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How can dragonflies discern bright and dark waters from a distance? The degree of polarisation of reflected light as a possible cue for dragonfly habitat selection

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SUMMARY

1. Based on the findings that some dragonflies prefer either 'dark' or 'bright' water (as perceived by the human eye viewing downwards perpendicularly to the water surface), while others choose both types of water bodies in which to lay their eggs, the question arises: How can dragonflies distinguish a bright from a dark pond from far away, before they get sufficiently close to see it is bright or dark?
2. Our hypothesis is that certain dragonfly species may select their preferred breeding sites from a distance on the basis of the polarisation of reflected light. Is it that waters viewed from a distance can be classified on the basis of the polarisation of reflected light?
3. Therefore we measured, at an angle of view of 20° from the horizontal, the reflection-polarisation characteristics of several ponds differing in brightness and in their dragonfly fauna.
4. We show that from a distance, at which the angle of view is 20° from the horizontal, dark water bodies cannot be distinguished from bright ones on the basis of the intensity or the angle of polarisation of reflected light. At a similar angle of view, however, dark waters reflect light with a significantly higher degree of linear polarisation than bright waters in any range of the spectrum and in any direction of view with respect to the sun.
5. Thus, the degree of polarisation of reflected light may be a visual cue for the polarisation-sensitive dragonflies to distinguish dark and bright water bodies from far away. Future experimental studies should prove if dragonflies do indeed use this cue for habitat selection.

Keywords: dark and bright freshwater habitats, dragonflies, habitat selection, polarisation vision, reflection polarisation

Introduction

The females of many aquatic insects, such as dragonflies or mayflies, must return to water to lay their eggs. Water bodies also often serve as rendezvous for both sexes. In Odonata many species are habitat generalists while others are highly specific in their ecological requirements (Corbet, 1999). Thus, we may ask by what proximate factors aquatic habitats are selected. As orientation in dragonflies is predominantly visual, we may ask for the cues by which specific water bodies are recognised (Wildermuth, 1994). Until the studies by Schwind (1991, 1995) polarisation of reflected light was not considered as a factor in habitat recognition by aquatic insects. The ventral region of the eye in many aquatic insects is sensitive to the polarisation of light in the visible and/or ultraviolet spectral ranges (Schwind, 1991, 1995; Tovée, 1995). These insects find their habitat on the basis of the horizontally polarised light reflected

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from the water surface (Schwind, 1984, 1985; Schwind & Horváth, 1993; Horváth, 1995; Kriska, Horváth & Andrikovics, 1998). On the other hand, the spectral sensitivity of the polarisation-sensitive photoreceptors of insects living in the water is generally matched to the spectral composition of underwater light, which is quite diverse in different types of aquatic habitats (Jerlov, 1976; Lythgoe, 1979). Aquatic insects detect polarisation in the region(s) of the spectrum, which is(are) characteristic of their preferred habitat(s) (Schwind, 1991, 1995).

The reflection-polarisation characteristics of water surfaces were studied theoretically as well as experimentally by Schwind & Horváth (1993), Horváth (1995), Horváth & Varjú (1997), Horváth, Gál & Wehner (1997) and Gál, Horváth & Meyer-Rochow (2001). Depth, turbidity, transparency, colour, surface roughness of the water and substratum composition, as well as the light itself, strongly influence the reflection-polarisation characteristics of water bodies. Polarised light reflected by water provides important information on the quality of freshwater habitats for polarotactic insects and can aid the orientation of these insects from a distance where other cues (e.g. atmospheric humidity, dimension and shape of the water body, undulation of the water surface, water plants on the surface and on the shore, temperature and odour) are still ineffective.

While monitoring the fauna of dark ponds in peatland and bright ponds in gravel pits in the Swiss midlands, we observed that some dragonflies preferred one or the other, whereas others were found in both types. It is a well-known optical phenomenon that two water bodies, being bright and dark to the human eye viewing downwards perpendicularly to their surface, cannot be distinguished from each other from a distance. Then the angle of view with respect to the water surface is very small (called the 'grazing' angle) and the amount of light reflected from the surface is equal for both dark and bright waters. This overwhelms the difference between the intensity of light coming from bright and dark waters, by which one can normally discern dark and bright waters (the amount of light coming from the water being much greater for bright, than for dark waters). Thus, the main question is to find how dragonflies distinguish a bright from a dark pond before they get sufficiently close to see them as such.

Since many dragonfly species find their aquatic habitat by polarotaxis (Horváth, Bernáth & Molnár, 1998; Wildermuth, 1998; Bernáth *et al*. 2001), we hypothesised that certain dragonflies can select from far away their preferred dark or bright water bodies, at least partly on the basis of reflection-polarisation information. Can dark and bright waters viewed from a distance, at a grazing angle of view, be classified on the basis of the degree and angle of linear polarisation of light reflected from them? In order to answer this question, we measured the reflection-polarisation characteristics, at an angle of view of 20°, for a number of dark and bright ponds inhabited by different dragonfly species.

Methods

Our field studies were carried out at two localities near Zurich, Switzerland: (1) Chomberg nature reserve, a former gravel pit near Winterthur (570 m a.s.l.), and (2) Ambitzgi/Böndler nature reserve, a moorland area with former peat diggings near Wetzikon (540 m a.s.l.), the two sites being situated 22 km apart from each other. The odonate fauna was monitored in a sample of six ponds at each locality. The water bodies at study site (1) appeared bright to the human eye viewing downwards perpendicularly to their surface, those at site (2) appeared dark. 'Bright' means shallow and clear water with a bright substratum, 'dark' refers to shallow and clear water with a dark substratum, from which light reflects only to a limited extent. The bright ponds were surrounded by forest, had a diameter of 5–10 m and a maximum depth of 0.3–0.4 m. The ponds were in an early successional stage, their surface being sparsely covered by aquatic vegetation. The colour was bright beige and the bottom consisted of gravel and clay. All dark ponds were situated in peatland. Their diameter ranged from 4 to 8 m and they had a maximum depth of 0.4–0.8 m. They were sparsely or moderately overgrown with emergent vegetation and surrounded by fenland and forest; their colour was dark brown and the substratum consisted of peaty mud.

The Odonata of the two localities were surveyed during the emergence and flying season from 1995 to 2000. On a total of 130 visits, the presence and the reproduction activities of the species at every water body were recorded. Special attention was paid to exuviae, because they give good evidence that the species had developed successfully in a corresponding water body. However, quantitative collection of exuviae was restricted to the Anisoptera as too many zygopteran exuviae are overlooked due to their small size.

The reflection-polarisation characteristics of these ponds were measured by videopolarimetry, using the method of Horváth & Varjú (1997) and Mizera *et al.* (2001), in summer 1997 and 1998, on calm days when the surface was flat. During the measurements, the viewing direction of the videocamera was always inclined downwards at 20°. We used this camera inclination in order to measure the reflection-polarisation characteristics of water surfaces from a relatively small grazing angle of view with respect to the horizontal, which simulates the view of dragonflies approaching a pond from a great distance. Video records were made using a Sony VX1E 3CCD camera with a field of view of 50° (horizontal) × 40° (vertical), able to measure in the red (wavelength of maximum sensitivity of the red-sensitive CCD-chip: λ_{max} = 650 nm with half band width = 40 nm), green (λ_{max} = 550 nm, half band width = 40 nm) and blue (λ_{max} = 450 nm, half band width = 40 nm) ranges of the spectrum. The reflection polarisation of the ponds was measured from three different directions of view with respect to the solar azimuth: the camera viewed either towards the solar azimuth, called 'towards the sun', or directly 'away from the sun' at 180° to the solar azimuth, or at right angles to these two directions, here called 'perpendicular to the sun'.

In the case of one bright and one dark pond from the 12 ponds studied, a Hamamatsu Beamfinder III camera with a field of view of 30° (horizontal) × 20° (vertical) was used, which is able to measure both in the ultraviolet and visible spectral regions (from 250 to 750 nm). For measurements with the Beamfinder III in the visible range of the spectrum we used the following B + W colour filters manufactured by Schneider Optics (Bad Kreuznach, Germany, http://www.schneideroptics.com): red, B + W 091; orange, B + W 040; yellow, B + W 022; green, B + W 061; blue, B + W 081; violet, B + W 484. The transmittivities T versus wavelength λ of these filters are shown in the left column of Fig. 3. The red, orange and yellow filters were 'long-pass' filters, transmitting equal light at wavelengths longer than a filter-specific threshold. The other filters had a $T(\lambda)$ curve with a maximum at a filter-specific wavelength. For the ultraviolet measurements with the Beamfinder III, we used the filter Hamamatsu UV A5194-01, the $T(\lambda)$ curve of which is also shown in the left column in Fig. 3. The polarimeter based on Beamfinder III was difficult to handle as it took a long time to measure in these seven spectral ranges, so measurements were taken only away from the sun and perpendicularly to the sun.

All measurements were made in a 4-h period around noon on cloudless and calm days. The solar zenith angles were slightly different, which might have caused small differences in the polarisation pattern of the skylight illuminating the water surface. During processing of the reflection-polarisation patterns of a given water surface, a rectangular 'window' with the greatest possible area, containing sunlit parts of the water surface without emergent vegetation, was always chosen from the investigated picture. Each window extended down to include the reflections at Brewster's angle (about 37° from the horizontal direction for the air–water interface) where reflected light is horizontally and approximately totally polarised (degree of polarisation, 100%) if the amount of light from the subsurface layers is negligible in comparison with the amount of surface-reflected light. Using t-test (Sachs, 1974), the average of the relative brightness, degree of linear polarisation and angle of polarisation calculated for the selected windows in the case of the six bright and six dark water surfaces were compared separately in the red (λ_{max} = 650 nm), green (λ_{max} = 550 nm) and blue (λ_{max} = 450 nm) spectral ranges for all three directions relative to the sun. Using Welch-test (Sachs, 1974), in the ultraviolet (λ_{max} = 360 nm) spectral region the distributions of the relative brightness, degree of polarisation and angle of polarisation on the surface of one dark and one bright pond were compared separately away from the sun and perpendicular to the sun.

Results

The dragonfly faunas of six bright and six dark ponds are summarised in Table 1. Five species, *Enallagma cyathigerum* (Charpentier), *Anax imperator* (Leach), *Libellula depressa* (Linnaeus), *Orthetrum cancellatum* (Linnaeus) and *Orthetrum brunneum* (Fonscolombe), were common only in bright ponds, although three of them, *E. cyathigerum*, *L. depressa* and *A. imperator*, also appeared sparsely or regularly, though in small numbers, at one or the other of the peat diggings.

Table 1 Dragonflies inhabiting bright and dark ponds as adults and/or larvae. Abundance classes: ++ = common; + = regular; (+) = sparse; – = absent. For further information see Methods and Results

	Six bright ponds in gravel pits		Six dark ponds in peatland	
	Adults	Exuviae	Adults	Exuviae
Enallagma cyathigerum (Charpentier, 1840)	++	++	(+)	–
Anax imperator (Leach, 1815)	++	++	+	(+)
Libellula depressa (Linnaeus, 1758)	++	++	(+)	–
Orthetrum cancellatum (Linnaeus, 1758)	++	++	–	–
Orthetrum brunneum (Fonscolombe, 1837)	++	++	–	–
Pyrrhosoma nymphula (Sulzer, 1776)	+	+	+	+
Coenagrion puella (Linnaeus, 1758)	++	++	++	++
Aeshna cyanea (Müller, 1764)	++	++	++	++
Libellula quadrimaculata (Linnaeus, 1758)	++	++	++	++
Sympetrum striolatum (Charpentier, 1840)	++	++	+	+
Lestes virens (Charpentier, 1825)	–	–	++	++
Lestes sponsa (Hansemann, 1823)	–	–	++	++
Lestes viridis (Vander Linden, 1825)	–	–	+	+
Coenagrion pulchellum (Vander Linden, 1825)	–	–	+	+
Aeshna juncea (Linnaeus, 1758)	–	–	+	+
Cordulia aenea (Linnaeus, 1758)	–	–	+	+
Somatochlora flavomaculata (Vander Linden, 1825)	–	–	+	+
Leucorrhinia pectoralis (Charpentier, 1825)	–	–	++	++
Sympetrum sanguineum (Müller, 1764)	–	–	+	+

Successful development (that is, finding of a few exuviae) was observed only in *A. imperator*. By comparison, nine species, *Lestes virens* (Charpentier), *Lestes sponsa* (Hansemann), *Lestes viridis* (Vander Linden), *Coenagrion pulchellum* (Vander Linden), *Aeshna juncea* (Linnaeus), *Cordulia aenea* (Linnaeus), *Somatochlora flavomaculata* (Vander Linden), *Leucorrhinia pectoralis* (Charpentier) and *Sympetrum sanguineum* (Müller), proved to be common or occurred regularly only at dark ponds, all of them being absent in bright ponds. A further five species, *Pyrrhosoma nymphula* (Sulzer), *Coenagrion puella* (Linnaeus), *Aeshna cyanea* (Müller), *Libellula quadrimaculata* (Linnaeus) and *Sympetrum striolatum* (Charpentier), were common in both types of pond, obviously showing no preference to dark or bright waters.

The following four abundance classes were recognised for Anisoptera (A) and Zygoptera (Z): *Adults*: the number of recorded individuals per visit at 'bright' and 'dark' ponds during the peak of the flight period: ++ = common: $A \geq 3$, $Z = 20$; + ≥ regular: $A \geq 1$, $Z \geq 5$; (+) = sparse: A varying (0–3), Z varying (0–3); – = absent: no records. *Exuviae* (n = total number of Anisoptera exuviae collected between 1995 and 2000): ++ = common: A = 100–1000, Z exuviae and freshly emerged adults frequently recorded; + = regular: A = 10–99, Z exuviae and freshly emerged adults repeatedly recorded; (+) = sparse: A = 1–10, Z exuviae and freshly emerged adults sporadically recorded; – = absent: no records. The results are shown in Table 1. Species that we recorded only exceptionally as adults were considered to be 'guest' species and are omitted from this analysis. Results of the optical observations are shown in Figs 1–6.

In the visible (red, green, blue) ranges of the spectrum there were no significant differences in brightness between dark and bright water bodies towards the sun (Fig. 1a). The same was true in the ultraviolet spectral range away from the sun and perpendicularly to the sun (Fig. 2a,b). In the green and red spectral ranges, however, the intensity of light reflected by bright waters was significantly higher than that reflected by dark ponds away from the sun (Fig. 1b) and perpendicularly (Fig. 1c).

The degree of polarisation of light reflected from bright or dark waters was the greatest for the blue range of the spectrum for any direction of view with respect to the sun (Figs 1d–f and 2c,d). Independently of the wavelength and the viewing direction with respect to the sun, the degree of polarisation of light reflected from dark water bodies was significantly higher than that reflected from bright waters

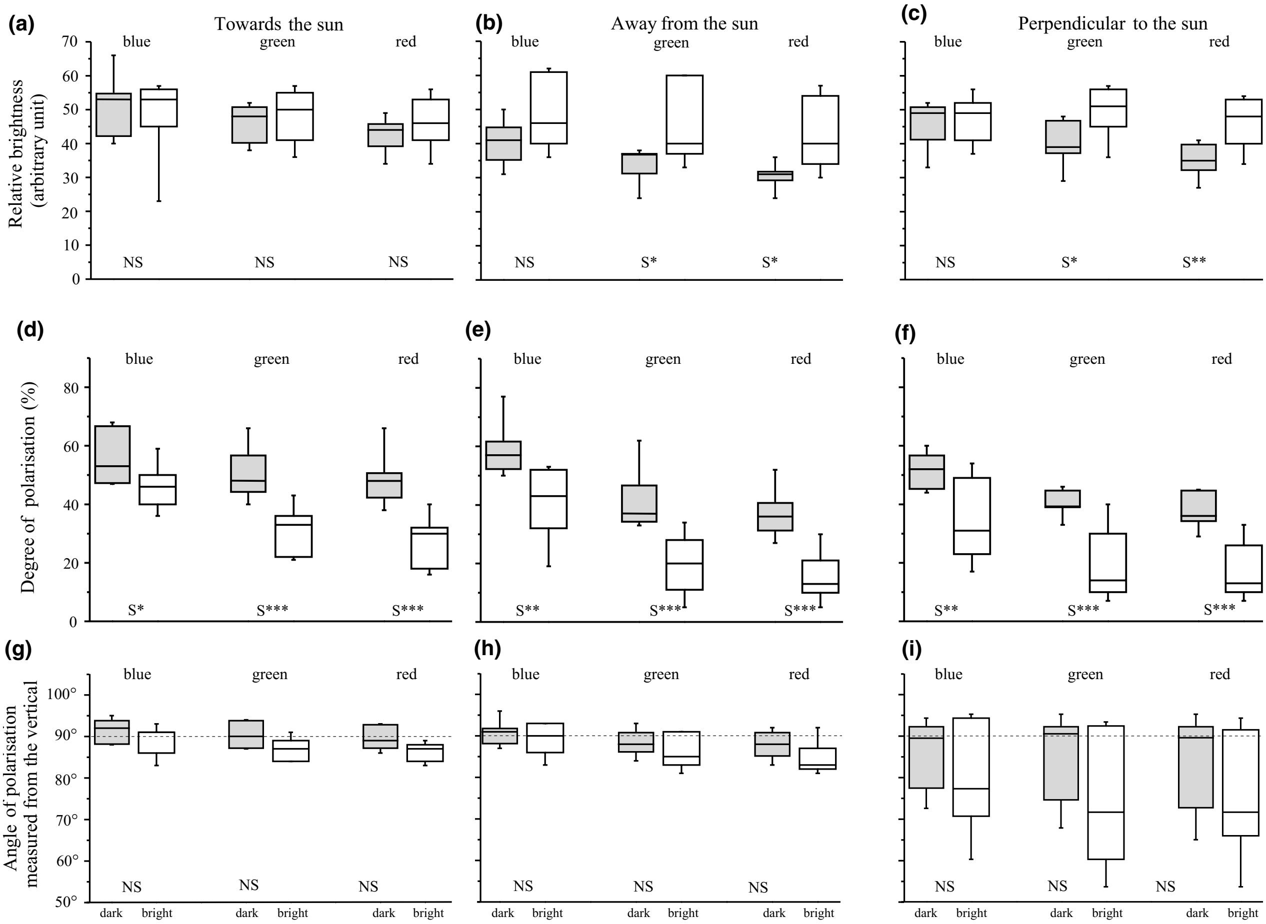


Fig. 1 Means (horizontal bars in boxes), quartiles (boxes), 5th and 95th percentile values (vertical bars protruding from boxes) of the relative brightness, degree of polarisation and angle of polarisation (with respect to the vertical; 0°, vertical; 90°, horizontal) measured by videopolarimetry (using a Sony 3CCD VX1E Hi8 video camera) at sunlit surfaces of six bright and six dark Swiss ponds in three different viewing directions (towards the sun, away from the sun, perpendicular to the sun) in the red ($\lambda_{max} = 650$ nm), green ($\lambda_{max} = 550$ nm) and blue ($\lambda_{max} = 450$ nm) spectral ranges. Data for dark or bright ponds are shown by dark grey or white boxes, respectively. *t*-Test (Sachs, 1974) was used; S*, $P < 0.05$; S**, $P < 0.01$; S***, $P < 0.001$; NS, not significant.

(Figs 1d–f and 2c,d). The differences in degree of polarisation of reflected light between dark and bright waters were the smallest in the blue range of the spectrum (Figs 1d–f and 2c,d).

Independently of the wavelength as well as the viewing direction, the average direction of polarisation of light reflected by waters is generally horizontal for both bright and dark water bodies (Figs 1g–i and 2e,f). However, the variation of the angle of polarisation of reflected light is small towards the sun (Fig. 1g) and away from the sun (Figs 1h and 2e), while it is large perpendicular to the sun for clear skies (Figs 1i and 2f).

The direction of polarisation of light reflected by bright water changes from horizontal to vertical from the shorter wavelengths towards the longer ones (Fig. 3), if the amount of vertically polarised light emanating from the subsurface overwhelms the amount of horizontally polarised surface-reflected light for longer wavelengths. Similar change in the direction of polarisation does not occur in the case of dark water bodies (Fig. 4).

Shadows also have a considerable effect on the reflection-polarisation characteristics of water bodies. In the case of dark waters, the horizontally polarised surface-reflected light always dominates, and thus the direction of polarisation is always horizontal for both the shaded and sunlit regions (right column of Fig. 4). The middle column of Fig. 4 shows that the degree of polarisation of light reflected from the shaded regions

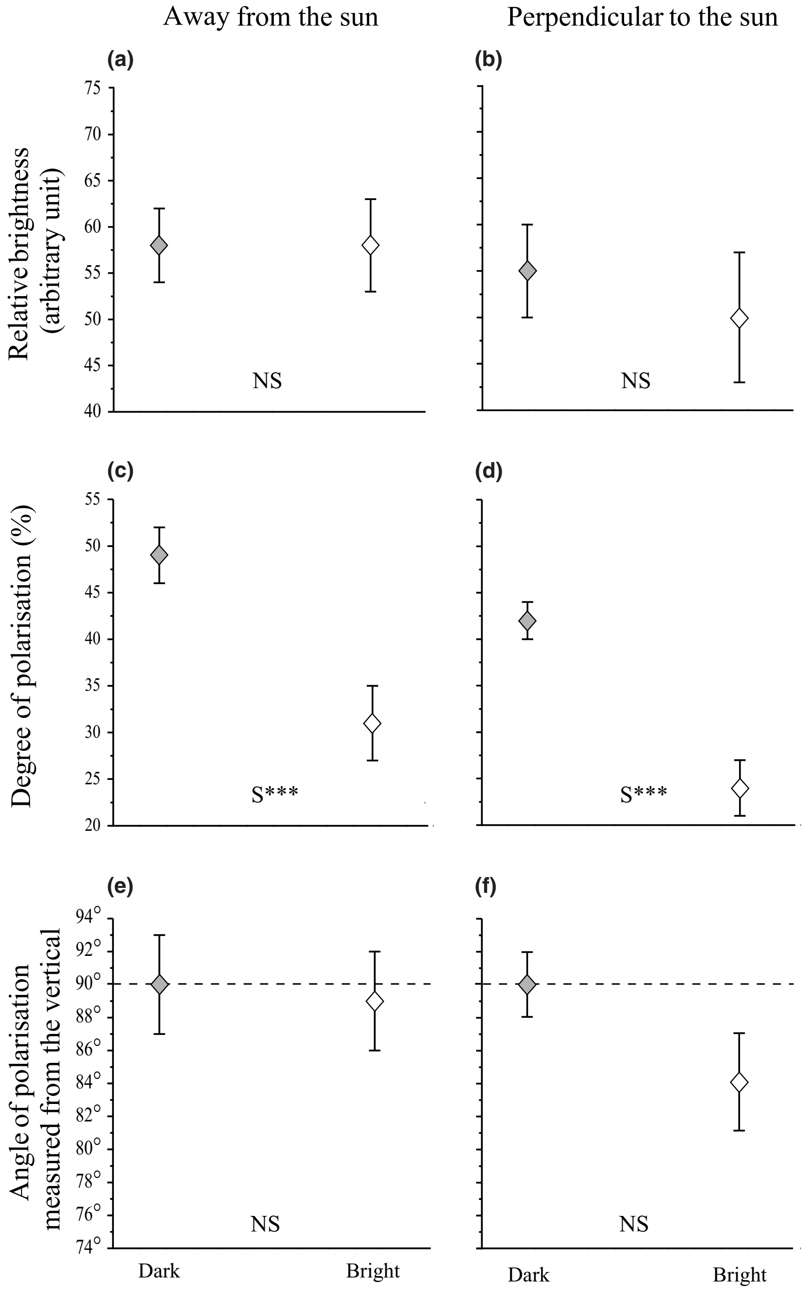
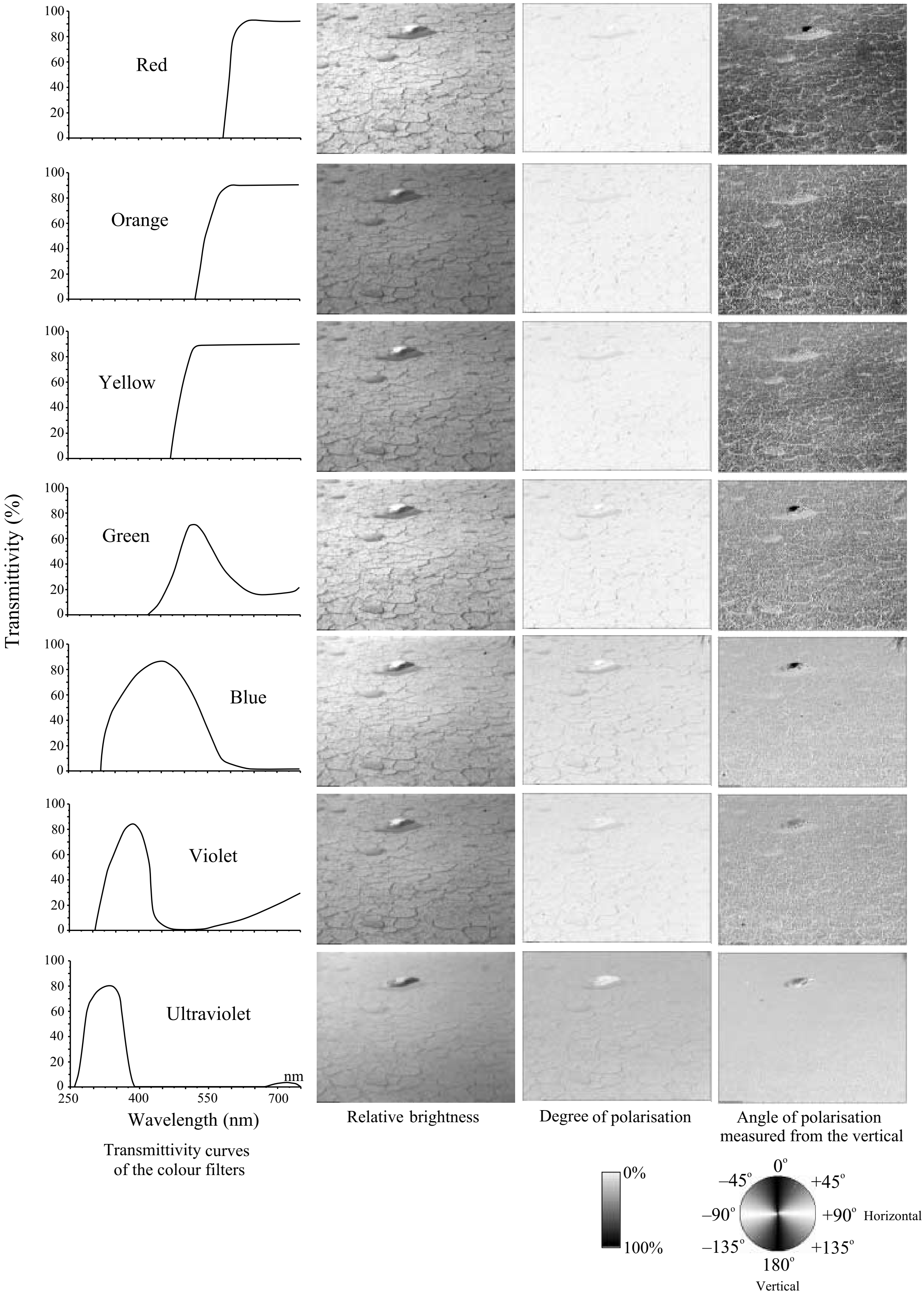


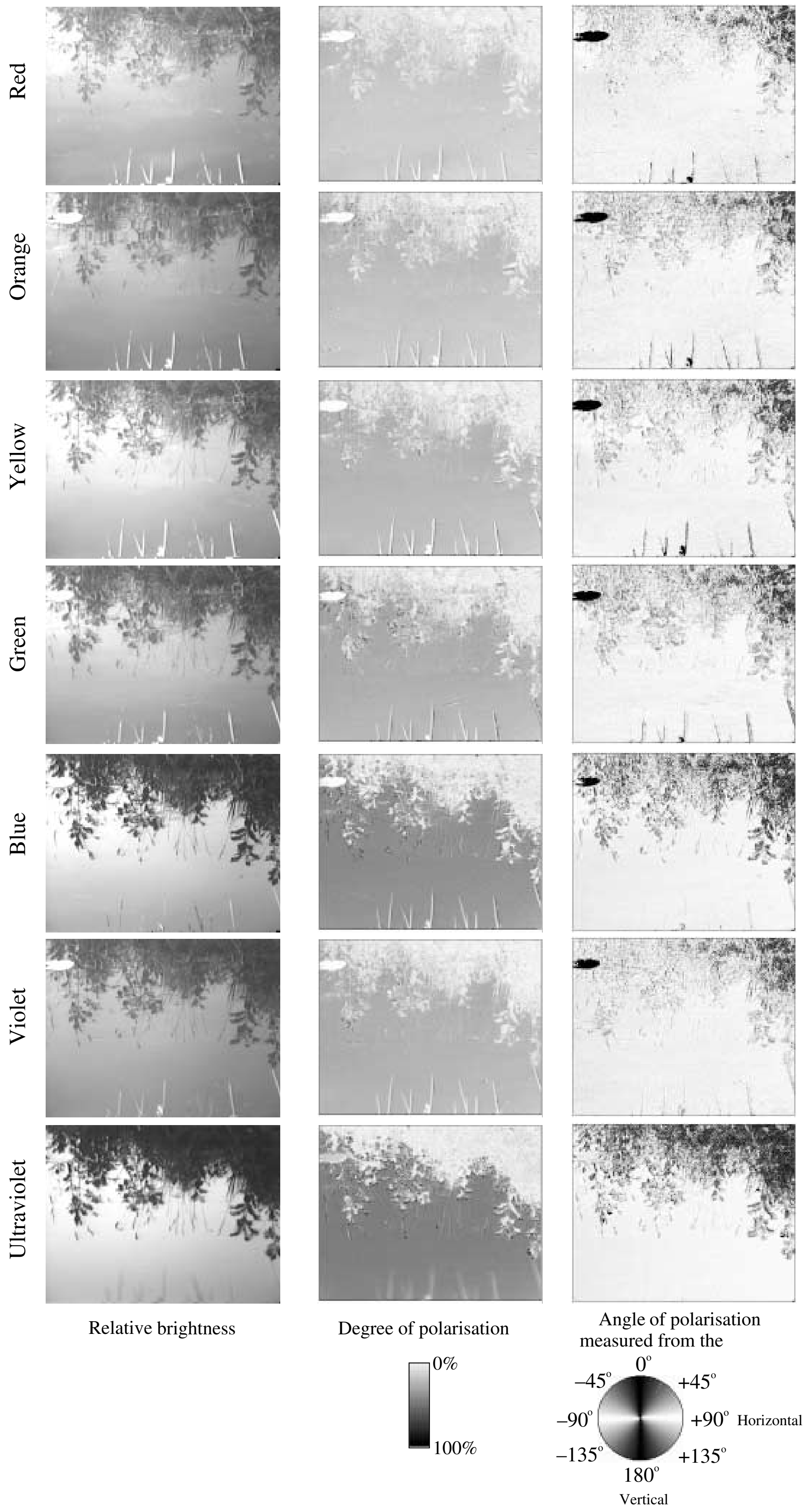
Fig. 2 Means (rhombi) and standard deviations (vertical bars protruding from rhombi) of the relative brightness, degree of polarisation and angle of polarisation (with respect to the vertical; 0°, vertical; 90°, horizontal) measured by videopolarimetry (using a Hamamatsu Beam Finder III) at sunlit surfaces of a dark and a bright pond in two different viewing directions (away from the sun and perpendicular to the sun) in the ultraviolet ($\lambda_{max} = 360$ nm) spectral range. Data for the dark or the bright pond are symbolised by dark grey or white rhombi, respectively. Welch-test (Sachs, 1974) was used; S***, $P < 0.001$; NS, not significant.

of dark waters is, however, lower than that reflected from the sunlit regions, because in the shaded areas the amount of horizontally polarised surface-reflected light is more or less reduced. The situation is quite different in the case of bright water bodies, where the net degree of polarisation of reflected light is generally low, due to the approximately equal amount of the horizontally polarised surface-reflected light component and the vertically polarised light component reflected from below the surface. In a given spectral

▶

Fig. 3 Transmittivity *T* versus wavelength λ of the colour filters used in the videopolarimetric measurements (left column) and reflection-polarisation (relative brightness *I*, degree of linear polarisation *p* and angle of polarisation α measured from the vertical) patterns of a bright pond in a gravel pit measured by videopolarimetry (using a Hamamatsu Beam Finder III mounted with different colour filters) in seven different ranges of the spectrum perpendicular to the sun with a viewing angle of 20° below the horizontal. The different values of *I*, *p* and α are represented by different grey tones as indicated in the bottom insets.


Red
Orange
Yellow
Green
Blue
Violet
Ultraviolet
Transmittivity (%)
100
80
60
40
20
0
250
400
550
700
nm
Wavelength (nm)
Transmittivity curves of the colour filters
Relative brightness
Degree of polarisation
Angle of polarisation measured from the vertical
0%
100%
0°
–45°
+45°
–90°
+90°
Horizontal
–135°
+135°
180°
Vertical


Red
Orange
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Green
Blue
Violet
Ultraviolet
Relative brightness
Degree of polarisation
0%
100%
Angle of polarisation measured from the
0°
–45°
+45°
–90°
+90°
Horizontal
–135°
+135°
180°
Vertical

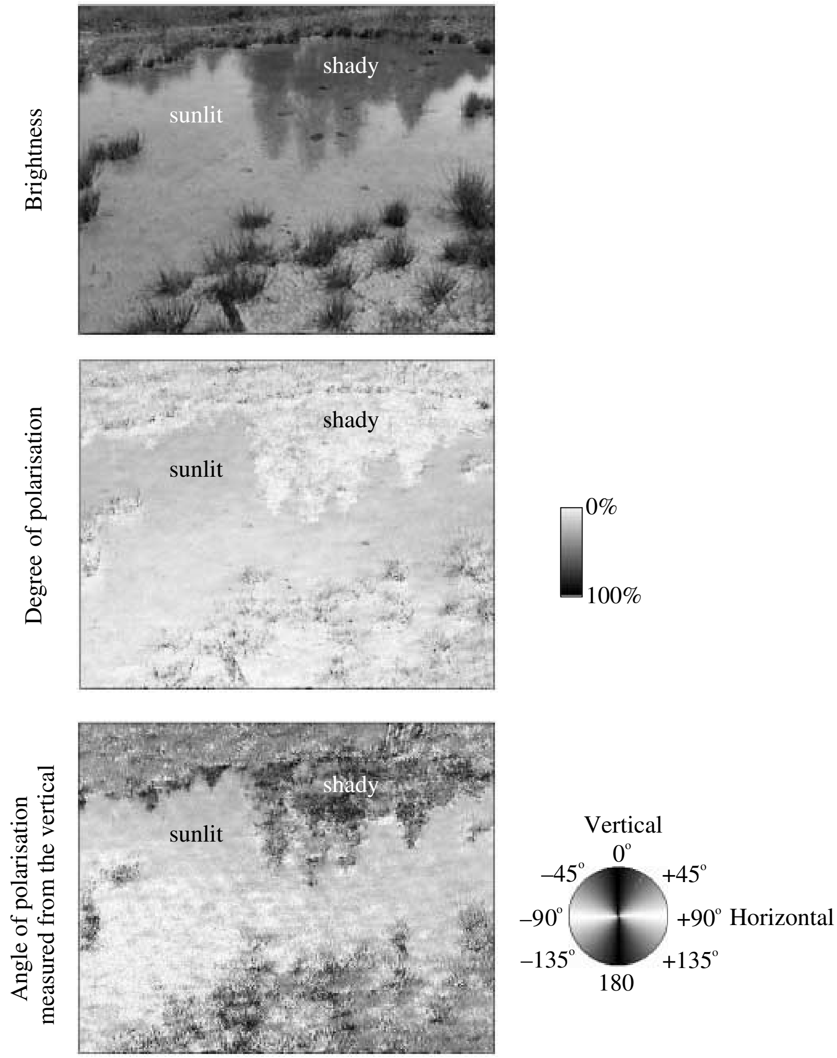

Fig. 5 Reflection-polarisation patterns of a sunlit bright pond with shady regions measured by videopolarimetry (using a Sony 3CCD VX1E Hi8 video camera) in the blue ($\lambda_{max} = 450$ nm) spectral range perpendicular to the sun with a viewing angle of 20° from the horizontal.

range the net direction of polarisation is horizontal if the surface-reflected component dominates, while the net direction of polarisation is vertical when the subsurface-reflected component dominates. Fig. 5 shows an example for a bright pond, in the sunlit or shaded regions of which the direction of polarisation is horizontal or vertical, and the degree of polarisation is higher or lower, respectively. Fig. 6 presents another bright pond, where the contrasts of the angle and degree of polarisation are contrary to those in Fig. 5. In Fig. 6, in the sunlit or shady regions of the bright pond, the direction of polarisation is vertical or horizontal, and the degree of polarisation is lower or higher, respectively. The degree of polarisation of bright water bodies is always much less than that of dark waters.

◀

Fig. 4 As Fig. 3 for a dark pond in a peat digging, measured away from the sun, and omitting the repetition of the $T(\lambda)$ curves of the colour filters used.

Discussion

Dark peat ponds and bright waters in gravel pits held different dragonfly faunas, some species unequivocally preferring one or the other type of water body. In some species there was no sharp distinction, however, and a number of species proved to be unspecialised with respect to their habitat. In general, earlier findings concerning the species composition of small water bodies in peatland, gravel pits and other

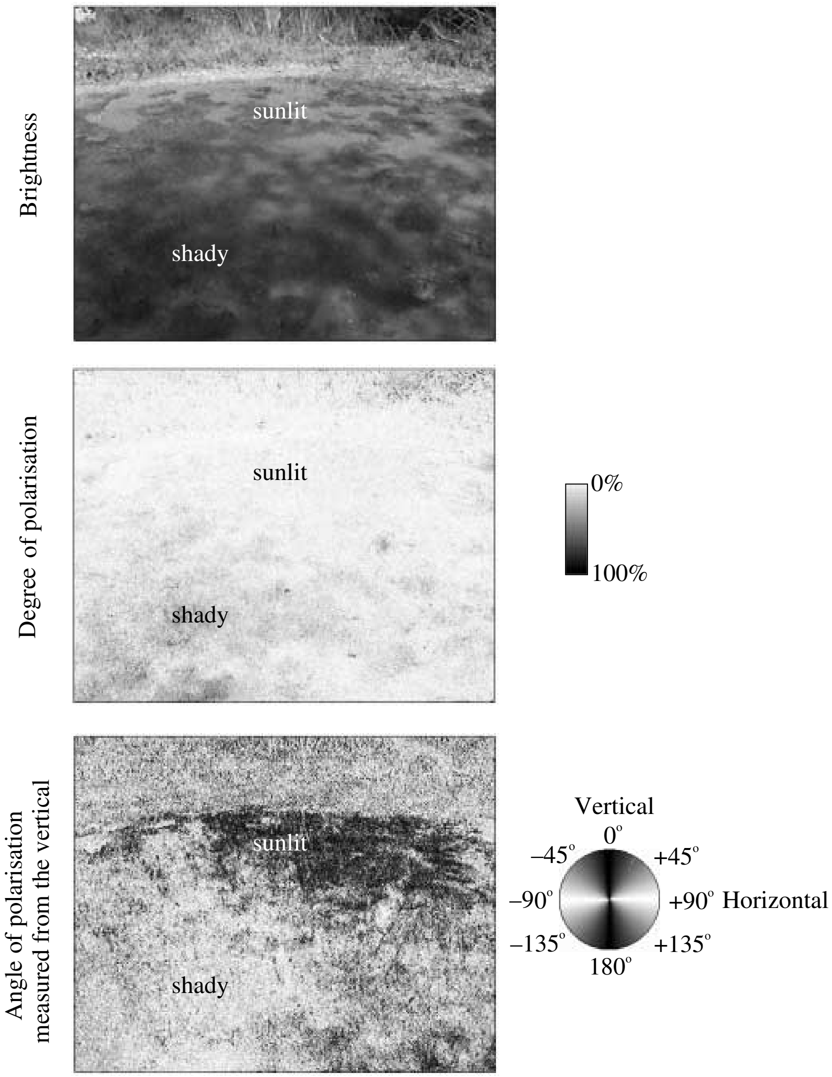

Fig. 6 As Fig. 5 for another shady bright pond with sunlit regions measured in the green (λ_{max} = 550 nm) spectral range away from the sun.

secondary biotopes in the Swiss midlands were confirmed (Wildermuth, 1980, 1992a,b; Wildermuth & Krebs, 1983, 1987).

The optical results are a consequence of the following phenomena. (1) Water surfaces reflect light almost independently of the wavelength. (2) The subsurface layers of dark water bodies absorb light almost independently of the wavelength. (3) The absorption of the subsurface layers of bright water bodies is higher at short wavelengths than at long ones. Hence, apart from the direction of the sun, and for sufficiently large angles of view with respect to the water surface, bright water bodies are generally brighter than dark ones, but only for longer wavelengths. This is because the contribution of the subsurface layers to the net reflectivity is weak for shorter wavelength in comparison with the surface reflection. This brightness difference disappears in the direction of the sun because of the dominance of the surface-reflected direct sunlight.

The reasons of the results obtained for the degree of polarisation of light reflected by ponds are manifold. First, the intensity of blue skylight reflected from the water surface is highest in the blue range of the spectrum. Second, independent of the wavelength and the viewing direction with respect to the sun, the subsurface layers of dark waters strongly absorb the penetrating light and the surface reflects horizontally polarised light with lower or higher degrees of polarisation depending on the angle of reflection. Thus, the degree of horizontal polarisation of surface-reflected light is barely reduced by the vertical polarisation of light originating from the subsurface regions. Third, in the case of bright waters the considerable amount of vertically polarised light emanating from the subsurface regions reduces significantly the degree of horizontal polarisation of the surface-reflected light. The longer the wavelength, the larger the amount of light emanating from the subsurface regions, and the lower the net degree of polarisation of reflected light.

The results obtained for the angle of polarisation of light reflected by ponds can be explained as follows. A clear blue sky has characteristic patterns of the degree and angle of polarisation, depending on the solar zenith angle. If the partially linear polarised skylight is reflected from the flat water surface, surface-specific patterns of the degree and angle of polarisation form because of the strong re-polarisation ability of the water surface (Schwind & Horváth, 1993; Horváth, 1995; Gál *et al*., 2001). The direction of polarisation of surface-reflected skylight is always horizontal in an annular zone, called the Brewster zone, from which totally polarised light is reflected. Towards the sun and away from the sun the direction of polarisation of incident skylight is always horizontal, which does not change the net horizontal direction of polarisation of light reflected by the water in these directions of view. Perpendicular to the sun, inside and outside the Brewster zone, surface-reflected skylight is diagonally or vertically polarised because of the diagonal or vertical direction of polarisation of the incident skylight. This effect more or less modifies the net angle of polarisation of light reflected by the water body and increases the variation of the angle of polarisation of bright waters.

The reflection-polarisation characteristics of dark and bright water bodies are also influenced by the roughness of the water surface. Under windy conditions the water surface undulates, which more or less distorts the reflection-polarisation patterns (Mobley, 1994; Shaw, 1999). Although in this case both the degree and angle of polarisation of light reflected from the water surface changes spatiotemporally, when averaged over time, a significant degree of polarisation difference between dark and bright waters remains, in spite of the rippling of the water surface. Emergent vegetation can, however, remove this difference due to the diffuse reflection and/or scattering of light at the surface and/or in the subsurface regions in the green range of the spectrum.

On the basis of the above analysis and discussion we conclude the following:

1 Dragonflies in this study, fell into three groups: (a) certain species prefer exclusively bright water bodies, while (b) other species prefer only dark water bodies, and (c) some species are ubiquitous, choosing dark and bright waters with equal frequency.

2 From long distances (at a small angle of view with respect to the water surface), dark water bodies cannot be distinguished from bright ones on the basis of the intensity of reflected light or its angle of polarisation. However, even at such small angles of view dark waters reflect light with a significantly higher degree of polarisation than bright waters in any range of the visible spectrum and in any direction of view with respect to the sun. Although in the ultraviolet spectral range, the reflection-polarisation characteristics are presented for only one dark and one bright pond as an example, conclusion (2) may also be extended to the ultraviolet region of the spectrum, because we do not know of any physical (optical) argument against it.

Conclusion (2) does not contradict the fact that the polarisation-blind human visual system discriminates between dark and bright waters by intensity differences. This distinction can be made only if the water bodies are relatively close to the observer, so that the viewing angle with respect to the horizontal is large. As a consequence, the amount of surface-reflected light is comparable with the amount of light originating from the subsurface layers. For small viewing angles from the water surface, the surface-reflected light overwhelms the light coming from the subsurface layers for both dark and bright waters. This effect makes it more difficult or even impossible to discriminate between dark and bright waters from a distance on the basis of the intensity of reflected light. From great distances the only optical cue that can be the basis of this distinction is the degree of polarisation of reflected light.

Water bodies possess many physical, chemical and biotic features. Although mechanical (Wildermuth, 1992b), thermal (Sternberg, 1990) and even olfactory (Steiner, 1948) characteristics can be used in the precise localisation of oviposition sites, dragonflies recognise their habitat mainly by visual cues (Wildermuth & Spinner, 1991; Wildermuth, 1993), one of them being the partially and horizontally linear polarised reflected light (Horváth *et al.*, 1998; Wildermuth, 1998). Depth, turbidity, transparency, colour, surface roughness of water and composition of the substratum greatly influence the reflection-polarisation characteristics of water bodies. The degree of polarisation of reflected light is a physical property that can be perceived from great distances and provides some information about the quality of the habitat. Thus, it may be the visual cue for polarisation-sensitive dragonflies enabling them to discern dark and bright water bodies from a distance. Future studies applying structural manipulations of natural substrata and choice experiments using dummies should prove whether dragonflies indeed use the degree of polarisation of reflected light in their habitat selection. However, one should bear in mind that polarised light is only one of the visual cues guiding dragonflies in the search of water habitats. In *Coenagrion mercuriale* (Charpentier), *Platycnemis pennipes* (Pallas) and *Leucorrhinia pectoralis* (Charpentier) it was shown experimentally that structural features of the habitat, such as emergent vegetation, are also important for the choice of the adults (Buchwald, 1989; Martens, 1996; Wildermuth, 1992a). Thus, different cues may act in combination or sequentially when a dragonfly in search of suitable breeding habitats approaches a water body.

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