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Reducing the Maladaptive Attractiveness of Solar Panels to Polarotactic Insects

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Abstract: *Human-made objects (e.g., buildings with glass surfaces) can reflect horizontally polarized light so strongly that they appear to aquatic insects to be bodies of water. Insects that lay eggs in water are especially attracted to such structures because these insects use horizontal polarization of light off bodies of water to find egg-laying sites. Thus, these sources of polarized light can become ecological traps associated with reproductive failure and mortality in organisms that are attracted to them and by extension with rapid population declines or collapse. Solar panels are a new source of polarized light pollution. Using imaging polarimetry, we measured the reflection–polarization characteristics of different solar panels and in multiple-choice experiments in the field we tested their attractiveness to mayflies, caddis flies, dolichopodids, and tabanids. At the Brewster angle, solar panels polarized reflected light almost completely (degree of polarization* $d \approx 100\%$*) and substantially exceeded typical polarization values for water (*$d \approx 30$*–*70%*). Mayflies (Ephemeroptera), stoneflies (Trichoptera), dolichopodid dipterans, and tabanid flies (Tabanidae) were the most attracted to solar panels and exhibited oviposition behavior above solar panels more often than above surfaces with lower degrees of polarization (including water), but in general they avoided solar cells with nonpolarizing white borders and white grates. The highly and horizontally polarizing surfaces that had nonpolarizing, white cell borders were 10- to 26-fold less attractive to insects than the same panels without white partitions. Although solar panels can act as ecological traps, fragmenting their solar-active area does lessen their attractiveness to polarotactic insects. The design of solar panels and collectors and their placement relative to aquatic habitats will likely affect populations of aquatic insects that use polarized light as a behavioral cue.*

Keywords: evolutionary trap, habitat selection, maladaptation, polarized light pollution

Reducción de la Atracción Inadaptiva de Placas Solares para Insectos Polarotácticos

Resumen: *Objetos construidos por humanos (e. g., edificios con superficies de vidrio) pueden reflejar luz polarizada horizontalmente tan potentemente los insectos acuáticos los confunden por cuerpos de agua. Los insectos que ovopositan en el agua son especialmente atraídos por tales estructuras porque estos insectos utilizan la polarización horizontal de luz de los cuerpos de agua para encontrar sitios para la puesta de huevos. Por lo tanto, estas fuentes de luz polarizada pueden convertirse en trampas ecológicas asociadas con el fracaso reproductivo y mortalidad de organismos que son atraídos a ellas y por extensión, con declinaciones poblacionales rápidas o colapso. Las placas solares son una fuente de contaminación por luz polarizada. Utilizando polarimetría de imágenes, medimos las características de reflexión-polarización de diferentes placas solares y, en experimentos de opción múltiple en el campo, probamos su atracción en efemerópteros, tricópteros, dolicopódidos y tabánidos. Las placas solares polarizaron la luz reflejada casi totalmente (nivel*

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de polarización d ≈ *100%) y excedieron sustancialmente los valores típicos de polarización del agua (*d *≈ 30–70%). Los efemerópteros, tricópteros, dípteros dolicopódidos y tábanos fueron los más atraídos a las placas solares y exhibieron comportamiento de ovoposición sobre las placas solares más a menudo que sobre superficies con niveles de polarización más bajos (incluyendo agua), pero en general evitaron las celdas solares con bordes blancos no polarizadores y rejillas blancas. Las superficies alta y horizontalmente polarizadoras que tenían celdas blancas no polarizadoras fueron entre 10 y 26 veces menos atractivas para insectos que las mismas placas sin divisiones blancas. Aunque las placas solares pueden actuar como trampas ecológicas, la fragmentación de su área solar activa no disminuye su atracción de insectos polarotácticos. El diseño de placas y colectores solares y su colocación en relación con hábitats acuáticos muy probablemente afectará poblaciones de insectos acuáticos que utilizan luz polarizada como una señal conductual.*

Palabras Clave: contaminación por luz polarizada, inadaptación, selección de hábitat, trampa evolutiva

Introduction

Rapidly changing environments have the potential to disrupt evolved behaviors because the environmental cues organisms use to direct their behavior may no longer elicit the outcome with which they were associated historically (Levins 1968). Evolutionary traps occur when rapid environmental change triggers organisms to make maladaptive behavioral decisions (Schlaepfer et al. 2002). Although evolutionary traps may be associated with any behavior (e.g., mate selection, navigation, nest-site selection), the most empirically and theoretically well-understood type of evolutionary trap is the ecological trap. Ecological traps are situations in which novel environmental conditions lead organisms to settle in poor-quality habitats (Dwernychuk & Boag 1972). They represent severe cases of behavioral maladaptation that can lead to population declines or extirpation (Delibes et al. 2001; Kokko & Sutherland 2001). Despite the awareness of ecological traps among ecologists and conservation biologists, fewer than 10 cases have been well documented (reviewed by Robertson & Hutto 2006, 2007; Hedin et al. 2008; Carrete et al. 2009; Resetarits & Binckley 2009).

Shiny dark-colored objects such as oil lakes and glass buildings can reflect highly and horizontally polarized light. Positively polarotactic aquatic insects that use horizontally polarized light to detect water are attracted to these objects (Schwind 1991; Horváth & Zeil 1996; Horváth et al. 1998; Wildermuth 1998; Kriska et al. 2008). Sunlight is unpolarized, because it consists of electromagnetic waves of different wavelengths and vibrating at all possible planes perpendicular to the direction of propagation, but light is completely linearly polarized when its waves oscillate only in a single plane. The smooth surface of water horizontally polarizes reflected sunlight and skylight, and this reflection is an evolutionarily reliable cue that indicates the presence of lakes and rivers to over 300 species of aquatic insects (e.g., Schwind 1995; Wildermuth 1998; Horváth & Kriska 2008). Polarized light pollution (Horváth et al. 2009) produced by human-made objects can be so severe that it creates ecological traps in which insects tend to mate above and oviposit on artificial surfaces, where they are subject to increased predation and reproductive failure (Kriska et al. 1998; Horváth & Varjú 2004).

In general, dark and smooth materials reflect light with a high degree of polarization and so are highly likely to attract polarotactic organisms. The use of photovoltaic solar cells and solar collectors as a source of energy is likely to increase dramatically yet the physical characteristics of the cells and collectors suggest they may represent a major new source of polarized light pollution (Figs. 1 & 2; Supporting Information). We examined the attractiveness of photovoltaic solar panels and artificial surfaces of varying brightness and smoothness to some polarotactic aquatic insects (*Philopotamus*: Trichoptera; dolichopodids: Diptera; mayflies: Ephemeroptera; tabanid flies: Tabanidae) and used imaging polarimetry (Horváth & Varjú 1997) to quantify the reflection–polarization characteristics of these surfaces.

Methods

Choice Experiments with Mayflies, Caddis Flies, and Dolichopodids

We conducted five experiments in the Hungarian Duna-Ipoly National Park at Dömörkapu, in which we monitored the response of Ephemeroptera, Trichoptera, and dolichopodid dipteran species to (1) white-framed solar cells and nonpolarizing surfaces, (2) white- and black-framed solar cells with an underlying polarizing plastic sheeting, (3) white- and black-framed solar cells in the absence of an underlying polarizing plastic sheeting, (4) shiny black surfaces with different nonpolarizing white grid patterns, and (5) white framing of solar cells in a solar panel versus a homogeneously black solar panel.

The insects we examined in the park emerged from a creek adjacent to the site of the experiments at dusk from May to July and swarmed above the water surface and portions of a dry asphalt road that reflected highly and horizontally polarized light near sunset. Insects mate in swarms that develop from 17:00 to 21:00 h, and fertilized females oviposit directly onto water or other horizontally polarizing surfaces immediately afterward (Horváth & Kriska 2008). In earlier field experiments performed

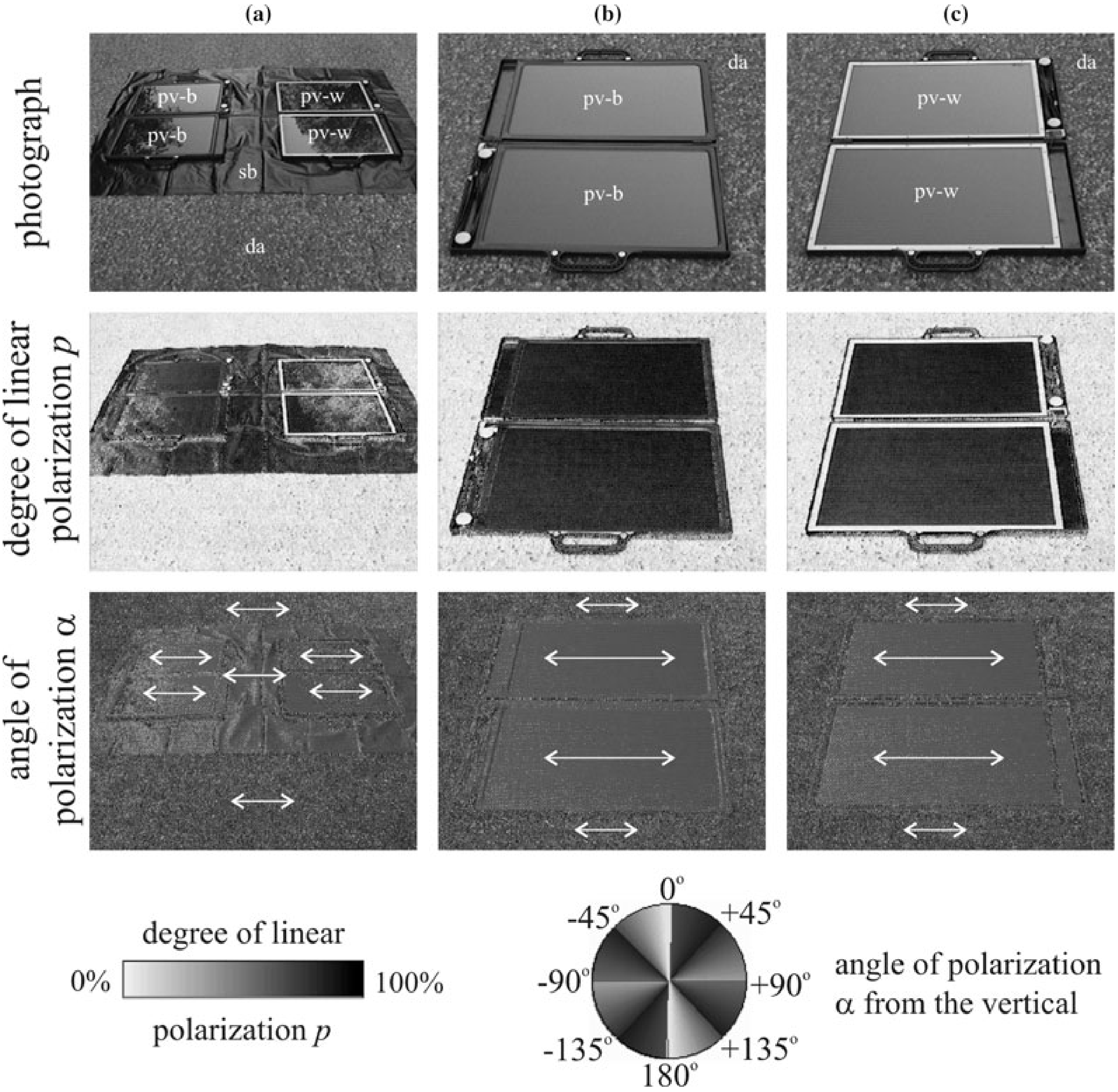

Figure 1. Photographs and reflection-polarization patterns of the shiny black (sb) plastic sheet (2 × 2 m; other surfaces 80 × 60 cm), white-framed photovoltaic solar cells (pv-w), black-framed photovoltaic solar cells (pv-b), shiny black plastic sheet (sb), and dry asphalt (da) measured in the green (550 nm) part of the spectrum after sunset. Double-headed arrows show the direction of polarization of reflected light. The polarimeter viewed toward the antisolar meridian and the angle of elevation of its optical axis was −35° from the horizontal.

at the same site (Kriska et al. 1998; Horváth & Varjú 2004; Horváth & Kriska 2008), these taxa more often reproduced over artificial surfaces that reflected highly and horizontally polarized light than over water, and displayed the same reproductive behavior above human-made, shiny, dark surfaces and water surfaces.

On 21 May 2008 we tested the relative attractiveness of white-framed solar cells and nonpolarizing test surfaces of different reflectivity to polarotactic taxa. We laid a sheet of shiny black plastic (2 × 2 m) flat on a dry asphalt road on which we placed a matte black cloth (80 × 60 cm), a matte white cloth, and a photovoltaic solar panel (13 W, Solar Generator, Conrad Electronic, Budapest, Hungary) of the same size equidistant from each other and the edges of the sheet (Supporting Information). The photovoltaic panel was composed of two white-framed (frame width 1 cm) photovoltaic solar cells (each 60 × 40 cm). The fourth test surface was an area of the black plastic sheeting equivalent in size to the other surfaces. We repositioned the test surfaces on the plastic

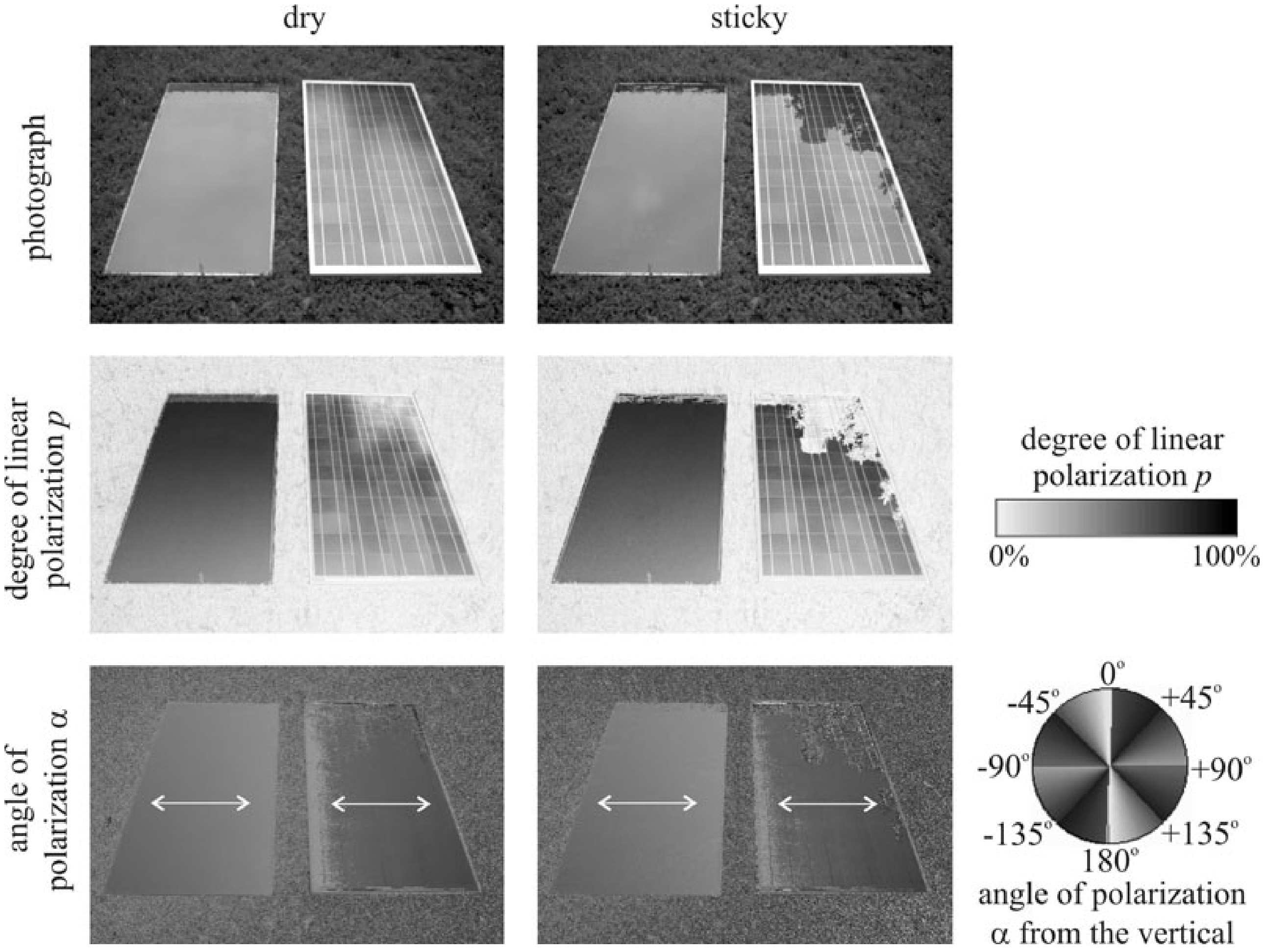

Figure 2. Photographs and reflection-polarization patterns of the two horizontal (dry and sticky) solar panels used in the choice experiments with mayflies, caddis flies, dolichopodids, and tabanids. Double-headed arrows show the direction of polarization of reflected light. The polarimeter viewed toward the antisolar meridian and the angle of elevation of its optical axis was $-35°$ from the horizontal.

sheet randomly every 30 min over the course of each experiment. Mayflies hover over and land repeatedly on surfaces prior to oviposition (Savolainen 1978; Supporting Information), so we inferred attractiveness from the number of mayflies (N_M) and the number of landings (N_L) made by individuals on each test surface.

On 22 May 2008 we tested whether the original white, nonpolarizing (degree of linear polarization of reflected light $d \approx 0\%$) frame (width 1 cm) around the two solar cells reduced their attractiveness to mayflies. The manufacturer (Conrad Electronic) described this white frame as purely decorative. We used two solar panels of identical size (80 × 60 cm) (Fig. 1a). The first had the original white frame. On the second, the white frame was covered with a highly ($d \approx 100\%$) and horizontally polarizing, shiny, black plastic tape (width 1 cm). We counted the number of mayflies and the number of landings made by individuals on both solar panels. These two panels were transposed on the black plastic sheet every 15 min throughout the 2-h experiment.

For 5 days between 23 and 30 May 2008, we tested mayfly attraction to a white-framed and a black-framed solar panel in the absence of the underlying polarizing plastic sheeting. The protocols were identical to the preceding experiment, but the underlying substrate of the two differently framed solar panels was a weakly polarizing ($d < 15\%$) section of the dry asphalt road (Figs. 1b-c).

For 8 days between 23 May to 3 June 2008, we tested the effect of nonpolarizing white grid patterns on the attractiveness of shiny black surfaces to mayflies. Given the typically deleterious effects of habitat fragmentation on the abundance and species richness of species in natural systems (e.g., Collinge 2000; Funk et al. 2005; Moore et al. 2008), we tested whether partitioning even highly and horizontally polarizing surfaces into smaller sections could make them unattractive to polarotactic insects. Because the operative nature of attraction of all known taxa of polarotactic aquatic insects to water is its polarized light signature (dragonflies: Wildermuth 1998;

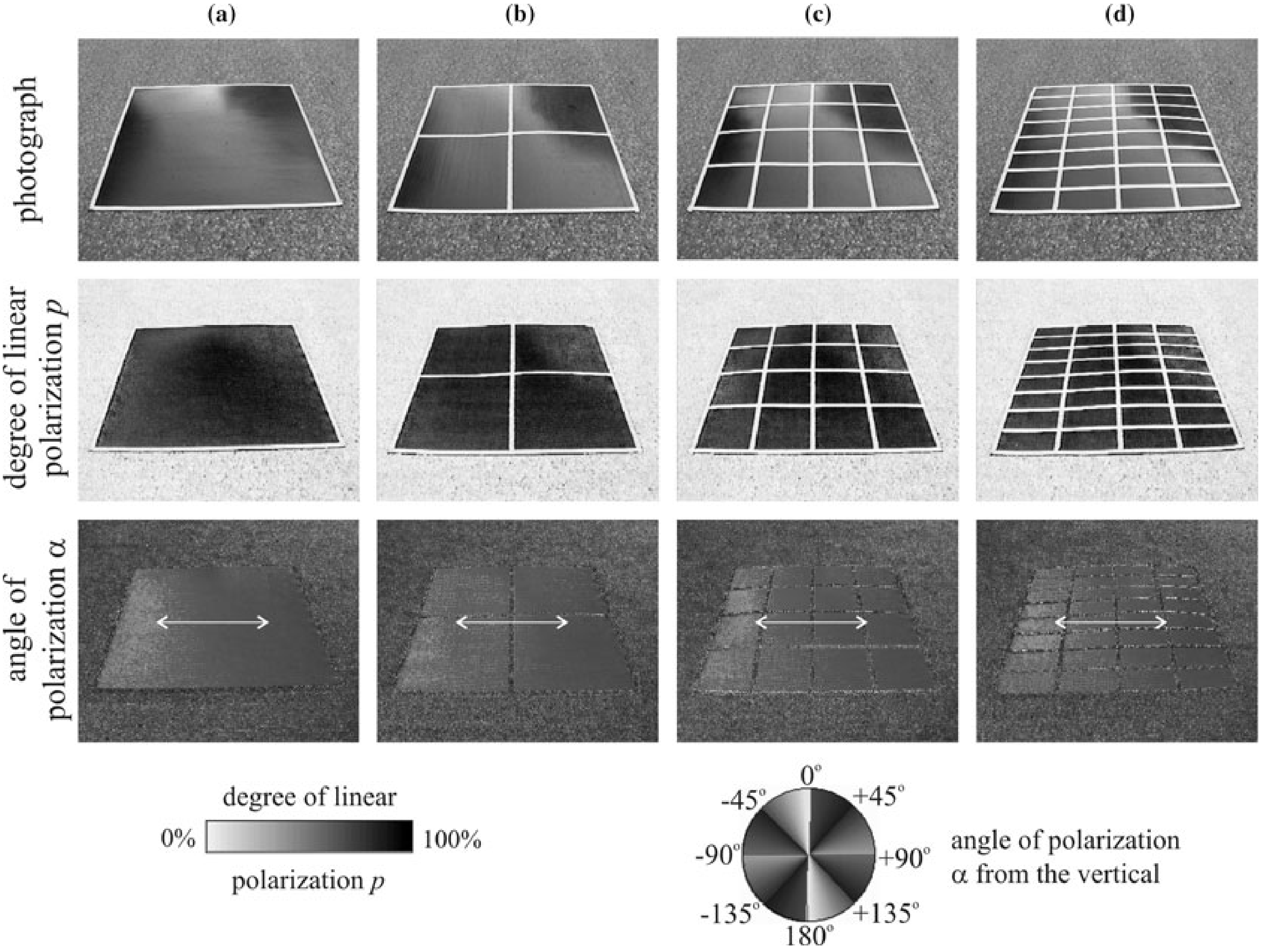

Figure 3. Photographs and reflection-polarization patterns of the four polarizing surfaces (2 × 2 m) used in the experiment with mayflies, caddis flies, and dolichopodids (Fig. 4). The white-framed surfaces (b, c, d) are orthogonally partitioned by nonpolarizing white tape. Double-headed arrows show the direction of polarization of reflected light. The polarimeter viewed toward the antisolar meridian and the angle of elevation of its optical axis was −35° from the horizontal.

78 aquatic beetles [Coleoptera] and 21 aquatic bugs [Heteroptera]: Csabai et al. 2006; 37 aquatic Coleopteran and Heteropteran taxa: Kriska et al. 2006), we created test surfaces of highly polarizing smooth black plastic (Bernáth et al. 2001). We made four shiny black plastic squares (2 × 2 m) with a white frame (width 1 cm) on their outer edge. Three of the white-framed squares were orthogonally partitioned by white tape (width 1 cm) with a low d (< 5%) that effectively fragmented the total area of black polarizing surface into smaller fragments (A, 1 section; B, 4 sections; C, 16; D, 32; Fig. 3). We covered surfaces with a colorless and odorless transparent paraffin oil, which made them sticky so that insects landing on them would be instantly trapped. Every 30 min we randomly repositioned test panels within their linear formation on an underlying substrate of weakly polarizing (d < 15%) dry asphalt road. Test surfaces were placed on the asphalt road 50 cm apart, parallel to the river, and exposed from 19:00 and 21:00 h. Trapped insects were collected at the end of each 2-h session, stored in alcohol, and later identified in the laboratory. We calculated the density of Emphemeroptera, Trichoptera, and dolichopodid Dipterans captured per unit black area on test surfaces. Ephemeropterans were identified to the species level.

We repeated the procedure we used with the shiny black surfaces fragmented by different white grid patterns with (1) a white-framed (width 1 cm) solar panel (100 W, RWE Schott Solar, Alzenau, Germany) composed of solar cells that were small, homogeneous, shiny black, and rectangular with narrow (width 0.2–0.5 cm) white margins (Fig. 2; Supporting Information) and (2) a homogenous black solar panel (40 W, DunaSolar, Budapest, Hungary) with no white partitioning (Fig. 2; Supporting

Table 1. The surface density[a] of polarotactic dolichopodids (Diptera) trapped by the homogeneous black and white-gridded solar panels

Date 2009	*Black*[b]	*White gridded*
3 June	111.9	15.8
8 June	185.7	47.3
9 June	136.9	55.8
10 June	75.0	32.7
12 June	135.7	78.8
14 June	161.9	32.7
15 June	77.4	43.6
16 June	109.5	46.1
17 June	98.8	40.0
18 June	92.9	49.7
Sum	1185.7	442.4

[a] *Surface density:* $n = m \times 1\ m^2/A$, *where* m *is the number of insects counted on the surface,* A *is the amount of black area;* n, *is the number of dolichopodids trapped by 1* m^2 *of sticky black surface. For the homogeneous black solar panel and the white-gridded solar panel* A *was 0.84 and 0.825* m^2, *respectively.*

[b] *On all dates for the black surface, the difference in the sum of* n *(*$\chi^2 = 338.4$, $df = 1$, $p < 0.0001$*) and the daily differences in* n *(*$\chi^2 = 8.9 - 84.5$, $df = 1$, $p < 0.005$*) were highly statistically significant.*

Information) to examine whether behavioral responses to test surfaces were representative of responses to manufactured solar panels. Narrow white cell divisions created 144 black squares that were slightly heterogeneous in size (Fig. 2; Supporting Information). We laid the panels on the dry asphalt road 1-m apart and exchanged their position every 30 min. Although the area of both surfaces was identical (1.2 × 0.7 m), the net black area of the panel with the white grid was slightly smaller (0.825 m^2) than the black area of the panel that was entirely black (0.84 m^2), so we calculated the number of insects captured per unit black area (Tables 1 & 2). For 10 days between 3 and 18 June 2009 between 18:00 and 21:00 h, we counted dolichopodids and mayflies because these taxa were the most abundant at the study site.

Choice Experiment with Tabanids

On 2 sunny, warm days (9 and 11 July 2009, between 10:00 and 18:00 h each day), we conducted experiments at a horse farm in Szokolya (47°52′N, 19°00′E), Hungary. We used the same two solar panels as in the experiment with sticky panels that trapped mayflies and dolichopodids, but the panels did not have sticky paraffin oil on them (Fig. 2). We laid both test surfaces horizontally on grassy ground 1-m apart and switched their positions every 30 min. We made sure both panels were in either sun or shade at the same time. Thus, their temperatures (measured by a digital contact thermometer with an accuracy of 0.25 °C) were the same. We counted the number of tabanid flies touching the dry solar panels and expressed the number of "captures" relative to the amount of black surface on the panels (Table 3). We did not use the paraffin oil to capture flies because we learned in a preliminary test that it did not capture tabanids. We acknowledge our method in this experiment is affected by pseudoreplication (i.e., the same tabanid individual may have been counted more than once). In spite of this, we believe the conclusions we drew from the number of tabanids touching the dry solar panels are valid because the attractiveness of the surfaces to tabanids is proportional to the number touching the surfaces.

Table 2. The surface density *n* of polarotactic mayflies (Ephemeroptera) trapped by the homogeneous black and white-gridded solar panels.

Mayfly species	*Black**	*White gridded*
Baetis rhodani	271.4	50.9
Ephemera danica	142.9	2.4
Rhithrogena semicolorata	60.7	18.2
Sum	475.0	71.5

**For the black surface the difference in the sum of* n *(*$\chi^2 = 296.4$, $df = 1$, $p < 0.0001$*) and the differences in* n *for all three species (*$\chi^2 = 21.8\text{-}149.5$, $df = 1$, $p < 0.0001$*) were highly statistically significant.*

We performed binomial χ^2 tests in Statistica (version 6.0) to compare numbers of captures, abundance, and touches among test surfaces for each insect taxon investigated.

Imaging Polarimetry

We measured reflection–polarization characteristics of solar panels and test surfaces by imaging polarimetry in the red (650 ± 40 nm = wavelength of maximal sensitivity ± half bandwidth of the detectors of the polarimeter), green (550 ± 40 nm), and blue (450 ± 40 nm) parts of the spectrum. Our method of imaging polarimetry is described in detail elsewhere (Horváth & Varjú 1997, 2004). We provide only the polarization patterns measured in the green spectral range. Similar patterns were obtained in the red and blue parts of the spectrum because the targets were colorless (black, gray, or white); thus, their reflection–polarization characteristics did not depend on the wavelength of light. Polarimetry was performed under clear skies after sunset or in full sun.

Results

At the Brewster angle ($\theta_{\text{Brewster}} = 56.3°$ from the vertical), solar cells ($d \approx 90\text{–}100\%$) and black plastic sheeting ($d \approx 100\%$) were strong horizontal polarizers of incident light compared with the matte black ($d < 20\%$) and white ($d \approx 0\%$) test surfaces (Figs. 1 & 2; Supporting Information). Mayflies were attracted to the black plastic sheeting ($N_M = 126$, $N_L = 281$) and avoided ($N_M = N_L = 0$) the matte white and matte black surfaces and the white-framed solar cells ($p < 0.0001$, df = 1, N_M: $\chi^2 = 126$, N_L:

Table 3. The surface densities n_{touch} and n_{time} of the numbers of polarotactic tabanids (N_T) and their landings (N_L) on the homogeneous black and the white-gridded dry solar panels and the temporal preference[a] of these tabanids.

	$\mathrm{n}_{tabanid}$		$\mathrm{n}_{touch-down}$		t *(sec)*	
Date (2009)	*black*[b]	*white gridded*	*black*[b]	*white gridded*	*black*[b]	*white gridded*
9 July	95.2	32.7	625	84.8	6,078.6	987.9
11 July	145.2	38.8	781	77.6	5,006	535.8
Sum	240.5	71.5	1406	162.4	11,084.5	1523.6

[a] *Temporal preference:* $\mathrm{t} = \mathrm{T} \times 1\ m^2/\mathrm{A}$, *where* T *is the time period spent by tabanids on a given test surface, the net black area of which is* A ($\mathrm{A}_{black} = 0.84\ m^2$, $\mathrm{A}_{whitegridded} = 0.825\ m^2$).

[b] *The differences in the sum of* $\mathrm{n}_{tabanid}$, $\mathrm{n}_{touchdown}$, *and* t *are statistically significant* ($\mathrm{n}_{tabanid} : \chi^2 = 90.5$, $df = 1$, $\mathrm{p} < 0.0001$; $\mathrm{n}_{touchdown} : \chi^2 = 984.5$, $df = 1$, $\mathrm{p} < 0.0001$; $\mathrm{t} : \chi^2 = 7248.6$, $df = 1$, $\mathrm{p} < 0.0001$). *The daily differences in* $\mathrm{n}_{tabanid}$, $\mathrm{n}_{touchdown}$, *and* t *are also statistically significant* ($\mathrm{n}_{tabanid} : \chi^2 = 29.6$–$60.4$, $df = 1$, $\mathrm{p} < 0.0001$; $\mathrm{n}_{touchdown} : \chi^2 = 435.1$–$574.6$, $df = 1$, $\mathrm{p} < 0.0001$; $\mathrm{t} : \chi^2 = 3604.2$–$3683.6$, $df = 1$, $\mathrm{p} < 0.0001$).

$\chi^2 = 281$). Mayflies avoided the white-framed solar cells ($N_M = N_L = 0$), but were attracted to the solar cells with polarizing black frames ($N_M = 43$, $N_L = 105$, $p < 0.0001$, df = 1, N_M: $\chi^2 = 43$, N_L: $\chi^2 = 105$; Fig. 1b). When we replaced the black plastic sheet with weakly polarizing dry asphalt ($d < 15\%$; Figs. 1b-c), the black-framed solar cells attracted 4.2 times more mayflies ($N_{M,\text{blackframed}} = 200$, $N_{M,\text{whiteframed}} = 48$, $\chi^2 = 93.1$, df = 1, $p < 0.0001$) and elicited 6.9 times more landings ($N_{M,\text{blackframed}} = 474$, $N_{M,\text{whiteframed}} = 69$, $\chi^2 = 302$, df = 1, $p < 0.0001$) than the white-framed solar cells (Supporting Information).

The relation between the number of orthogonal white stripes on a sticky test surface and the captures per unit black area for all taxa was negative (Fig. 4; Supporting Information). Captures per square meter were 26.5 and 10.3 times higher on the unpartitioned surface relative to the most highly partitioned surface for Trichopterans and dolichopodids, respectively. Mayfly captures per square meter were 16.7 times higher on the unpartitioned surface relative to the most highly partitioned surface, and responses were similar among the four mayfly species we captured (Supporting Information).

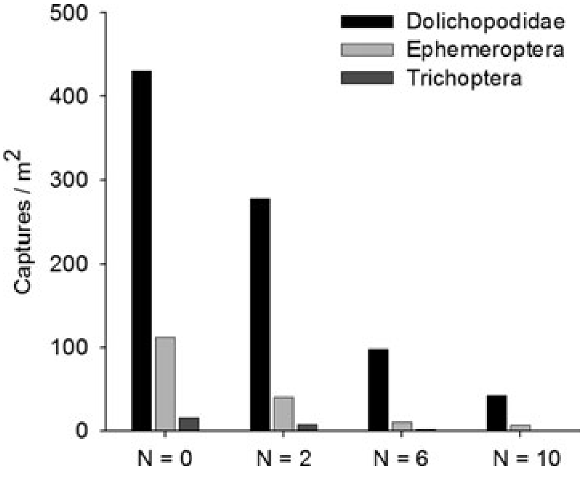

Figure 4. The surface density (captures per square meter) of polarotactic dolichopodid (Diptera), mayflies (Ephemeroptera), and Philopotamus *(Trichoptera) trapped by a highly and horizontally polarizing sticky surface with different numbers* (N) *of orthogonal white strips (Fig. 3).*

Captures ($1186/\mathrm{m}^2$) of dolichopodids on the homogeneous black solar panel were 2.7 times higher than captures ($442/\mathrm{m}^2$) on the partitioned white-gridded panel, which is a highly statistically significant difference (Table 1). The homogeneous panel ($475/\mathrm{m}^2$) attracted mayflies 6.6 times more than the partitioned panel ($72/\mathrm{m}^2$) (Table 2). We obtained similar results for the experiment with tabanid flies (Table 3). The homogeneous black solar panel ($240.5/\mathrm{m}^2$) attracted tabanids 3.4 times more than the white-gridded panel ($71.5/\mathrm{m}^2$). Tabanids touched down ($1406/\mathrm{m}^2$) on the homogeneous panel 8.7 times more frequently than on the white-gridded panel ($162.4/\mathrm{m}^2$). After landing, tabanids stayed ($11084.5/\mathrm{m}^2$) on the homogeneous panel 7.3 times longer period than on the white-gridded panel ($1523.6/\mathrm{m}^2$).

Figure 2 shows the reflection–polarization patterns of the two sticky and dry solar panels we used in the experiment with mayflies, caddis flies, dolichopodids, and tabanids, respectively. The dry and sticky solar panels had nearly the same reflection–polarization characteristics. Both the white frame and the white grid of the partitioned solar panel reflected weakly polarized or unpolarized light, whereas the other shiny black surface regions reflected highly polarized light as did the entire surface of the homogeneously black solar panel. The direction of polarization of light reflected from both panels was always horizontal when the plane of reflection was vertical.

Discussion

Our results demonstrate that photovoltaic solar panels produce polarized light pollution (Horváth et al. 2009). White-framed and white-gridded solar panels, however, were much less attractive to polarotactic aquatic insects than homogeneous black panels. Thus, the former panels induce much less polarized light pollution. The degree of polarization of light reflected from water bodies is typically <70%. Because of the near total ($d \approx 100\%$ at the Brewster angle) and horizontal polarization of light reflected from solar panels, polarotactic aquatic insects are likely to prefer artificial surfaces over natural bodies of water and to oviposit on the artificial surfaces. This polarization-induced attraction represents a severe form of ecological trap (Robertson & Hutto 2006) for polarotactic insects that will result in reproductive failure of eggs laid on artificial surfaces (e.g., Watson 1992; Vondel 1998; Kriska et al. 2006; Horváth et al. 2007), death from exhaustion, and increased risk of predation (Kriska et al. 1998; Horváth & Varjú 2004; Horváth & Kriska 2008). The solar panels we used were oriented horizontally to mimic the orientation of natural water bodies. Solar panels are often elevated above the ground and tilted at an angle to maximize interception of solar radiation. Orientation and elevation appear to be generally unimportant in mitigating behavioral responses of polarotactic insects to artificial polarizing reflectors. Vertical glass surfaces are highly effective at horizontally polarizing light (Malik et al. 2008) and attracting polarotactic aquatic insects to oviposit en masse even many stories above ground level (Kriska et al. 2008). It is well documented that aquatic beetles, water bugs and dragonflies are attracted to and oviposit on the roof, hood, and trunks of dark-colored highly polarizing automobiles that are elevated and tilted at various heights and angles (e.g., Jäch 1997; Nilsson 1997; Wildermuth & Horváth 2005). Consequently, we expect that tilted and even highly elevated solar panels will attract these insects. Elevation may even increase the distances at which such structures can be detected.

Our results show that a dense nonpolarizing (e.g., white) grid partitioning the solar-active area of solar panels reduces or eliminates the polarized light pollution of these highly and horizontally polarizing artificial surfaces. There is a trade-off, however, between the amount of solar-active surface and nonpolarizing grid: such grids will reduce the performance of these panels. The decrease in energy production associated with the application of a grid is proportional to the total surface area of the grid. The white-gridded solar panel (RWE Schott Solar) we used had a total surface area of 0.840 m^2, and the surface area of the white grid was 0.015 m^2. Thus, the solar-active (black) area was 0.825 m^2. This means there would be a 1.8% loss of effective (i.e., energy producing black) surface area in this panel, but a statistically significant reduction of the attractiveness of the panel to polarotactic insects. Thus, the cost of effectively eliminating the attractive effect of polarized light pollution on the taxa we investigated amounts to a relatively small drop in performance of solar panels.

The cognitive or behavioral mechanism reducing the attractiveness of partitioned solar panels to polarotactic insects is unclear. Because fragmenting polarizing surfaces reduced their attractiveness, patch size may be a habitat-selection cue to aquatic insects, as has been observed in terrestrial and aquatic vertebrates (e.g., Herkert 1994; Funk et al. 2005; Moore et al. 2008). Another, more proximate, potential mechanism is that the low spatial resolution of the insect compound eye reduces polarization contrast, rendering the appearance of a white-gridded solar panel as less polarized and therefore less attractive than might be expected on the basis of our high-resolution polarization patterns. Although distinguishing between these two mechanisms is outside the scope of this paper, the possibility of a sensory origin rather than a more cognitive origin of the reduction in attractiveness facilitates mitigation of the ecological trap solar panels present.

The potential effects of polarized light pollution associated with solar panels on populations of aquatic insects remains unclear, but they are predicted to cause rapid and potentially large population declines (Delibes et al. 2001; Donovan & Thompson 2001), especially when located near natural wetlands and water bodies. The ubiquity of strong artificial polarizers in rural and urban environments has not been quantified. Until the population-scale effects of artificial polarizers on affected taxa are clarified, we urge caution in the placement of solar arrays and selection of panel design, particularly where rare or endangered species may be directly or indirectly affected. Solar farms, on which solar panels cover large areas, are rapidly increasing throughout Europe, Africa, and the United States. As artificial polarizers become a more common component of modern landscapes, intense selective pressure could trigger rapid evolution of novel habitat-selection cues (Kokko & Sutherland 2001). This possibility is contingent on the existence of other environmental signals that are tightly correlated with the presence of suitable water bodies. Because horizontally polarized light is the most reliable visual cue associated with water bodies under variable illumination conditions (Horváth & Varjú 2004), rapid evolution of cue use that facilitates evolutionary escape may be unlikely, especially if exploiting novel cues requires the evolution of new or enhanced sensory modalities.

Our results illustrate the attractiveness of highly and horizontally polarizing surfaces to polarotactic insects and show that both the degree and the direction of polarization of reflected light are important to mayflies, dolichopodids, Trichopterans, and tabanid flies in selecting among potential habitats. We also demonstrated that the increasing fragmentation of polarizing surfaces by a white grid reduces their attractiveness to polarotactic insects. This fact can be used to eliminate the trap effect associated with solar panels. By partitioning the active (i.e., highly and horizontally polarizing) surface of a panel into smaller subpanels with nonpolarizing (e.g., white) borders (Figs. 2 & 3), the surface is fragmented and becomes much less attractive. Substantial variation exists in the degree of partitioning associated with commercially manufactured solar cells and collectors and the width of the white panel partitions may determine whether adjacent panel sections are perceived as separate habitat patches or a single continuous patch. Although the relative effectiveness of partitioning solar panels appears taxon specific, the 10- to 26-fold reduction in attractiveness we found is biologically significant, which suggests partitioning will be an effective conservation measure for these and other polarotactic taxa. Because solar collectors and photovoltaic solar panels share polarization-relevant physical characteristics (i.e., they are smooth and dark colored), we expect polarized light pollution to be associated with solar collectors as well and that partitioning their surfaces with nonpolarizing strips should similarly reduce their attractiveness to polarotactic insects. New technologies such as three-dimensional solar cells that use vertically aligned arrays of carbon nanotubes (Camacho et al. 2007; Currie et al. 2008) reflect only a small amount of diffuse light with weak and not always horizontal polarization, and so should produce little polarized light pollution.

Ecological traps represent severe threats to animal populations (Delibes et al. 2001; Kokko & Sutherland 2001) and may contribute to ongoing declines of native species worldwide. Because ecological traps are predicted to arise from rapid environmental changes, including climate change, habitat fragmentation (Schlaepfer et al. 2002), and introductions of nonnative species (Schlaepfer et al. 2003), they are almost certainly more common than is recognized. Consequently, identifying methods to realign the attractiveness of habitats with their value for survival and reproduction is critical. Successful management of "behavioral landscapes" will require new conceptual approaches.

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Supporting Information

Color versions of Figs. 1-3, supplementary Figs. S1-S5, as well as supplementary Tables S1-S4 and their legends are available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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