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Why is it advantageous for animals to detect celestial polarization in the ultraviolet? Skylight polarization under clouds and canopies is strongest in the UV

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Abstract

The perception of skylight polarization in the ultraviolet (UV) by many insect species for orientation purposes is rather surprising, because both the degree of linear polarization and the radiance of light from the clear sky are considerably lower in the UV than in the blue or green. In this work we call this the "UV-sky-pol paradox". Although in the past, several attempts have been made to resolve this paradox, none of them was convincing. We present here a possible quantitative resolution to the paradox. We show by a model calculation that if the air layer between a cloud and a ground-based observer is partly sunlit, the degree of linear polarization p of skylight originating from the cloudy region is highest in the UV, because in this spectral range the unpolarized UV-deficient cloudlight dilutes least the polarized light scattered in the air beneath the cloud. Similarly, if the air under foliage is partly sunlit, p of downwelling light from the canopied region is maximal in the UV, because in this part of spectrum the unpolarized UV-deficient green canopylight dilutes least the polarized light scattered in the air beneath the canopy. Therefore, the detection of polarization of downwelling light under clouds or canopies is most advantageous in the UV, in which spectral range the risk is the smallest that the degree of polarization p is lower than the threshold p_{tr} of polarization sensitivity in animals. On the other hand, under clear skies there is no favoured wavelength for perception of celestial polarization, because p of skylight is high enough ($p > p_{tr}$) at all wavelengths. We show that there is an analogy between the detection of UV skylight polarization and the polarotactic water detection in the UV. However, insects perceive skylight polarization by UV or blue or green receptors. The question, why they differ in the spectral channel used for the detection of celestial polarization cannot be answered at the present time, because data are insufficient. Nevertheless, we present here one possible atmospheric optical reason why certain visual systems involved in detecting celestial polarization, are specifically tuned to the UV part of the spectrum.

Keywords: Polarization sensitivity; Skylight polarization; UV-sky-pol paradox; Polarimetry; Cloudy sky; Canopy

1. Introduction

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 (Labhart and Meyer, 1999). The spectral type of the DRA receptors is ultraviolet (UV) in flies, honeybees, desert ants, certain scarab beetles and spiders; blue in crickets, desert locusts and cockroaches, but green in cockchafers (Table 1). However, the detection of skylight polarization in the UV is rather surprising, because both the degree of linear polarization p_{sc} and the radiance I_{sc} of light from the clear sky are considerably lower in the UV than in the blue or green (Figs. 1 and 2). In this work we call this the "ultraviolet paradox of the perception of skylight polarization", or simply "UV-sky-pol paradox" further on.

Why do many insects detect skylight polarization in the UV? Although in the past several attempts have been made to answer this question, none of them is convincing. In this work we first briefly survey some explanations why UV could be advantageous to perceive

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Table 1
Known wavelengths λ_{POL} at which the sensitivity of photoreceptors detecting skylight polarization is maximal in different species

Species	λ_{POL} (nm)	References
Calliphora erythrocephala, *Musca domestica* (flies)	330–350	Smola and Meffert (1978), Hardie et al. (1979), Hardie (1984), Philipsborn and Labhart (1990)
Apis mellifera (honeybee)	345–350	Helversen et al. (1974), Labhart (1980)
Bombus hortorum (bumblebee)	353 and 430	Meyer-Rochow (1981)
Cataglyphis bicolor (desert ant)	380–410	Duelli and Wehner (1973)
Cataglyphis setipes (desert ant)	380–400	Frantsevich et al. (1976, 1977)
Lethrus apterus, *Lethrus inermis* (scarab beetles)	350	Frantsevich et al. (1976, 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), Herzmann and Labhart (1989), Brunner and Labhart (1987)
Schistocerca gregaria (desert locust)	450	Eggers and Gewecke (1993)
Leucophaea maderae (Madeira cockroach)	<471	Loesel and Homberg (2001)
Melolontha melolontha (cockchafer)	~520	Labhart et al. (1992)
Parastizopus armaticeps (beetle)	~540	Bisch (1999)

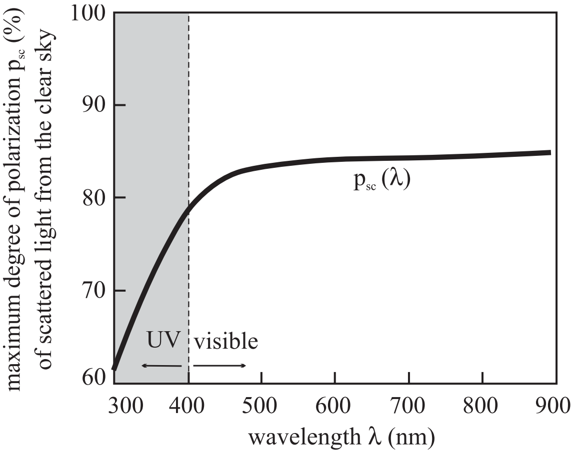

Fig. 1. Degree of linear polarization p_{sc} versus wavelength λ of scattered light from the clear sky measured at 90° from the sun in a clear atmosphere for a solar elevation of 10° (after Coulson, 1988, p. 285).

skylight polarization, in order to show that a more reliable explanation is necessary. Then we show by a model calculation that perception of celestial polarization in the UV has the advantage that under cloudy skies and green canopies the degree of linear polarization of skylight is maximal. A possible reason why crickets prefer the blue against the UV part of the spectrum for detection of skylight polarization is briefly discussed. Finally we show that there is an analogy between the detection of UV skylight polarization and the polarotactic water detection in the UV.

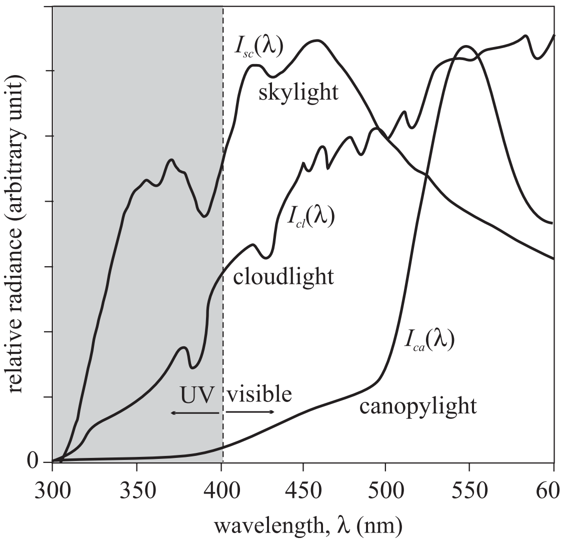

Fig. 2. $I_{sc}(\lambda)$: radiance of scattered light from the clear sky measured by Hess (1939) at 90° from the sun under clear sky conditions. $I_{cl}(\lambda)$: radiance of white cloudlight measured by Coemans et al. (1994, p. 1464) at an elevation of 40° under a thick cloud deck. $I_{ca}(\lambda)$: radiance of green canopylight transmitted through the leaves of cottonwood (*Populus deltoides*) (after Gates, 1980, p. 216).

2. Some explanations why UV could be advantageous to perceive skylight polarization

(1) In the literature of animal polarization sensitivity a frequently occurring misbelief is that the degree of linear polarization p_{sc} of scattered light from the clear sky is highest in the UV. Some researchers (e.g. Waldvogel, 1990; Beason and Semm, 1991; Helbig, 1991; Tovée, 1995) tried to explain in this way why certain animals may detect skylight polarization in the UV. However, measurements by Coulson (1988), for example, have clearly shown that under clear atmospheric conditions p_{sc} of skylight decreases considerably with decreasing wavelength λ (Fig. 1).

(2) The explanation of Frisch (1967) that the celestial polarization pattern might be the least sensitive to "atmospheric disturbances" in the UV, is frequently cited (e.g. Duelli and Wehner, 1973;

Wehner, 1976; Dacke et al., 2002). However, these enigmatic atmospheric disturbances have never been precisely defined.

(3) Other authors (e.g. Hawryshyn, 1992) suggested that the relatively large proportion of UV in the light from clear skies partially accounts for the use of UV for the detection of polarization. However, Fig. 2 demonstrates that the radiance I_{sc} of scattered skylight is much lower in the UV than in the blue, where it is maximal.

(4) Mazokhin-Porshnyakov (1969) suggested that using UV light, 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 might help insects to distinguish phototactically "sky" from "ground". However, since skylight and ground-reflected light can reach the eye always from above and below, respectively, an appropriate regionalization of the photoreceptors can simply eliminate the confusion of skylight with ground-reflected light, independently of the wavelength sensitivity of the receptors. Indeed, this is the case in many insects (e.g. honeybees, desert ants and crickets), in which it is only the DRA that is sensitive to skylight polarization, and this area is oriented towards the sky, so that the ambiguities envisaged by Mazokhin-Porshnyakov (1969) do not arise.

(5) 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 (e.g. Wehner, 1976). However, if there are distinct skylight polarization detectors as well as motion/form detectors in separate eye regions, both detector types can function in the same spectral range. Indeed, the detection of motion and form is mediated by receptors being distinct from receptors in the polarization-sensitive DRA, so that the mentioned confusion does not arise.

(6) UV receptors might have evolved originally as skylight detectors and might have been incorporated into the E-vector detecting system only later (e.g. Wehner, 1994). However, this hypothesis does not explain why the photoreceptors used originally as simple photometric skylight detectors should have been sensitive to UV. We have already mentioned that the radiance of skylight in the UV is much smaller than in the blue or green (Fig. 2), which feature is rather disadvantageous for a photometric skylight detector.

(7) 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 (e.g. Brines and Gould, 1982; Cockell, 1998). The reasons for this 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 solar UV radiation might have been greater during earlier epochs of evolution. However, this hypothesis is hard to test, because from the past there are no reliable data about the temporal change of the solar UV radiation reaching the earth's surface.

(8) It was also proposed that using UV receptors in skylight navigation might be advantageous in exploiting spectral gradients across the sky (e.g. Wehner, 1984, 1989; Wehner and Rossel, 1985). However, the celestial radiance gradients are much stronger in the blue than in the UV, therefore in the UV the sky is much more homogeneous than in the blue (Hess, 1939; Nagel et al., 1978; Coulson, 1988; Coemans et al., 1994). Thus, the UV sensitivity of the DRA would be rather disadvantageous in detecting the celestial radiance gradients.

(9) According to Brines and Gould (1982), under partly cloudy meteorological conditions, or under extensive vegetation 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. 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. 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 the degree of linear polarization 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.

(10) Pomozi et al. (2001) showed by full-sky imaging polarimetry that in the visible part of the spectrum

the shorter the wavelength λ, the more pronounced is the continuation of the clear-sky E-vector pattern underneath clouds, if regions of the clouds and parts of the air layer between the clouds and the earth's surface are directly lit by the sun. The scattering of direct sunlight on cloud particles and in the air columns underneath the clouds results in the same E-vector pattern as that present in the clear sky. The light from cloudy sky regions can be used for the polarization compass if the degree of linear polarization p is higher than a threshold p_{tr} and the deviation of the angle of polarization from that of the corresponding clear sky is smaller than a threshold. Pomozi et al. (2001) proved experimentally that the proportion k of the celestial polarization pattern useful for animal orientation is greater than about 83% under clear skies at wavelengths $\lambda = 650\,\text{nm}$ (red), 550 nm (green) and 450 nm (blue) calculated for a polarization-sensitive model retina with parameters characteristic to the DRA of field crickets (*Gryllus campestris*). Thus, under clear skies there is no selective advantage for shorter wavelengths, because the extent of the polarized clear sky usable for orientation is great enough in all parts of the visible spectrum. Pomozi et al. (2001) have also shown that in the visible spectrum and under partly cloudy skies, the shorter the λ, the greater is k. This phenomenon may have a selective advantage for blue wavelengths. Hence, the extension of the clear-sky E-vector pattern into celestial areas covered by clouds is more useful for an E-vector compass when the skylight is perceived in the blue (B) rather than in the green (G) or red (R). Pomozi et al. (2001) could measure celestial polarization patterns and derive k-values only in the visible part of the spectrum ($\lambda > 400\,\text{nm}$), because UV light was not transmitted through their fisheye lens. Unless full-sky polarization measurements are available in the UV ($200\,\text{nm} < \lambda < 400\,\text{nm}$), calculations can provide the relation between k_{UV} and k_B, k_G, k_R for cloudy skies. In this work such a model calculation is presented.

3. Materials and methods: calculation of the degree of linear polarization of downwelling light versus wavelength under clouds and canopies

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) and Pomozi et al. (2001), $k(\lambda)$ is essentially determined only by the degree of linear polarization $p_{sky}(\lambda)$ of skylight. If $p_{sky}(\lambda)$ at any particular direction in the sky is greater than the threshold of polarization sensitivity $p_{tr}(\lambda)$ in a given animal, the skylight from this direction can be used for polarization compass orientation. The higher the $p_{sky}(\lambda)$ in the whole sky, the greater is $k(\lambda)$. The skylight originating from a cloudy celestial region and reaching a ground-based observer is composed of (i) the practically unpolarized cloudlight with radiance $I_{cl}(\lambda)$ and degree of linear polarization $p_{cl}(\lambda) \approx 0$—due to the diffuse scattering of light by cloud particles, apart from the direction of rainbow scattering in water clouds (Können, 1985; Coulson, 1988)—, and (ii) the scattered light with $I_{sc}(\lambda)$ and $p_{sc}(\lambda) > 0$ from the air layer between the clouds and the observer (Fig. 3). Thus, $p_{sky}(\lambda)$ is, per definition, the polarized radiance $a(\lambda, h)p_{sc}(\lambda)I_{sc}(\lambda)$ divided by the total radiance $a(\lambda, h)I_{sc}(\lambda) + I_{cl}(\lambda)$:

$$p_{sky}(\lambda) = a(\lambda, h)p_{sc}(\lambda)I_{sc}(\lambda)/[a(\lambda, h)I_{sc}(\lambda) + I_{cl}(\lambda)], \quad \text{with} \quad 0 \leqslant a(\lambda, h), \tag{1}$$

where $a(\lambda, h)$ is a factor describing the wavelength-dependent effect of the air layer with thickness h underneath the clouds. In other words, $a(\lambda, h)$ characterizes the contribution of $I_{sc}(\lambda)$ relative to $I_{cl}(\lambda)$: The greater the h, the smaller is the relative contribution of $I_{cl}(\lambda)$ of cloudlight reaching the observer. This phenomenon can be described by the increase of factor $a(\lambda, h)$. On the other hand, decreasing thickness h of the air layer between a cloud and a ground-based observer, the number of scattering events decreases, which can be described by the decrease of $a(\lambda, h)$, because then the relative contribution of $I_{sc}(\lambda)$ of light scattered in the air beneath clouds decreases. Since measurements of a are not available yet, as a first approximation we assume

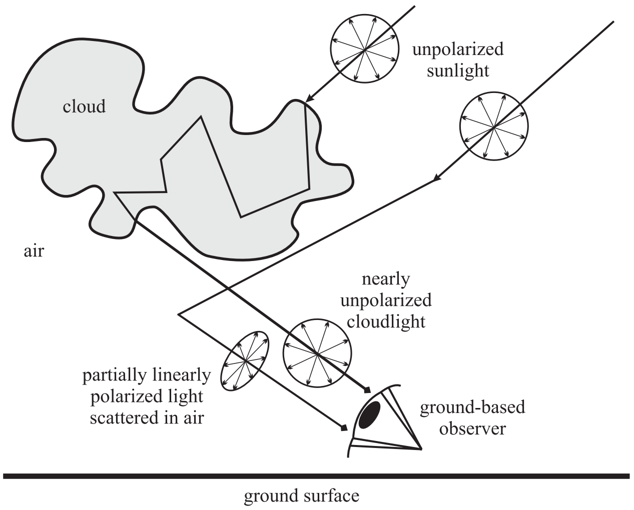

Fig. 3. Schematic representation of the two components of light from cloudy sky regions reaching a ground-based observer. Unpolarized sunlight is scattered in the air and/or in a cloud. Direct cloudlight is unpolarized (apart from the direction of rainbow scattering in water clouds), while light scattered in air is partially linearly polarized.

that a is independent of λ. Although the dependence of a on h is also unknown, it is clear from the above that a increases with h: If a cloud would be in the immediate vicinity of the observer, the contribution of light scattered in the air beneath the cloud would be zero, thus $a(h=0)=0$. When a cloud would be at a huge distance from the observer (e.g. for high altitude cirrus clouds or clouds at the horizon), then the contribution of cloudlight would be small in comparison with that of light scattered in the air between the observer and the cloud.

One can similarly calculate the influence of the weighting of unpolarized green light transmitted through foliage and linearly polarized light scattered in the air beneath foliage on the degree of linear polarization p_{ca} of downwelling light under a canopy, if the air beneath the foliage is illuminated partly by direct sunlight, as usually in forests, for example. Under canopies, the same calculation can be performed as under clouds, but in the former case the radiance $I_{cl}(\lambda)$ of white cloudlight should be replaced by the radiance $I_{ca}(\lambda)$ of green light transmitted by the canopy, called "canopylight" further on:

$$p_{ca}(\lambda, a) = a p_{sc}(\lambda) I_{sc}(\lambda)/[a I_{sc}(\lambda) + I_{ca}(\lambda)], \quad \text{with} \quad 0 \leqslant a. \tag{2}$$

4. Results

Figs. 1 and 2 show measured functions $p_{sc}(\lambda)$ and $I_{sc}(\lambda)$ of scattered light from a clear sky at 90° from the sun. Fig. 2 represents the spectrum $I_{cl}(\lambda)$ of cloudlight measured under a thick cloud deck, when the total radiance $aI_{sc}(\lambda) + I_{cl}(\lambda)$ of skylight is practically the same as the radiance $I_{cl}(\lambda)$ of cloudlight (because $a \approx 0$). Using these particular functions without any loss of generality, Fig. 4A shows $p_{sky}(\lambda, a)$ calculated on the basis of Eq. (1). We can see in Fig. 4 that

- if $a < 2.5$ (when cloudlight dominates, that is, the air layer between the clouds and the observer is thinner than a certain threshold), $p_{sky}(\lambda, a)$ is maximal in the UV ($\lambda < 400\,\text{nm}$);
- if $a > 2.5$, the maximum of $p_{sky}(\lambda, a)$ is in the visible part of the spectrum ($\lambda > 400\,\text{nm}$);
- if $a > 10$, $p_{sky}(\lambda, a)$ approximates $p_{sc}(\lambda)$ of the clear sky (Fig. 1).

The reasons for these characteristics are the following: Although the polarized radiance $ap_{sc}I_{sc}$ of skylight is larger 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 λ from blue to UV, the denominator of the expression of $p_{sky}(\lambda, a)$ given in Eq. (1) decreases more drastically than the nominator, resulting in $p_{sky}(UV, a)$ becoming higher than $p_{sky}(B, a)$. Fig. 4B shows the optimal (for orientation by means of skylight polarization) wavelength λ_{max}, where $p_{sky}(\lambda, a)$ is maximal as a function of the control parameter a.

Fig. 2 shows the radiance $I_{ca}(\lambda)$ 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 (Vanderbilt et al., 1985a, b). Consequently, the same phenomenon occurs as under clouds, as shown in Fig. 5: the degree of linear polarization $p_{ca}(\lambda, a)$ of light from the canopy (composed of the partially linearly polarized light scattered in the air layer beneath the canopy and the UV-deficient unpolarized greenish canopylight) is maximal in the UV if $a < 0.8$. Hence, also under canopies the detection of polarization of downwelling light is most advantageous in the UV. This may be important for those insects with polarization-sensitive DRA that live under canopies and orient by means of the E-vector pattern of downwelling light.

5. Discussion

In this work we showed how the weighting (described by the control parameter a) of unpolarized white cloudlight or unpolarized green canopylight and linearly polarized 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 height 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} is maximal always in the UV. However, the question is whether the maximum of p_{ca} is higher than the threshold p_{tr} for polarization sensitivity (about 5% for crickets and 10% for honeybees; Wehner, 1994). 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 $p_{ca} > p_{tr}$. The experimental spectro-polarimetric study of this question could be an interesting task of future research.

On the basis of the above, we propose the following possible resolution of the UV-sky-pol paradox:

1. There is no favoured wavelength for perception of skylight polarization under clear skies, because p_{sc} of light from clear skies is high enough ($p_{sc} > p_{tr}$) at all wavelengths, thus the proportion k of the celestial

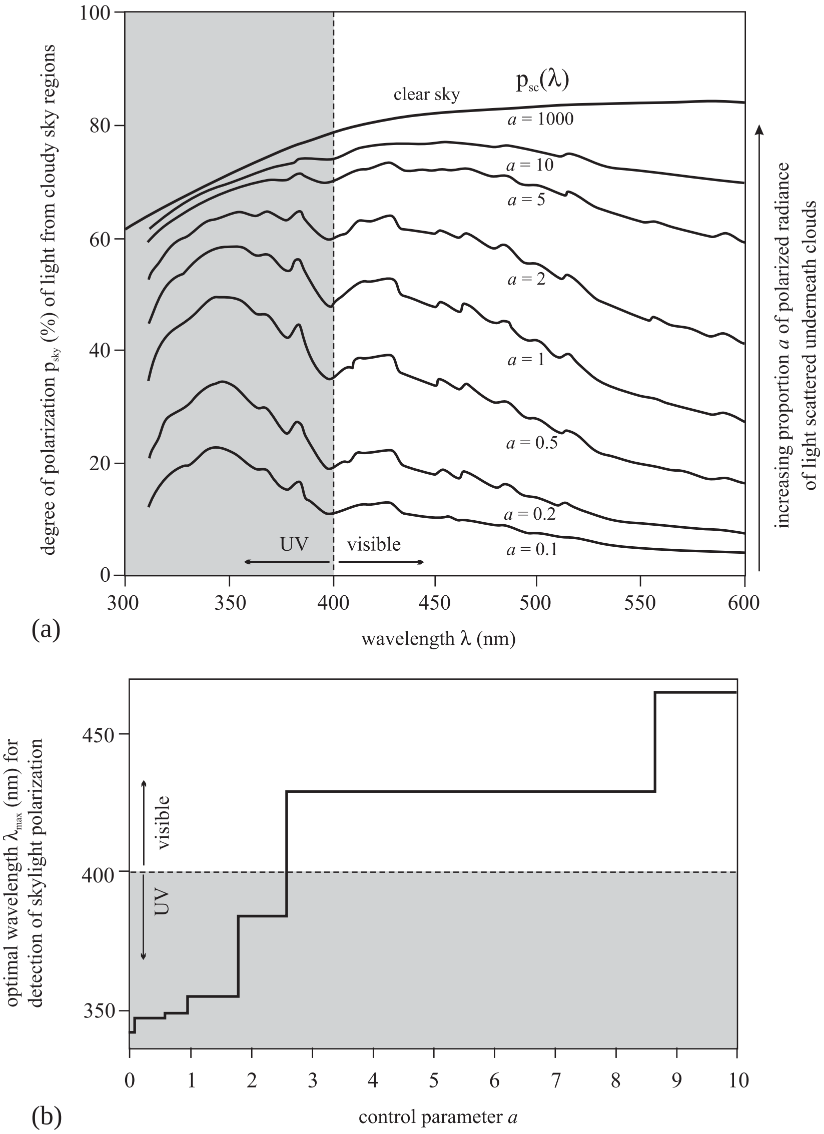

Fig. 4. (a) The degree of linear polarization $p_{sky}(\lambda, a)$ of light from cloudy sky regions calculated on the basis of Eq. (1) for different values of the control parameter a, using the functions $p_{sc}(\lambda)$ in Fig. 1, as well as $I_{sc}(\lambda)$ and $I_{cl}(\lambda)$ in Fig. 2. Increasing a means increasing proportion of the polarized light scattered underneath clouds. (b) Wavelength λ_{max}, where $p_{sky}(\lambda, a)$ is maximal as a function of a.

polarization pattern useful for animal 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 air columns under clouds are partly sunlit, the degree of linear polarization p_{sky} of skylight originating from the cloudy regions is the highest in the UV, because in this spectral range the unpolarized UV-deficient cloudlight dilutes least the polarized light scattered in the air beneath the clouds.

Some of the above arguments were presented in favour of the perception of celestial polarization in the UV under clouds and canopies. However, several insect species detect skylight polarization in the blue or green (Table 1). Why do not all the insects use UV-sensitive photoreceptors for this task? This question remains unanswered. Certainly, other important physical, biological or environmental factors may still exist, which determine the optimal wavelength range of the detection of skylight polarization in a particular animal species. However, at least in the case of crickets there is a possible explanation why they perceive skylight in the blue. We can see in Fig. 4A that $p_{sky}(\lambda, a)$ is always relatively high in the violet and blue ($400\,\text{nm} < \lambda < 470\,\text{nm}$) 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

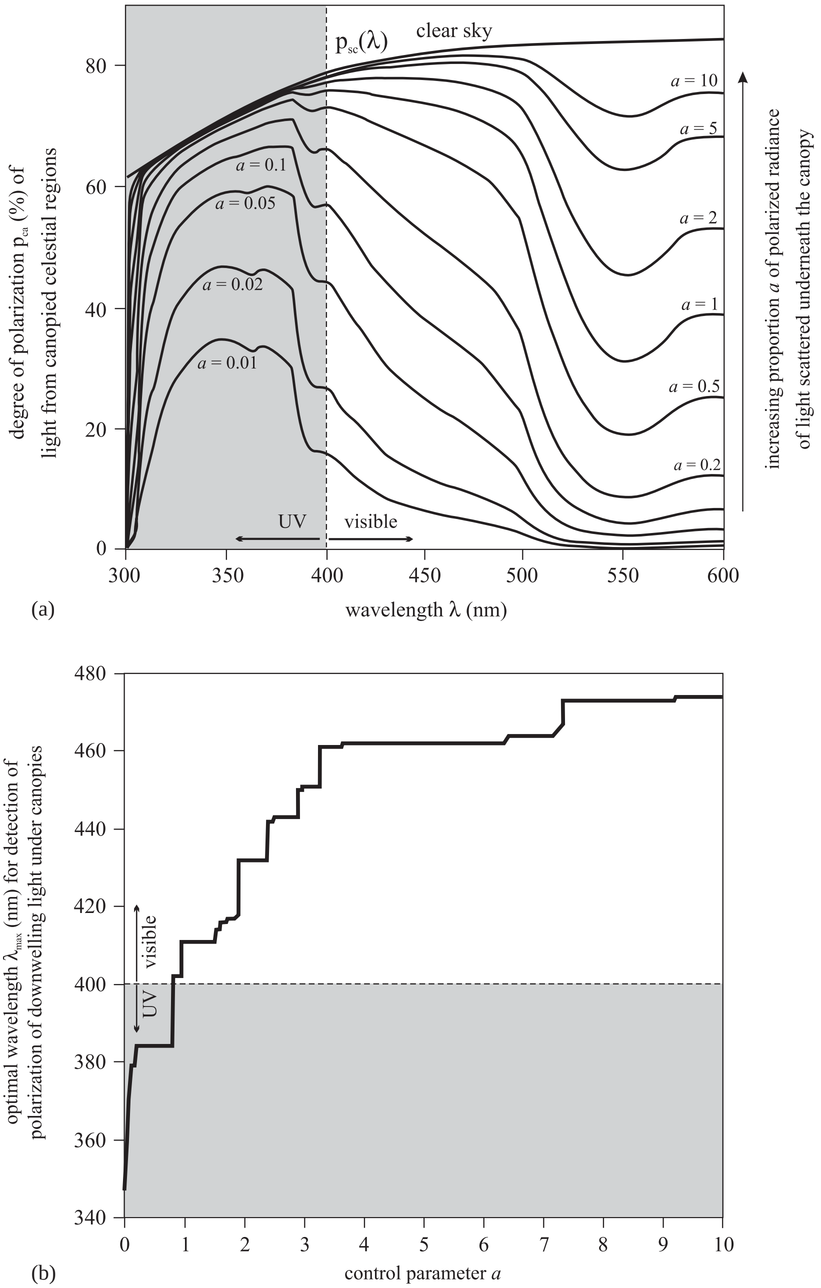

Fig. 5. As Fig. 4 for the downwelling light under a canopy calculated on the basis of the expression of $p_{ca}(\lambda, a)$ given in Eq. (2) using the functions $p_{sc}(\lambda)$ in Fig. 1, as well as $I_{sc}(\lambda)$ and $I_{ca}(\lambda)$ in Fig. 2. Increasing a means increasing proportion of the polarized light scattered underneath the green foliage.

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 under clear skies, when the degree of skylight polarization is high enough for all wavelengths: The radiance of the UV component of sunlight and light from the clear sky is low relative to that of the blue and green components (Fig. 2). At twilight under clear skies, the absolute light radiance is more likely to fall below the sensitivity threshold of a polarization-sensitive visual system operating in the UV rather 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 the UV, has been interpreted in this way (Labhart et al., 1984; Herzmann and Labhart, 1989). The crickets *Acheta domestica*, *G. bimaculatus* and *G. 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. According to Zufall et al. (1989), the combination of blue 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 1). However, the question is whether this "radiance 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. 2), detection of skylight may be more disadvantageous in the UV than in the blue. On the other hand, under cloudy skies p_{sky} is the highest in the UV (Fig. 4), thus perception of skylight polarization could be more advantageous in the UV than in the blue. The question is, which effect is the stronger.

The spectral aspects of the detection of polarization of light reflected from water surfaces are discussed by Schwind (1991, 1995) and Bernáth et al. (2002). Here we mention only that the majority of the known polarotactic water-seeking insect species exploit UV wavelengths to seek for water, because the amount of light originating from the underwater region is minimal in the UV, thus the degree of linear polarization 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. Possible reasons for this are discussed by Schwind (1991, 1995). Note that considering the optimal wavelength range, there is an analogy between the perception of skylight polarization and the detection of polarization of light reflected from water surfaces. Both tasks are most efficient in the UV, the reason for which is the same: The degree of linear polarization of skylight and water-reflected light is highest in the UV if there is a background—a cloud (or canopy) in the sky (Fig. 3) 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 degree of polarization of the biologically relevant light (downwelling skylight and water-reflected light) is highest in the UV.

Finally, we would like to emphasize that although in this work we discussed only some atmospheric optical aspects of insect polarization vision, our results are true also for all animals that detect celestial polarization. We considered insects, because (apart from the spider *Drassodes cupreus*) only in certain insect species it is known which spectral range they perceive celestial polarization in (Table 1). Although it was demonstrated behaviourally in many species (e.g. in the grass shrimp, *Palaemonetes vulgaris*; Goddard and Forward, 1991) that they can use celestial polarization for orientation, it is generally unknown in which part of the spectrum they detect skylight polarization. On the other hand, in several species (e.g. in the rainbow trout, *Oncorhynchus mykiss*, Hawryshyn, 1992; for review see: Horváth and Varjú, 2003, Chapter 28, pp. 293–316), it was shown that perception of polarization happens in different parts of the spectrum, but usually it is unknown whether this capability is used for detection of skylight polarization. After reviewing the literature, in Table 1 we listed all the species we found, in which (i) it is proven that they can detect skylight polarization, and (ii) the wavelengths of their maximal polarization sensitivity are known.

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