



## Degrees of polarization of reflected light eliciting polarotaxis in dragonflies (Odonata), mayflies (Ephemeroptera) and tabanid flies (Tabanidae)

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### ABSTRACT

With few exceptions insects whose larvae develop in freshwater possess positive polarotaxis, i.e., are attracted to sources of horizontally polarized light, because they detect water by means of the horizontal polarization of light reflected from the water surface. These insects can be deceived by artificial surfaces (e.g. oil lakes, asphalt roads, black plastic sheets, dark-coloured cars, black gravestones, dark glass surfaces, solar panels) reflecting highly and horizontally polarized light. Apart from the surface characteristics, the extent of such a 'polarized light pollution' depends on the illumination conditions, direction of view, and the threshold  $p^*$  of polarization sensitivity of a given aquatic insect species.  $p^*$  means the minimum degree of linear polarization  $p$  of reflected light that can elicit positive polarotaxis from a given insect species. Earlier there were no quantitative data on  $p^*$  in aquatic insects. The aim of this work is to provide such data. Using imaging polarimetry in the red, green and blue parts of the spectrum, in multiple-choice field experiments we measured the threshold  $p^*$  of ventral polarization sensitivity in mayflies, dragonflies and tabanid flies, the positive polarotaxis of which has been shown earlier. In the blue (450 nm) spectral range, for example, we obtained the following thresholds: dragonflies: *Enallagma cyathigerum* ( $0\% < p^* \leq 17\%$ ), *Ischnura elegans* ( $17\% \leq p^* \leq 24\%$ ). Mayflies: *Baetis rhodani* ( $32\% \leq p^* \leq 55\%$ ), *Ephemera danica*, *Epeorus silvicola*, *Rhithrogena semicolorata* ( $55\% \leq p^* \leq 92\%$ ). Tabanids: *Tabanus bovinus*, *Tabanus tergstinus* ( $32\% \leq p^* \leq 55\%$ ), *Tabanus maculicornis* ( $55\% \leq p^* \leq 92\%$ ).

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### 1. Introduction

As a rule of thumb, insects with aquatic larvae detect water by means of the horizontal polarization of light reflected from the water surface (Schwind, 1991, 1995; Horváth and Varjú, 2004; Lerner et al., 2008), with the yet only known exception of the yellow fever mosquito, *Aedes aegypti* (Bernáth et al., 2008). Polarotactic aquatic insects are attracted to sources of horizontally polarized light. The unfortunate consequence of this positive polarotaxis is that aquatic insects can be deceived by artificial surfaces reflecting highly and horizontally polarized light. Such surfaces are crude and waste oil lakes (Horváth and Zeil, 1996; Horváth et al., 1998; Bernáth et al., 2001), asphalt roads (Kriska et al., 1998), black plastic sheets used in agriculture (Wildermuth, 1998; Kriska et al., 2007), black, red or dark-coloured cars (Wildermuth and Horváth, 2005; Kriska et al., 2006), polished black gravestones (Horváth et al., 2007), dark glass surfaces (Kriska et al., 2008; Malik et al., 2008), but even shiny black photovoltaic

solar panels and sun collectors (Horváth et al., 2009), for example. These human-made shiny dark surfaces may act as polarized ecological traps for polarotactic insects, because such surfaces are inappropriate for the development of eggs laid onto them by the deceived and attracted insects, which can also perish due to exhaustion, or dehydration (Horváth and Varjú, 2004; Horváth and Kriska, 2008).

All adverse effects of such artificial surfaces on polarotactic aquatic insects attracted to such artificial surfaces are summarized in the term 'polarized light pollution' introduced recently (Horváth et al., 2009). The extent of polarized light pollution of a given human-made surface depends on the surface characteristics, illumination conditions, direction of view, and the threshold  $p^*$  of polarization sensitivity of a given aquatic insect species.  $p^*$  means the minimum degree of linear polarization  $p$  of reflected light that can elicit positive polarotaxis from a given insect species.

Species-specific values of  $p^*$  may also have a deep ecological meaning. In aquatic environments turbidity and plant density are constraints on predator-prey interactions involving aquatic invertebrates (Van de Meutter et al., 2005). These physical parameters are not directly accessible to flying aquatic insects searching for suitable places for their offsprings. However, the

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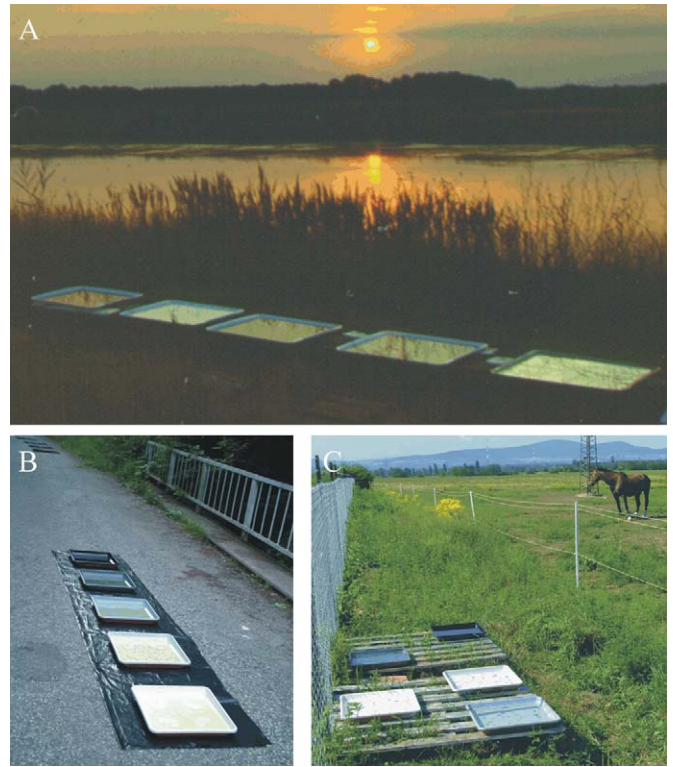
degree of polarization  $p$  of reflected light is a remotely perceivable and reliable physical predictor of aquatic oviposition sites (Bernáth et al., 2002). The higher the  $p^*$  of an aquatic insect, the more probable that it will prefer darker, deeper, or clearer water bodies and avoid brighter, shallow, turbid, or eutrophic ones (Bernáth et al., 2004).

Unfortunately the literature does not contain reliable quantitative values of  $p^*$  in aquatic insects. Schwind (1995) hypothesized that the value of  $p^*$  for the ventral polarization-sensitive eye region in aquatic beetles and bugs studied by him may be much higher ( $p^* \approx 35\%$ ) than that of the polarization-sensitive dorsal-rim area of the eye in the field cricket, *Gryllus campestris* ( $p^* \approx 5\%$  for blue light; Labhart, 1996) and the honey bee, *Apis mellifera* ( $p^* \approx 11\%$  for ultraviolet light; von Frisch, 1967; Rossel and Wehner, 1984).

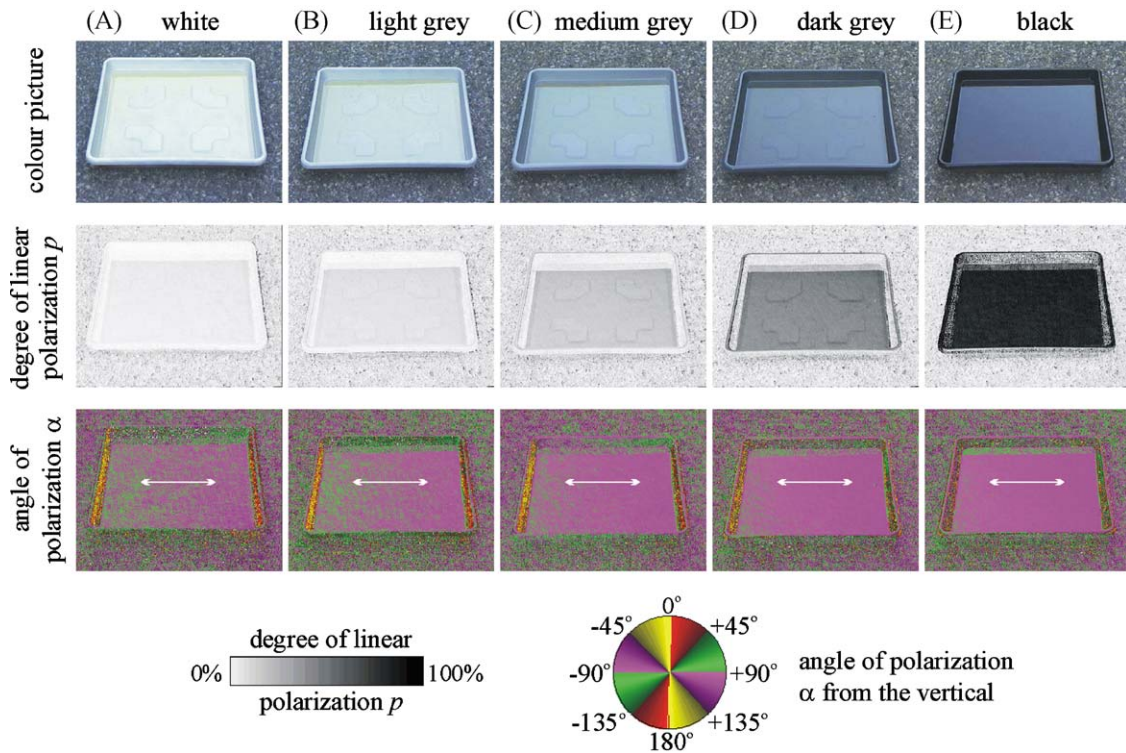
The aim of this work is to provide data on  $p^*$  in dragonflies, mayflies, and tabanid flies. Using imaging polarimetry in the red, green and blue parts of the spectrum, in multiple-choice field experiments we measured the threshold  $p^*$  of ventral polarization sensitivity in mayflies, dragonflies and tabanid flies, the positive polarotaxis of which has been shown earlier (mayflies: Kriska et al., 1998, 2007; dragonflies: Wildermuth, 1998; Horváth et al., 1998, 2007; Bernáth et al., 2002; tabanid flies: Horváth et al., 2008). This work presents the first experimentally supported values of  $p^*$  in mayflies, dragonflies and tabanids. The knowledge of  $p^*$  in aquatic insects allows one to measure and monitor the extent of polarized light pollution of artificial surfaces in the human-made optical environment.

**2. Materials and methods**

We captured dragonflies, mayflies and tabanid flies with the use of colourless (white, light grey, medium grey, dark grey, black) liquid traps (Fig. 1) reflecting horizontally polarized light with different degrees of linear polarization  $p$  (Fig. 2). From the numbers



**Fig. 1.** Arrangement of the five salad-oil-filled trays in the 1st (A), 2nd (B) and 3rd (C) experiment at Kunfehértó (A), Dömörkapu (B) and Göd (C), in Hungary.



**Fig. 2.** Reflection–polarization characteristics of shady salad-oil-filled white (A), light grey (B), medium grey (C), dark grey (D) and black (E) trays used in the choice experiments and measured by imaging polarimetry in the blue (450 nm) part of the spectrum (see also Table 4). In the  $\alpha$ -patterns double-headed arrows show the always horizontal direction of polarization of reflected light. When the test surfaces were sunlit, their polarization patterns were quite similar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

**Table 1**

Number of different dragonfly species (males and females together) trapped in the 1st experiment (Fig. 1A).

Dragonfly species	Salad-oil-filled tray			
	White	Light grey	Dark grey	Black
<i>Ischnura elegans</i>	6	22	32	30
<i>Erythromma viridulum</i>	2	4	8	14
<i>Lestes macrostigma</i>	0	1	5	4
<i>Enallagma cyathigerum</i>	17	15	24	19
Sum	25 (12.3%)	42 (20.7%)	69 (34.0%)	67 (33.0%)

of captured insects we determined the lower ( $p_{\min}$ ) and upper ( $p_{\max}$ ) limits of  $p^*$  in the investigated positively polarotactic insect species.

The first choice experiment was performed with dragonflies between 24 July and 8 August 1997 in a large field about 500 m away from a small alkaline lake (a typical emergence site of dragonflies) at Kunfehértó (46°22'N, 19°23'E) in the southern part of the Hungarian Great Plain (Fig. 1A and Table 1). The traps were left in the field continuously and checked every day. The trays were covered by wooden boards every day from sunset to sunrise, furthermore when it was raining. The distance between the neighbouring trays was 50 cm, and their positions were changed randomly once daily at sunset. This regular shuffling of the trays served to prevent possible artefacts originating from inequalities in the immediate vicinity (e.g. vegetation, prevailing winds). (For further details see Horváth et al., 1998.) In this experiment only four grey (white, light grey, dark grey, black) test surfaces were used; the bottom of the fifth tray was shiny aluminium foil serving as a control, reflecting weakly and non-horizontally polarized light. Since the aluminium test surface served only to prove the positive polarotaxis in dragonflies, and is irrelevant in the determination of the threshold  $p^*$  of the degree of polarization that can elicit positive polarotaxis, the numbers of dragonflies trapped by the aluminium tray were not used in the statistical analysis and are not given in Table 1.

The second choice experiment was conducted with mayflies at Dömörkapu (47°40'N, 19°03'E), in Hungary, between 11 May and 3 June 2008 from 19 to 21 h (=local summer time = UTC + 2 h) every day. Five (white, light grey, medium grey, dark grey, black) salad-oil-filled trays (Fig. 1B) were put on an asphalt road running in the immediate vicinity of a mountain creek, a typical emergence site of mayflies, which was studied thoroughly by Kriska et al. (1998). The trays were underlaid by a horizontal shiny black plastic sheet of 70 cm × 300 cm. The function of this highly and horizontally polarizing black plastic sheet was to attract polarotactic mayflies to the experimental area from greater distances. The order of the trays was changed randomly and hourly, because the investigated mayflies swarmed only near sunset, between 19 and 21 h. Since the trays were always in the shade of the neighbouring trees, their

**Table 2**

Number of different mayfly species (males and females together) trapped in the 2nd experiment (Fig. 1B).

Mayfly species	Salad-oil-filled tray				
	White	Light grey	Medium grey	Dark grey	Black
<i>Baetis rhodani</i>	0	1	2	20	39
<i>Epeorus silvicola</i>	0	0	2	12	60
<i>Ephemera danica</i>	1	8	14	31	195
<i>Rhithrogena semicolorata</i>	14	14	17	69	440
Sum	15 (1.6%)	23 (2.4%)	35 (3.7%)	132 (14.1%)	734 (78.2%)

**Table 3**

Number of different tabanid species (males and females together) trapped in the 3rd experiment (Fig. 1C).

Tabanid species	White	Light grey	Medium grey	Dark grey	Black
<i>Atylotus loewianus</i>	–	–	–	1	2
<i>Haematopota italica</i>	–	–	–	1	2
<i>Tabanus bovinus</i>	–	1	–	9	13
<i>Tabanus maculicornis</i>	–	–	–	–	16
<i>Tabanus tergustinus</i>	1	1	3	11	50
Sum	1 (0.9%)	2 (1.8%)	3 (2.7%)	22 (19.8%)	83 (74.8%)

temperature was always the same. The mayflies trapped by these trays were collected, stored in alcohol, and later identified (Table 2).

The third choice experiment was done with tabanid flies in a Hungarian horse school at Dömörkapu (47°43'N, 19°09'E) between 11 July and 7 September 2008. Five (white, light grey, medium grey, dark grey, black) salad-oil-filled trays (Fig. 1C) were put on the grassy ground, 50 cm apart from each other, and their order was changed randomly once daily at sunset. They were covered by wooden boards every day from sunset to sunrise, and also when it was raining. The tabanids trapped by these trays were collected, stored in alcohol, and later identified (Table 3).

The reason for the different temporal changes of test surfaces in the choice experiments was that the investigated dragonflies and tabanid flies were active throughout the whole day, while the studied mayflies swarmed only near sunset. Thus, the order of the trays in the experiment with mayflies should have been changed much more frequently (hourly) than in the case of dragonflies and tabanids (once daily).

The reflection–polarization characteristics of the test surfaces (salad-oil-filled trays) used in all three experiments were measured by imaging polarimetry in the red ( $650 \pm 40$  nm = wavelength of maximal sensitivity  $\pm$  half bandwidth of the CCD detectors of the polarimeter), green ( $550 \pm 40$  nm) and blue ( $450 \pm 40$  nm) parts of the spectrum. In this work we present only the polarization patterns of the shady trays measured in the blue spectral range (Fig. 2). Quite similar patterns were obtained in the red and green parts of the spectrum, and if the trays were sunlit. The method of imaging polarimetry has been described in detail by Horváth and Varjú (1997). The polarimetric measurements of the test surfaces were performed under clear sky. The optical axis of the polarimeter viewed toward the antisolar meridian at the Brewster angle  $\theta_{\text{Brewster}} = \arctan(n) \approx 56.3^\circ$  from the vertical calculated for the refractive index  $n \approx 1.5$  of salad-oil. At the Brewster angle the surface-reflected ray of light is perpendicular to the refracted ray penetrating into the oil, resulting in the highest possible degree of polarization up

**Table 4**

Degree of linear polarization  $p$  (average  $\pm$  standard deviation) of light reflected from the salad-oil-filled white, light grey, medium grey, dark grey and black trays (Fig. 1) used in the choice experiments and measured by imaging polarimetry in the red (650 nm), green (550 nm) and blue (450 nm) parts of the spectrum at the Brewster angle  $\theta_{\text{Brewster}} = 56.3^\circ$  from the vertical averaged for the whole tray surface (Fig. 2). The physical reason for the standard deviation of  $p$  is that the direction of view changed within the field of view ( $40^\circ$  horizontal  $\times$   $30^\circ$  vertical) of the polarimeter. The wavelength-dependency of  $p$  can be explained by the slightly yellowish colour of the salad-oil in the trays, and the blueness of skylight illuminating the trays.

	Degree of linear polarization $p$ (%)		
	Red (650 nm)	Green (550 nm)	Blue (450 nm)
White	6.8 $\pm$ 1.6	7.3 $\pm$ 1.5	17.0 $\pm$ 3.4
Light grey	11.0 $\pm$ 2.1	11.1 $\pm$ 1.9	23.5 $\pm$ 4.7
Medium grey	23.2 $\pm$ 3.1	20.7 $\pm$ 2.8	31.8 $\pm$ 5.6
Dark grey	47.7 $\pm$ 4.9	45.7 $\pm$ 4.4	55.4 $\pm$ 5.6
Black	90.3 $\pm$ 6.1	88.7 $\pm$ 5.7	91.9 $\pm$ 5.3



**Table 5**

Lower ( $p_{\min}$ ) and upper ( $p_{\max}$ ) limits of the polarization sensitivity threshold  $p^*$  eliciting positive polarotaxis from the investigated polarotactic dragonflies, mayflies and tabanids estimated on the basis of the choice experiments (Tables 1–3) and reflection–polarization measurements (Table 4) with the assumption that their polarization sensitivity functions in the red, or green, or blue part of the spectrum.

Species	$p_{\min} \leq p^* \leq p_{\max}$ (%)			
	Red (650 nm)	Green (550 nm)	Blue (450 nm)	Between oil trays
Dragonflies				
<i>Enallagma cyathigerum</i>	0–6.8	0–7.3	0–17.0	White
<i>Ischnura elegans</i>	6.8–11.0	7.3–11.1	17.0–23.5	White–light grey
Mayflies				
<i>Baetis rhodani</i>	23.2–47.7	20.7–45.7	31.8–55.4	Medium grey–dark grey
<i>Ephemera danica</i>				
<i>Epeorus silvicola</i>	47.7–90.3	45.7–88.7	55.4–91.9	Dark grey–black
<i>Rhithrogena semicolorata</i>				
Tabanid flies				
<i>Tabanus bovinus</i>				
<i>Tabanus tergustinus</i>	23.2–47.7	20.7–45.7	31.8–55.4	Medium grey–dark grey
<i>Tabanus maculicornis</i>	47.7–90.3	45.7–88.7	55.4–91.9	Dark grey–black

of reflected light. Thus, the data in Table 4 are the maximum  $p$ -values a polarotactic insect approaching these traps can ever perceive. Earlier, Horváth et al. (1998) measured the reflection–polarization characteristics of the salad-oil-filled trays used to trap dragonflies at an angle of view of  $70^\circ$  from the vertical. In the present work we repeated this measurement, but now the direction of view was the Brewster angle ( $56.3^\circ$ ). This is the reason for the fact that now we obtained higher  $p$ -values (Tables 4 and 5) than earlier (Horváth et al., 1998, Table 2, p. 294).

The temperature  $T$  of the salad-oil in the trays was measured by a digital contact thermometer with an accuracy of  $\Delta T = \pm 0.25^\circ\text{C}$ . When the trays were shady (at low solar elevations, or under cloudy skies), the temperature of the oil in them was the same, while in sunshine the darker the trays, the higher was the oil temperature.

For the statistical analyses of the insects captured by the oil trays in the 1st and 2nd experiments one-way ANOVA (model I) with an estimated experimentwise error rate of 0.05 was used. Orthogonal comparisons were performed to assess the probable  $p^*$  threshold value of the degree of linear polarization  $p$ , separating unattractive trays from polarotaxis-eliciting ones: The (i) white tray against light grey, dark grey and black together; (ii) light grey tray against dark grey and black together; and (iii) dark grey tray against the black one were tested. Analogous method with four comparisons including the medium grey tray was used to analyse the numbers of mayflies captured by the oil trays in the 2nd experiment.

Data recorded in the 3rd experiment were not eligible for ANOVA, thus the  $\chi^2$ -test was used. Comparisons were carried out using repeated tests for all trays (Comp 0), then omitting dark trays started with the black one (Comp 1 – Comp 3). The overall experimentwise error rate was decreased to 0.0127 following the Dunn–Šidák method.

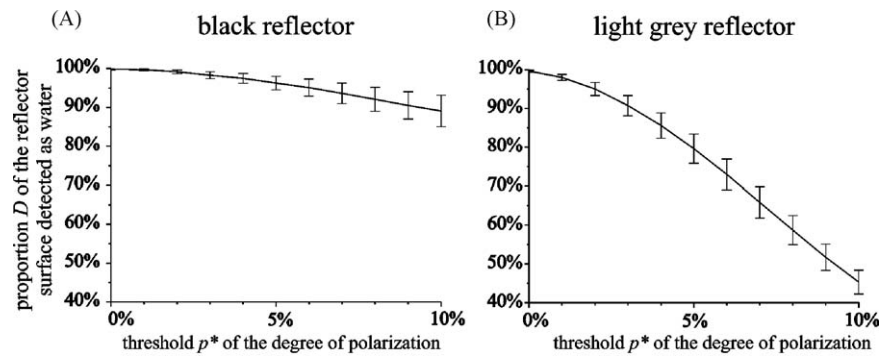
The darker the trap surface, the higher the  $p$  of reflected light (Fig. 2 and Table 4) in all spectral ranges. Since the direction of polarization of light reflected from all five traps was always horizontal (Fig. 2), all traps should be attractive to positively polarotactic dragonflies, mayflies and tabanid flies, given the  $p$  of trap-reflected light was not lower than the species-specific threshold  $p^*$  of polarization sensitivity. Thus, we assume that  $p^*$  must fall between the  $p$  (measured at the Brewster angle) of light reflected from the brightest tray among the trays catching similar numbers of individuals, and the  $p$  (measured at the Brewster angle) of light reflected from the darkest trays among the trays capturing significantly less individuals of a given insect species. Since the trapped insects were killed instantly, pseudoreplication was excluded. All statistical analyses were done with the use of the computer program Statistica 6.0.

### 3. Results

In all three choice experiments (Fig. 1) we obtained the following clear tendencies: the darker the colourless, shiny, horizontally polarizing test surface, the higher the degree of polarization  $p$  of reflected light (Fig. 2 and Table 4), and the larger the attractiveness to dragonflies (Table 1), mayflies (Table 2), and tabanid flies (Table 3). The white and light grey salad-oil-filled trays trapped only 12.3% and 20.7% of the total number of dragonflies. The white, light grey and medium grey trays trapped only 1.6%, 2.4% and 3.7% of mayflies. Similarly, the white, light grey and medium grey trays trapped only 0.9%, 1.8% and 2.7% of tabanids. On the other hand, the dark grey tray captured 34.0%, 14.1%, and 19.8%, of dragonflies, mayflies and tabanids, respectively. Finally, the black tray trapped 33.0%, 78.2%, and 74.8% of dragonflies, mayflies and tabanids, respectively.

Most individuals captured in the 1st experiment belonged to either the two dragonfly species *Ischnura elegans* or *Enallagma cyathigerum* (90 and 75 individuals, respectively), thus these data were analysed separately. The remaining 47 individuals of dragonflies *Erythromma viridulum* and *Lestes macrostigma* were pooled and analysed together. In the case of *I. elegans* the white tray was significantly less attractive, while the differences between the other three (light grey, dark grey, black) trays were statistically not significant, clearly presenting a threshold  $p^*$  between the  $p$ -values of light reflected from the white and the light grey trays (Table 5). For *E. cyathigerum* no statistically significant differences were found (see Supporting Online Material), thus the positive polarotaxis in this species proved by the salad-oil-filled aluminium tray (Horváth et al., 1998) indicates a threshold  $p^*$  not higher than the  $p$ -value of light reflected from the white tray (Table 5). In the case of the pooled data, the results were similar to those of the ones found for *I. elegans* (Supporting Online Material).

For the investigated mayflies and tabanid flies quite similar results were obtained: in the mayfly *Baetis rhodani*, and the tabanid flies *Tabanus bovinus* and *Tabanus tergustinus* the threshold  $p^*$  of polarization sensitivity ranged between the  $p$ -values of light reflected from the medium grey and the dark grey trays, while in mayflies *Ephemera danica*, *Epeorus silvicola* and *Rhithrogena semicolorata*, and the tabanid fly *Tabanus maculicornis*  $p^*$  ranges between the  $p$ -values of light reflected from the dark grey and the black trays (Table 5). The numbers of captured individuals of tabanids *Atylotus loewianus* and *Haematopota italica* were not enough for statistical analysis. Table 5 summarizes the lower ( $p_{\min}$ ) and upper ( $p_{\max}$ ) limits of  $p^*$  in the investigated polarotactic dragonflies, mayflies and tabanid flies, for which statistically



**Fig. 3.** Proportion  $D$  of the whole lower hemispherical field of view in which a given polarotactic aquatic insect can detect water (by means of the horizontal polarization of reflected light) as a function of the threshold  $p^*$  of the degree of polarization. It is assumed that positive polarotaxis is elicited by the reflected light, if (1) it is partially linearly polarized with degrees of polarization  $p > p^*$ , and (2) its direction of polarization deviates from the horizontal with angles less than  $5^\circ$ .  $D$  was calculated for the reflection–polarization patterns of a black and a light grey horizontal reflector mimicking dark and bright waters, and measured by imaging polarimetry. For more details see Bernáth et al. (2004).

significant estimates can be given on the basis of our choice experiments (Tables 1–3) and reflection–polarization measurements (Table 4).

#### 4. Discussion

Insects orienting on the basis of the celestial polarization pattern use the direction of polarization of skylight, because it is the most stable optical variable of the sky (Horváth and Varjú, 2004). Insects most probably do not rely on the degree of polarization  $p$  of skylight for navigation, because it is highly susceptible, even to minor atmospheric disturbances (Coulson, 1988). On the other hand, the brightness (intensity of light coming from water) of a water body cannot be perceived at small angles relative to the water surface, because the light coming from water is then overwhelmed by the light reflected from the water surface. Thus, from a remote distance the brightness of water bodies can be guessed only from the  $p$  of water–returned light. This characteristic  $p$  of water–reflected light correlates with the depth and turbidity (Bernáth et al., 2002), which affect the predator–prey interactions, and are closely related with nutrient concentration and oxygen balance in lake ecosystems. Thus the degree of polarization  $p$  of water–reflected light is of highly useful for water–seeking flying aquatic insects, the larvae of which develop in water.

Highly and horizontally polarized light is a quite stable optical cue of dark/deep water bodies, thus positive polarotaxis with a high threshold  $p^*$  of the degree of polarization can guide aquatic insects to dark/deep waters in most cases. On the other hand, shallow and bright (e.g. alkaline) water bodies reflect weakly polarized light (with low  $p$ ), because the large amount of light coming from the water (scattered back from the bottom, or the suspended particles) is vertically polarized due to refraction at the water surface, and thus reduces the effect of the horizontally polarized light reflected from the water surface. Aquatic insect species bound to find such bright water bodies may possess a lower threshold  $p^*$  and/or fly predominantly at sunset or sunrise to exploit the decrease of the depolarizing backscattered light component coming from water (Csabai et al., 2006).

Although the stimulus series used in our choice experiments (series of test surfaces reflecting light with increasing degree of polarization  $p$  and decreasing intensity  $I$ ) seems to confound  $p$  and  $I$ , this is not a serious problem at all. The reason for this is that in earlier multiple-choice experiments it has been shown that the investigated dragonfly (Horváth et al., 1998, 2007; Wildermuth, 1998; Bernáth et al., 2001, 2002), mayfly (Kriska et al., 1998, 2007; Horváth and Varjú, 2004) and tabanid fly (Horváth et al., 2008) species possess true polarization vision and positive polarotaxis, that is they are attracted to the horizontal polarization rather than

to the intensity of reflected light. Consequently, the preference of the dragonflies, mayflies and tabanids studied by us for higher  $p$ -values does not reflect the avoidance of brighter surfaces, reflecting light with lower  $p$ .

If dragonflies ovipositing into bright waters would possess a polarization sensitivity threshold  $p^* \approx 35\%$ , as suggested by Schwind (1995) for certain water bugs and aquatic beetles, their aquatic habitats would remain hidden from them in most of their active period (Bernáth et al., 2004). But even a small decrease of  $p^*$  can dramatically increase their chance to reliably locate bright waters (Fig. 3). However, a low  $p^*$  also increases their susceptibility to polarized light pollution induced by horizontally polarizing artificial reflectors (Horváth et al., 2009). This is well supported by the low values of  $p^*$  of *E. cyathigerum* and *I. elegans*, the larvae of which live in small, bright alkaline lakes: according to Tables 1 and 5, the polarization sensitivity threshold  $p^*$  eliciting positive polarotaxis from *I. elegans* ranges between 6.8 and 23.5%, while for *E. cyathigerum* we found  $0\% < p^* \leq 6.8\text{--}17.0\%$ , depending on the wavelength range of the perception of polarization.

The low  $p^*$  obtained for *E. cyathigerum* is remarkable. It is almost as low as the electrophysically determined polarization sensitivity threshold in the upward pointing dorsal-rim ommatidia of the field cricket, *G. campestris* ( $p^* \approx 5\%$  for blue light; Labhart, 1996) and the honey bee, *A. mellifera* ( $p^* \approx 11\%$  for ultraviolet light; von Frisch, 1967; Rossel and Wehner, 1984). If the aluminium-bottomed salad-oil-filled tray with very high albedo and variable direction of polarization of reflected light used by Horváth et al. (1998) have had caught at least as much *E. cyathigerum* individuals as the darker and always horizontally polarizing trays, it would be credible that *E. cyathigerum* relies on the intensity of reflected light instead of polarization. However, the aluminium tray did not attract any *E. cyathigerum*, thus it is also positively polarotactic. The larvae of both *E. cyathigerum* and *I. elegans* can be found in small ponds in the northern hemisphere. While *I. elegans* larvae are less susceptible to predation, *E. cyathigerum* larvae are more capable to tolerate poor water quality and even extreme low oxygen concentrations (Steiner et al., 2000). Hence, very shallow, easily hot-growing alkaline ponds are still suitable for *E. cyathigerum*, while they are inappropriate for *I. elegans*. Since these microhabitats are characterized by high albedo (brightness) and low degrees of polarization  $p$ , the very low  $p^*$  allows *E. cyathigerum* to utilise them. Contrary to this,  $p^*$  between 6.8 and 23.5% allows *I. elegans* to ignore such shallow, bright waters.

Setting the threshold values  $20.7\% \leq p^* \leq 91.9\%$  (depending on the wavelength) found in the investigated mayfly and tabanid species (Tables 2, 3 and 5) are significantly higher than those in the studied dragonflies (Tables 1 and 5) living around bright alkaline

ponds. The water habitat of mayflies at Dömörkapu is a fast flowing creek. At Gőd, situated on the bank of the river Danube, small and dark water bodies compose the habitat of the larvae of the investigated tabanids. Both aquatic habitats are characterized by higher degrees of polarization of water-reflected light. Thus, it is not surprising, that we found as high  $p^*$ -values as 20.7–91.9%, which range involves also the value  $p^* \approx 35\%$  estimated by Schwind (1995) for certain aquatic bugs and water beetles, preferring darker waters. Depending on the spectral range of polarization sensitivity, we found  $20.7\% \leq p^* \leq 55.4\%$  for *B. rhodani*, while  $45.7\% \leq p^* \leq 91.9\%$  for *E. danica*, *E. silvicola* and *R. semicolorata* (Tables 2 and 5). Similar is the case for the studied tabanids: *T. maculicornis* with  $45.7\% \leq p^* \leq 91.9\%$  prefers darker water bodies than *T. bovinus* and *T. tergestinus* with  $20.7\% \leq p^* \leq 55.4\%$  (Tables 4 and 5). All these demonstrate well that the species-specific  $p^*$ -values in aquatic insects possess an important visual ecological meaning.

Setting the value of  $p^*$  allows a behavioural adaptation in polarotactic water detection. Since  $p$  of water-reflected light is a quite reliable optical cue of the turbidity and depth of water bodies (Bernáth et al., 2002), the fine tuning of their  $p^*$  would be a simple way for aquatic insects to select habitats for their larvae, and may be a factor forming aquatic communities. Since early experience on water turbidity is known to permanently affect the foraging behaviour of transferred dragonfly larvae (Van de Meutter et al., 2005), it is logical to assume that the physical characteristics of the habitat experienced in larval period may fine tune also the preference of the imagoes. The adaptation of aquatic insect species or populations to the optical characteristics of their preferred habitats raise exciting visual ecological questions, which were not investigated until now.

We would like to emphasize, that the thresholds  $p^*$  of the degree of polarization in Table 5 are derived from behavioural tests. As outcomes of the signal processing of the entire central nervous system, they may differ from those could be measured by electrophysiology, and usually noted simply as polarization sensitivity (PS). Individuals captured by trays with  $p$  of reflected light lower than  $p^*$  demonstrate that  $p^*$  may vary in the populations. We should also note, that in Table 5 we gave the values of  $p^*$  for the red, green and blue parts of the spectrum, because the wavelength ranges of polarization sensitivity of the ventral eye region in the investigated dragonfly, mayfly and tabanid fly species are still unknown. Finally, we note that we considered here only the threshold  $p^*$  acting as lower limit of the degree of polarization eliciting polarotaxis in aquatic insects. One could also suppose an upper threshold  $p^{**}$  of reflected light eliciting positive polarotaxis. However, there are no experimental data supporting the existence of such an upper limit, and the several confirmed cases of 'polarized light pollution' (Horváth et al., 2009) renders it highly improbable.

In all cases, males and females of a given dragonfly, mayfly and tabanid fly species were trapped and considered together in our choice experiments. This is important, because one of the functions of positive polarotaxis in these aquatic insects is the need of females to detect suitable oviposition sites. On the other hand males may look for the same sites to find mates, like in the case of males of the investigated dragonfly species. Since there were not enough data on the gender distribution for our five different oil-filled traps, the possible sex-dependence of the threshold  $p^*$  of polarization sensitivity in a given aquatic insect species would be an important task of future research.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jinsphys.2009.08.013.

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