Imaging polarimetry of glass buildings: why do vertical glass surfaces attract polarotactic insects?

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Recently it was observed that the *Hydropsyche pellucidula* caddis flies swarm near sunset at the vertical glass surfaces of buildings standing on the bank of the Danube river in Budapest, Hungary. These aquatic insects emerge from the Danube and are lured to dark vertical panes of glass, where they swarm, land, copulate, and remain for hours. It was also shown that ovipositing *H. pellucidula* caddis flies are attracted to highly and horizontally polarized light stimulating their ventral eye region and thus have positive polarotaxis. The attraction of these aquatic insects to vertical reflectors is surprising, because after their aerial swarming, they must return to the horizontal surface of water bodies from which they emerge and at which they lay their eggs. Our aim is to answer the questions: Why are flying polarotactic caddis flies attracted to vertical glass surfaces? And why do these aquatic insects remain on vertical panes of glass after landing? We propose that both questions can be partly explained by the reflection–polarization characteristics of vertical glass surfaces and the positive polarotaxis of caddis flies. We measured the reflection–polarization patterns of shady and sunlit, black and white vertical glass surfaces from different directions of view under clear and overcast skies by imaging polarimetry in the red, green, and blue parts of the spectrum. Using these polarization patterns we determined which areas of the investigated glass surfaces are sensed as water by a hypothetical polarotactic insect facing and flying toward or landed on a vertical pane of glass. Our results strongly support the mentioned proposition. The main optical characteristics of "green," that is, environmentally friendly, buildings, considering the protection of polarotactic aquatic insects, are also discussed. Such "green" buildings possess features that attract only a small number of polarotactic aquatic insects when standing in the vicinity of fresh waters. Since vertical glass panes of buildings are abundant in the man-made optical environment, and polarotactic aquatic insects are spread worldwide, our results are of general interest in the visual and behavioral ecology of aquatic insects. © 2008 Optical Society of America

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1. Introduction

Recently Kriska *et al.* [1] observed that the *Hydropsyche pellucidula* caddis flies swarm at dusk at the vertical glass surfaces of buildings standing on the bank of the Danube river in Budapest, Hungary. These aquatic insects emerge from the Danube and are lured to the vertical glass surfaces, where they swarm, land and copulate (see Figs. 1 and 2). The landed individuals often move randomly on the vertical panes of glass, fly off, and land again within a few tens of seconds, and this is repeated for hours. In choice experiments it was shown [1] that ovipositing *H. pellucidula* caddis flies are attracted to highly and horizontally polarized light stimulating their ventral eye region and thus have positive polarotaxis. Kriska *et al.* [1] also observed that highly polarizing vertical

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Fig. 1. (Color online) (a) Mass swarming of the *H. pellucidula* caddis flies (white spots) in front of the vertical glass surfaces of the northern building of Eötvös University in Budapest, Hungary, on 1 May 2007. (b) Numerous individuals of *H. pellucidula* (black spots) landed on vertical glass surfaces.

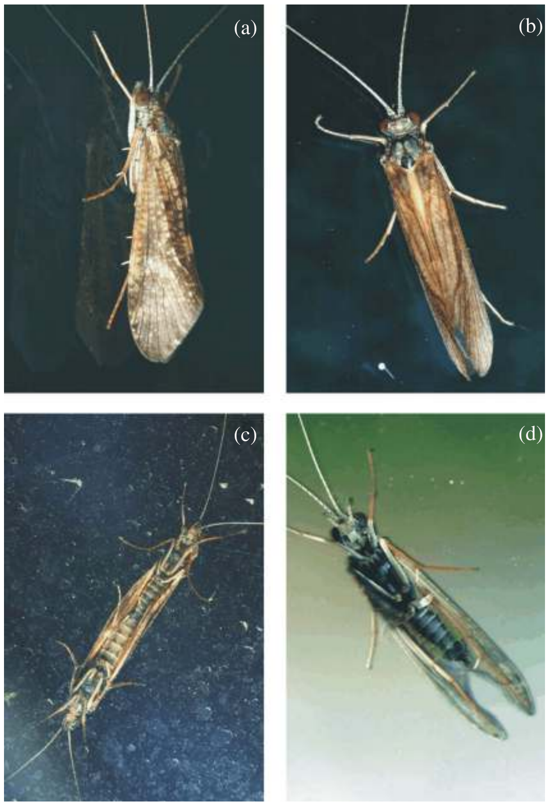

Fig. 2. (Color online) *H. pellucidula* landed on the outside surface of a vertical glass pane of the northern building of the Eötvös University photographed from (a), (b) outside and (c), (d) inside the building. A copulating pair of *H. pellucidula* is seen in Picture C.

black glass surfaces were significantly more attractive to both female and male *H. pellucidula* than weakly polarizing white ones. Under natural conditions these caddis flies detect water by the horizontal polarization of water-reflected light [2], and this is the reason for their positive polarotaxis. It was suggested [1] that after their emergence from the river, *H. pellucidula* caddis flies are lured to buildings by their dark silhouettes and the glass-reflected horizontally polarized light, and after sunset the attraction of these insects may also be strengthened by positive phototaxis elicited by the lights from buildings.

This behavior of *H. pellucidula* was not expected, because these insects are attracted only to horizontally polarized light [1], while depending on the direction of view, vertical glass panes can reflect light with all possible directions of polarization. It is well-known that polarotactic aquatic beetles (coleoptera), aquatic bugs (heteroptera), stoneflies (plecoptera), caddis flies (trichoptera), mayflies (ephemeroptera), and dragonflies (odonata) are deceived by and attracted to various artificial shiny dark horizontal surfaces such as oil lakes [3–6], asphalt roads [7]; black plastic sheets laid on the ground [5,6,8]; roofs, boots, and bonnets of black, red, or dark-colored cars [9,10]; and horizontal parts of black gravestones [11]. The attraction of *H. pellucidula* caddis flies to vertical reflectors is surprising, because after their aerial swarming they must return to the horizontal surface of water bodies from which they emerge and at which they lay their eggs.

Our aim is to answer the following two questions: (1) Why are flying polarotactic caddis flies attracted to vertical glass surfaces? And (2) why do these insects remain on vertical panes of glass after landing? We propose that both questions can be partly explained by the reflection–polarization characteristics of vertical glass surfaces and the positive polarotaxis of caddis flies. We measured the reflection–polarization patterns of shady and sunlit, black and white vertical glass surfaces from different directions of view under clear and overcast skies by imaging polarimetry in the red, green, and blue parts of the spectrum. Using these polarization patterns we determined which areas of the investigated glass surfaces are sensed as water by a hypothetical polarotactic insect facing and flying toward or landed on a vertical pane of glass. Since vertical glass panes of buildings are abundant in the man-made optical environment, and polarotactic aquatic insects, e.g., caddis flies [12,13], are spread worldwide, our results are of general interest in the visual and behavioral ecology of aquatic insects.

2. Materials and Methods

The reflection–polarization characteristics of the northern building of the Eötvös University (see Fig. 3) were measured by videopolarimetry in the red (650 ± 40 nm), green (550 ± 40 nm), and blue (450 ± 40 nm) parts of the spectrum from four different directions of view on 8 May 2006 between 19:00 and 19:15 h (Universal Time Code [UTC] plus 2) in the middle of the swarming period of the caddis flies, which lasted from 17:00 to 21:00 h. During these measurements the sky was clear and cloudless, the sun was shining, and the solar elevation was $\theta = 9.4°$. The angle of elevation of the optical axis of the videopolarimeter was $+35°$ relative to the horizon. The geometry of these measurements is shown in Fig. 3(a). The method of videopolarimetry has been described in detail elsewhere [14].

The reflection–polarization characteristics of the southern building of the Eötvös University (see Fig. 4) were measured by 180° field of view imaging polarimetry in the red (650 ± 40 nm), green (550 ± 40 nm), and blue (450 ± 40 nm) parts of the spectrum from four different directions of view on 9 May 2006 between 14:35 and 14:50 h (UTC plus 2) for a high solar elevation of $\theta = 51.8°$. During these measurements the sky was clear and cloudless, and the sun was shining. The optical axis of the polarimeter was horizontal. The geometry of these measurements is shown in the middle area of Fig. 4. Depending on the direction of view relative to the solar azimuth, both buildings were illuminated by the sun and the light from the clear sky.

The method of 180° field of view imaging polarimetry has been described in detail elsewhere [15]. Here we mention only that the polarization patterns of the vertical glass surfaces in Figs. 4–9 are visualized as high-resolution color-coded two-dimensional (2D) circular maps. The three-dimensional hemispherical field of view of the polarimeter's fish-eye lens is represented in two dimensions by a polar-coordinate system, where angular distance θ from the center of the circular pattern and azimuth angle φ from the vertical are measured radially and tangentially, respectively ($\theta_{\text{center}} = 0°$, $\theta_{\text{half radius}} = 45°$, and $\theta_{\text{perimeter}} = 90°$). If the polarimeter's optical axis was vertical, pointing to the zenith, for example, in this 2D coordinate system, the zenith would correspond to the center and the horizon to the perimeter of the circular map.

The reflection–polarization patterns of a black vertical glass surface and a white vertical glass surface of the northern building of the Eötvös University (see Figs. 5–9 and Table 1) were measured in May 2007 by 180° field of view imaging polarimetry in the red (650 ± 40 nm), green (550 ± 40 nm), and blue (450 ± 40 nm) parts of the spectrum under the following three illumination conditions: (1) a shady glass surface under a clear sky (see Figs. 5 and 7) measured from Direction of View 5 in Fig. 3(a), (2) a shady glass surface under an overcast sky (see Figs. 6 and 8) measured from Direction of View 5 in Fig. 3(a), and (3) a sunlit glass surface under a clear sky (see Fig. 9) measured from Direction of View 3 in Fig. 3(a). The vertical black glass pane (nontransparent, absorbing light completely) was an ornamentation, while the vertical white glass surface was a transparent window with a nontransparent curtain composed of vertical bars of white, matte cloth. The dimensions of both the black and white glass surfaces were 2 m × 2 m, and they were positioned 15 cm apart. The polarimeter's tripod was placed on the sill of these glass surfaces. The polarimetric measurement was performed at noon under a clear sky when both glass surfaces were in shadow and faced north. Since the glass surfaces of the investigated building were always in shadow, we selected another window with a white curtain on the southern wall of the building to measure its reflection–polarization patterns under sunlit conditions from Direction of View 3 in Fig. 3(a). Apart from their illumination, both investigated white glass surfaces were the same. Unfortunately polarimetric measurements under sunlit conditions could not be done with a vertical black glass surface, because all black glass ornamentations approachable with our polarimeter were on the northern wall, thus always shady. During measurements the optical axis of the polarimeter was horizontal. To ensure a maximum part of the 180° field of view of the polarimeter was filled by the mirroring glass surface, the fish-eye lens was at a distance of 10 cm from the glass pane, and the camera optics was focussed to infinity, because we wanted to measure the polarization pattern of the sky (being in the infinity) reflected from the vertical glass surface.

The dorsoventral symmetry axis of all polarotactic aquatic insects is a distinguished reference direction, because these insects are attracted to light, whose direction of polarization is exactly or nearly perpendicular to this axis, while light with a direction of polarization parallel or tilted to this axis is unattractive [16–19]. Such polarotactic aquatic insects consider to be water only those areas that reflect light with degrees of linear polarization p higher than the threshold $p*$ of their polarization sensitivity and with angles of polarization α differing from the direction perpendicular to their dorsoventral symmetry plane by less than a certain threshold $\Delta\alpha*$ in that part of the spectrum in which the polarization of reflected light is perceived. Therefore a hypothetical polarotactic aquatic insect was assumed to take those areas of a vertical glass surface to be water, from which light is reflected under the following two conditions: (i) a degree of p higher than $p* = 10\%$, and (ii) a deviation $|\alpha - 90°|$ of α from the direc-

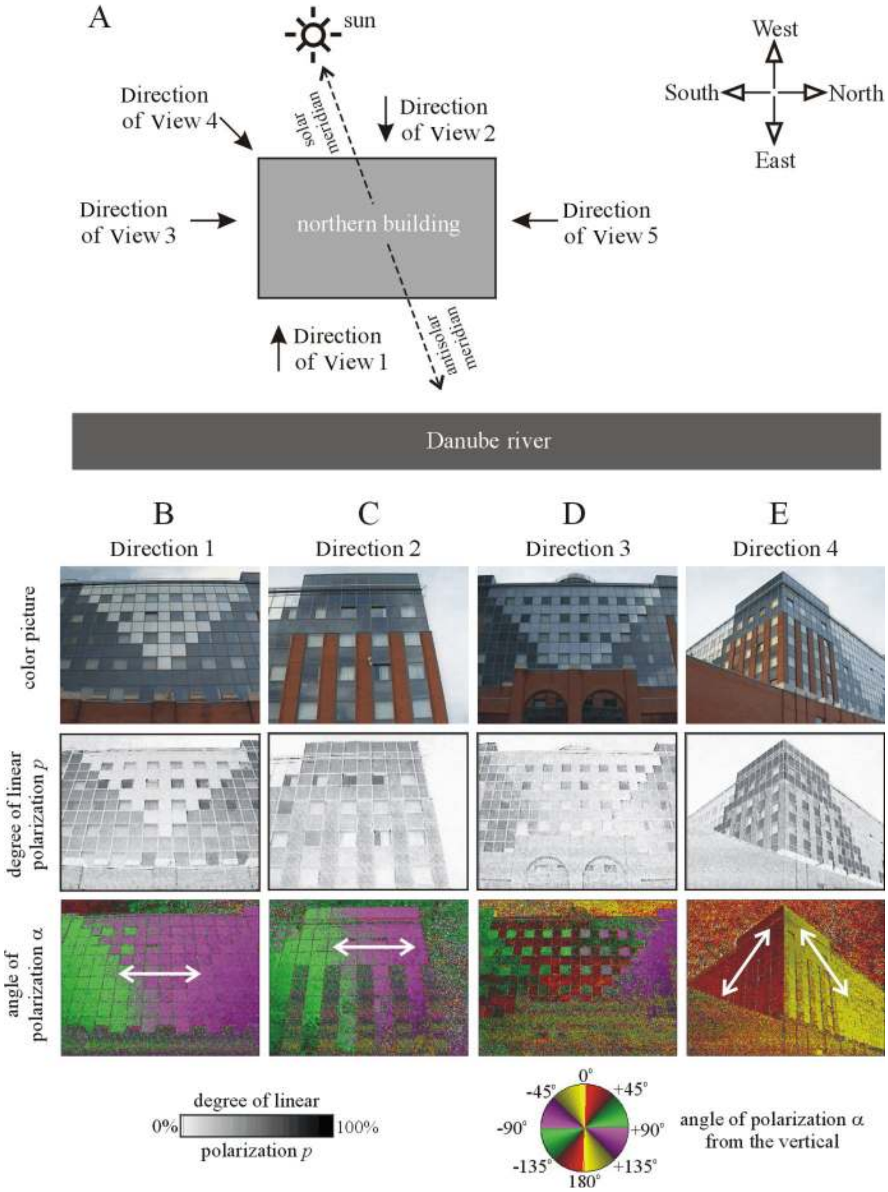

Fig. 3. (Color online) (a) Geometry of the northern building of Eötvös University on the bank of the Danube river with Directions of View 1, 2, 3, 4, and 5 of the polarimeter. (b)–(e) Color photograph and patterns of p and α (measured from the vertical) of the northern building at the vertical glass surfaces at which *H. pellucidula* caddis flies swarmed. In the α patterns the white double-headed arrows show the average directions of polarization of light reflected from the vertical glass surfaces. The reflection–polarization patterns were measured in the green (550 nm) part of the spectrum, and they were practically the same as those in the red (650 nm) and blue (450 nm) spectral ranges.

tion normal to the insect's dorsoventral symmetry axis smaller than $\Delta\alpha* = 5°$. The whole eye of this hypothetical aquatic insect was assumed to be polarization sensitive. We introduce the quantity percentage W of a vertical glass surface detected as water, which is the angular proportion W of the viewing directions (relative to the angular extension of the field of view containing the reflecting glass surface) for which both conditions are satisfied. In other words, W gives the proportion of the field of view in which the vertical glass surface is sensed as water by polarization. The higher the W value for a vertical glass surface, the more attractive it is to water-seeking polarotactic aquatic insects.

The investigated glass surfaces (2 m × 2 m) did not fill the entire 180° field of view of our polarimeter, thus in the calculation of the W values, we did not consider those peripheric areas of the circular polarization patterns that fell outside these surfaces. These nonconsiderable areas are masked out by a circular X pattern in Figs. 5–9. Furthermore, within the considered glass surfaces at some places, the polarization pictures became underexposed (e.g., at the mirror image of the polarimeter), or overexposed (e.g., at the mirror image of the too bright sky re-

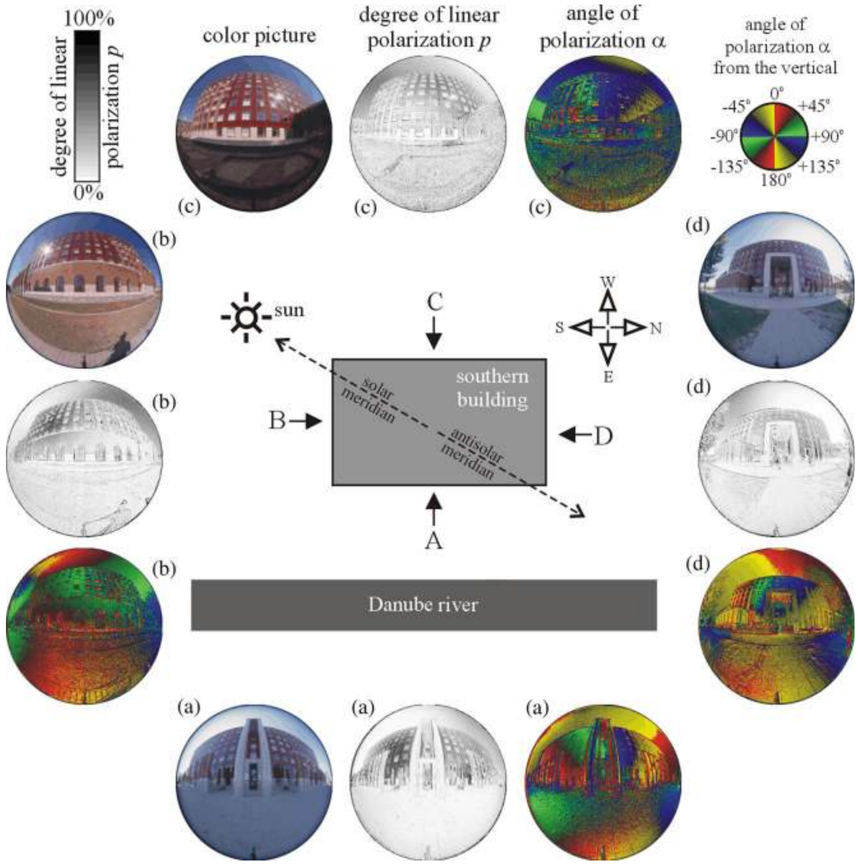

Fig. 4. (Color online) Middle: Geometry of the southern building of Eötvös University on the bank of the Danube river with Directions of View A, B, C, and D of the polarimeter relative to the solar meridian. Periphery: 180° field of view color photograph and patterns of p and α (measured from the vertical) of the southern building at the vertical glass surfaces at which *H. pellucidula* swarmed. The reflection–polarization patterns were measured by 180° field of view imaging polarimetry in the green (550 nm) part of the spectrum, and they were similar to those in the red (650 nm) and blue (450 nm) spectral ranges.

gions). Since the reflection–polarization characteristics of the underexposed or overexposed regions of the glass surfaces were unknown, these unevaluable glass areas were masked out. Because of the unavoidable reflection of its sill, the shady regions of the sunlit window (see Fig. 9) were considered unevaluable, since the reflection–polarization characteristics of shady surfaces greatly differ from those of sunlit ones. These unevaluable glass areas are filled by a checkered pattern in Figs. 5–9, and their proportions are given in Tables 2 and 3.

At a given glass surface, the values of W were calculated for two situations: (A) The model polarotactic aquatic insect was assumed to face and fly toward the vertical glass surface. Since the dorsoventral symmetry axis of the insect's head was then vertical, α was measured from the vertical in this case [see Figs. 5(c), 6(c), 7(c), 8(c), 9(c), 10, and 11 and Table 2). (B) The model polarotactic aquatic insect was assumed to be landed on the vertical glass surface, and the insect faced an arbitrary direction parallel to the glass. Since the dorsoventral symmetry axis of the insect's head was then always perpendicular to the glass surface, α was measured from the local meridian passing through the observed point of the glass surface [see Figs. 5(d), 6(d), 7(d), 8(d), 9(d), and 12 and Table 3). This meridian is always perpendicular to the glass surface.

3. Results

Figure 3(a) and the middle part of Fig. 4 show the geometry of the buildings on the bank of the Danube river with directions of view of our polarimeter relative to the solar meridian. Figures 3(b)–3(e) display the color photographs and the patterns of the degree of linear polarization p and angle of polarization α (from the vertical) of the vertical glass surfaces of the northern building at which *H. pellucidula* caddis flies swarmed. In the color photographs we can see that the vertical walls of the building were patchy, because they were covered by different glass surfaces; in addition to the transparent glass windows, there were also gray and black nontransparent vertical glass surfaces. The latter function simply as architectural decoration. In some of the transparent glass windows, the white blinds (curtains) were dropped, which resulted in the bright appearance of the windows. If the blinds were raised, the windows appeared dark due to the small amount of light coming from the dark rooms. Some of the tiltable windows were partly open. The amount of light reflected from such tilted glass panes was different

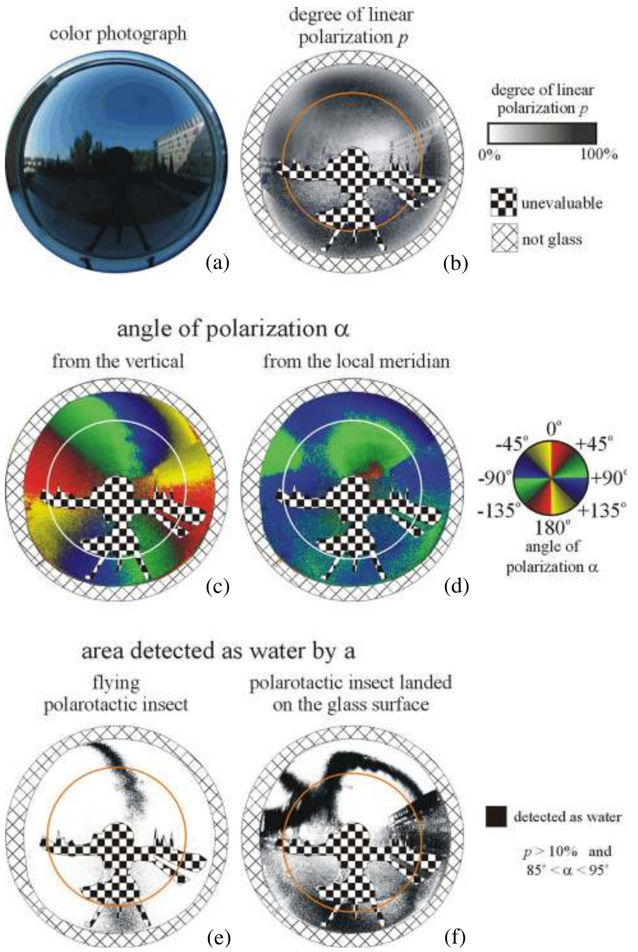

Fig. 5. (Color online) (a) Color photograph and patterns of (b) p and (c), (d) α of a shady black vertical glass surface measured by 180° field of view imaging polarimetry in the blue (450 nm) part of the spectrum from Direction of View 5 in Fig. 3(a). (c) α of reflected light is measured from the vertical or (d) from the local meridian passing through the point observed. (e) Area (black) of the vertical glass surface detected as water by a hypothetical polarotactic aquatic insect flying perpendicular to the glass. (f) Area (black) of the vertical glass surface detected as water by a hypothetical polarotactic insect landed on the glass. The insect was assumed to consider a surface to be water if the reflected light has the following polarization characteristics: $p > 10\%$ and $85° < \alpha < 95°$. It was also assumed that the insect's entire eye is polarization sensitive. (b)–(f) In the circular patterns the Brewster angle is shown by circles. The horizontal optical axis of the polarimeter passes through the center of a given circular pattern, the perimeter of which represents angles of view perpendicular to the optical axis.

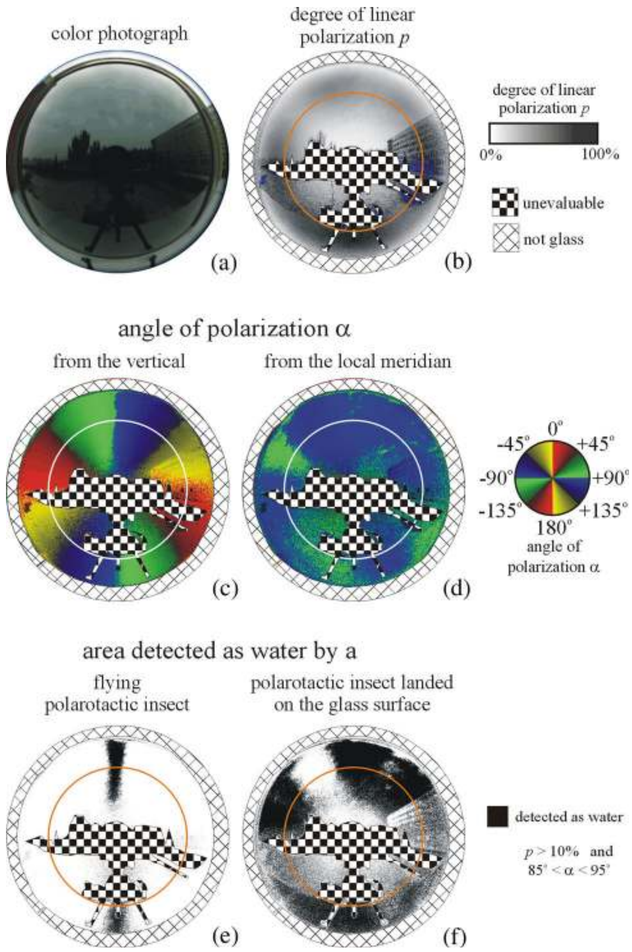

Fig. 6. (Color online) As Fig. 5 under a totally overcast sky.

from that reflected from the vertical glass surface of the closed (nontilted) windows. The vertical surface of the red bricks of the walls was moderately shiny due to its moderate smoothness.

According to our polarimetric measurements, the darker a glass surface, the higher the p of reflected light. Since the glass surfaces covering the walls are colorless (from white through gray to black), p of light reflected from them was practically independent of the wavelength. The light reflected from the vertical shiny red bricks of the building's walls was also partially polarized, p of which was the lowest in the red part of the spectrum and the highest in the blue spectral range. These all correspond to the rule of Umow [20]. The p pattern of the building's walls was patchy, because p of reflected light depends on both the brightness and the tiltedness of the reflecting surface.

The pattern of α of a given vertical wall of the buildings depended strongly on the direction of view relative to the solar meridian. According to Figs. 3(b) and 3(c), the direction of polarization of reflected light was horizontal for the walls facing toward the solar or antisolar meridian if they were viewed from directions parallel to the solar–antisolar meridian. Comparing Figs. 3(c) and 3(e), we can see that the direction of polarization of light reflected from the same wall surface was different when viewed from different directions, horizontal in Fig. 3(c) but oblique in Fig. 3(e). The same can be established if the α patterns in Figs. 3(d) and 3(e) are compared. In the α pattern of Fig. 3(d), we can see that the direction of polarization of light reflected from the vertical glass surfaces not facing toward the solar or antisolar meridian depended also on the brightness of the glass pane; the darker glass panes reflected nearly horizontally polarized light, while the direction of polarization of light reflected from the bright-

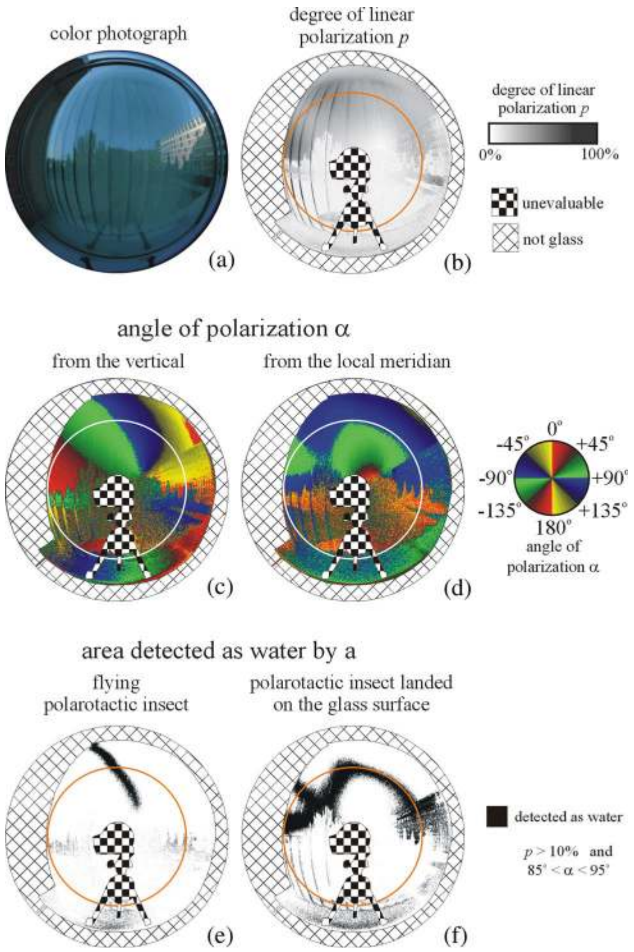

Fig. 7. (Color online) As Fig. 5 for a shady vertical pane of a glass window, behind which there is a white curtain. The sky was clear and cloudless. This white glass surface was next to the black glass in Fig. 6.

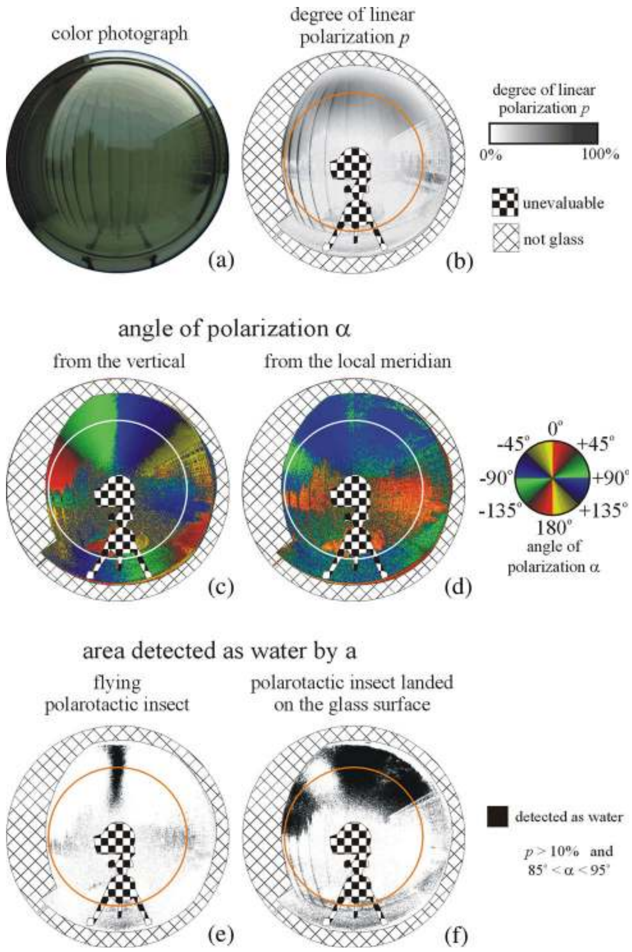

Fig. 8. (Color online) As Fig. 7 under a totally overcast sky.

er panes was oblique. Hence the glass panes were facing nonparallel to the solar or antisolar meridian reflected light, whose direction of polarization was not always horizontal.

The caddis flies investigated by Kriska *et al.* [1] swarmed prior to and near sunset when the solar elevation angle θ was low. The reflection–polarization characteristics of the northern building of Eötvös University are shown in Fig. 3 for $\theta = 9.4°$. Figure 4 shows the reflection–polarization patterns of the southern building of Eötvös University for four different directions of view relative to the solar meridian when the solar elevation was high, $\theta = 51.8°$. We can see that, depending on the direction of view, certain parts of the skylighted or sunlit vertical glass surfaces of the building reflect nearly horizontally polarized light (shaded by green and blue coding angles of polarization $+45° < \alpha < +135°$), but other regions reflect nearly vertically polarized light (shaded by red and yellow coding $-45° < \alpha < +45°$). p of glass-reflected light also depends strongly on the direction of reflection. Figures 3 and 4 demonstrate well that buildings with vertical glass surfaces always have such parts from which nearly horizontally polarized light is reflected for both low and high solar elevations.

Figures 5(a)–5(d), 6(a)–6(d), 7(a)–7(d), 8(a)–8(d), and 9(a)–9(d), show the reflection–polarization patterns of the investigated black and white, shady and sunlit vertical glass surfaces measured under clear and overcast skies in the blue (450 nm) part of the spectrum. Similar patterns were obtained for the red and green spectral ranges. Table 1 contains the values of p averaged for all vertical glass surfaces (without the unevaluable regions) in Figs. 5–9 measured in the red, green, and blue parts of the spectrum. Figures 5(c), 6(c), 7(c), 8(c), and 9(c) represent the patterns of α of the vertical glass surfaces when α is measured from the vertical, that is, from the vertical dorsoventral symmetry axis of the head of a flying aquatic insect facing and approaching perpendicular to the glass pane (Fig. 1).

According to Figs. 5(b), 5(c), 6(b), 6(c), 7(b), 7(c), 8(b), 8(c), 9(b), and 9(c), the light reflected from the so-called Brewster zone (an annular region, the center line of which is a circle at a nadir angle of $\theta_B = 57.5°$, where $\theta_B = \arctan n$ is the Brewster angle for the refractive index $n = 1.5$ of glass) of vertical glass surfaces is maximally polarized, and the direction of polarization of light reflected from the Brew-

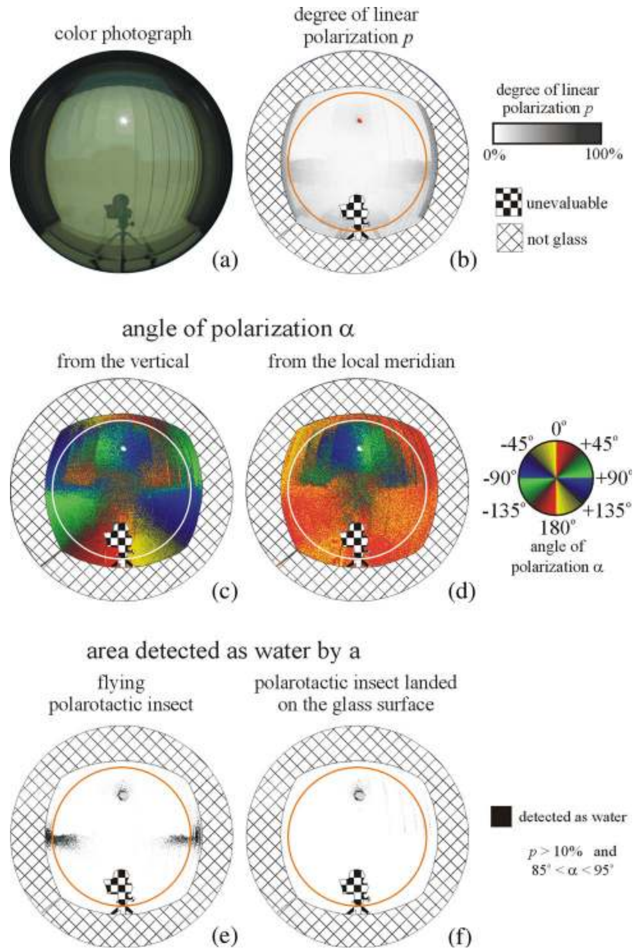

Fig. 9. (Color online) As Fig. 5 measured under a clear sky from Direction of View 3 in Fig. 3(a) for a sunlit vertical pane of a glass window, behind which there is a white curtain.

ster zone can be horizontal, tilted or vertical. The black glass surface [see Figs. 5(b) and 6(b)] reflects light with much higher p (average $39\% \le p_{black} \le 52\%$) than the white one [see Figs. 7(b), 8(b), and 9(b); average $10\% \le p_{white} \le 20\%$], and p of light reflected from the sunlit white glass [see Fig. 9(b)] is considerably lower (average $8\% \le p_{white} \le 10\%$) than that from the shady white glass [see Figs. 7(b) and 8(b); average $14\% \le p_{white} \le 18\%$].

To a flying polarotactic aquatic insect, only the highly [shown as dark gray shadows in Figs. 5(b), 6(b), 7(b), 8(b), and 9(b)] and exactly or nearly horizontally polarizing [shown as bright blue and green in Figs. 5(c), 6(c), 7(c), 8(c), and 9(c)] areas of the vertical glass surfaces can be attractive (see Figs. 10 and 11). Figures 5(e), 6(e), 7(e), 8(e), and 9(e) show the areas of the vertical glass surfaces detected as water by a hypothetical flying polarotactic aquatic insect whose above-mentioned polarization sensitivity thresholds are $p* = 10\%$ and $\Delta\alpha* = 5°$ and whose entire eye is assumed to be polarization sensitive. Only two narrow, approximately vertical patches of the shady black and white vertical glass surfaces can be attractive to such an insect [see Figs. 5(e), 6(e), 7(e), and 8(e)], because only these glass regions reflect exactly or approximately horizontally polarized light with high enough p. The center of both patches is positioned on the Brewster zone. The other parts of the vertical shady glass surfaces are unattractive to flying polarotactic insects, because the polarization of light reflected by them is not horizontal or not strong enough. On the other hand, on the white sunlit vertical glass surface, there are two horizontally elongated patches that are considered to be water by flying polarotactic insects [see Fig. 9(e)]. These patches are atypical, because they occur only due to the mirror image of a neighboring building on the horizon.

Figures 5(d), 6(d), 7(d), 8(d), and 9(d) show the α patterns of the investigated vertical glass surfaces if α is measured from the local meridian (as a reference direction) passing through the point observed. This choice of reference direction corresponds with the situation when a polarotactic aquatic insect is landed on the vertical glass surface and looks into an arbitrary direction parallel to the glass; then the insect's dorsoventral symmetry plane is always perpendicular to the glass surface (see Fig. 12). The direction of polarization of light reflected from the vertical black glass surface is practically always exactly or approximately parallel to the glass [see Figs. 5(d) and 6(d)], while the direction of polarization of light reflected from the vertical white glass surface can be perpendicular, tilted, or parallel to the glass. Figures 5(f), 6(f), 7(f), 8(f), and 9(f) show the regions of the vertical glass surfaces detected as water by the hypothetical polarotactic aquatic insect landed on the glass, whose polarization sensitivity thresholds are $p* = 10\%$ and $\Delta\alpha* = 5°$ and whose entire eye is assumed to be polarization sensitive. Then the glass surface is perpendicular to the insect's dorsoventral symmetry plane (see Fig. 12). The areas of the vertical shady black and white glass surfaces sensed polarotactically as water by an aquatic insect landed on the glass are placed along the Brewster zone [see Figs. 5(f), 6(f), 7(f), and 8(f)]. On the other hand, almost the entire surface of the sunlit white vertical glass is not detected polarotactically as water [see Fig. 9(f)].

Tables 2 and 3 contain the proportion W of the vertical glass surfaces in Figs. 5–9 detected as water by a hypothetical polarotactic aquatic insect flying toward [see Figs. 5(c), 6(c), 7(c), 8(c), and 9(c) and Table 2] or

Table 1. Degree of Linear Polarization *p* (%, Average ± StandardDeviation) in the Red (650 nm), Green (550 nm), and Blue (450 nm) Parts of the Spectrum Averaged for the Entire Vertical Glass Surface (without the Unevaluable Underexposed or Overexposed Regions Displayed as a Checkered Pattern) in Figs. 5–9

Glass	Illumination	Sky	Figure	Red	Green	Blue
Black	Shady	Clear	5(b)	52 ± 21	43 ± 19	44 ± 22
Black	Shady	Overcast	6(b)	45 ± 23	39 ± 21	41 ± 22
White	Shady	Clear	7(b)	16 ± 10	14 ± 11	18 ± 13
White	Shady	Overcast	8(b)	10 ± 8	11 ± 9	20 ± 14
White	Sunny	Clear	9(b)	8 ± 6	8 ± 7	10 ± 10

Table 2. Proportion *W* (%) of the Vertical Glass Surfaces in Figs. 5–9 Detected as Water by a Hypothetical Polarotactic Aquatic Insect Flying Toward the Glass [see Figs. 5(c), 6(c), 7(c), 8(c), and 9(c)] Calculated in the Red (650 nm), Green (550 nm), and Blue (450 nm) Parts of the Spectrum[a]

Glass	Illumination	Sky	Figure	Red			Green			Blue		
				W	*N*	*U*	*W*	*N*	*U*	*W*	*N*	*U*
Black	Shady	Clear	5(c)	5.3	82.1	12.6	4.8	87.5	7.7	4.5	80.5	15.0
Black	Shady	Overcast	6(c)	5.7	81.7	12.6	5.5	86.5	8.0	5.3	77.1	17.6
White	Shady	Clear	7(c)	3.6	76.8	19.6	3.3	77.1	19.6	4.3	76.1	19.6
White	Shady	Overcast	8(c)	4.7	77.0	18.3	4.7	77.1	18.2	6.0	75.7	18.3
White	Sunny	Clear	9(c)	2.6	60.5	36.9	2.6	60.5	36.9	3.0	60.1	36.9

[a]The insect was assumed to consider a surface as water if the reflected light has the following two polarization characteristics: (1) $p > 10\%$ and (2) $85° < \alpha < 95°$. It was also assumed that the insect's entire eye is polarization sensitive. *N* (%) is the proportion of the glass surface that is not sensed as water by the insect, because condition (1) or (2) is not satisfied. *U* (%) is the proportion of the glass surface that is unevaluable due to underexposure or overexposure (see the checkered areas in Figs. 5–9). $W + N + U = 100\%$.

landed on [see Figs. 5(d), 6(d), 7(d), 8(d), and 9(d) and Table 3] the glass surface calculated for $p* = 10\%$ in the red, green, and blue parts of the spectrum. From Tables 2 and 3, the following trends can be read: (i) At a given sky condition (clear or overcast) and in a given spectral range (red, green, or blue), *W* of a polarotactic insect is higher for black glass than for white glass, especially for an insect landed on the glass. (ii) At a given glass surface and spectral range, *W* is larger under an overcast sky than under a clear sky. (iii) *W* is lowest for the sunlit white vertical glass surface. (iv) Apart from the sunlit white vertical glass [see Figs. 9(c) and 9(d)], *W* is much larger for a polarotactic insect landed on a given vertical glass surface [see Figs. 5(d), 6(d), 7(d), and 8(d) and Table 3] than that for an insect facing and flying toward the same glass [see Figs. 5(c), 6(c), 7(c), and 8(c) and Table 2]. (v) *W* more or less depends on the wavelength of light.

4. Discussion

In Tables 2 and 3, *N* is the proportion of the glass surface that is not sensed as water by the hypothetical polarotactic aquatic insect, while *U* is the ratio of the glass surface, the polarizing ability of which is unevaluable due to underexposure or overexposure, or being the reflection of the window sill, possessing different reflection–polarization characteristics from that of sunlit areas or areas reflecting the sky. The unevaluable glass regions originate predominantly from the underexposed (dark) mirror image of the polarimeter. Note that $W + N + U = 100\%$. The light rays forming the polarimeter's mirror image are reflected nearly perpendicular from the glass surface, and consequently their degree of linear polarization is approximately zero. Thus if the polarization characteristics of the unevaluable glass regions could be evaluated, these glass regions would mainly contribute to the areas that are not sensed as water by polarotactic insects. In other words, *U* would mainly enhance the value of *N* rather than the value of *W*. Hence the above-mentioned trends remain valid in spite of these unevaluable glass regions (*U* in Tables 2 and 3).

We used $p* = 10\%$ and $\Delta\alpha* = 5°$ as the thresholds of polarization sensitivity and polarotaxis in our imaginary polarotactic insect, which are characteristic to the highly polarization-sensitive ultraviolet receptors in the specialized dorsal rim area of the compound eye in the honey bee *Apis mellifera* [19]. Since in aquatic insects the values of thresholds $p*$ and $\Delta\alpha*$ are unknown, and they are certainly species specific, we set these threshold values arbitrarily. However, with increasing $p*$, *W* decreases monotonically, and increasing $\Delta\alpha*$ results in the monotonous increase of *W*. Since there are no sudden changes, local extrema, breaking points, or plateaus in $W(p*)$ and $W(\Delta\alpha*)$ curves, we cannot establish any criterion for a threshold value that could be preferred. This fact has the important consequence that the values of thresholds $p*$ and $\Delta\alpha*$ can indeed be chosen arbitrarily, and the actual choice concerns neither the relative values of *W* calculated for vertical glass surfaces with different brightnesses nor the conclusions drawn from them. Thus the arbitrary use of $p* = 10\%$ and $\Delta\alpha* = 5°$ is not a serious restriction. A similar approach was used by Bernáth *et al.* [21]. Furthermore when we set $p* = 35\%$ as Schwind [18] hypothesized for certain aquatic

Table 3. As Table 2 for a Hypothetical Polarotactic Aquatic Insect Landed on the Glass Surface [see Figs. 5(d), 6(d), 7(d), 8(d), and 9(d)]

Glass	Illumination	Sky	Figure	Red			Green			Blue		
				W	*N*	*U*	*W*	*N*	*U*	*W*	*N*	*U*
Black	Shady	Clear	5(d)	32.7	54.7	12.6	38.0	54.3	7.7	35.2	49.8	15.0
Black	Shady	Overcast	6(d)	45.8	41.6	12.6	50.3	41.7	8.0	43.6	38.8	17.6
White	Shady	Clear	7(d)	8.6	71.8	19.6	11.6	68.8	19.6	16.1	64.3	19.6
White	Shady	Overcast	8(d)	7.1	74.6	18.3	16.9	64.9	18.2	23.3	58.4	18.3
White	Sunny	Clear	9(d)	0.4	62.7	36.9	0.4	62.7	36.9	0.7	62.4	36.9

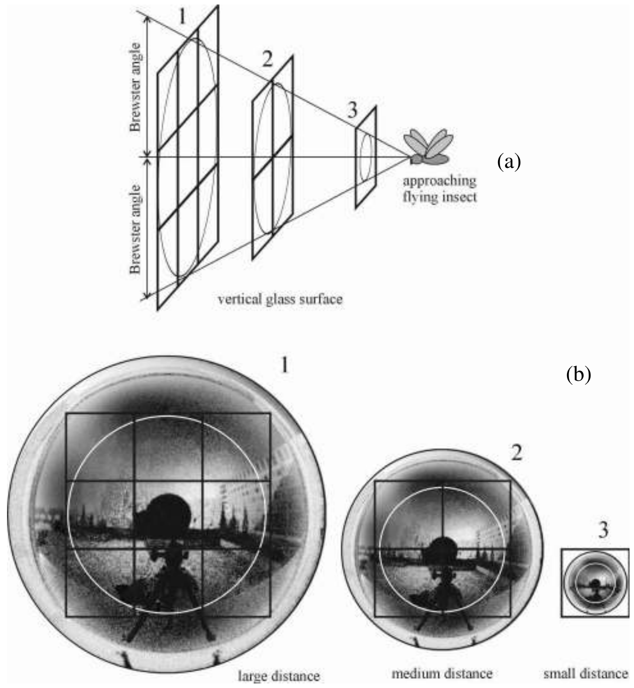

Fig. 10. (a) Flying insect approaching vertical wall of a building covered by a quadratic grid of glass surfaces. The smaller the distance d of the insect from the wall (d decreases from 1 to 3), the fewer quadratic glass surfaces fall within a given field of view (here coinciding with twice of the Brewster angle) of the insect. (b) 180° field of view pattern of p seen by a flying polarotactic insect approaching perpendicular to the glass-covered vertical wall in (a) for a (1) large, (2) medium, and (3) small distance. The Brewster angle is shown as a white circle.

beetles and bugs, we obtained practically the same results and conclusion as for $p* = 10\%$.

A. Why Are Polarotactic Caddis Flies Attracted to Vertical Glass Surfaces?

The reflection–polarization characteristics of vertical glass surfaces positioned on different sides of the investigated building near sunset (see Fig. 3) depend on the illumination conditions. We measured these polarization features of the building from directions of view similar to those of the caddis flies emerging from the Danube river. If an observer looks at a vertical glass surface from below, the light perceived by the observer can have the following three major components:

1. the skylight reflected specularly from the outer surface of the pane of glass,
2. the sunlight reflected specularly from the outer glass surface (if the reflected sun is directly imaged by the smooth reflector), and
3. the light coming from the room behind the window.

Since the glass surfaces of the investigated buildings are smooth, the tiny amount of sunlight scattered on the slightly rough glass surface can be neglected relative to these three components. Assuming that

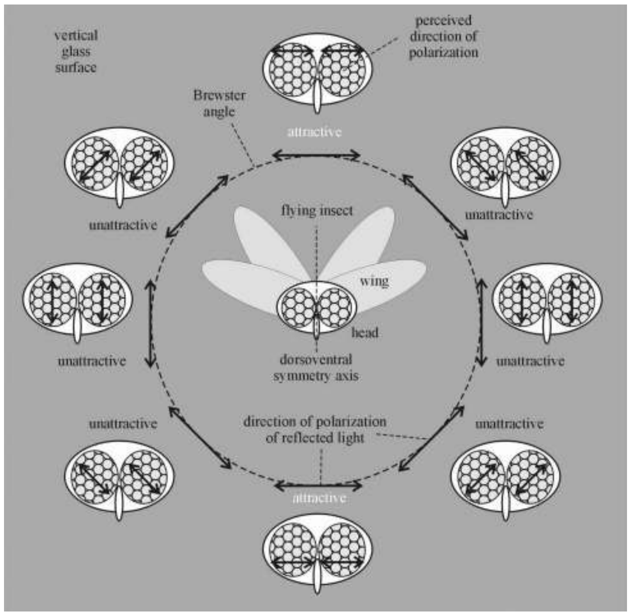

Fig. 11. How a flying polarization-sensitive insect approaching perpendicular to a vertical glass surface perceives the direction of polarization (double-headed arrows) of light reflected from the glass at the Brewster angle (dashed circle). A polarotactic aquatic insect is attracted to the reflected light only if the perceived direction of polarization is exactly or nearly perpendicular to its dorsoventral symmetry axis. If the perceived direction of polarization is parallel or tilted to this symmetry axis, the reflected light is unattractive to the insect.

light leaves the room after multiple diffuse reflections from different objects, the third component can be considered as nearly unpolarized. This unpolarized third component can only reduce the net degree of linear polarization p of light originating from the glass pane but cannot change the net direction of polarization, which is the most important variable of light considering the attraction of polarotactic aquatic insects, being lured only by exactly or nearly horizontally polarized light. The direction of polarization of light reflected from a smooth glass surface is always perpendicular to the plane of reflection determined by the incident and reflected light as well as the local normal vector of the reflecting surface [22]. Thus, seen from below, the downwelling skylight reflected from the vertical glass surface is always nearly horizontally polarized, because the plane of reflection is then nearly vertical.

All reflections must obey the law of reflection, so the direct rays from the sun can only dominate reflection–polarization if the reflected sun is directly imaged; we normally see this as glare, as can be seen, for example, in Fig. 4(b) on the upper left-hand side of the building. For directions of view where glare is not occurring, there is no direct image of the sun. If a surface is sufficiently smooth, the sun will have no effect. While glass surfaces are not perfectly smooth, they do exhibit properties close to a mirror, so they reflect mainly specularly. Still, since they are slightly rough, they scatter some direct sunlight. This scattering does affect the reflection–

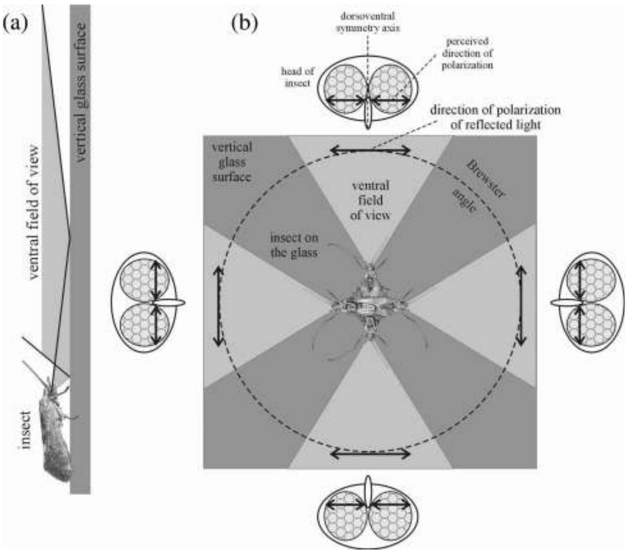

Fig. 12. (a) Side view of a light beam (light gray) reflected from a vertical glass surface and received by the ventral eye region of an insect landed on the glass. (b) How a polarization-sensitive insect landed on a vertical glass surface and looking into different directions (here only four such directions are shown) perceives the direction of polarization (double-headed arrows) of light reflected from the glass at the Brewster angle (dashed circle). Since the perceived direction of polarization is always perpendicular to the insect's dorsoventral symmetry axis (independently of the direction of view), the light reflected from the Brewster angle is always attractive to a polarotactic aquatic insect landed on the glass.

polarization, but it may or may not dominate it, depending on the surface roughness. Thus for windows and smooth glass surfaces, direct sunlight cannot dominate the polarization signature in regions where there is no glare.

If the sun is occluded by clouds and thus there is no direct sunlight, then seen from below all vertical glass surfaces of the building reflect nearly horizontally polarized light, irrespective of the direction of view relative to the solar meridian. This is the optical reason for the observation of Kriska *et al.* [1] that under cloudy conditions, when the sun was occluded by clouds, the *H. pellucidula* caddis flies swarmed at all four sides of the investigated buildings, because all vertical glass surfaces then reflected approximately horizontally polarized light.

For View 3 in Fig. 3, the windows reflect light from the sky above and behind to the south. When the sun is near sunset, the sky directly to the north and the south (and the band through the center of the sky connecting the north to the south) is highly polarized at an angle parallel to the vertical plane of reflection. Therefore, looking north or south, an observer will only see vertically polarized light. The sky that illuminates the south wall of the building is dominated by a vertical component. Although Fresnel reflection from a glass surface can polarize unpolarized light, it cannot change the direction of polarization of illuminating partially linearly polarized light. Therefore the building cannot reflect the vertically polarized skylight to become horizontally polarized light; it can only attenuate it. For this reason the light reflected by the building's south wall will be primarily vertically polarized at sunset, and thus polarotactic insects will not be attracted to it. This is the optical reason why Kriska *et al.* [1] observed the *H. pellucidula* caddis flies to swarm in sunshine predominantly at vertical glass surfaces on the sides of the buildings facing the antisolar meridian [Direction of View 1 in Fig. 3(a)] and solar meridian [Direction of View 2 in Fig. 3(a)], and swarming occurred only sporadically on the side of the buildings facing Direction of View 3 in Fig. 3(a).

The above analysis is valid only for the swarming period of *H. pellucidula* when the solar elevation is low. During the day, especially for high solar elevations near noon, the reflection–polarization patterns of glass buildings are more complex. However, in these situations there are also always such regions of the glass-covered vertical buildings' walls from which exactly or nearly horizontally polarized light is reflected, as demonstrated in Fig. 4. Thus glass buildings near water can attract not only polarotactic aquatic insects swarming near sunset [21] but also polarotactic aquatic insects flying during the day [23].

As with many other aquatic insect species [21,23], the *H. pellucidula* caddis flies swarm near sunset in the vicinity of water at vertical objects (e.g., bushes, trees, and buildings), and after copulation the fertilized females return to the water to lay their eggs. Kriska *et al.* [1] showed with choice experiments that female *H. pellucidula* are attracted to highly and horizontally polarized light (positive polarotaxis), which means that these insects find water by means of the horizontally polarized water-reflected light as well, like aquatic insects in general [16–19]. Kriska *et al.* [1] also showed that the highly polarizing dark (black or dark gray) vertical glass surfaces are significantly more attractive to both female and male *H. pellucidula* than the weakly polarizing bright (white or light gray) vertical glass surfaces. This further strengthens the finding that *H. pellucidula* is positively polarotactic.

Because of their positive polarotaxis, *H. pellucidula* can be deceived by and attracted to various sources of horizontally polarized light. Using imaging polarimetry we showed that the light reflected from the vertical glass surfaces of buildings is horizontally polarized from certain directions of view and under certain illumination conditions [see Figs. 3, 4, 5(c), 6(c), 7(c), 8(c), and 9(c)]. Figure 10(a) shows a flying insect approaching the vertical wall of a building covered by a quadratic grid of glass surfaces. The smaller the distance of the flying insect from the wall, the fewer quadratic glass panes fall within the field of view of the Brewster angle. Figure 10(b) shows schematically the 180° field of view pattern of the degree of linear polarization p perceived by a flying polarization-sensitive insect approaching perpendicular to a glass-covered vertical wall for a (1) large, (2) medium, and (3) small distance. Figure 11 represents how a flying polarization-sensitive insect approaching perpendicular to a vertical glass surface could perceive the directions of polarization of light reflected from different parts of the glass at the Brewster angle. A polarotactic aquatic insect is attracted to the reflected light only if the perceived direction of polarization is exactly or nearly perpendicular to its dorsoventral symmetry axis. If the perceived direction of polarization is parallel or tilted to this axis, the reflected light is unattractive to the insect [19]. The black areas in Figs. 5(e), 6(e), 7(e), 8(e), and 9(e) show those regions of the investigated vertical black and white glass surfaces that are sensed as water by a flying polarotactic aquatic insect whose entire eye is assumed to be polarization sensitive (see also Table 2); these black areas are very attractive to a flying polarotactic aquatic insect if they fall within the field of view of the insect's polarization-sensitive eye region. This can be one of the reasons why after their emergence from the Danube river, the polarotactic flying *H. pellucidula* can be lured to the glass-covered vertical walls of buildings on the river bank.

It is still unknown which parts of the eye in *H. pellucidula* are polarization sensitive. According to the choice laboratory experiments of Kriska *et al.* [1], it is known that ovipositing female *H. pellucidula* have positive polarotaxis if their ventral eye region is stimulated by highly and horizontally polarized light. If the eye of *H. pellucidula* had only a ventral polarization-sensitive eye region like the backswimmer *Notonecta glauca* [16], for example, then a flying *H. pellucidula* could be attracted only to the horizontally polarized light reflected from the lower black patch in Figs. 5(e), 6(e), 7(e), and 8(e). In this case vertical panes of glass could attract *H. pellucidula* only if the flying insects approach the glass surface at an appropriately large height, ensuring that the highly and horizontally polarized glass-reflected light can stimulate their ventral eye region. *H. pellucidula* can be attracted to the buildings first by their conspicuous dark silhouettes against the brighter sky. This phenomenon is well-known and called the marker effect [24]. Note that in Table 2, the proportion W of the vertical glass surface sensed as water by a flying polarotactic insect is slightly higher for the black glass than for the white glass. Since darker glass surfaces reflect light with higher p than brighter ones [see Table 1 and Figs. 5(b), 6(b), 7(b), 8(b), and 9(b)], black and dark gray vertical panes of glass should be more attractive to polarotactic caddis flies than white and light gray ones. This prediction is corroborated by the observation of Kriska *et al.* [1] that highly polarizing vertical dark glass surfaces were significantly more attractive to both female and male *H. pellucidula* than weakly polarizing bright ones.

In Figs. 5(e), 6(e), 7(e), and 8(e) , the lower black patch sensed as water by a polarotactic flying insect is not as striking as the upper one. The reason for this is that this lower patch was more or less covered by the mirror image of the tripod of our polarimeter. Of course this problem does not occur for a flying polarization-sensitive caddis fly, which can thus see well also this lower patch.

We would like to emphasize that the attraction of *H. pellucidula* to vertical glass surfaces can be only partly explained by the reflection–polarization characteristics of vertical glass reflectors and the positive polarotaxis of caddis flies. There are certainly other factors that play an important role in this attraction: We have already mentioned the marker effect of the dark silhouettes of buildings against the bright sky, and the positive phototaxis elicited by the room lights at dusk. Both phenomena result in caddis flies being lured to buildings. Other important factors may be the air temperature and humidity or the strength and direction of wind, for example. All these environmental parameters are more or less influenced around buildings and thus surely affect the swarming of caddis flies. Kriska *et al.* [1] also observed, for instance, that *H. pellucidula* do not swarm at and do not stay for a longer period (for hours) at or on sunlit and windy glass surfaces, because they can dry out easily and cannot fly in strong wind.

B. Why Do Polarotactic Caddis Flies Remain on Vertical Glass Surfaces after Landing?

After the flying polarotactic caddis flies emerging from the Danube river have been attracted to vertical glass surfaces, they land on the glass and remain there for hours, especially on black glass panes [1]. In our opinion this can also be partly explained by means of the polarization of glass-reflected light and the polarotaxis of caddis flies.

Figure 12(a) shows schematically the light beam reflected from a vertical glass surface and received by the ventral eye region of an insect landed on the glass. If the ventral eye region of this insect is polarization sensitive, it perceives the polarization patterns shown in Figs. 5(b), 5(d), 6(b), 6(d), 7(b), 7(d), 8(b), 8(d), 9(b), and 9(d) and senses more or less areas of the glass surface as water [see Figs. 5(f), 6(f), 7(f), 8(f), and 9(f)]. Figure 12(b) represents how such a polarotactic insect landed on a vertical glass surface and looking into different directions senses the direction of polarization of light reflected from the glass at the Brewster angle. Since the perceived direction of polarization is always perpendicular to the insect's dorsoventral symmetry axis, independently of the direction of view, the light reflected from the Brewster angle is always attractive to the insect if it has positive polarotaxis. According to Table 3 the proportion W of the vertical glass surface sensed as water by a landed polarotactic insect is much higher for black glass than for white glass, because dark glass surfaces are much stronger polarizers than bright ones. This may be one of the reasons for why *H. pellucidula* observed by Kriska *et al.* [1] remained for hours on the dark vertical glass surfaces after landing, and why the vertical dark glass surfaces were significantly more attractive to *H. pellucidula* than the bright ones.

When a caddis fly landed on a vertical glass surface recognizes that the glass is not water, it either flies away or remains on the glass, which, however, may be considered henceforward as a solid substratum on which the insect can rest or walk around. If the insect flies off the vertical glass, its polarization-based attraction can be again elicited by the mechanism described in Subsection 4.A (see Figs. 10 and 11). This may be the reason for the observation by Kriska *et al.* [1] that *H. pellucidula* swarm for hours at dark vertical glass surfaces; they land on and fly off the dark glass many times during swarming.

The explanation of why the caddis flies stay on the glass after landing when other sensory modes get information is that the polarization signal is a supernormal stimulus [19]. It has been observed in numerous other polarotactic aquatic insect species (e.g., mayflies, water bugs, aquatic beetles, and dragonflies) that all their sensory modes are overwhelmed by the highly and horizontally polarized light reflected from various artificial surfaces such as dark crude oil [3–6], asphalt roads [7], black plastic sheets [6,8], black or dark-colored car bodies [9,10], and black gravestones [11]. All these highly and horizontally polarizing man-made surfaces act as ecological traps for polarotactic aquatic insects [25–27]; these insects are deceived by, attracted to, and killed by the mentioned surfaces due to exhaustion and dehydration, because the deceived insects remain there in spite of the signals of their other sensory organs.

C. "Green" Buildings Considering Aquatic Insect Protection

Kriska *et al.* [1] showed that the polarotactic caddis flies *H. pellucidula* attracted to vertical glass surfaces can be trapped if the tiltable windows are open, and thus such glassy buildings can be ecological traps for mass-swarming caddis flies *sensu* [25]. On the basis of the observations of Kriska *et al.* [1] and the results presented in this paper, we can establish the main optical characteristics of "green," that is, environment-friendly, buildings considering the protection of polarotactic aquatic insects. These "green" buildings possess features that attract a small number of polarotactic aquatic insects when standing in the vicinity of fresh waters:

- Since a smooth glass surface strongly polarizes the reflected light, a "green" building must minimize the used glass surfaces. All unnecessary panes of glass should be avoided, which would have only an ornamental function. The buildings in Figs. 1, 3, and 4, for example, have plenty of decorative glass surfaces; almost the entire upper wall surface is covered by unnecessary gray and black glass panes composing 80% of the entire glass area. Practically the only necessary glass surfaces on a building are the windows, and all other glass covering could be spared.
- Since all smooth surfaces highly polarize the reflected light, a "green" building has to avoid bricks with shiny-looking, that is, smooth, surfaces. The optimal is the use of bricks with matte surfaces.
- Since, according to the rule of Umow [20], the darker a surface, the higher p of reflected light, a "green" building must especially avoid the use of shiny dark (black, dark gray, or dark-colored) surfaces. A building covered by dark decorative glass surfaces functions as a gigantic highly and, from certain directions of view, horizontally polarizing light trap for polarotactic aquatic insects. The windows of dark rooms can also attract polarotactic insects. If the bright curtains are drawn in, p of light reflected from the window is considerably reduced, and thus the window becomes unattractive to polarotactic insects.
- Since aquatic insects usually do not perceive red light [17–19] and thus a red shiny surface seems dark and highly polarizing to them [10], a "green" building has to avoid the use of shiny red surfaces. Since the outer walls of the southern building of Eötvös University (see Fig. 4), for example, are covered by huge dark red vertical glass surfaces as ornamentations, furthermore the bricks of both the northern and southern buildings have a shiny red surface, these buildings are not "green" at all.
- The surfaces of a "green" building must not be too bright either, because near and after sunset they reflect a large amount of city light, which can also lure insects by phototaxis. The optimal compromise is the use of medium gray and matte surfaces, which reflect light only moderately with a weak and usually nonhorizontal polarization.
- If a building possesses the above-mentioned optical features, it will attract only a small number of polarotactic and phototactic insects. A further important prerequisite of the environment-friendly character is that the glass windows of a "green" building must not be tiltable around a horizontal axis of rotation. As Kriska *et al.* [1] have shown, if partly open, such tiltable windows can easily trap the insects attracted to them in the room. The optimal solution would be the application of windows that can be opened by rotation around a vertical axis. If a building stands near fresh water and has the mentioned unfavorable tiltable windows, it can easily be made "green" by keeping the windows closed (if possible) during the main swarming period of the polarotactic and phototactic insects swarming in the surroundings.

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