# 8 Which Part of the Spectrum is Optimal for Perception of Skylight Polarization?

In many insect species the perception of skylight polarization is mediated by a group of anatomically and physiologically specialized ommatidia in an upward-pointing narrow dorsal rim area (DRA) of the compound eye. The ommatidia in the DRA contain two sets of monochromatic and highly polarization-sensitive photoreceptors with orthogonal microvilli. The spectral type of the receptors in the DRA is ultraviolet (UV) in flies, honeybees, desert ants, scarab beetles and spiders, blue in crickets, desert locusts and cockroaches, while green in the beetles *Melolontha melolontha* and *Parastizopus armaticeps* (Table 8.1).

However, the perception of skylight polarization in the UV is rather surprising, because both the radiance $I$ and the degree of linear polarization $p$ of skylight in the UV are considerably lower than in the blue and green (Figs. 8.1 and 8.2), furthermore the atmospheric absorption of light is much higher in the UV than for longer wavelengths (e.g. Henderson 1970). We call this the "ultraviolet paradox of perception of skylight polarization", simply "UV-sky-pol paradox" further on. In the opinion of Wehner (1994a, p. 110), there is no particular region of the spectrum predestined to be used preferentially for detection of the E-vector of skylight under all possible sky conditions.

## 8.1 A Common Misbelief Concerning the Dependence of the Degree of Skylight Polarization on Wavelength

Some researchers are not aware of the UV-sky-pol paradox due to an erroneous belief considering the wavelength dependency of polarization of light from the clear sky. In the literature of animal polarization sensitivity a frequently occurring misbelief is that $p$ of scattered blue skylight is the highest in the UV. Several biologists tried to explain by this misinformation why certain animal species detect the skylight polarization in the UV. We mention here the following typical examples for this delusion:

1. Waldvogel (1990, p. 352): "In insects, the visual cells that are responsive to the **ultraviolet** - where **skylight polarization is most pronounced** - are also sensitive to polarization."
2. Beason and Semm (1991, p. 107): "Polarized light detection probably occurs in the **UV wavelengths**, because **the greatest degree of polarization occurs at those frequencies**."
3. Helbig (1991, p. 288): "Since **natural skylight is most strongly polarized in the UV**, much of the natural polarization is taken away by the cage covers with increasing absorption below 400 nm."
4. Tovée (1995, p. 456): "So shorter wavelengths, such as **UV light**, are scattered and **polarized more than longer wavelengths**."
5. Shashar et al. (1995b, p. 215): "A growing portion of the literature shows that vision in the **ultraviolet (UV) range** (300-400 nm) is closely related to sensitivity to **partially linearly polarized light** (PLPL) … Further, the characteristics of PLPL are expected to change according to the wavelength observed, and should be **especially strong in the short end of the spectrum**."

From the context it was always obvious that these researchers wrote about polarization of light from the clear sky rather than about light from clouds. However, polarization measurements (e.g. Coulson 1988, p. 285) have shown that under clear atmospheric conditions $p$ of scattered skylight decreases with decreasing wavelength $\lambda$ (Fig. 8.1A). The reason for this has already been explained in Chapter 7. Figure 8.1B shows the dispersion of $p_{max}(\lambda)$ of skylight for a turbid, dusty atmosphere. Dust considerably reduces $p_{max}$ in the long-wavelength (orange, red, infrared) range, while in the short-wavelength (blue, UV) range it has only a minor effect, $p$ in the UV being essentially the same as that for the clear atmosphere. Due to this reduction, $p_{max}$ in the UV is about as low as $p_{max}$ for $\lambda >$ 650 nm. However, for $\lambda <$ 650 nm, $p_{max}$ is the lowest in the UV.

## 8.2 Why do Many Insects Perceive Skylight Polarization in the UV?

Several hypotheses have been published which tried to solve the UV-sky-pol paradox. In this section we describe these hypotheses and give their criticism, finally we expound a convincing solution of the paradox. However, we should emphasize that several insect species perceive the skylight polarization in the blue or green (Table 8.1). Why do not use these insects UV-sensitive photoreceptors for detection of skylight polarization? Below some arguments are presented for the advantage of perception of celestial polarization in the blue and especially in the UV. However, also another important physical, biological or environmental factors may exist still, which determine the optimal wavelength range of detection of skylight polarization in a particular animal species.

Sometimes it is simply declared without any explanation, that the UV spectral range is the least or the best reliable for perception of skylight polarization. We mention only one example: "In *Cataglyphis*, polarized light patterns in the ultraviolet apparently provide the primary compass information …, ultraviolet wavelengths are the least reliable for performing these tasks, so why insects use only those wavelengths for polarized light orientation is puzzling in itself" (Able 1989, pp. 252-253). Similar declarations cannot help to solve the UV-sky-pol paradox.

### 8.2.1 Is the Celestial Polarization Pattern More Stable in the UV?

Zdenek Sekera claimed in his communication to Karl von Frisch (1967, p. 382) that UV wavelengths are the least sensitive to "atmospheric disturbances". Relying on this suggestion, Frisch (1967) postulated that UV polarization patterns of skylight might be more advantageous as cues for orientation not only because the UV 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. In other words, atmospheric disturbances may affect the E-vector direction of skylight, and such disturbances may have an increased effect on the longer wavelengths, and the least influence on UV skylight. Although in the 1960's neither the experimental nor the theoretical basis was available for this assumption and the evidence for this conjecture were very slim, this idea has become widely accepted in the literature, because any strategy that could extend the conditions under which successful orientation is possible would certainly constitute a major selective advantage.

The statement of Sekera (cf. Frisch, 1967, p. 382), that "the celestial polarization pattern might be the least sensitive to atmospheric disturbances in the UV spectral region", has been frequently cited in the literature. Here we refer only to three examples:

- Duelli and Wehner (1973, p. 50): "The **polarization pattern** looks about the same in different spectral regions. With **increasing wavelengths**, however, the pattern is getting more and **more susceptible to atmospheric disturbances**."
- Wehner (1976, p. 110): "It is **in the ultraviolet** range of wavelengths that the **polarization of skylight is least affected by atmospheric disturbances** and is therefore the most stable."
- Dacke et al. (2002, p. 215): "The high polarization sensitivity of the **UV receptors** in *Pachysoma striatum* further supports the use of this spectral class for the analysis of the sky compass. At these short wavelengths the **sky polarization pattern** is also the most stable under different weather conditions."

However, the major problem with such too general statements is, that these "atmospheric disturbances" have never been precisely defined. It remained unclear what do "susceptibility to atmospheric disturbances" or "stability of the celestial polarization pattern under different weather conditions" exactly mean.

### 8.2.2 Was the UV Component of Skylight Stronger in the Past?

It is a logical assumption that the sensitivity maximum of the monochromatic polarization-sensitive photoreceptors perceiving polarized skylight may be adapted to the wavelength where the radiance of skylight is maximal. Such spectral adaptations of certain receptors to the dominant radiation field of the optical environment are common in visual systems (e.g. Lythgoe 1979). Since in the present atmosphere of the earth the radiance of skylight is maximal in the blue (Fig. 8.2), the receptors detecting polarized skylight should be blue sensitive.

Brines and Gould (1982) suggested that a possible reason why UV wavelengths are used by skylight detectors in certain animals may be that in the era when polarization sensitivity has evolved in these animals, the UV component of skylight might have been stronger than it is today. The reasons could be that the atmosphere might have attenuated the UV flux of sunlight to a lesser degree than it does today, and/or the magnitude of UV radiation of the sun might have been greater during earlier epochs of evolution. Although the total energy emitted by the sun fluctuates by a tiny 0.1% over an 11-year solar cycle, and solar UV radiation changes three times as strongly during a cycle as total radiation (Pearce 1998), furthermore the composition of the earth's atmosphere has dramatically changed during the history of the biosphere, the major problem with this hypothesis is that from the past there are no reliable data about the temporal change of the UV radiation reaching the earth's surface. Thus this idea is hard to evaluate. If we accepted this hypothesis, the period, during which the UV component of skylight might have been stronger than nowadays, should have been in the near past on the time scale of evolution, else the sensitivity maximum of skylight detectors should have been adapted to the present situation, namely to the blue maximum of skylight radiation (Fig. 8.2).

Let us estimate, in which spectral range would function optimally a monochromatic crossed-analyzer in the DRA of insects. If the E-vector of partially linearly polarized incident light is parallel (par) or perpendicular (perp) to the microvilli, the amount $Q$ of skylight absorbed by a polarization-sensitive photoreceptor can be calculated as follows (Horváth et al. 2002c):

$$Q_{par} = c \int_0^\infty A(\lambda)\, I(\lambda)\, [PS+1+(PS-1)\, p(\lambda)]\, d\lambda,$$

$$Q_{perp} = c \int_0^\infty A(\lambda)\, I(\lambda)\, [PS+1-(PS-1)\, p(\lambda)]\, d\lambda, \quad (8.1)$$

where $c$ is a constant, $\lambda$ is the wavelength of light, $A(\lambda)$ is the absorption function of the receptor (Fig. 8.3A), $I(\lambda)$ and $p(\lambda)$ are the radiance (Fig. 8.2) and the degree of linear polarization (Fig. 8.1A) of scattered skylight, $PS$ is the polarization sensitivity describing the fact that if the E-vector of totally linearly polarized light is parallel to the microvilli, then a receptor absorbs $PS$-times more amount of light than in the case when the E-vector is perpendicular to the microvilli. The difference between $logQ_{par}$ and $logQ_{perp}$ is:

$$\Delta(\log Q) = \log Q_{par} - \log Q_{perp} = \log(Q_{par}/Q_{perp}). \quad (8.2)$$

The basis of E-vector contrast sensitivity of crossed-analyzers in the DRA is to compare $logQ_{par}$ and $logQ_{perp}$, that is, to evaluate the difference $\Delta(logQ)$. The greater this difference, the better is the functioning of the detection of skylight polarization. Thus, maximizing $\Delta(logQ)$ is optimal for receptors in the DRA. Using Eqns. (8.1) and (8.2), $\Delta[logQ(\lambda_{max})]$ was calculated as a function of $\lambda_{max}$ for the graphs $p(\lambda)$ and $I(\lambda)$ in Figs. 8.1A and 8.3A, where $\lambda_{max}$ is the wavelength where the receptor's absorption $A(\lambda)$ (Fig. 8.3A) is maximal. The result is shown by graph 1.0 in Fig. 8.3B for $PS$ = 7, which is a typical value for crickets, for example. One can see that this graph has a maximum at 458 nm. Hence, under the recent atmospheric radiation circumstances the most effective polarization-sensitive photoreceptor has an absorption maximum in the blue. In spite of this fact Hymenoptera and Diptera, for example, use for this purpose UV ($\lambda$ < 400 nm) receptors. Thus, the functioning of these receptors is not as effective as could be in this regard.

Following the hypothesis of Brines and Gould (1982), let us estimate the necessary magnitude of the "ancient level" of UV radiation of scattered skylight, which would ensure that the maximum of $\Delta[logQ(\lambda_{max})]$ of photoreceptors in the DRA is shifted to the UV part of the spectrum. $\Delta[logQ(\lambda_{max})]$ was calculated for the series of $I_n$, $n$ = 1.0, 1.5, 2.0, 2.5, 3.0 shown in Fig. 8.3A, where $I_{1.0}$ is the recent radiance of skylight, while $I_{1.5}$, $I_{2.0}$, $I_{2.5}$ and $I_{3.0}$ are imaginary radiance curves derived in such a way that the UV part ($\lambda$ < 400 nm) of $I_{1.0}(\lambda)$ was multiplied by factor $n$. The results are shown by graphs 1.5, 2.0, 2.5 and 3.0 in Fig. 8.3B (for $PS$ = 7), from which one can read that if the total radiance of UV skylight were about twice as high as today, the maximum of $\Delta[logQ(\lambda_{max})]$ would be shifted to the UV.

Hence, if the ancient UV level of skylight had been at least twice higher than the recent one, it would have been advantageous for the skylight detectors to function in the UV. However, the minuscule periodic variation of the solar flux could not account for a considerable (e.g. twice) increasing of the UV level of skylight in the past. Much greater variations in the UV radiation from the sun are improbable during the evolution in the case of a star like the sun. Thus, it is very unlikely that an earlier enhancement of the solar UV radiation could be the clue of the solution of the UV-sky-pol paradox.

What about the absorption of UV light in the earth's atmosphere? The attenuation of the UV flux of solar radiation in the atmosphere is governed predominantly by the concentration of ozone ($O_3$) in the stratospheric ozone layer, which is the greater, the higher the oxygen ($O_2$) level. The link between UV level and atmospheric oxygen concentration is that UV radiation converts oxygen into ozone. However, this cannot be the clue of the solution of the UV-sky-pol paradox, because the detection of skylight polarization in animals functions between 345-400 nm (Table 8.1), and in this range of the spectrum the absorption of ozone is practically zero. In the visible spectrum, the ozone has one absorption maximum at 600 nm, while in the UV range there are three maxima at 255, 314 and 344 nm (Rozenberg 1966). Due to absorption by the ozone layer, practically 300 nm is the effective wavelength cut-off for UV light incident on the earth's surface. Thus, the change of the oxygen and ozone concentration in the atmosphere does not influence the UV level of sunlight and skylight in that part of the spectrum, where the detection of skylight polarization by animals happens.

### 8.2.3 Relatively Large Proportion of UV Radiation in Skylight?

According to Hawryshyn (1992, p. 166), "Even though it is potentially harmful, the relatively large proportion of ultraviolet radiation in scattered light at least partially accounts for the use of these wavelengths for the detection of polarization."

However, Fig. 8.2 shows that the radiance of skylight is much lower in the UV than in the blue, where it is maximal. The maximal proportion of blue radiation in scattered skylight could account for the use of blue (rather than UV) wavelengths for the detection of skylight polarization.

### 8.2.4 Mistaking Skylight for Ground-Reflected Light?

Mazokhin-Porshnyakov (1969) suggested that by using UV wavelengths, animals would be fairly sure that they use polarized skylight for orientation rather than polarized light reflected from the ground, which is richer in long-wavelengths than skylight. In other words, using UV light might help to distinguish phototactically "sky" from "ground". This argumentation was taken over by Wehner in some of his review articles:

- Wehner (1982, p. 88, 89, 123): "The polarization sensitivity of many insect species functions in the UV, because the **light from the radiant sky is rich in UV but light reflected from the surface of the earth is not**. In other words, **the intensity contrast between sky and ground is maximal in the UV**, which is advantageous for **discrimination the sky from the ground**."
- Wehner (1983, pp. 360-361): "As **the scattered light from the radiant sky is rich in ultraviolet components, but reflected light from terrestrial objects is not**, it seems likely that ultraviolet receptors have evolved in the functional context of exploiting skylight cues for one or another type of navigational purpose."
- Wehner (1984, pp. 285-286): "Why do ultraviolet receptors play such a special role in skylight navigation? … As **scattered skylight is rich in ultraviolet, but reflected light from the ground is not** (with the remarkable exception of light reflected from water surfaces), any visual system whose spectral range extends into the ultraviolet is advantageous in **discriminating between sky and ground**, e.g. in detecting the sky when taking off the ground, or in any kind of course control in which skylight is involved."
- Wehner (1994a, p. 125): "... the widespread use of UV receptors for analysing e-vector patterns in the sky might well be an evolutionary heritage derived from

> some kind of skylight detecting mechanism. Note that the **light from the sky is the most ubiquitous source of UV radiation** in an insect's environment."

In reality, this idea originates from Frisch and Lindauer (1954), who as first discussed the concurrence of sky and earth in the orientation of honeybees.

Since skylight and ground-reflected light can reach the eye always from above and below, respectively, an appropriate regionalization of photoreceptors in the eye can simply eliminate the confusion of skylight with ground-reflected light (earthlight). The skylight analysers and earthlight detectors should be separately arranged in the eye in such a way, that only the former can see the sky, while the latter can view only towards the ground. Then, both the skylight and earthlight detectors can function in the same, e.g. visible range of the spectrum, and using the UV wavelengths for skylight detection is unnecessary. Hence, the anatomical separation of the adequate photoreceptors can simply solve the problem of distinguishing "sky" from "ground", independently of receptor wavelength sensitivity. Indeed, this is the usual case in insects: It is only the DRA of insect compound eyes, which is sensitive to skylight polarization, and this area is oriented towards the sky, so that the ambiguities envisaged by Mazokhin-Porshnyakov (1969) and Wehner (1982, 1983, 1984, 1994a) do not arise. Thereby, confusion of sky with ground would not occur, because they are viewed by different eye regions.

### 8.2.5 Confusion of Motion and Form for Celestial Polarization?

In the opinion of Wehner (1976), UV wavelengths may be used for orientation by means of skylight polarization so that polarization can be analysed separately from motion and form, the detection of which is mediated by receptors sensitive for longer wavelengths. However, an appropriate division of labour between receptors in the eye as well as an appropriate eye regionalization can eliminate the confusion of information from motion and form with polarization information from the sky. If there are separate skylight polarization detectors as well as motion/form detectors in separate eye regions, both detector types can function in the same spectral range, and using other (e.g. UV) wavelengths for skylight detection is not necessary. Indeed, the detection of motion and form is mediated by receptors being distinct from receptors in the polarization-sensitive DRA, so that the confusion envisaged by Wehner (1976) does not arise.

On the other hand, longer wavelengths can "mask" the effects of polarized UV light for bees if the source is small (Brines and Gould 1979). In this effect colour-opponent neurons can play an important role (Kien and Menzel 1977). Kirschfeld (1973a) has observed similar "masking" of the effect of polarized UV light by long wavelengths in optomotor experiments, and Edrich et al. (1979) as well as van der Glas (1977) have also shown that longer wavelengths can influence orientation. These results demonstrate that UV receptors are not always involved alone in orientation and in the detection of skylight polarization.

### 8.2.6 Have been UV Receptors Originally Skylight Detectors and Involved Only Later Into the E-vector Detecting System?

According to Wehner (1989b, p. 80), "It is also very likely indeed that ultraviolet receptors evolved originally as a means of detecting skylight rather than for extending the spectral range of the insect's colour vision system." Wehner (1982, 1994a) hypothesized that UV receptors might have been incorporated into the E-vector detecting system only later. Bees, for example, take an UV but unpolarized beam of light for the sky, particularly for a point lying within the antisolar half of the celestial hemisphere. 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 exhibited by many insect species have their sensitivity maxima in the UV (Wehner 1981).

The major problem with this hypothesis is that it does not explain why the photoreceptors used originally as simple "photometric" skylight detectors should have been sensitive to UV instead of blue or green, for instance. The radiance of skylight in the UV is much smaller than in the blue and green (Fig. 8.2), which feature should be rather disadvantageous to a photometric skylight detector.

### 8.2.7 Maximizing "Signal-to-Noise Ratios" by UV Photopigments Under Low Degrees of Skylight Polarization?

In a theoretical approach, Seliger et al. (1994) surmised that rhodopsin absorption spectra with peaks in the blue (450 nm) maximize detection efficiencies under conditions of high $p$ of skylight. On the other hand, rhodopsin absorption spectra peaking in the UV (350 nm) may maximize "signal-to-noise ratios" for the detection of polarized skylight at the other extreme of low $p$. Photopigments that are most efficient under conditions of high $p$ (under clear skies) would have their maximum sensitivity at 450 nm, whereas UV (350 nm) photopigments would maximize the signal-to-noise ratio under low $p$ (under cloudy skies), where the biologically significant "signal" is the net plane-polarized single-scattered Rayleigh skylight, while the "noise" is the unpolarized, multiply-scattered skylight.

However, we shall see in Chapter 8.2.10 that the degree of linear polarization $p_{sky}(\lambda)$ of skylight given by Eqns. (8.3) and (8.4) should be maximized, rather than the "signal-to-noise ratio" as suggested by Seliger et al. (1994), in order to solve the UV-sky-pol paradox.

### 8.2.8 In the Spectral and Intensity Domain the Celestial Band of Maximum Polarization is Less Pronounced in the UV than in the Blue

– In the opinion of Wehner (1984, p. 286), "Why do ultraviolet receptors play such a special role in skylight navigation? … It might also be advantageous in exploiting spectral gradients across the sky."
– According to Wehner and Rossel (1985, p. 20), "… within the bee's visual system information about skylight polarization is mediated exclusively by the ultraviolet receptors. Recall that those parts of the (anti-solar) sky that exhibit the most saturated ultraviolet tinge are also the ones that exhibit maximum polarization. Apparently, this important physical property of skylight patterns has been incorporated into the bee's visual system."
– Wehner (1989b, p. 80): "In the ant's POL area there are three times as many ultraviolet receptors per ommatidium as in the remainder of the eye, and the ultraviolet receptors of the POL area exhibit the highest polarization sensitivities of all photoreceptors of bees and ants. In terms of their adaptive significance, these functional properties of the system make a lot of sense. With increasing angular distance from the sun, skylight is increasingly dominated by short-wavelength radiation, and the parts of the sky that exhibit the highest degree of polarization also exhibit the most saturated ultraviolet tinge."

However, the same is true for the blue wavelengths of skylight (e.g. Hess 1939; Nagel et al. 1978; Coulson 1988): Those parts of the sky that exhibit the most saturated blue tinge are also the ones that exhibit maximum $p$. What is more important, the intensity gradients of skylight are much higher in the blue than in the UV, therefore in the UV the sky is more homogeneous than in the blue (Coemans et al. 1994b). Thus, the cited argument is not sound and is unable to explain why just the UV-sensitive photoreceptors are used for detection of skylight polarization. The UV sensitivity of the polarization-sensitive photoreceptors in the DRA would be rather disadvantageous in detecting the celestial UV intensity gradients. Using the blue part of the spectrum would be more advantageous due to the fact that in the blue the sky is more heterogeneous than in the UV. Consequently, the celestial band of maximum $p$ (at $90^o$ from the sun) is more pronounced in the blue than in the UV. In the UV this band merges into the homogeneous UV surrounding.

### 8.2.9 The Proportion of Celestial Polarization Pattern Useful for Animal Orientation is Higher in the Blue than in the Green or Red

Pomozi et al. (2001b) proved experimentally that the proportion $q$ of the celestial polarization pattern available for use in animal navigation measured in the red, green and blue spectral ranges are greater than about 80% for clear skies. Thus, under clear sky conditions there is no selective advantage for the shorter wavelengths, because the extent of the polarized clear sky usable for orientation is great enough in all parts of the visible spectrum (see Chapter 7.6). More serious is the consequence of the wavelength-dependency of $q$ if the sky is cloudy, because under such frequently occurring meteorological conditions $q$ often can be considerably reduced. Pomozi et al. (2001b) have also proven that in the visible spectrum and under partly cloudy skies, the shorter the wavelength, the greater the proportion $q$. This phenomenon may have a selective advantage for shorter wavelengths. Hence, the extension of the E-vector pattern of clear sky into celestial areas covered by clouds is more useful for an E-vector compass when the skylight is perceived in the blue rather than in the green or red.

The above features of cloudy and clear skies are demonstrated in Figs. 8.4 and 8.5, where the patterns of the angle of polarization of a partly cloudy sky and a corresponding clear sky measured by full-sky imaging polarimetry in the red, green and blue are shown. We see in these figures that the E-vector pattern of the cloudy sky is most similar to that of the corresponding clear sky in the blue. This conclusion is based on many similar full-sky imaging polarimetric measurements. Figures 8.4 and 8.5 demonstrate quantitatively what Karl von Frisch and Zdenek Sekera could have only suspected (see Chapter 8.2.1): The celestial E-vector pattern at shorter wavelengths is most stable and less disrupted under cloudy conditions. In other words, the shorter the wavelength, the weaker the disturbing effect of clouds on the E-vector distribution of skylight, at least in the visible part of the spectrum.

### 8.2.10 Perception of Skylight in the UV Maximizes the Extent of the Celestial Polarization Pattern Useful for Compass Orientation Under Cloudy Skies

According to Brines and Gould (1982), under partly cloudy meteorological conditions, or under extensive vegetation[1] UV wavelengths may have advantages over longer ones in animal polarization orientation, because both spuriously polarized and unpolarized light resulting from reflections from the clouds or the vegetation may cause more troublesome interference at longer wavelengths. They proposed that the UV sensitivity of the E-vector detection in many animals may be at least partly an adaptation for perceiving celestial polarization patterns under conditions when useful scattering can occur only relatively close to an animal. They argued that under clear sky conditions there may be no selective advantage for a visual system that detects skylight polarization at wavelengths where $p$ is high. They suggested that the necessary selection pressure to use UV-sensitive skylight polarization detectors has been provided by light scattering beneath the clouds, because these scattering events produce E-vector patterns with nearly the same E-vector orientation seen in a clear sky, and result in higher $p$ in the UV.

[1] Bees must often fly with most of their view of the sky obscured by vegetation. This is a constant problem for the tropical honeybees (the ancestors of all bees) living and dancing on exposed limbs in the dense tropical forests (Wilson 1971, p. 266). Brines and Gould (1982) hypothesized that under many circumstances, typical and biologically significant E-vector patterns may exist against overhead vegetation at UV wavelengths.

Barta and Horváth (2003) formed this idea into a quantitative model, which gave a satisfactory solution of the UV-sky-pol paradox. They have proven that the perception of skylight in the UV maximizes the proportion $q(\lambda)$ of the celestial polarization pattern useful for polarization compass, as suggested by Brines and Gould (1982), who, however, were not able to determine $q(\lambda)$ quantitatively in the full sky. With full-sky imaging polarimetry Pomozi et al. (2001b) could measure celestial polarization patterns and calculate $q(\lambda)$ only in the visible part of the spectrum, because UV light was not transmitted by their fisheye lens. Until full-sky polarization measurements are not available in the UV, model calculations can provide the relation between $q(UV)$ and $q(blue)$ for cloudy skies.

Let us consider the model of Barta and Horváth (2003). Since under partly cloudy conditions the E-vector pattern of cloudy celestial regions is approximately the same as that of the corresponding clear sky regions as shown experimentally by Brines and Gould (1982) as well as Pomozi et al. (2001b), $q(\lambda)$ is essentially determined only by the degree of linear polarization $p_{sky}(\lambda)$ of skylight. If $p_{sky}(\lambda)$ at a particular direction in the sky is higher than the threshold of polarization sensitivity, the skylight from this direction can be used for polarization compass. The higher the $p_{sky}(\lambda)$ in the whole sky, the larger is $q(\lambda)$. The skylight originating from a cloudy celestial region and reaching a ground-based observer is composed of (i) the cloudlight with a wavelength-dependent radiance $I_{cl}(\lambda)$ and degree of linear polarization $p_{cl}(\lambda)$, and (ii) the scattered light with $I_{sc}(\lambda)$ and $p_{sc}(\lambda)$ from the air layer between the clouds and the ground (Fig. 8.6). Since the E-vector direction of both components are approximately the same, the net degree of linear polarization $p_{sky}(\lambda)$ of skylight is the net polarized radiance $a_{cl}(\lambda,h)p_{cl}(\lambda)I_{cl}(\lambda) + a_{sc}(\lambda,h)p_{sc}(\lambda)I_{sc}(\lambda)$ divided by the total radiance $a_{cl}(\lambda,h)I_{cl}(\lambda) + a_{sc}(\lambda,h)I_{sc}(\lambda)$:

$$p_{sky}(\lambda) = [a_{cl}(\lambda,h)p_{cl}(\lambda)I_{cl}(\lambda)+a_{sc}(\lambda,h)\, p_{sc}(\lambda)I_{sc}(\lambda)]/[a_{cl}(\lambda,h)I_{cl}(\lambda)+a_{sc}(\lambda,h)I_{sc}(\lambda)], \qquad (8.3)$$

where $a_{cl}(\lambda,h)$ and $a_{sc}(\lambda,h)$ are factors describing the wavelength-dependent effect of the thickness $h$ of the air layer underneath the clouds. Due to the absorption of cloudlight in the atmosphere, the larger the $h$, the lower is the relative contribution $a_{cl}(\lambda,h)$ of the radiance $I_{cl}(\lambda)$ of cloudlight reaching the observer. On the other hand, increasing the thickness $h$ of the air layer between a cloud and the observer, the number of scattering events increases resulting in the increase of the relative contribution $a_{sc}(\lambda,h)$ of the radiance $I_{sc}(\lambda)$ of light scattered in the air beneath clouds. Since at all wavelengths the degree of polarization $p_{cl}(\lambda)$ of cloudlight is practically zero due to the diffuse scattering of light by the cloud particles (Können 1985; Coulson 1988), the following approximation can be made:

$$p_{sky}(\lambda, a) \approx a_{sc}(\lambda,h)p_{sc}(\lambda)I_{sc}(\lambda)/[a_{cl}(\lambda,h)I_{cl}(\lambda) + a_{sc}(\lambda,h)I_{sc}(\lambda)] =$$

$$= ap_{sc}(\lambda)I_{sc}(\lambda)/[I_{cl}(\lambda) + aI_{sc}(\lambda)], \quad \text{where} \quad a = a_{sc}(\lambda,h)/a_{cl}(\lambda,h), \quad 0 \le a \le \infty. \qquad (8.4)$$

Since measurements of $a = a_{sc}(\lambda,h)/a_{cl}(\lambda,h)$ are not available yet, as a first approximation we assume that the quotient $a(h)$ is independent of $\lambda$. Although the dependence of $a(h)$ on $h$ is also unknown, it is clear that $a$ increases with increasing $h$:

– If a cloud would be in the immediate vicinity of the observer, then the contribution of light scattered in air beneath the cloud would be zero, thus $a(h=0) = 0$.
– When a cloud would be at a huge distance from the observer, then the contribution of cloudlight could be neglected in comparison with that of light scattered in the air between the observer and the cloud. This means that $a(h=\infty) = \infty$, and if $a \rightarrow \infty$ then $p_{sky} \rightarrow p_{sc}(\lambda)$.

Figures 8.1A and 8.2 show the measured functions $p_{sc}(\lambda)$ and $I_{sc}(\lambda)$ of scattered skylight at 90° from the sun. Figure 8.2 shows also the function $I_{cl}(\lambda)$ of cloudlight measured by Coemans et al. (1994b) under a thick cloud deck, when the total intensity $aI_{sc}(\lambda)+I_{cl}(\lambda)$ of skylight is practically the same as the intensity $I_{cl}(\lambda)$ of cloudlight (because $a \approx 0$). Using these particular functions without any loss of generality, Fig. 8.7A shows $p_{sky}(\lambda)$ calculated on the basis of Eqn. (8.4) for different values of the control parameter $a$. We can see in Fig. 8.7 that

- if $a < 2.5$ (when the cloudlight dominates, that is, the air layer between the clouds and the observer is thinner than a threshold), $p_{sky}(\lambda,a)$ is maximal in the UV;
- if $a > 2.5$, the maximum of $p_{sky}(\lambda,a)$ is in the visible part of the spectrum;
- if $a > 10$, $p_{sky}(\lambda,a)$ approximates $p_{sc}(\lambda)$ of the clear sky (Fig. 8.1A).

The reason for this is the following: Although the polarized radiance $ap_{sc}I_{sc}$ of skylight is more intense in the blue (B) than in the ultraviolet (UV) because $p_{sc}(B) > p_{sc}(UV)$ and $I_{sc}(B) > I_{sc}(UV)$, in the UV the radiance $I_{cl}(UV)$ of cloudlight is much smaller than the radiance $aI_{sc}(UV)$ of light scattered in the air beneath clouds. In other words, changing the wavelength $\lambda$ from blue to UV, the denominator of the expression of $p_{sky}(\lambda,a)$ given in Eqn. (8.4) decreases more drastically than the nominator, resulting in that $p_{sky}(UV,a)$ becomes higher than $p_{sky}(B,a)$. Figure 8.7B shows the wavelength $\lambda_{max}$ where $p_{sky}(\lambda,a)$ is maximal as a function of the control parameter $a$. $\lambda_{max}$ is optimal for orientation by means of skylight polarization.

The measurements of Brines and Gould (1982) support that the above theoretical prediction is correct. They measured $p_{sky}$ against several isolated cumulus clouds at 350, 500, 600 nm and obtained that $p_{sky}$ was the highest in the UV (Table 8.2).

## 8.3 Resolution of the UV-Sky-Pol Paradox

The essence of the resolution of the UV-sky-pol paradox proposed by Brines and Gould (1982), Pomozi et al. (2001b) as well as Barta and Horváth (2003) is the following:

1. There is no favoured wavelength for perception of skylight polarization under clear skies, because the proportion of the celestial polarization pattern useful for orientation is large enough at all wavelengths in the UV and visible parts of the spectrum.
2. Under partly cloudy skies, the E-vector patterns characteristic to clear skies approximately continue beneath the clouds, especially for blue and UV wavelengths.
3. If the clouds are near enough to the ground-based observer and the air columns under clouds are partly sunlit, the degree of linear polarization of skylight originating from the cloudy regions is the highest in the UV, because the nearly unpolarized UV-deficient cloudlight dilutes the least the polarized light scattered in the air beneath the clouds. Thus, detection of skylight polarization in the UV maximizes the extent of the celestial polarization pattern useful for polarization compass under cloudy skies.

## 8.4 E-Vector Detection in the UV also Maximizes the Proportion of the Celestial Polarization Pattern Useful for Orientation Under Canopies

Let us consider the influence of the weighting of unpolarized green light transmitted through a foliage and linearly polarized blue light scattered in the air beneath the foliage on the degree of linear polarization $p_{ca}(\lambda)$ of downwelling light under a canopy, if the air beneath the foliage is illuminated partly by direct sunlight, as usually in forests, for example. This is important for those insects with polarization-sensitive DRA that live under canopies and orient by means of the E-vector pattern of downwelling light. Under canopies, the same calculation can be performed as under clouds, but in the former case the intensity $I_{cl}(\lambda)$ of white cloudlight should be replaced by the intensity $I_{ca}(\lambda)$ of green light transmitted by the canopy, called "canopylight" further on:

$$p_{ca}(\lambda, a) \approx a p_{sc}(\lambda) I_{sc}(\lambda) / [a I_{sc}(\lambda) + I_{ca}(\lambda)]. \quad (8.5)$$

Figure 8.2 shows the intensity $I_{ca}(\lambda)$ of canopylight transmitted through the leaves of cottonwood (*Populus deltoides*). Similarly to the cloudlight, the canopylight is most deficient in the UV and is practically unpolarized due to the diffuse scattering in the leaf tissue (e.g. Gates 1980). Consequently, the same phenomenon occurs as under clouds, as shown in Fig. 8.8: the degree of linear polarization $p_{ca}(\lambda,a)$ of light from the canopy (composed of the partially linearly polarized bluish light scattered in the air layer beneath the canopy and the UV-deficient unpolarized greenish canopylight) is maximal in the UV if $a < 0.10$. Hence, detection of polarization of downwelling light in the UV also maximizes the extent of the celestial polarization pattern useful for polarization compass under canopies.

In this chapter we showed how the weighting (described by the control parameter $a$) of unpolarized white cloudlight or unpolarized green canopylight and linearly polarized blue light scattered in the air beneath clouds or canopies affects the degree of linear polarization $p(\lambda,a)$ of downwelling light under clouds or canopies, respectively. The only important difference between the effects of clouds and canopies is that clouds can also be at huge (practically infinite) distances from the ground-based observer (meaning great $a$-values), while the distance of canopies from the ground can range between 0 m and only about some 10 m (meaning small $a$-values). Thus, under canopies, $p_{ca}(\lambda,a)$ is maximal always in the UV. However, the question is whether the maximum of $p_{ca}(\lambda,a)$ is higher than the threshold $p^*$ for polarization sensitivity (about 5% for crickets and 10% for honeybees). In other words, the question is if the polarized light scattered in the thin air layer beneath the canopy can be enough intense (relative to the unpolarized canopylight) to ensure that $p_{ca}(\lambda,a) > p^*$. The experimental spectro-polarimetric study of this question could be an interesting task of future work.

## 8.5 Analogy Between Perception of Skylight Polarization and Polarotactic Water Detection Considering the Optimal Spectral Range

The spectral aspects of the detection of polarization of light reflected from water surfaces are discussed in Chapters 16-20. Here we mention only that the majority of the known polarotactic water-seeking insect species exploit UV wavelengths to seek for water (Table 8.3), because the amount of light originating from the underwater region is minimal in the UV, thus $p$ of light reflected from the water surface is maximal in the UV. However, also some known polarotactic water insect species detect water in the visible part of the spectrum (Table 8.3).

Note that considering the optimal wavelength range, there is an analogy between perception of skylight polarization for orientation and detection of the polarization of light reflected from water surfaces to find water bodies. Both tasks are most efficient in the UV, the reason for which is the same (Figs. 8.6 and 12.1): $p$ of both skylight and water-reflected light is highest in the UV if there is a background – a cloud or canopy in the sky and the bottom or particles suspended in water –, which reflects nearly unpolarized light. The amount of light originating from this background is minimal in the UV, thus the net $p$ of the biologically relevant light (downwelling skylight and water-reflected light) is highest in the UV.

## 8.6 Analogy of the UV-Sky-Pol Paradox in the Polarization Sensitivity of Aquatic Animals

Interestingly, UV sensitivity is frequently coupled with sensitivity to linear polarization also in aquatic animals. Several fish species (e.g. Hawryshyn 1992) as well as mantis shrimps (Marshall et al. 1991a,b) use their UV photoreceptors to perceive underwater polarization. However, the role of UV polarization sensitivity in the underwater world by these animals is as yet unknown.

What is the unique property of the UV part of the spectrum that has such importance to underwater polarization sensitivity? The common answer to this question sounds: "The underwater UV light field undergoes fewer changes during the day, and was more stable on an evolutionary scale, than other regions of the visible range. This stability is important when polarization sensitivity is used for navigation" (Shashar 1995, p. 203). This recalls the similarly frequently cited opinion that the skylight polarization should be more stable against atmospheric disturbances mentioned in Chapter 8.2.1. Unless these "changes", "stabilities" and "disturbances" are not exactly defined and their existence and importance experimentally are not proven, one can do nothing with such hypotheses.

Note, however, that crustaceans generally perceive polarization between 440 and 580 nm (e.g. Goldsmith 1972; Schwind 1999), and the polarization-sensitive photoreceptors of cephalopods are maximally sensitive near 500 nm. According to Cronin and Shashar (2001), this may be explained by the fact that $p$ of underwater light increases with increasing wavelength, at least above 450 nm (Ivanoff and Waterman 1958b). The question is whether this trend does also continue below 450 nm.

## 8.7 Why do Crickets Perceive Skylight Polarization in the Blue?

We can see in Fig. 8.7A that $p_{sky}(\lambda,a)$ is always relatively high in the violet and blue (400 nm < $\lambda$ < 470 nm) for a given $a$-value. Thus, under partly cloudy conditions the violet-blue wavelength region is the second optimal spectral range to detect skylight polarization for orientation. Crickets perceive the celestial polarization in the blue, the reason for which is still unknown. Using the blue part of the spectrum may have the following advantage against the UV range under clear skies, when the degree of skylight polarization is high enough for all wavelengths: The intensity of the UV component of sunlight and light from the clear sky is low relative to that of the blue and green components (Fig. 8.2). At twilight under clear skies, the absolute light intensity is more likely to fall below the sensitivity threshold of a polarization-sensitive visual system operating in the UV than in the blue.

In the context of the detection of skylight polarization, the finding that the photoreceptors in the DRA of the twilight-active field cricket *Gryllus campestris* operate in the blue rather than in the UV, has been interpreted in this way by Labhart et al. (1984) as well as Herzmann and Labhart (1989). Crickets (*Acheta domestica*, *Gryllus bimaculatus* and *Gryllus campestris*) are active not only during the day but also during crepuscular periods (dusk and dawn) as well as at night and all have highly polarization-sensitive blue receptors in their DRA specialized to perceive skylight polarization for orientation. According to Zufall et al. (1989), the combination of blue sensitivity and polarization sensitivity in the DRA may be a common adaptation of insects that are active at very low light intensities, as opposed to day-active insects (e.g. honeybees, desert ants and flies) which predominantly use UV receptors as detectors for skylight polarization (Table 8.1).

However, the question is whether this "intensity argument" holds also for cloudy conditions: On the one hand, since under cloudy skies the UV component of skylight is much weaker than under clear skies (Fig. 8.2), detection of skylight may be more disadvantageous in the UV than in the blue. On the other hand, under cloudy skies the degree of linear polarization $p_{sky}$ of skylight is the highest in the UV (Fig. 8.7), thus perception of skylight polarization could be more advantageous in the UV than in the blue. The question is, which effect is the stronger.

## 8.8 Concluding Remark

The question why insects differ in their spectral channel used for polarization detection cannot be answered at the present time, because too little data are available. One would have to correlate the spectral channels of a large number of insect species with their biology and ecology (e.g. under what sky conditions are they normally active) to obtain an answer. Theory alone will not clarify the situation. Clearly, honeybees, for instance, have an advantage in that they can exploit the weak UV (but stronger than blue) polarization under clouds, whereas under clear skies the polarization is normally strong enough at all wavelengths. But why do other insects not take advantage of this? The explanation of this remains an interesting future task.

# Tables

**Table 8.1.** Wavelengths $\lambda_{max}^{POL}$ at which the sensitivity of photoreceptors detecting skylight polarization is maximal in insects and spiders.

| species | $\lambda_{max}^{POL}$ (nm) | reference |
|---|---|---|
| *Calliphora erythrocephala*, *Musca domestica* (flies) | 330-350 | Smola & Meffert (1978), Hardie et al. (1979), Hardie (1984), Philipsborn & Labhart (1990) |
| *Apis mellifera* (honeybee) | 345-350 | Helversen & Edrich (1974), Labhart (1980) |
| *Cataglyphis bicolor* (desert ant) | 380-410 | Duelli & Wehner (1973) |
| *Cataglyphis setipes* (desert ant) | 380-400 | Frantsevich et al. (1977) |
| *Lethrus apterus*, *Lethrus inermis* (scarab beetles) | 350 | Frantsevich et al. (1977) |
| *Pachysoma striatum* (desert dung beetle) | 350 | Dacke et al. (2002) |
| *Drassodes cupreus* (spider) | 350 | Dacke et al. (1999) |
| *Gryllus campestris* (field cricket) | 433-435 | Labhart et al. (1984), Brunner & Labhart, 1987), Herzmann & Labhart (1989) |
| *Schistocerca gregaria* (desert locust) | 450 | Eggers & Gewecke (1993) |
| *Leucophaea maderae* (Madeira cockroach) | < 471 | Loesel & Homberg (2001) |
| *Melolontha melolontha* (cockchafer) | ~520 | Labhart et al. (1992) |
| *Parastizopus armaticeps* (beetle) | ~540 | Bisch (1999) |

**Table 8.2.** Average degree of linear polarization $p_{sky}$ of skylight measured by Brines and Gould (1982) at three wavelengths $\lambda$ against 20 different small cumulus clouds under hazy and clear atmospheric conditions. (After Table 2 of Brines and Gould 1982, p. 88).

| $p_{sky}$ (%) | $\lambda$ (nm) | sky condition |
|---|---|---|
| 10 | 350 | hazy |
| 7 | 500 | hazy |
| 6 | 600 | hazy |
| 37 | 350 | clear |
| 23 | 500 | clear |
| 17 | 600 | clear |

**Table 8.3.** Polarotactic insects detecting water or moist substrata by means of the horizontal polarization of reflected light studied by multiple-choice field experiments (Schwind 1991, 1995). The known spectral ranges in which the polarization of reflected light is perceived are given in brackets (after Table 1 of Schwind 1995, p. 446).

| |
|---|
| HETEROPTERA<br>**Corixidae**: *Sigara nigrolineata* (360 nm), *Sigara lateralis* (360 nm)<br>**Pleidae**: *Plea leachi*<br>**Saldidae**: *Saldula saltatoria* |
| EPHEMERIDAE: *Cloeon* sp. (450-480 nm) |
| COLEOPTERA<br>**Dytiscidae**: *Agabus bipustulatus* (480-520 nm), *Bidessus nasutus, Guignotus pusillus* (360 nm), *Hydroporus* sp. (390-420 nm), *Laccophilus minutus* (430-450 nm), *Potamonectes* sp., *Rhantus pulverosus* (500 nm), *Scarodytes halensis*<br>**Haliplidae**: *Neohaliplus lineato* (530-550 nm), *Haliplinus lineolatus* (530-550 nm), *Peltodytes caesus*<br>**Hydrophilidae**: *Anacaena limbata* (390-420 nm), *Enochrus quadripuctatus, Helophorus aquaticus* (< 360 nm), *Helophorus brevipalpis* (< 360 nm), *Helophorus flavipes* (< 360 nm), *Helophorus griseus* (< 360 nm), *Helophorus minutua* (< 360 nm), *Helochares lividus* (380-390 nm), *Hydraena* sp., *Hydrobius fuscipes* (370-400 nm), *Laccobius sinatus* (370-390 nm), *Limnoxenus niger*<br>**Hyfraenidae**: *Limnebius crinifer* (360-380 nm)<br>**Sphaeridiinae**: *Megasternum boletophagum, Cryptopleurum minutum, Cercyon* sp. |

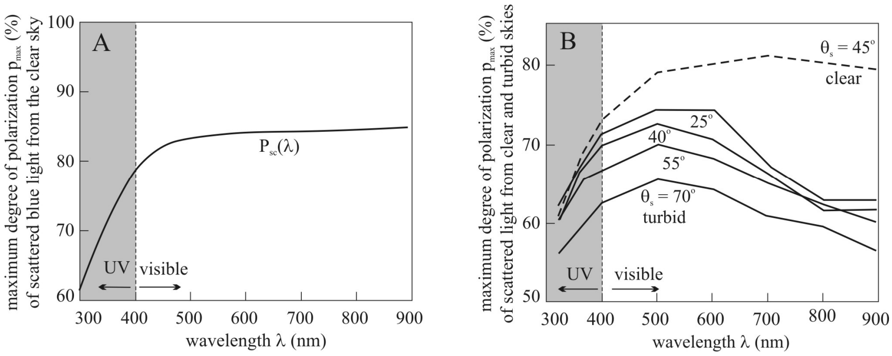


**Fig. 8.1.** A: Degree of linear polarization $p_{sc}$ versus wavelength $\lambda$ of scattered blue skylight measured under a clear sky at a solar elevation of 10° (after Fig. 5.6 of Coulson 1988, p. 285). B: As A measured in an atmosphere when it was turbid, dusty (continuous) and clear (dashed) (after Fig. 5.9 of Coulson 1988, p. 291).

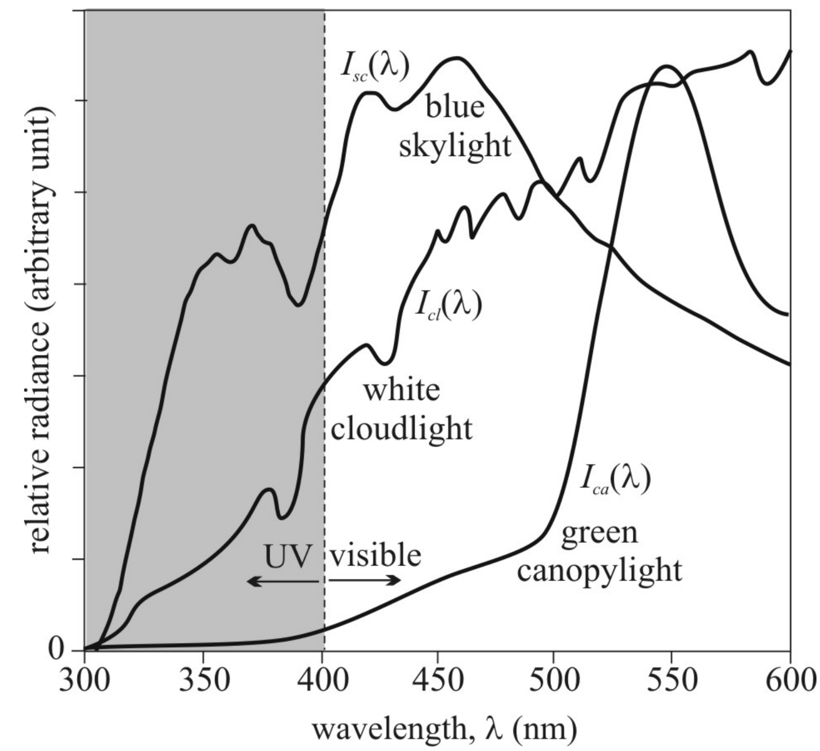


**Fig. 8.2.** Relative radiances as a function of the wavelength $\lambda$. $I_{sc}(\lambda)$: radiance of scattered blue skylight measured by Hess (1939) at 90° from the sun under clear sky conditions (after Fig. 4 of Seliger et al. 1994, p. 481). $I_{cl}(\lambda)$: radiance of white cloudlight measured by Coemans et al. (1994b) at an elevation of 40° under a thick cloud deck (after Fig. 4b of Coemans et al. 1994b, p. 1464). $I_{ca}(\lambda)$: radiance of green canopylight transmitted through the leaves of cottonwood (*Populus deltoides*) (after Fig. 8.20 of Gates 1980, p. 216).

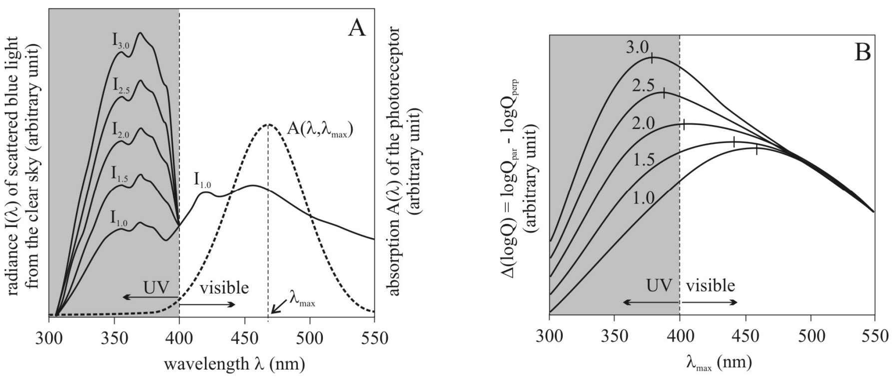


**Fig. 8.3.** A: Real and imaginary relative radiances $I_n(\lambda)$, $n$ = 1.0, 1.5, 2.0, 2.5, 3.0 of scattered blue light from the clear sky as a function of the wavelength $\lambda$. The Gaussian function $A(\lambda,\lambda_{max})$ with 50 nm half bandwidth is the absorption function of a photoreceptor, the sensitivity maximum of which is at $\lambda_{max}$. $I_{1.0}(\lambda)$: The radiance of blue skylight today (after Fig. 4 of Seliger et al. 1994, p. 481). $I_n(\lambda)$, $n$ = 1.5–3.0: Imaginary radiances of blue skylight obtained in such a way, that the UV part ($\lambda$ < 400 nm) of $I_{1.0}(\lambda)$ is multiplied by a factor $n$ ranging from 1.5 to 3.0. B: The difference $\Delta(logQ) = logQ_{par} - logQ_{perp}$ of the logarithms of the amounts of skylight absorbed by a polarization-sensitive ($PS$ = 7) photoreceptor with microvilli direction parallel (par) and perpendicular (perp) to the E-vector of polarized skylight as a function of $\lambda_{max}$ calculated for the series of $I_n(\lambda)$ shown in A. The maxima (marked by vertical bars) of $\Delta(logQ)_{1.0}$, $\Delta(logQ)_{1.5}$, $\Delta(logQ)_{2.0}$, $\Delta(logQ)_{2.5}$ and $\Delta(logQ)_{3.0}$ are at $\lambda_{max}$ = 458, 442, 404, 390 and 380 nm, respectively.

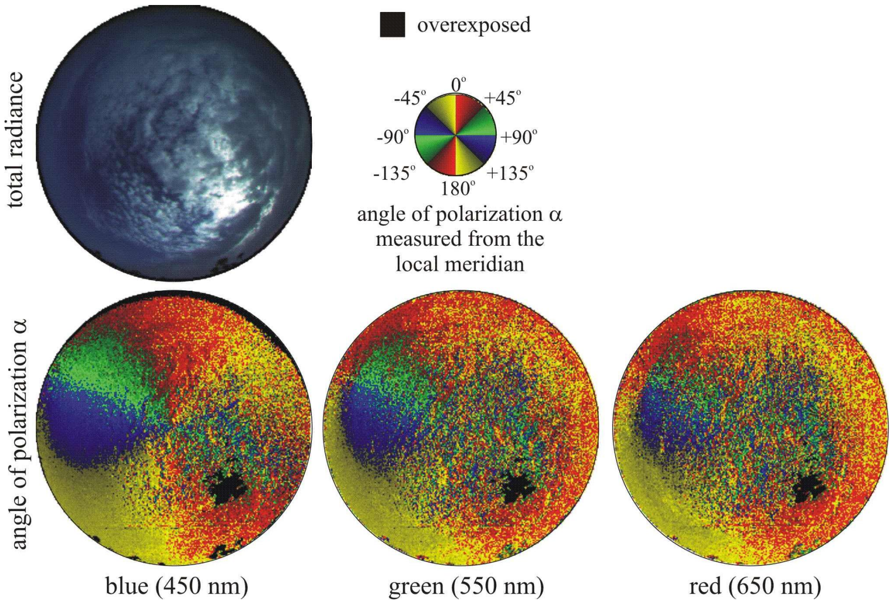


**Fig. 8.4.** Patterns of the angle of polarization of a partly cloudy sky measured by full-sky imaging polarimetry in Tunisia in August 1999. The sun is occluded by clouds, but its approximate position is within the overexposed (chequered) region of the sky.

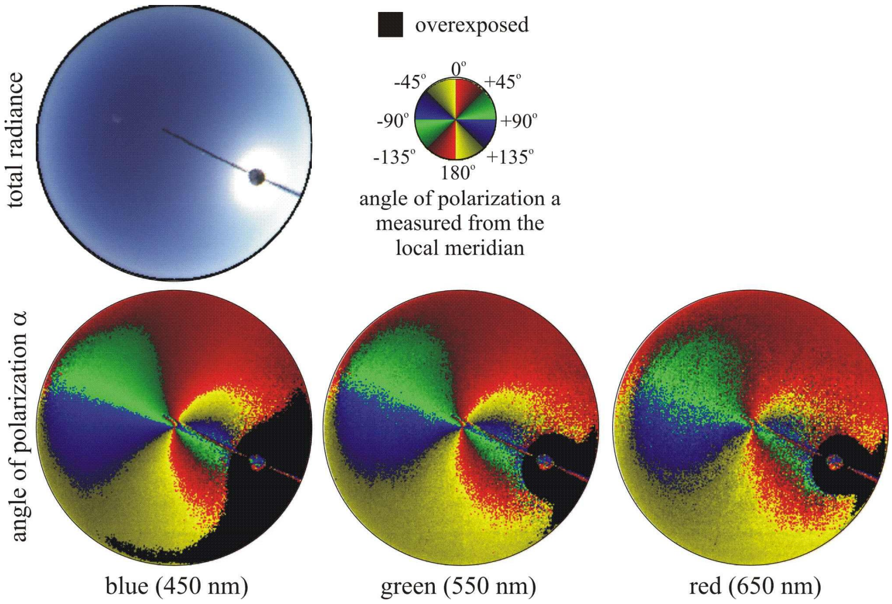


**Fig. 8.5.** Patterns of the angle of polarization of a clear sky measured by full-sky imaging polarimetry in Tunisia in August 1999 approximately at the same solar zenith angle as in the case of the cloudy sky in Fig. 8.4. In the circular pictures the radial bar with a small disk is the sun occulter. The sun is positioned behind the disk.

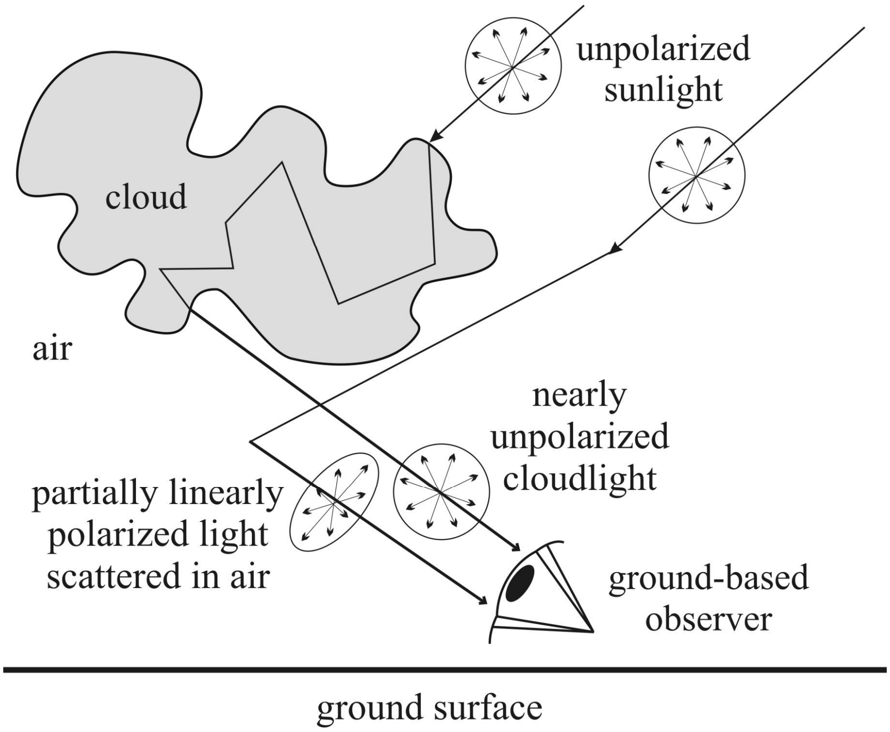


**Fig. 8.6.** Schematic representation of the two components of cloudlight reaching a ground-based observer. Unpolarized sunlight is scattered in the air and/or in a cloud. Direct cloudlight is nearly unpolarized, while light scattered in air is partially linearly polarized. (After Fig. 3 of Barta and Horváth 2003).

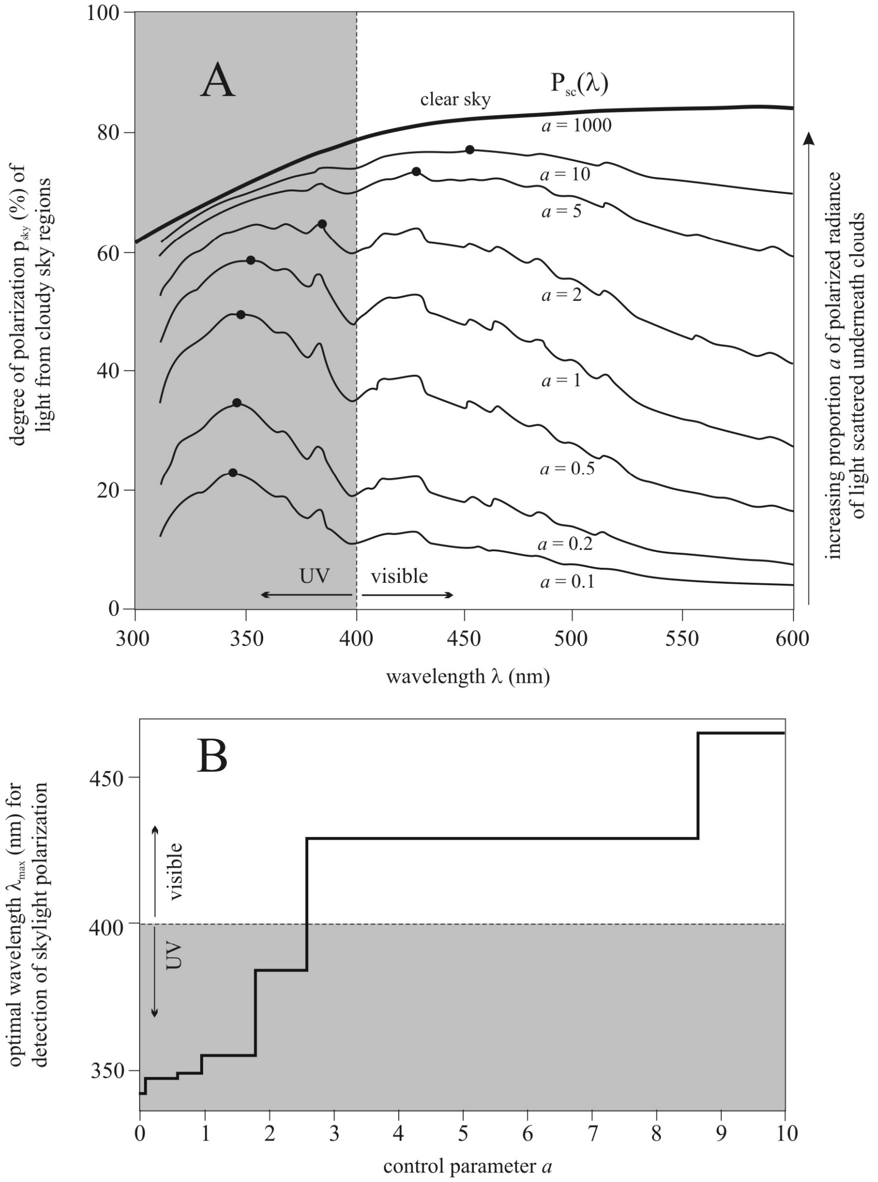


**Fig. 8.7.** A: The degree of polarization $p_{sky}(\lambda,a)$ of light from cloudy sky regions calculated on the basis of Eqn. (8.4) for different values of the control parameter $a$, using the functions $p_{sc}(\lambda)$ in Fig. 8.1A, and $I_{sc}(\lambda)$ and $I_{cl}(\lambda)$ in Fig. 8.2. Increasing $a$-values mean increasing proportion of the polarized radiance of light scattered underneath clouds. The positions of the local maxima of the curves are marked by dots. B: Wavelength $\lambda_{max}$ where $p_{sky}(\lambda,a)$ is maximal as a function of the control parameter $a$. $\lambda_{max}$ is optimal for orientation by means of skylight polarization. (After Fig. 4 of Barta and Horváth 2003).

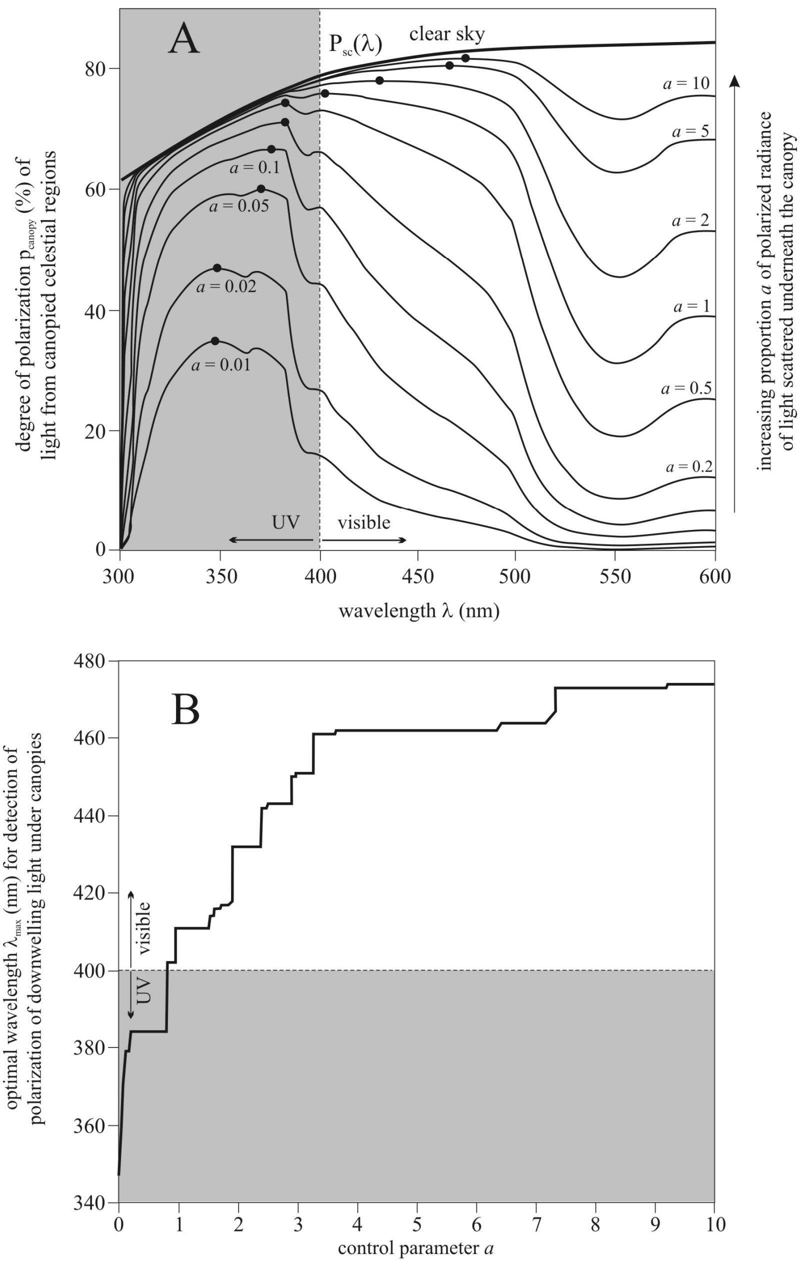


**Fig. 8.8.** As Fig. 8.7 for the downwelling light under a canopy calculated on the basis of the expression of $p_{ca}(\lambda,a)$ given in Eqn. (8.5) using the functions $p_{sc}(\lambda)$ in Fig. 8.1A, as well as $I_{sc}(\lambda)$ and $I_{ca}(\lambda)$ in Fig. 8.2. Increasing $a$ means increasing proportion of the polarized light scattered underneath the green foliage. (After Fig. 5 of Barta and Horváth 2003).