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RESEARCH

Disentangling the visual cues of an evolutionary trap for aquatic insects

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Abstract

Aquatic insects use polarized light as a reliable visual cue for locating water surfaces given their need to locate sites for oviposition. However, many man-made surfaces polarize light more strongly than natural waterbodies creating an evolutionary trap in which many species preferentially lay their eggs on these polarizing artificial surfaces. Previous work has shown that the attractiveness of artificial surfaces to aquatic insects is diminished by adding non-polarizing gridlines to these surfaces. However, it is unknown how this mitigation affects aquatic insect preferences. We tested two alternative hypotheses about how aquatic insects judge the quality of potential oviposition sites. The visual averaging hypothesis states that insects judge the quality of a surface based on the percent area of the surface that is polarizing. An alternative hypothesis is that the quality of a polarizing surface is judged by the degree to which it is fragmented by non-polarizing elements. This experiment was conducted using oil tray traps as artificial polarizers whose percentage of polarizing area and the presence/absence of fragmentation was manipulated. Only Diptera were captured in sufficient numbers to test the hypotheses. Our findings for the dominant family in our captures, Dolichopodidae, were consistent with the visual averaging hypothesis – increasing the percent area that was non-polarizing significantly decreased captures, but the fragmentation of a polarizing surface had no significant effect on the number captured. For the other families of aquatic Diptera combined, however, there was a complex interactive effect of percent area of a surface that was polarizing and its fragmentation by non-polarizing gridlines. For the conservation of aquatic insects, these findings support the effectiveness of reducing the attractiveness of artificial polarizing surfaces such as solar panels by adding non-polarizing elements, but also show that for some aquatic insects, it is important to consider if the non-polarizing elements fragment the surface.

Keywords Light pollution · Ecological trap · Oviposition site · Diptera · Flies · Polarized light

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Extended author information available on the last page of the article

Introduction

An evolutionary trap is a circumstance whereby rapid changes in the environment cause an evolutionarily adaptive response (e.g., a behavior or physiological change) to a cue to suddenly become unreliable such that the response leads to reduced fitness (Schlaepfer et al. 2002). Since adaptive behavioral responses to cues evolve over many generations, rapid environmental change can decouple or invert relationships between choices and their past consequences for fitness (Levins 1968; Kriska et al. 1998). This can lead to rapid population declines and local extinctions (Kokko and Sutherland 2001; Fletcher et al. 2012). Due to the pervasiveness and rapidity of human-induced environmental changes, the evolutionary traps resulting from them are a substantial threat to the conservation of biodiversity (Schlaepfer et al. 2002; Robertson and Blumstein 2019).

One category of evolutionary trap is the ecological trap, in which individuals choose a habitat that offers inferior opportunities for survival and/or reproduction (Gates and Gysel 1978; Robertson et al. 2017). A clear example of humans creating an ecological trap occurs when adult female aquatic insects, because of their use of horizontally polarized light to locate waterbodies and preference for highly polarizing surfaces, fail to reproduce because they lay their eggs on anthropogenic surfaces that strongly polarize incident light (Kriska et al. 1998; Robertson et al. 2017). Several common man-made surfaces that are dark and smooth such as asphalt, dark colored-automobiles, and solar panels are stronger polarizers of incident light than are natural waterbodies (Horváth et al. 2009). The preference of aquatic insects for ovipositing on surfaces that are the most highly polarizing could be an adaptation that not only guides aquatic insects to water bodies in the first place, but can also variously indicate deeper water, water with light absorbing and dark-colored substrates (e.g., rock, mud, algae) or dark light-absorbing suspended particles and calmer, less rippled areas of waterbodies that reflect a higher percentage of polarized light (Horváth and Varju 2004). Natural water bodies polarize roughly 30%−80% of light (Horváth and Varju 2004), while some anthropogenic surfaces can polarize as much as 95%−100% of the light they reflect, attracting insects to oviposit on them even when oriented vertically (e.g. windows, Horváth et al. 2014).

There is a need for cost-effective mitigation strategies in the face of global expansion of photovoltaics and other artificial polarizers that are known to act as evolutionary traps for aquatic insects (Black and Robertson 2020; Horváth et al. 2010), but whose impact on populations is unclear. Studies have shown that the addition of non-polarizing gridlines that fragment large, contiguous areas of a polarizing surface such as a solar panel can lower the attractiveness of these surfaces to aquatic insects, offering a potential means of mitigating the adverse impacts of man-made polarizing surfaces. One possible explanation is that the preference of aquatic insects is affected by the fragmentation (breaking up) of large continuous areas of highly polarizing surface, such that small patches are less preferred, a phenomenon known to occur in some aquatic insect taxa (Resetarits et al. 2019; Scott et al. 2021). Even so, the attractiveness of surfaces to aquatic insects can be reduced by increasing the width of non-polarizing gridlines, which suggests that it may not be the fragmentation of a polarizing surface per se that affects its attractiveness as an oviposition site. Black and Robertson (2020) proposed the visual averaging hypothesis as an alternative explanation. This hypothesis states that insects assess the quality of a potential oviposition site based on the overall proportion of incident light that is polarized by the surface. However, no study to date has yet explicitly compared whether visual averaging or fragmentation of polarizing surfaces contributes the most to altering the preferences of aquatic insects.

Here, we tested two alternative hypotheses about how non-polarizing gridding patterns reduce the attractiveness of artificial polarizers to aquatic insects, the visual averaging hypothesis, and the fragmentation hypothesis. We conducted a field experiment to test these hypotheses by isolating the effects of the percentage of area of a surface that was polarizing from the effects of the fragmentation of a polarizing surface on the attractiveness of artificial surfaces to aquatic insects. Percent area that was polarizing was manipulated independently of fragmentation using two levels of fragmentation and four levels of percent area that was polarizing. The factors affecting the attractiveness of potential oviposition sites were tested by exposing wild populations of aquatic insects to oil-filled trays in which the characteristics of polarization were manipulated using established protocols (Kriska et al. 2009).

Materials and methods

The field experiment was conducted during six trapping sessions from mid-June to mid-July, 2023 at Oxbow Farm, at a site along the Shenandoah River, in Warren County, VA. We intended for the experiment to focus on three orders of aquatic insects, Trichoptera (caddisflies), Ephemeroptera (mayflies), and Diptera (true flies), because they are known to be sensitive to polarized light (Wunderer and Smola 1982; Horváth et al. 2010; Száz et al. 2016). However, only Diptera were captured in sufficient numbers for testing our hypotheses. We tested the hypotheses using black- and white-painted oil-filled trays that were painted to manipulate the percentage of the surface that was polarizing and the fragmentation of the polarizing surface. Black-painted areas of the trays reflect strongly polarized light, while areas painted white reflect unpolarized light (Kriska et al. 2009). The percentage of the tray surface (41 × 61 cm, width × length) that was polarizing and the fragmentation of the polarizing surface were manipulated by varying the widths, lengths, and spatial orientations of white lines (Fig. 1; additional information in Online Resource). The four levels of non-polarizing area were 0 (control), 2.2, 6.5, and 11%. For the three levels > 0%, we used line widths of 0.27, 0.81, and 1.38 cm. The percentages of non-polarizing areas were chosen to be consistent with a previous study (Black and Robertson 2020) that investigated how the width of non-polarizing white gridlines affected the oviposition preferences of aquatic insects. For each level of percent area > 0% that was non-polarizing, we manipulated whether the polarizing area was fragmented (i.e., fully subdivided) or not (Fig. 1) using two different orientations (perpendicular or parallel) for the white, non-polarizing lines. Because the areas of perpendicular lines of non-zero width overlap where they intersect, whereas parallel lines do not intersect, we maintained constant percentages of non-polarizing areas (2.2, 6.5, or 11%) across both fragmentation levels by holding the lengths of non-overlapping portions of the lines constant (See Fig. S3 for details).

The outer lips of the trays were not included in the calculations of percent area that was non-polarizing. However, the tray lips were painted to ensure that the white lines on a fragmented tray would reach the end of the tray, thus fully fragmenting the polarized area. This was done by painting white lines (0.81 cm in width) on the lips on each side of a tray that connected to the lines in the fragmented tray design. The lips of the trays on the unfragmented trays were painted in the same manner (Fig. 1).

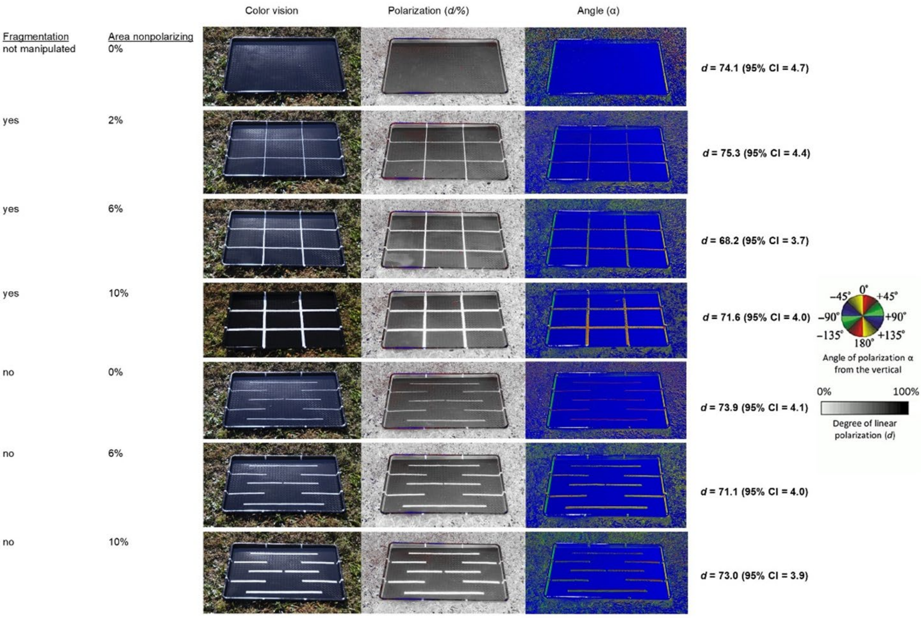

Fig. 1 Color photographs (left column) and reflection-polarization characteristics, including the degree *d* of linear polarization of reflected light (middle column) and angle α measured clockwise from the vertical and degree *d* of linear polarization of reflected light (right column), of the seven sun-lit, oil-filled trays painted with non-polarizing gridlines that either fragment or do not fragment the polarizing surface and make up different percentages (0, 2.2, 6.5, or 11%) of the surface area. The left column (color vision) represents what the DSLR camera images and as viewed by the human eye in the 380–750 nm spectral range. Comparison of color vision to degree of polarization demonstrates that the black, but not the white portions of our treatments horizontally polarize light within the visual range. In the middle column, red and blue pixels represent portions of the image that were over- or under-exposed, respectively

We measured the reflection-polarization characteristics of oil-filled trays using imaging polarimetry (Horváth and Varjú 2004) on a cloud-free day. Our polarimeter was a Canon EOS Rebel T6 DSLR camera aimed downward at the oil-filled trays at the Brewster's angle $\theta_{\mathrm{Brewster}} = \arctan$ (refractive index of oil = 1.5) = 56.3° from the vertical which results in the highest possible degree of polarization. We imaged trays while pointing in the direction of the sun at 10:00 am and 3 degrees to the right to avoid the direct reflection of the sun on our test surfaces. Three images were taken of each object with the polarization filter at different angles, then processed via Algonet© software into images illustrating the degree (*d*) and angle (α) of polarization at each pixel (Fig. 1). We subsampled the degree of polarization in the black-painted and highly polarizing sections of the tray in 5 small 30-pixel circular subsamples so we could calculate a mean and 95% confidence interval. We calculated values in the red, green and blue portions of the visual spectrum (380–700 nm) separately but reported only values in the blue portion because the degrees of polarization were similar across each portion of the visible spectrum.

Insect collections were carried out on 6 days (6/16, 6/25, 6/27, 6/29, 7/3, 7/11). During each of these days, collections began at 7 p.m. and ended 60–90 min later (Horváth et al. 2010; Horváth and Kriska 2008; Horváth and Csabai 2014). The trays were placed 0.5 m apart at seven locations arrayed parallel to the river 1–2 m from the water. Each day, the seven tray types (treatments) were randomly assigned to one of the seven locations in the line of trays parallel to the water body (Kriska et al. 2009). The trays were leveled by shimming them with flat stones and polystyrene foam sheets and filled with vegetable oil to polarize surface-reflected light and capture insects that touched-down on the surface. After each 60–90 min collection period, the oil within a tray and aquatic insects were poured through cheesecloth to separate the insects from the oil. Lastly, the cheesecloth was placed into a Whirlpak bag and submerged in 80% ethanol to preserve the specimens (Robertson and Horváth 2018).

Identification of Diptera families, carried out under a dissecting scope, was based on McAlpine (1981, 1987, 1989). Voucher specimens are retained at Blandy Experimental Farm (Boyce, Virginia). A family's larval habitat was categorized as "aquatic" if some or all its species are known to have an aquatic larval phase, "not aquatic" if none of its species have aquatic larvae, or "unknown" (McAlpine 1981, 1987, 1989; Smith 1989).

Because the captured Diptera belonged predominantly to the family Dolichopodidae, with low numbers captured in any other family with aquatic larvae, the effects of percent area that was non-polarizing and fragmentation of the polarizing surface on number of captures were tested separately for Dolichopodidae and those in any other family with aquatic larvae. The analyses were carried out using generalized linear mixed-effects models. Due to overdispersion when using a Poisson distribution, we specified the negative binomial distribution and log-link function. To examine the independent and interacting effects of non-polarizing area and fragmentation we excluded the trays with 0% non-polarizing area because fragmentation is necessarily absent for this treatment level. In cases where there was not a significant interaction, we also tested the effects of non-polarizing area on captures across all levels of this factor (0%, 2.2%, 6.5%, and 11%) by omitting fragmentation as an explanatory variable. A random effect for collection day (1–6) was included in each model. The analysis were performed using the software language R using the 'glmer' function from the 'lme4' package (Bates et al. 2015). *Post hoc* multiple comparisons were conducted using Tukey's HSD test using the "emmens" package (Lenth 2023).

Results

Diptera identification and habitat classification

A total of 810 Diptera representing 21 families were captured (Table 1). Most of the captures (65.6%) were Dolichopodidae (long-legged flies), while other families were much less abundant (Table 1). 87% of the captures belonged to families that tend to oviposit in aquatic habitat (Table 1).

Table 1 Counts of captured diptera by family. The primary oviposition habitat for each family as aquatic, not aquatic, or unknown was categorized based on McAlpine (1981, 1987, 1989) and Smith (1989)

Family	Count
Aquatic	
Dolichopodidae	531
Ceratopogonidae	56
Chironomidae	30
Empididae	30
Phoridae	23
Tipulidae	18
Ephydridae	9
Culicidae	4
Muscidae	4
Scatophagidae	1
Simuliidae	1
Not aquatic	
Anthomyiidae	25
Sciaridae	23
Psychodidae	18
Chloropidae	17
Sphaeroceridae	10
Asilidae	3
Mycetophilidae	3
Pipunculidae	1
Unknown	
Diastatidae	2
Asteiidae	1

Polarizing area and fragmentation

In the analysis testing for potential independent and interacting effects of non-polarizing area and fragmentation of the polarizing surface on captures of Dolichopodidae (i.e., the analysis excluding the tray with 0% non-polarizing area), there were no significant effects of non-polarizing area ($\chi^2=3.916$, df=2, $P=0.141$) or fragmentation ($\chi^2=0.001$, df=1, $P=0.980$) and there was no significant non-polarizing area × fragmentation interaction ($\chi^2=1.978$, df=2, $P=0.372$; Fig. 2). Captures of other aquatic Diptera were not significantly affected by non-polarizing area ($\chi^2=5.981$, df=2, $P=0.050$) or fragmentation ($\chi^2=0.169$, df=1, $P=0.681$), but captures of these flies were significantly affected by an interaction of non-polarizing area and fragmentation ($\chi^2=11.913$, df=2, $P=0.002$; Fig. 2). For other aquatic Diptera, *post hoc* tests (Tukey's HSD) of the effects of fragmentation within each level of non-polarizing area revealed significant ($P<0.05$) effects of fragmentation within the two lower levels of non-polarizing area, 2.2% and 6.5%, but not within the highest level of non-polarizing area (11%; Fig. 2). In contrast to the trays with 2.2% non-polarizing area, in which fragmentation of the polarizing surface had a negative effect on captures of other aquatic Diptera, fragmentation had a positive effect on captures in the trays with 6.5% non-polarizing area.

Given that the effects of non-polarizing area on captures of Dolichopodidae were not significantly affected by the fragmentation of the polarizing surface, we tested the effects of non-polarizing area on captures of this family across all experimental levels of non-polariz-

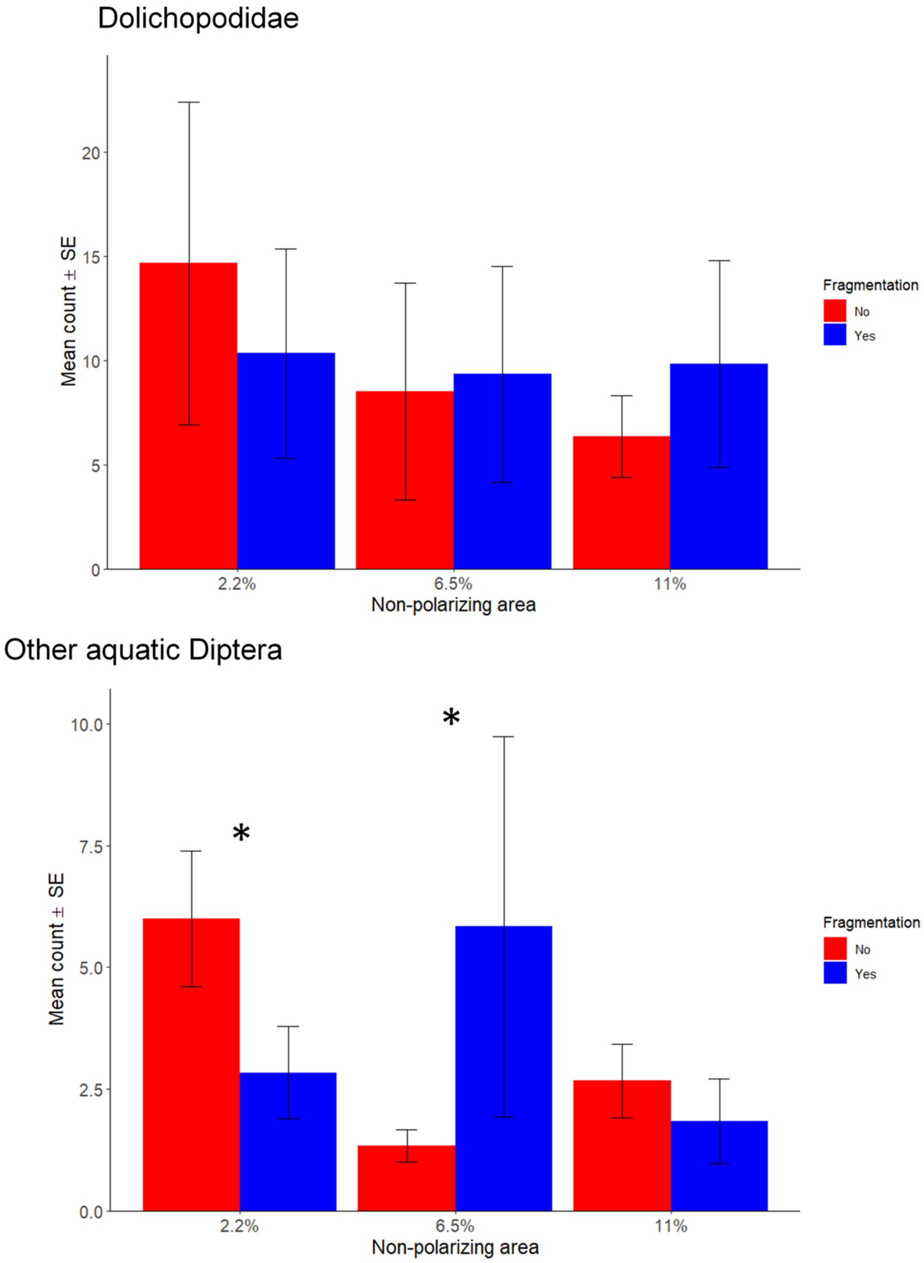

Fig. 2 Effect of the percentage of the surface that was non-polarizing and fragmentation of the polarizing surface on the number of captures of Dolichopodidae (top) and other families of aquatic Diptera combined (bottom). Data are means ± 1 SE (N = 36). Asterisks denote levels of non-polarizing area with significant (Tukey's HSD, $P < 0.05$) effects of fragmentation of the polarizing surface

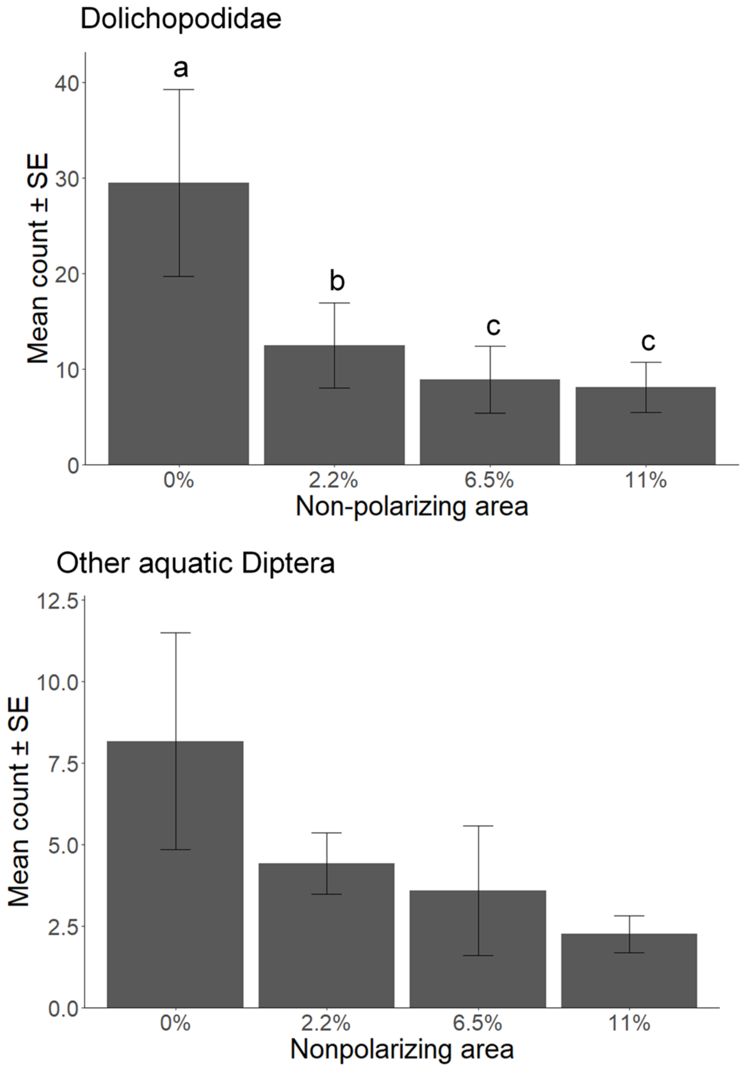

Fig. 3 Effect of the percentage of the surface that was non-polarizing on the number of captures of Dolichopodidae (top) and other aquatic Diptera (bottom). Data are means ± 1 SE ($N = 42$). For Dolichopodidae, different letters denote significant differences (Tukey's HSD, $P < 0.05$). Given the significant interaction between non-polarizing area and fragmentation of the polarizing surface for other aquatic Diptera, we did not test for independent effects of non-polarizing area on their captures

ing area (including 0%). We found that the number of Dolichopodidae captured decreased significantly with increasing amounts of non-polarizing area ($P < 0.001$; Fig. 2). On average, the number of Dolichopodidae captured dropped by 57.6% with the increase in non-polarizing area from 0% to 2.2%, with smaller incremental decreases (though not always significantly based on Tukey's HSD *post hoc* comparisons) with each increase in the percent of non-polarizing area (Fig. 3).

Discussion

While the findings of two prior studies (Horváth et al. 2010; Black and Robertson 2020) contributed to the conceptual development of the visual averaging hypothesis, the experiments, because they did not manipulate percent non-polarizing area independently from the fragmentation of a polarizing surface, preclude making conclusions about the relative roles of visual averaging vs. the fragmentation of polarizing surfaces in oviposition site selection in aquatic insects. In Black and Robertson's (2020) study for example, the width of non-polarizing gridlines affected captures of aquatic insects, but the fragmentation of polarizing areas was not manipulated. Consistent with the visual averaging hypothesis, the present study showed that the attractiveness of surfaces to adults of the dominant aquatic family of Diptera in our collections, Dolichopodidae, increased with the percent of the surface that polarized light, whereas the presence/absence of fragmentation of the polarizing surface did not affect its attractiveness. In contrast to our findings with Dolichopodidae, the overall attractiveness of surfaces to Diptera from other families was influenced by a complex interaction between polarizing area and fragmentation of the polarizing area.

For Dolichopodidae, the cognitive and sensory mechanisms whereby the percentage of a surface that polarizes light influences its attractiveness as an oviposition site while the fragmentation of the polarizing surface is not important are unclear. The anatomy of insect visual systems may play a role. First, an insect's compound eyes have low resolution compared to a camera-type eye (e.g., a human eye; Land 2005). In addition, the shapes of the lenses of the compound eyes cannot change to focus on an object (Wunderer and Smola 1982; Feller et al. 2021). Because of these anatomical features, Dolichopodidae adults may not have perceived whether the non-polarizing strips fragmented the polarizing surfaces. Alternatively, the spatial arrangement of polarizing and non-polarizing areas in a natural waterbody may tend to be a less reliable indicator of site quality than is the proportion of the surface that polarizes light. However, we cannot rule out that fragmentation of polarizing surfaces is important to Dolichopodidae on different scales. For example, it is possible that their preferences for oviposition sites are influenced by the fragmentation of polarizing surfaces over areas that are larger than the trays we used in our experiment.

Determining the mechanisms that led to the interacting effects of the percentage of the surface that was polarizing and fragmentation of the polarizing surface on the attractiveness of surfaces to the other aquatic families of aquatic Diptera will likely require additional research to document these responses for individual Diptera families. Prior research has revealed taxonomic variation in aquatic insects in their sensitivity to polarized light (Kriska et al. 2009) and visual resolution (Feller et al. 2021). Results from studies on individual families (other than Dolichopodidae) on the independent and interacting effects of the portion of a surface that is polarizing and fragmentation of the polarizing surface might differ substantially from what we found by pooling these families.

Black and Robertson (2020) showed that the addition of grids of white non-polarizing lines to solar panels was a viable means of disarming the evolutionary trap to aquatic insects. In addition, the attractiveness of surfaces decreased with thicker non-polarizing grid lines. However, line widths that led to even small reductions in the proportion of photovoltaically active surfaces led to dramatic declines in attractiveness. Our results confirm this conclusion but suggest there is taxonomic variation in whether there is an interactive effect of the area of non-polarizing grid lines and the fragmentation of the polarizing surface by such grid lines. For Dolichopodidae, we found no effects of the fragmentation of polarizing surfaces on their attractiveness. It is premature, however, to conclude that for Dolchopodidae there is no effect of the configuration of polarizing versus non-polarizing areas on a surface. The attractiveness of a surface could be influenced by the distribution or shapes of polarizing vs. non-polarizing areas on a surface and there are an untold number of such spatial arrangements. The phenomenon of aliasing, for example, in which stripping on objects interferes with the ability of insects to judge their motion relative to the object (Mouy 2025) emphasizes the importance of particular spatial arrangements. Photovoltaic solar panels are a rapidly expanding source of polarized light pollution (Horváth et al. 2009) whose demographic impact on aquatic insects and other phototactic organisms (e.g. birds) remain unclear. Investigations of the attractiveness of solar panels to aquatic insects in the landscapes in which they are placed have not yet been conducted to evaluate if they can act as evolutionary traps. Indeed, the polarizing surfaces of both polycarbonate and thin-film solar panels are typically interrupted by non-polarizing grid lines, suggesting that engineering considerations have resulted in designs that may already repel aquatic insects. Empirical studies evaluating the attractiveness of photovoltaics in situ paired with manipulative sensory studies like our own that seek to mimic the configurations of the polarizing, solar-active portions of photovoltaic panels will be needed to evaluate this possibility.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10682-025-10378-9.

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Author contributions B.A.R. and K.J.H. contributed to the study conception. N.W.F., B.A.R., P.W.C., and K.J.H. contributed to the study design. Material preparation, data collection, and analysis were performed by N.W.F., C.M.C.S., W.S.L., and K.J.H. The first draft of the manuscript was written by N.W.F and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Data supporting the findings of this study have been deposited in figshare and are available to reviewers with a private link ([https://figshare.com/s/e471b22fbb5c85a41ec2](https:/figshare.com/s/e471b22fbb5c85a41ec2)).

Declarations

Competing interests The authors declare no competing interests.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent to publish Not applicable.

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