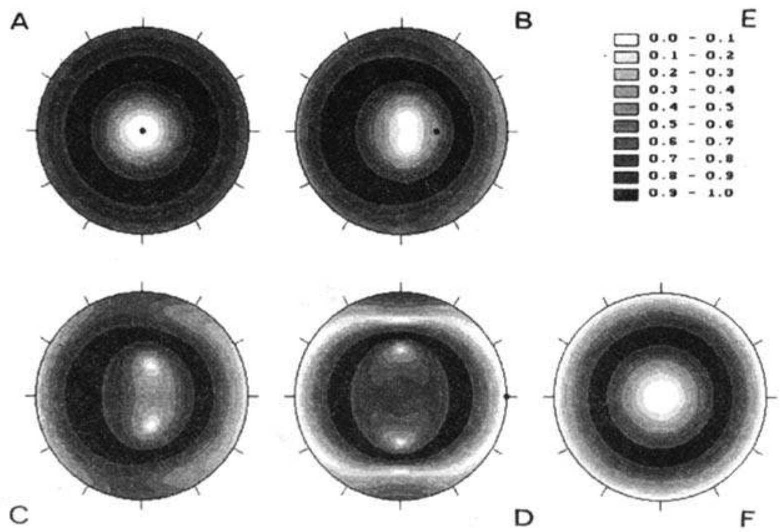


Fig. 4 As Fig. 1 for the degree of polarization of skylight reflected from the flat water surface. The "mirror sun" is represented by a dot. (F) As (A–D) for unpolarized light from an overcast sky

One can see in Fig. 4 and 5 that an annular Brewster zone occurs at the water surface where the degree of polarization approaches 100% and the reflected E-vector is mainly horizontal. The shape of this Brewster zone depends on the zenith distance of the sun. The area, from which mainly horizontal E-vectors are reflected, contracts gradually as the Sun approaches the horizon **(Fig. 5).** At sunset this area is extended towards and away from the sun, and perpendicularly to the solar meridian there are two patches, from which mainly vertically polarized light is reflected (Fig. 5D). The butterfly-like patches (with vertical polarization) in Fig. 5B–D correspond to the neutral points of the degree of polarization pattern of reflected light in Fig. 4B–D.

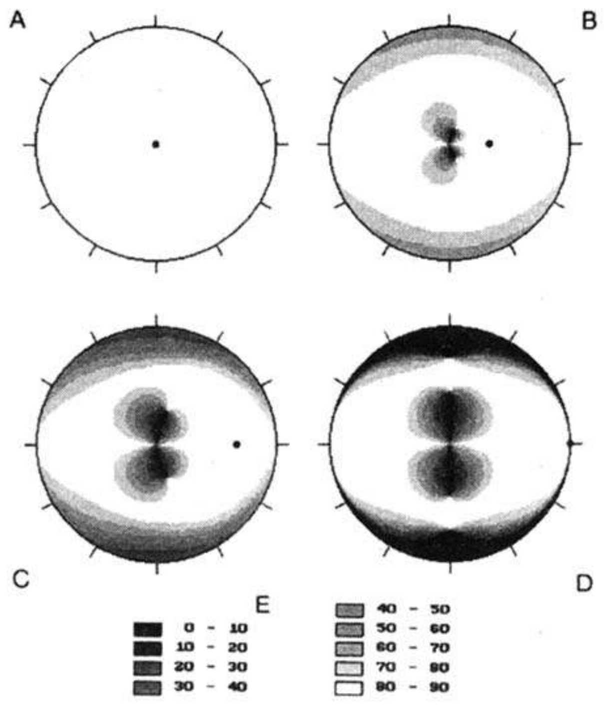


Fig. 5 As Fig. 2 for the direction of polarization of skylight reflected from the flat water surface. Since all the reflected E-vectors are horizontal when the sun is at the zenith, pattern A is homogeneous white

In nature, the reflection-polarization patterns calculated for the flat water surface (Fig. 4, 5) are influenced by the polarization of light coming from water and by the glittering of the water surface due to ripples. If the body of water is shallow, the light reflected and depolarized by the bottom and vertically repolarized by refraction at the water surface, changes the characteristics of the polarization pattern visible at water surfaces. Ripples reduce or even destroy the reflection-polarization calculated for the flat water surface. The light scattered and polarized by particles suspended in water contribute, too, to the polarization pattern at the water surface.

Polarization-Sensitive Photoreceptors

In 1923 F. Santschi discovered that ants could find their way even if they could see only a blue patch of the sky. In 1949 K. von Frisch observed a similar ability in honeybees. He demonstrated that bees are able to detect polarized skylight and use it as a compass cue. Since 1970 even vertebrates (e.g. reptiles, fishes and birds) have been claimed to deduce some kinds of navigational information from the patterns of polarized light in the sky.

The ability of some animals to detect polarized light is due to the specialization of their visual cells. In all animals the visual pigment rhodopsin is present in the photoreceptor membrane in the form of elongated molecules. The rhodopsin molecules absorb a maximum of the incoming light intensity when the direction of polarization is parallel to their dipole axis. This effect is called the dichroism. In insects the photoreceptor membranes are bent into arrays of narrow tubes, the microvilli as can be seen in **Fig. 6.** The rhodopsin molecules in the microvillar membrane are preferentially aligned parallel to the microvillar axis. This orientation results in the maximum absorption of polarized light when the direction of polarization coincides with the microvillar axis.

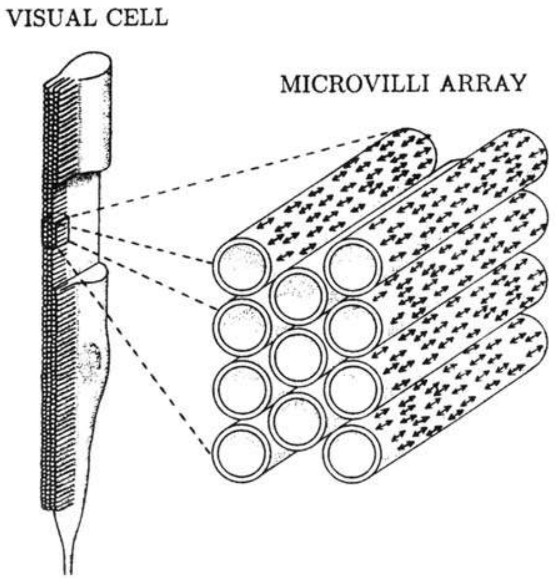


Fig. 6 Left: A photoreceptor cell of insects. Right: An enlarged part of the microvilli array in the insect photoreceptor. The axes of rhodopsin molecules (double-headed arrows) are preferentially parallel to the longitudinal axis of tubelike microvilli. This arrangement results in the dichroism in the visual cell

The common orientation of the rhodopsin molecules in the insect photoreceptor membrane is not in itself enough to allow the analysis of light polarization. Different kinds of receptors, each maximally sensitive to a different direction of polarization, must interact in order to determine unambiguously any direction of polarization. In the most simplest case two perpendicularly oriented microvilli systems are needed to detect polarized light. The temporal responses of these orthogonal analyzers to polarized light with rotating direction of polarization are phase shifted by 90°. If these two crossed systems interact with each other, the degree and direction of polarization of the incident light can be determined by a proper underlying neural network.

Polarization Vision in Honeybees and Desert Ants

The honeybee *Apis* and the desert ant *Cataglyphis* (native to North Africa) are two examples for insects that navigate by means of the polarization pattern of the sky. Both are social insects that routinely return to their colony after foraging trips. Since the investigations by K. von *Frisch* with honeybees it is well-known that they detect polarized skylight and use it as a compass cue. The polarization vision and E-vector navigation of the desert ant Cataglyphis was studied by R. *Wehner*. Cataglyphis is a running forager and a solitary hunter. It does not forage along a scout's scent trail as many other ant species. Its desert habitat is nearly lacking in conspicuous landmarks, so that it must rely almost exclusively on skylight cues to guide it on its forays. After Cataglyphis leaves its underground nest it meanders until it captures prey. Then, it runs straight back to its nest. Honeybees and desert ants possess a polarization and ultraviolet-sensitive retina region positioned at the uppermost dorsal margin of the eye. This region of the eye is called the "POL area", which is characterized by a number of functional specializations that maximize the polarization sensitivity. Other parts of the eye are insensivite to polarization because of the twist of the photoreceptors.

In order to determine directions honeybees and desert ants need a compass, whose fundamental reference direction is the orientation of the sun. If the Sun is not visible, because it is occluded by clouds or landmarks, bees and ants must rely on the celestial polarization pattern, which has a symmetry plane formed by the solar and anti-solar meridian (see Fig. 1, 2). They can solve the problem of inferring the azimuthal position of the sun from the polarization pattern of the sky. There is a simple trick, by which insects can distcriminate between the solar and the anti-solar meridian: Cataglyphis does so by referring to spectral information in the sky.

The insect E-vector navigation is made more difficult by some disturbing celestial and meteorological factors. On the one hand, owing to the daily westward movement of the sun across the sky, the symmetry plane, and with it the whole polarization pattern rotates about the celestial hemisphere (Fig. 1, 2). On the other hand, the sky is usually partly or totally clouded. Since the discovery of F. Santschi and the studies of K. von Frisch, we know that bees and ants effectively cope with these problems even if they can see only a blue patch of the sky.

Polarization Vision of Water Insects and Insects Living on Moist Substrates

Till the investigations by R. Schwind (at the Institute for Zoology of the University of Regensburg in the late 1980s and the early 1990s) little attention has been paid to the significance of polarized light reflected from shiny surfaces as a cue to orientation for animals sensitive to this source of polarization. Among the few investigations that have been done in this topic, one can mention the microvillar specializations in the ventral retina of dolichopodids, gerrids and dragonflies. The specializations in dolichopodids and gerrids were explained as polarizing filters for eliminating water surface glare, a hindrance in their prey capture; and those in dragonflies were taken to be horizon detectors for flight over water or rather water detectors. In 1984 R. Schwind discovered that flying backswimmers *Notonecta glauca,* detect bodies of water by the polarization of the reflected light. Polarized ultraviolet (UV) light with horizontal E-vector elicits a plunge reaction in Notonecta, whereas unpolarized UV light is ineffective even if its intensity is several times higher. The ability to discriminate polarized light with a horizontal E-vector from unpolarized light regardless of intensity is mediated by a two-channel orthogonal microvilli system. This is a set of two different UV-receptor types, one with horizontally and the other with vertically arranged microvilli. Polarized light reflected from water surfaces produces a difference in the outputs of the two types. This difference provides the basis for the intensity-independent discrimination of the polarization of light.

Are other water insects or insects living on moist subtrates detecting polarization of reflected light in a way similar to Notonecta, or are they simply responding phototactically to relatively intense reflected light? Could light, reflected from the bottom of waters and scattered by particles suspended in water, affect the polarization of reflected light in certain wavelength ranges? Do different ecological groups take advantage of these differences by adapting their polarization vision to their own special habitat? Do seasonal changes appear in the preference of some species for certain reflecting surfaces? To answer these questions, R. *Schwind* tested light polarized by reflection in the field for its attractiveness to flying insects. By comparing the attractiveness of different reflecting surfaces with defined reflection characteristics, he showed that polarized reflected light attracts a variety of insects to water or to a moist substrate. These insects include bugs and beetles living as adults in, on, or near water; beetles living in moist decaying plant debris or dung; and nematocerans, living as adults on land, but developing in water. Unpolarized light failed to attract any of these insects. There are numerous other observations of water insects being deceived by artificial shiny surfaces such as glass panes, car roofs or wet asphalt streets. These artifical surfaces have also a strong reflection polarization.

The observations by R. Schwind showed that glittering from water ripples is not necessary to attract water insects, and the intensity gradient is not decisive in recognizing water by aquatic insects. Polarization is the only factor to explain the attractiveness of light reflected from water surfaces. It might be that the specific gradients of polarization, as seen in the reflection-polarization patterns in Fig. 4 and 5, visible on flat water surfaces, are also needed for water detection and identification.

The reactions of insects to polarized light from shiny surfaces are variable. R. Schwind could distinguish three main response groups. The first group is attracted whenever the degree of polarization is high in the UV-range, irrespective of the degree of polarization in other wavelength ranges, and irrespective of colour or brightness of the background beneath the polarizing, reflecting surface. The polarization vision of these insects operates in the UV-range. This type is able to detect a puddle with a bright bottom as well as a dark pond, for in nature light is highly polarized in the UV-range in both. The second group is attracted only by the reflecting surface over dark background, where the reflected light is highly polarized at all wavelengths visible to insects. On the one hand, if the insect polarization vision operates for wavelengths larger than 500 nm, then the POL-system is advantageous to insects living in deeper turbid ponds where the intensity in UV is low. With this system they find only the appropriately dark pond attractive. On the other hand, if the POL-system operates in the short wavelength range and different receptors measure intensity at wavelengths larger than 500 nm, then too high intensity causes avoidance of water. The third group ranges between the above mentioned two different extreme types.

There are some visual differences between water insects and those living on moist substrates. The Hydrophilinae live in water and the Sphaeridiinae inhabit moist substrates, for example. The latter have to recognize shiny polarizing substrates on a bright background, therefore they must have a POL-system operating in the UV-range, but this need not necessarily be the case with the former. Some *Helophorus* species change their behaviour in the course of the year. Compared with early spring individuals after hibernation, the newly hatched *Helophorus griseus* generation in early summer prefers brighter surfaces. But by fall they change behaviour and prefer darker water bodies. The newly hatched individuals look for bright puddles in early summer for feeding and then for dark ponds in autumn, which are too deep to freeze down to the bottom. In spring they disperse and populate habitats suitable for breeding. The seasonal changes of their preference of different surfaces show that their visual system is involved in their choice of suitable aquatic habitats.

Aquatic insects and insects living on moist substrates are surely influenced in their choice of habitats by non-optical factors, too. Their optical system, however, narrows their choices before other factors become operative. Some insects may make use of cues other than polarized light to detect water bodies. Insects inhabiting running waters (e. g. plecopterans living near brooks) may not locate their habitats with help of polarization vision at all, because polarization is distorted by waves and ripples.

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