

Susceptibility to ecological traps is similar among closely related taxa but sensitive to spatial isolation



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Ecological traps are maladaptive behavioural scenarios in which animals prefer to settle in habitats with the lowest survival and/or reproductive success. Aquatic insect species, for example, are attracted to sources of horizontally polarized light associated with natural water bodies, but today they commonly prefer to lay their eggs upon asphalt roads and buildings that reflect an unnaturally high percentage of polarized light. Ecological traps are a rapidly emerging threat to the persistence of animal populations, but the degree to which species vary in their susceptibility to them remains uninvestigated. We designed a field experiment to (1) assess the relative susceptibility of aquatic flies (Diptera) to a single maladaptive behavioural cue: variation in degree of horizontally polarized light (d), and (2) quantify how the isolation of an ecological trap from a high-quality habitat affects its relative attractiveness. We exposed wild dipterans to experimental test surfaces varying in d at three distances from natural streams and mapped behavioural reaction norms of habitat preference as a function of d and distance from high-quality habitat. All seven of the dipteran families were captured most in traps with progressively higher d values, especially those ($d = 90\text{--}100\%$) that exceeded that of natural water bodies ($30\text{--}80\%$). In most taxa, the height and slope of numerical responses to d were influenced by the distance of an ecological trap from a natural water body. Our results illustrate that dipterans have broadly evolved the use of a habitat selection behaviour that treats more strongly polarized light sources as indicative higher-quality habitats, making them broadly susceptible to ecological traps driven by polarized light pollution. We also found that the spatial isolation of ecological traps from higher-quality, but less attractive, habitats can either increase or reduce species' susceptibility to them.

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Ecological traps are scenarios in which, due to some human-induced rapid environmental change (Robertson, Rehage, & Sih, 2013), a poor-quality habitat becomes more attractive than available high-quality habitats that would lead to greater survival or reproductive success (Dwernychuk & Boag, 1972; Schlaepfer, Runge, & Sherman, 2002). Traps occur because animals use indirect cues to assess the ultimate value of potential habitats during settlement, but these cues can be manipulated independently of the fitness conditions to which they have been correlated over evolutionary time (Robertson & Hutto, 2006). The result is that an animal can prefer to settle in, and compete over, the most dangerous and low-quality habitats. This extreme form of

maladaptive behaviour is an increasing conservation reality affecting a broad taxonomic range of animals (Robertson et al., 2013) and, perhaps most disturbingly, is sometimes a consequence of interventions designed to restore ecosystems or species (Hawlena, Saltz, Abramsky, & Bouskila, 2010; Severns, 2011). Given that ecological traps can lead to rapid population declines or even extinctions (Delibes, Ferreras, & Gaona, 2001; Donovan & Thompson, 2001; Fletcher, Orrock, & Robertson, 2012; Hale, Trembl, & Swearer, 2015; Hawlena et al., 2010; Kokko & Sutherland, 2001), that they can be difficult to identify and that researchers are infrequently looking for them (Robertson & Hutto, 2006), it is concerning that we still know relatively little about the underlying sensory-cognitive, behavioural and ecological mechanisms that cause them.

A species' susceptibility to being ecologically trapped can be defined as the relative tendency of a single misleading environmental cue to trigger a maladaptive behaviour that an animal

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prefers over higher-fitness alternatives. In this sense, interspecific susceptibility to evolutionary traps could vary when (1) species differ in their ability to use and weigh ancillary environmental cues in adaptive decision making, or (2) species differ in their relative tendency to prefer more extreme or intense forms of a cue than those that occur in nature (Robertson et al., 2013; Tinbergen, 1951). Yet, susceptibility to traps could also vary among taxa if species are more or less likely to encounter them in space, as a function of their typical range of movement, for example. An ecological trap in close proximity to a high-quality habitat may be disproportionately effective in attracting individuals to settle because it is more easily detected. Alternatively, animals might find spatially isolated ecological traps disproportionately attractive due to a paucity of other settlement options in close proximity. The degree to which species vary in their sensory-cognitive and spatial susceptibility to ecological traps remains uninvestigated. This knowledge is crucial in that it illustrates how robust wildlife species are to ecological novelty, the degree to which an animal's likelihood of getting trapped is context dependent and whether conservation scientists can anticipate whether strategies designed to eliminate an ecological trap affecting one species will be effective in eliminating it for other species also caught in that trap.

Perhaps the most well-understood example of an ecological trap occurs when emergent aquatic insects are attracted to lay their eggs upon man-made objects that are strong sources of horizontally polarized light (reviewed in Horváth, Kriska, Malik, & Robertson, 2009; Horváth & Zeil, 1996; Schwind, 1985). The dominant terrestrial source of polarized light on earth has always been the water surface, due to its ability to reflect horizontal polarization stronger than vertical polarization, the consequence of which is horizontally polarized water-reflected light with maximal degree (or percentage) of polarization at the Brewster angle (Horváth & Varjú, 2004; Horváth, 2014). In response to this highly reliable and nearly unique environmental cue, natural selection has shaped all known insects that require fresh water bodies to survive or reproduce with an eye capable of detecting the angle of polarized light (Horváth & Varjú, 2004; Horváth, 2014). The percentage (or degree) of horizontal polarization of water-reflected light (hereafter d) depends on the smoothness of the water surface and on the reflectivity of the water body (bottom and/or suspended materials), with darker, smoother objects reflecting a higher d (also known as 'Umow's law': Umow, 1905). The d for natural water bodies ranges from ~30% to 80% (Horváth, 2014), but humans have populated the earth with objects that act as artificial polarizers that commonly polarize 95–100% of reflected sunlight (e.g. solar panels: Horváth et al., 2010; glass buildings: Kriska, Bernáth, Farkas, & Horváth, 2009; automobiles: Kriska, Csabai, Boda, Malik, & Horváth, 2006; asphalt: Kriska, Horváth, & Andrikovics, 1998). Adults of insect species with aquatic life-history phases commonly prefer to swim on, dive into (Kriska et al., 2006; Schwind, 1985, 1991, 1995) or sexually display and mate above, then touch down and lay eggs on (Horváth, 2014; Horváth et al., 2010; Kriska et al., 1998, 2006; Kriska, Malik, Szivák, & Horváth, 2008; Lerner et al., 2008, 2011) artificial polarizing surfaces that approximate or exceed the d of water.

Current evidence suggests that polarized light is the most important, perhaps only, sensory cue that many freshwater aquatic insect species use in locating water bodies (Horváth, 2014; but see Bernáth, Horváth, & Meyer-Rochow, 2012). When exposed to a higher versus lower degree of polarization, insects are typically more attracted to the higher value (Boda, Horváth, Kriska, Blahó, & Csabai, 2014; Horváth & Zeil, 1996; Horváth, Bernáth, & Molnár, 1998; Horváth, Móra, Bernáth, & Kriska, 2011; Kriska et al., 1998). A behavioural reaction norm is a visualization of the behavioural responses produced by individuals as a function of different environments or stimuli. Because the shape of a reaction norm

determines whether or not there is an ecological trap present, demonstrating relative susceptibility to artificial polarizers versus water bodies requires higher-resolution behavioural maps that compare attraction among d values typical of land (<30%) or water (~30–80%; Horváth, 2014) and those that are only produced by man-made objects (80–100%; but see Lerner et al., 2008; Chironomidae; Kriska et al., 2009; Odonata).

We designed a field-based experiment to (1) assess the relative susceptibility of ecologically similar aquatic insect taxa to ecological traps triggered by a single maladaptive behavioural cue: variation in the d of horizontally polarized light, and (2) quantify how distance from a natural, high-quality habitat affects the relative attractiveness of ecological traps. We chose aquatic flies (Diptera) as our focal taxon because they are an abundant and diverse group of aquatic insect known to be attracted to horizontally polarized light: Dolichopodidae (Horváth et al., 2010), Ceratopogonidae (Robertson et al., 2017), Empididae (Robertson et al., 2017), Simuliidae (Robertson et al., 2017), Chironomidae (Horváth et al., 2011; Lerner et al., 2011, 2008; Robertson et al., 2017). We created behavioural reaction norms by examining the numerical response of insects caught in oil traps that varied in the percentage of reflected sunlight they polarized (d), and we examined the influence of trap distance from natural water bodies in shaping reaction norms by placing rows of traps varying in their d at three distances from river banks.

METHODS

Study Sites and Experimental Design

We designed the experiment with five polarization treatments (Fig. 1a). Two represented degrees of polarization (87% and 99%) that do not exist in nature, but are typical of artificial polarizers (e.g. Horváth et al., 2010; Kriska et al., 1998, 2008). Two treatments (28% and 51%) were typical of natural bodies of water, and the final (16%) was only typical of certain (white) man-made objects or land (reviewed in Horváth, 2014). Two of our treatments mimicked the visual characteristics of natural water bodies, and did so at each of the three distances we examined in our experiment. We interpret relative captures among these water-typical polarization treatments between distance categories as reflective of the underlying distribution of insects in each taxon. Within distance categories, differences in relative captures are indicative of the relative preferences that individuals have for each polarization treatment. We selected study sites on five tributaries of the Hudson River in southern New York State, U.S.A. (Fig. 1b). Study locations were located in sparsely populated areas along heavily forested river corridors. We chose residential properties that maintained mown lawns extending from the high water line inland at least 60 m to ensure sufficient area for our experiment and so that vegetation would not impede insect lines of sight towards experimental test surfaces.

In 2012, we trapped flying emergent aquatic insects under clear skies three times at each site: 19 May–3 June (Visit 1); 4–16 June (Visit 2); 19–25 June (Visit 3). Each trapping session lasted for 120 min, ending exactly 30 min after sunset. Diurnal aquatic insect taxa are most active at sunset, in part because polarotactic water detection is easiest at lower solar elevations (Bernáth, Gál, & Horváth, 2004). Furthermore, at low sun elevations the reflected polarization cues are more stable and reliable in comparison to the intensity cues (Lerner et al., 2008). We placed one of each of five shades (white, black and three shades of grey) of oil-trap in a row parallel to the riverbank at three distances: 5 m, 10 m, 50 m (Fig. 1b). Each row of trays was centred upon a 2 × 8 m piece of black plastic tarpaulin that acted as a strong polarizer attracting insects to the general location of the experimental trays (Kriska

et al., 1998). Trays were spaced 0.5 m apart from each other. To avoid potential capture bias associated with the spatial relationship of trays to each other, the edges of the tarpaulin or other environmental features (e.g. prevailing wind), we began the experiment with trays placed in a random shade order within rows and rotated and transposed their relative positions within their row every 20 min according to a predetermined and standardized algorithm (position 1 → position 3, 3 → 5, 5 → 2, 2 → 4, 4 → 1).

At the conclusion of each sampling visit, tray contents were poured through fine cheesecloth to separate oil from insects. Insects were labelled and stored in 80% ethanol for later identification to the family level. While numerical responses to variation in d are most statistically convenient for mapping reaction norms, biomass is typically a better indicator of the ecological functions (e.g. nutrient cycling, decomposition, translocation of materials) that arthropods play in ecological communities (Saint-Germain et al., 2007). We estimated the dry biomass of each individual via published length–biomass regressions for respective families (Hodar, 1996; Sabo, Bastow, & Power, 2002). Aquatic dipteran families were defined as families whose larvae typically require water bodies in which to mature (Johnson & Triplehorn, 2004). The insects in this study were collected under the guidelines outlined by the New York Department of the Environmental Conservation, License to Collect or Possess: Scientific No. 1632.

Polarization Trap Design and Imaging

We used oil-filled trays painted white, black and three shades of grey to capture insects and assess their relative preference for test surfaces varying in their light polarization signature (Figs 1a and 2). Reflection–polarization characteristics of oil-filled trays were measured using imaging polarimetry (Horváth & Varjú, 2004) in the red (650 ± 40 nm = wavelength of maximal sensitivity \pm half bandwidth of the polarimeter detector), green (550 ± 40 nm) and blue (450 ± 40 nm) parts of the light spectrum. We illustrate the polarization patterns of trays in the blue spectral range only (Fig. 2) because patterns obtained by visualizing the red and green parts of the spectrum were similar.

We captured images of test surfaces using an imaging polarimeter modified from a Canon DSLR camera. This method involves the capture of three images taken through a polarized light filter placed at three different angles, which are then processed into composite imagery using Polarworks software developed by Dr Ramón Hegedüs (Horváth & Varjú, 1997). We performed polarimetric measurements under clear skies with the optical axis of the polarimeter viewed towards the anti-solar meridian at the Brewster angle $\theta_{\text{Brewster}} = \arctan(n) \approx 56.3^\circ$ from the vertical calculated for the refractive index ($n \approx 1.5$) of salad oil. At the Brewster angle, light reflected from the surface is perpendicular to the refracted ray penetrating the oil, resulting in the highest possible degree of polarization. We created two darker test surfaces that reflected light at the Brewster angle with higher d values (black: $98\% < d < 100\%$; dark grey: $d = 87 \pm 5\%$) than water is capable of reflecting, two shades of grey that were typical of natural water bodies (medium grey: $d = 51 \pm 4\%$; light grey: $d = 28 \pm 3\%$), and one white tray that reflected light with $d = 16 \pm 2\%$ being lower than natural water bodies in general. Before deploying trays in the field experiment we verified that they polarized reflected sunlight approximately horizontally with $85^\circ \leq \alpha \leq 95^\circ$ (Fig. 2).

Statistical Analyses

We examined the effect of distance of an artificial polarizer from the river and the d (percentage of polarization of reflected sunlight) associated with a test surface on (1) the number of captured

individuals within each dipteran family, (2) a weighted index of abundance reflective of captures of the entire dipteran community and (3) the estimated biomass of all dipterans captured. Family-specific analyses serve to illustrate the behavioural preferences of each taxon. Our second goal was to understand whether dipterans, as an order, respond maladaptively to supernormally strong to polarized light sources and as a function of distance. To do so, we created a standardized metric of abundance designed to eliminate results being biased towards responses typical of more abundant families. We adjusted captures of each family associated with each test surface to be a fraction of the total number of captures in each row for that site. Each of these totals was divided by the total number of families included in the analyses of total dipterans (see Results) and then fractions for each family were added together to represent a single metric reflective of total dipteran captures per treatment that gave equal weight to each family. We treated both distance from water and the d values emerging from polarimetry of test surfaces as quantitative variables.

Because the timing of captures has the potential to bias estimates of behavioural preferences for experimental treatments, we

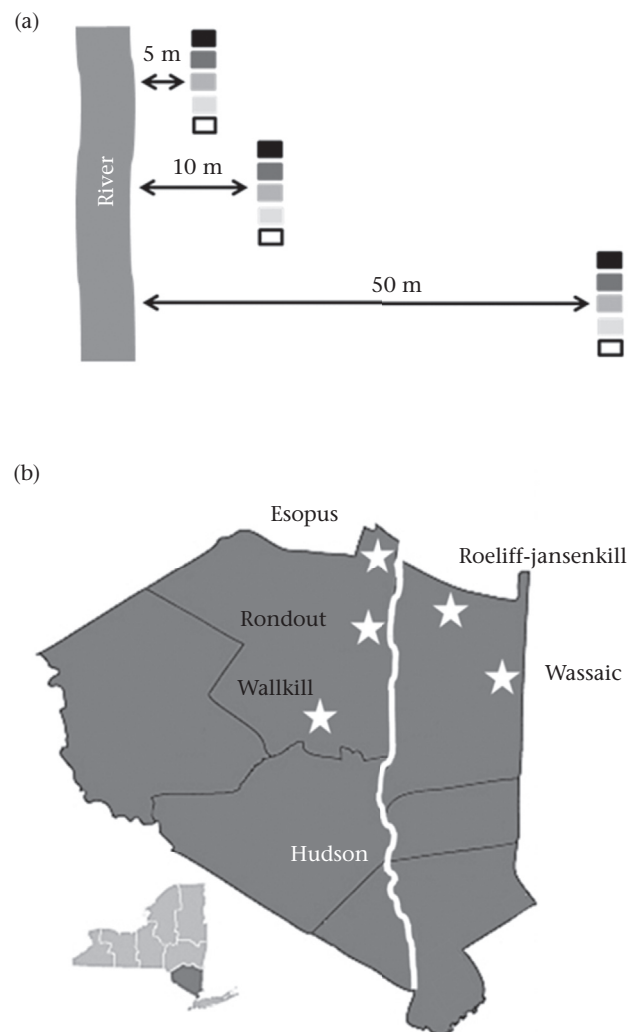


Figure 1. (a) The spatial arrangement of oil-filled polarization traps of five shades at each study site. Squares represent trays of different shades in three rows placed at three distances from each river and perpendicularly offset from each other. (b) Locations of polarized light experiments in the Hudson Valley region of southern New York State. Stars indicate locations of experimental sites on five tributaries of the Hudson River (in white) located in three of the six counties shown.

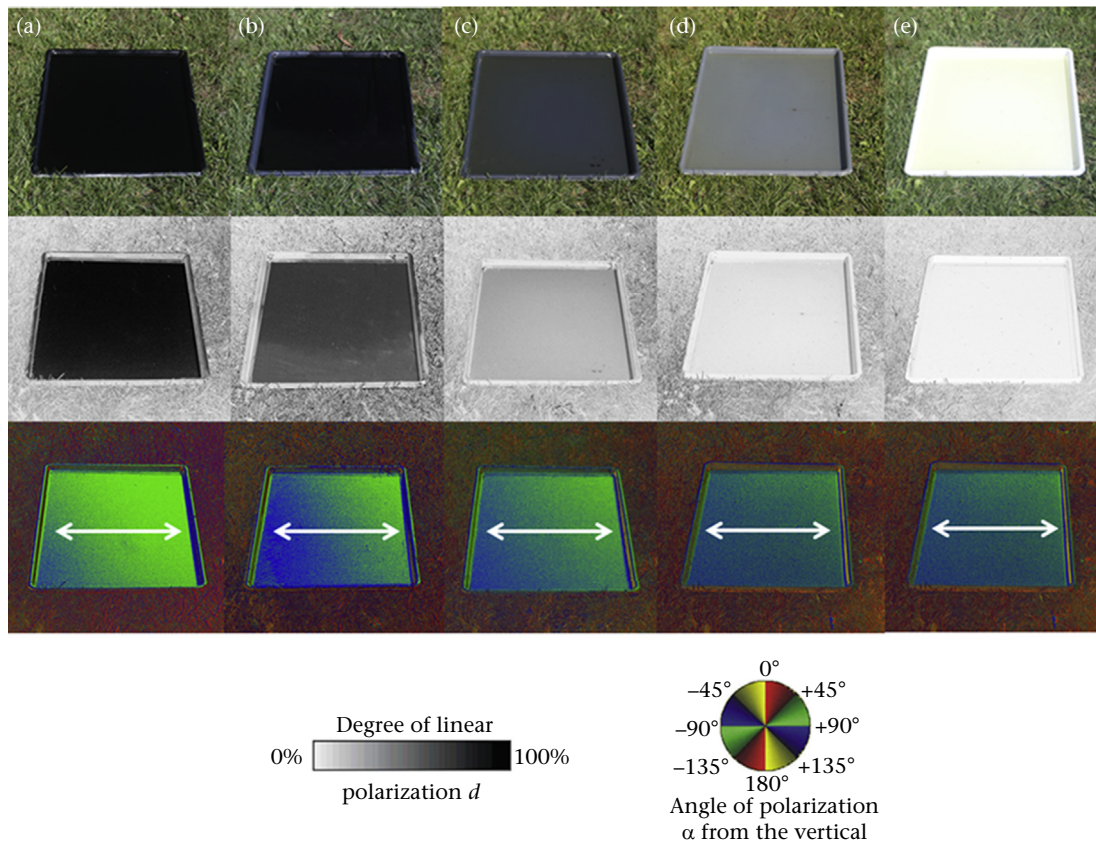


Figure 2. The reflection–polarization characteristics of salad oil-filled (a) black, (b) dark grey, (c) medium grey, (d) light grey and (e) white trays used in the choice experiments and measured by imaging polarimetry in the blue (450 nm) part of the spectrum. Below the top row of coloured images the middle row shows pixels with a higher degree of polarization in darker grey. The bottom row of images are coloured to reflect the angle of polarization (α patterns). Double-headed arrows show the horizontal direction of polarization of reflected light. When viewed toward the solar meridian, polarization patterns were similar.

conducted preliminary analyses to determine whether captures changed over the course of our experiment as a function of time. We used generalized linear mixed models to model distance and d as fixed variables, and Julian date of sampling session and study site as random variables, in predicting captures for each family, for all dipterans combined and for total dipteran biomass. Family and total dipteran captures best fit a Poisson distribution while biomass fit a normal distribution. In all cases Julian date and study site were unimportant in explaining the dependent variable (all $P > 0.12$). For this reason, we combined observations for all three visits prior to analysis and used simple Poisson regression in our final analyses of captures and a general linear model in our biomass analysis. Poisson regression models fit the data well and produced very similar results to those of mixed models so we present results of Poisson regressions only.

RESULTS

We captured a total of 6720 adult aquatic dipterans in 12 families: Chironomidae (nonbiting midges), Empididae (dance flies), Dolichopodidae (long-legged flies), Simuliidae (black flies), Ceratopogonidae (biting midges), Phoridae (humpbacked flies), Psychodidae (sand flies), Chaoboridae (phantom midges), Culicidae (mosquitos), Ephydriidae (shore flies), Sciomyzidae (marsh flies) and Tabanidae (deer flies). We focused our analysis on seven families that were captured in sufficient abundance to examine statistically (Table 1). Fit of data to Poisson models was good ($\hat{c} = 0.95$ – 3.72).

All seven dipteran families were captured in greater numbers in trays with increasingly higher values of d , but numerical responses

of aquatic dipteran families to d as a function of distance from water were diverse (Fig. 3). The reaction norm of chironomids was steepest at a distance of 10 m (distance: $\chi^2 = 191.2$, $P < 0.0001$; d : $\chi^2 = 1229.4$, $P < 0.0001$; distance* d : $\chi^2 = 73.8$, $P < 0.0001$; Fig. 3a). In contrast, the reaction norm of simuliids became steeper as distance from water decreased (distance: $\chi^2 = 23.7$, $P < 0.0001$; d : $\chi^2 = 278.8$, $P < 0.0001$; distance* d : $\chi^2 = 29.4$, $P < 0.0001$; Fig. 3b). Two families (Dolichopodidae and Ceratopogonidae) exhibited reaction norms that were steeper at 50 m than at 5 m, but whose reaction norms at 10 m did not show a clear increase in captures with increasing d . In both the ceratopogonids (distance: $\chi^2 = 80.0$, $P < 0.0001$; d : $\chi^2 = 57.6$, $P < 0.0001$; distance* d : $\chi^2 = 40.3$, $P < 0.0001$; Fig. 3c) and the dolichopodids (distance: $\chi^2 = 159.6$, $P < 0.0001$; d : $\chi^2 = 52.5$, $P < 0.0001$; distance* d : $\chi^2 = 20.4$, $P = 0.009$; Fig. 3d), captures were actually lower at $d = 100\%$ than at $d = 90\%$ (post hoc LSD: Ceratopogonidae: $P = 0.01$; Dolichopodidae: $P = 0.05$).

For the family Empididae, captures were a positive function of d , and were greater further from water, but there was no significant interaction effect of distance and d (distance: $\chi^2 = 19.0$, $P < 0.0001$; d : $\chi^2 = 23.7$, $P < 0.0001$; distance* d : $\chi^2 = 9.0$, $P = 0.34$; Fig. 3e). In the remaining two families, captures were a positive function of d but were unaffected by the distance from water (Psychodidae: distance: $\chi^2 = 2.1$, $P < 0.38$; d : $\chi^2 = 46.6$, $P < 0.0001$; distance* d : $\chi^2 = 3.4$, $P = 0.84$; Fig. 3f; Phoridae: distance: $\chi^2 = 5.1$, $P < 0.08$; d : $\chi^2 = 31.8$, $P < 0.0001$; distance* d : $\chi^2 = 7.2$, $P = 0.51$; Fig. 3g).

The collective response of all seven aquatic dipteran families combined (Fig. 3h) was most similar to that of the family Psychodidae (Fig. 3f) in that the traps with a d value approximating water

Table 1

Abundance and biomass of the seven most abundant families of emergent aquatic dipterans captured during the course of the experiment

Family	Common name	Captures	Biomass (mg)	% Total biomass ^a
Psychodidae	Sand flies	143	0.1	0.4
Phoridae	Humpbacked flies	441	0.3	1.4
Ceratopogonidae	Biting midges	633	0.4	1.8
Simuliidae	Black flies	567	1.0	4.2
Dolichopodidae	Long-legged flies	992	3.4	14.8
Chironomidae	Midges	2790	5.1	22.2
Empididae	Dance flies	961	12.8	55.2

^a Indicates the relative contribution of biomass of each family to the total of the seven families.

($d = 50\%$) were more attractive than the less typical and much lighter-shaded traps, but traps with d values of 90–100% were substantially, and progressively, more attractive as measured by relative captures (distance: $F_{2,68} = 0.01$, $P = 0.99$; d : $F_{4,68} = 17.4$, $P < 0.0001$; Fig. 3h). The estimated dry biomass of aquatic dipterans increased with d and with the distance of the traps from water (distance: $F_{2,68} = 34.5$, $P < 0.0001$; d : $F_{4,68} = 31.9$, $P < 0.0001$; distance $\times d$: $F_{8,68} = 1.2$, $P = 0.99$; Fig. 3i).

DISCUSSION

We mapped reaction norms of numerical responses of aquatic flies to variation in the percentage of horizontally polarized light (d) and found that all seven families were captured in traps with stronger polarized light signatures. Increasing preference for these artificial water bodies with higher fractions of reflected horizontally polarized light was generally robust to the distance that they were placed from rivers. Besides indicating that these families all use polarized light as a habitat and/or oviposition selection cue, all seven dipteran families exhibited strongest behavioural responses to d values (90–100%) exceeding that of natural water bodies (~30–80%), indicating that evolution has predisposed them to being caught in ecological traps associated with artificially strong sources of polarized light. As important, we found that the height and slope of reaction norms were, in several taxa, influenced by the distance of an ecological trap from a natural water body. This shows for the first time that the spatial isolation of ecological traps from higher-quality, but less attractive, habitats can shape the degree to which animals are maladaptively attracted to them.

Previous research has demonstrated that the d of horizontal polarization is used as an oviposition and habitat selection cue in a diversity of aquatic taxa (e.g. mosquitos (Culicidae): Bernáth et al., 2012; dragonflies (Odonata): Wildermuth, 1998; nonbiting midges (Chironomidae): Lerner et al., 2008, 2011; horse flies: Horváth, Majer, Horváth, & Kriska, 2008; aquatic Heteroptera and Coleoptera: Schwind, 1991, 1995; Trichoptera: Kriska et al., 2008). However, studies examining responses to more than a dichotomous high versus low value of d have been only accomplished by Horváth et al. (2009) for four species of mayfly (Ephemeroptera), and by Lerner et al. (2008) for chironomids. Three of those species exhibited generally linear unimodal numerical responses to increasing d , but a fourth strongly avoided intermediate values of d . This would allow it to avoid a 'severe' evolutionary trap (Robertson & Hutto, 2006) associated with artificially high degrees of polarized light. In contrast, we found that reaction norms of aquatic Diptera were all positive with respect to d but varied in their slope (steepest: Chironomidae; shallowest: Dolichopodidae). Some families exhibited flatter, more unimodal responses (e.g. Dolichopodidae) while reaction norms of others (e.g. Chironomidae) approached shallow exponential shapes, indicating that preference for traps was nonadditively (e.g. multiplicatively) related to the degree of polarization. Collectively, and independent of these exact shapes, insects in all seven families were most attracted to

polarized light with d values of 90–100% that exceed that of natural water bodies, indicating that all have evolved a susceptibility to both weak ($d \approx 90\%$) and strong ($d \approx 100\%$) ecological traps created by man-made artificial polarizers, most likely as a by-product of historical selection for a unimodal-type attraction response to typical d values of water-polarized light (i.e. 'super-normal releasers' (Tinbergen, 1951).

Spatial context (e.g. scale dependence, habitat connectivity) is known to shape adaptive habitat selection behaviour across a diversity of animal taxa (Burgess, Treml, & Marshall, 2012; Ciarniello, Boyce, Seip, & Heard, 2007; Donovan, Jones, Annand, & Thompson, 1997), but the role of context in shaping animal preferences for deceptively attractive resources like ecological traps has so far been ignored. If individuals' preferences for ecological trap habitat are dependent not just upon the relative attractiveness of the ecological trap's associated environmental cues, but also its availability, proximity to alternative habitats and/or their detectability, then the evolved behavioural reaction norms that predispose animals to ecological traps should vary in their shape as a function of their isolation from alternative habitat patches. For example, Lerner et al. (2008, 2011) found that chironomid midges that used polarize light as an oviposition cue were less choosy in their oviposition site preference and laid eggs in low- d patches when large patches of natural river habitat were restricted. We found great variation in the relative preference of dipteran families for ecological traps as a function of their isolation from free-flowing rivers. Midges (Chironomidae) exhibited one of the steepest reaction norms, and therefore showed an exaggerated preference for trap habitats, at intermediate distance (10 m) from the river, while black flies (Simuliidae) showed a greater relative preference for traps when they encountered them further from the stream. In this way, chironomids in our study did not exhibit a distance $\times d$ pattern (steeper reaction norms in proximity to river) consistent with the mechanism identified by Lerner et al. (2008, 2011). Two families (Phoridae, Psychodidae) did not shift their reaction norm in response to distance from river, suggesting their behavioural responses to variation in the d of horizontally polarized light are independent of their spatial context.

Behavioural reaction norms for ceratopogonids and dolichopodids were increasing functions of d at 5 m and 50 m from rivers, and were moderately steeper at greater distances from the river. However, reaction norms for these families at the 10 m distance were atypically shaped, suggesting avoidance of the strongest ($d = 100\%$) ecological trap. This pattern is actually predicted as an adaptively evolved response to the fitness cost of ovipositing in an ecological trap, but such a response should be independent of distance to water and only likely to evolve in more heavily urbanized areas, which were not characteristic of our study sites. The diversity of ways in which habitat preference varied with trap isolation could emerge as a function of the capability of different taxa to detect alternative habitats at a distance, the relative availability of alternative habitats combined with the short period (~1–4 days) that these taxa have to mate and oviposit (Lerner et al., 2008),

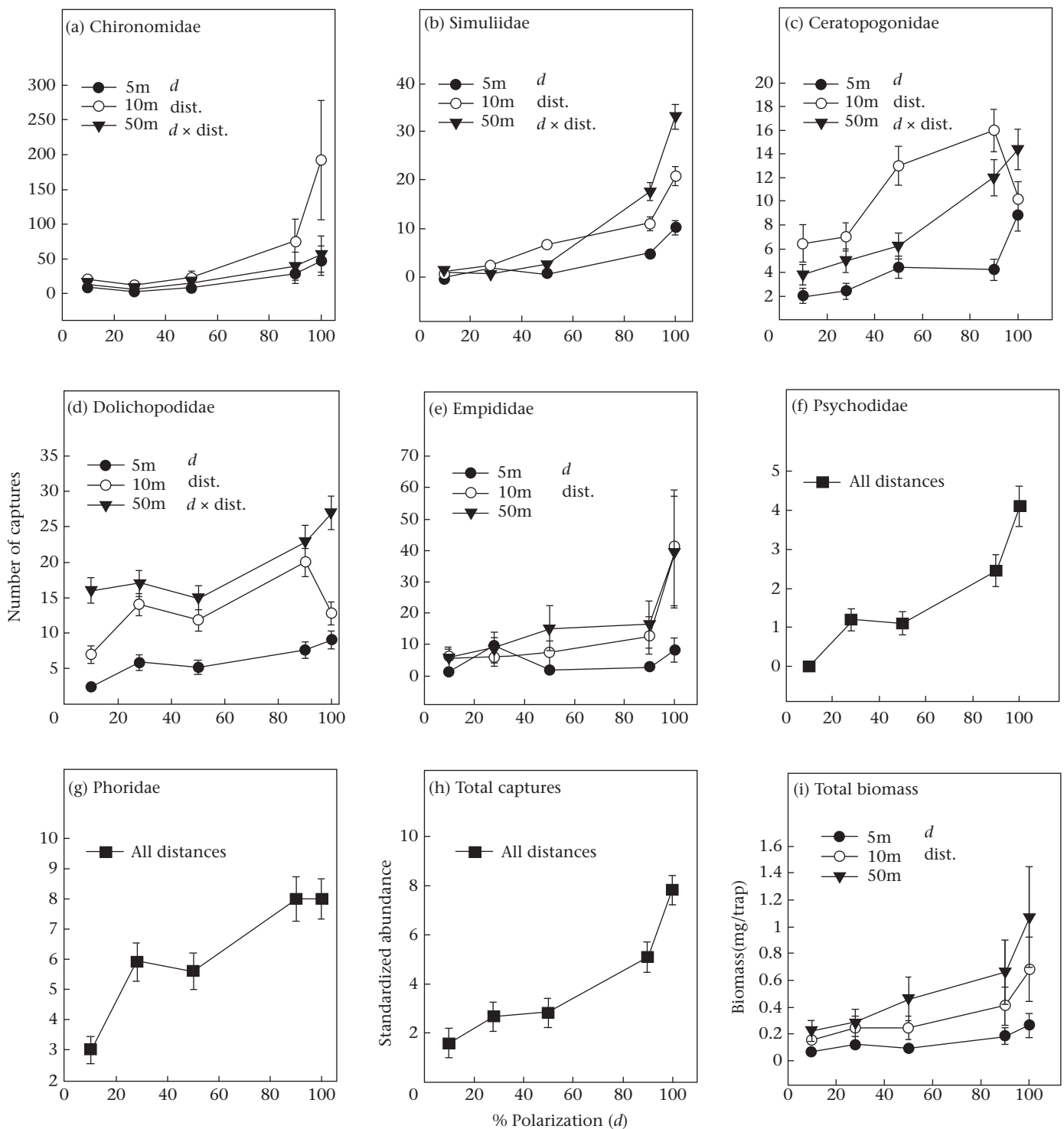


Figure 3. Captures of aquatic dipterans in polarized light traps as a function of the percentage d of horizontally polarized light reflected by the trap and the distance of the trap from the edge of five rivers in the Hudson Valley of New York State. Shaded oil-filled trays (Fig. 2) reflected 16% (white), 28% (light grey), 51% (medium grey), 87% (dark grey), or 99% (black) of reflected sunlight. One tray of each type was placed in a row at 5 m (filled circles), 10 m (open circles) or 50 m (filled triangles) from a river bank. Graphs show the abundance of captures in each tray–distance combination (\pm SE) for seven families of aquatic-breeding dipterans (a–g) and for the abundance of all seven families of aquatic dipterans captured (h). The dry biomass of captures is also estimated (i). Within each graph, significant main effects from Poisson regressions (a–g) or glms (h–i) are indicated for the effect of the percentage of polarization of traps (d), the distance from water (dist.), or interaction effects ($d \times$ dist.) on abundance or biomass. Where distance from water was unimportant in explaining dipteran abundance (f–h), only the estimated marginal means for d are given (black squares). The units in (h) reflect captures standardized to give equal weight to each of the seven families in (a)–(g).

limitations on the mobility of taxa that constrain their ability to detect and choose among alternatives, attraction to concentrations of food, or the avoidance of predators or challenging microhabitats (e.g. windy, hot). Indeed, the diversity of family-specific responses that we observed seems inconsistent with any single ecological or behavioural mechanism. Our study did not test for the influence of other habitat selection cues that dipterans might use in guiding their behaviour. Indeed, the *d* of water bodies is currently known to be the predominant habitat selection cue used by aquatic insect species and entirely explains the maladaptive oviposition of a diverse array of taxa upon windows, roads, solar panels and automobiles (Horváth, 2014), but *Aedes aegypti* mosquitos are also known to use olfactory cues (Bernáth et al., 2012; Wildermuth, 1998). Avoidance of whiter traps, which are better reflectors of light, is unlikely because certain aquatic insects are also attracted to intense unpolarized light sources (Boda et al., 2014; Nowinszky, Kiss, Szentkirályi, Puskás, & Ladányi, 2012; Nowinszky & others, 2003; Perkin, Höcker, & Tockner, 2014; Szaz et al., 2015), which can synergistically enhance their attraction to polarized light sources (Boda et al., 2014; Robertson et al., 2017) or even cause them to ignore polarized light (Robertson et al., 2017).

Regardless, our findings indicate that strong sources of polarized light pollution (e.g. asphalt roads, solar panels, glass buildings) placed further from rivers in our study region create ecological traps for aquatic flies, and that these traps are more attractive for some species and less attractive for others. The fitness penalty of arthropod attraction to artificial polarizers is severe in that adults perish and oviposition always results in complete reproductive failure because eggs desiccate and perish out of water (Horváth et al., 2010; Kriska et al., 1998, 2008, 2006; Szaz et al., 2015). The supernormal strength of *d* associated with artificial polarizers commonly leads to individuals being unable to escape the area (also known as ‘the polarization captivity effect’; Horváth et al., 2009) and they exhaust themselves and die or are eaten by predators (Horváth, Majer, Horváth, Szivák, & Kriska, 2008; Robertson, 2010; reviewed in ; Robertson et al., 2013). Whether ecological traps driven by artificial polarized light will, or have already led to, population declines in aquatic arthropods, as mathematical simulations (Fletcher et al., 2012; Kokko & Sutherland, 2001) suggest, remains unclear, but unpolarized light pollution represents a global threat to biodiversity and species persistence (Gaston, Bennie, Davies, & Hopkins, 2013; Höcker, Wolter, Perkin, & Tockner, 2010; Longcore & Rich, 2004) and unpolarized light can be strongly and horizontally polarized by man-made objects to create ecological traps at night (Szaz et al., 2015).

Of the over 50 extant examples of ecological traps (reviewed by Robertson et al., 2013), all have been identified only after their accidental creation. The use of field experiments that reveal behavioural reaction norms appears to be a promising way to predict conditions under which future ecological novelty will create ecological traps as it allows an explicit and quantitative comparison of behavioural responses to environmental cues that span historical and novel levels of variation. Our focus on polarized light as a quantitative habitat selection cue was convenient because it is so closely and uniquely associated with water (Horváth, 2014), which itself is a resource key to the survival of a broad taxonomic range of insects. Yet, this approach could be adapted to predict maladaptive behavioural responses in other contexts (e.g. mate selection, food choice, navigation and orientation; ‘evolutionary traps’ sensu Robertson et al., 2013; Schlaepfer et al., 2002) as the result of multiple cues and cue types (e.g. presence/absence, categorical, quantitative) and how they are weighted by organisms in assessing behavioural options. For example, nocturnally active aquatic insects are attracted to sources of both horizontally polarized and unpolarized light and these two ecological traps can act

synergistically to create even more attractive, and therefore demographically costly, ecological traps (Boda et al., 2014). Another benefit of employing reaction norms in understanding and managing ecological traps is that they are also capable of revealing when evolution or learning is adapting organisms to trap conditions (Schlaepfer, Sherman, Blossey, & Runge, 2005) by reshaping reaction norms in such a way that they guide individuals away from previously attractive, but poor-quality, habitats.

Understanding the mechanisms by which anthropogenic impacts can trigger maladaptive behaviour like evolutionary traps is critical both to ecological and evolutionary theory and central to the development of conservation strategies to eliminate traps where they threaten species persistence (Hawlena & Bouskila, 2006; Hawlena et al., 2010; Kessler et al., 2015; Schlaepfer et al., 2005; Van der Meer, Fritz, Blinston, & Rasmussen, 2014) and to prevent their creation in the first place (Robertson et al., 2013). Our findings indicate the aquatic dipterans are broadly susceptible to ecological traps triggered by supernormally strong polarized light sources, and the similarity of their respective reaction norms suggests that this susceptibility is a consequence of the evolution of similar habitat selection algorithms. The more variable ways in which spatial isolation affected preference for ecological traps in our study indicates that attraction to traps is contextualized by life-history traits, and that the potential for habitat acting as an ecological trap in one spatial context could, in theory, be adaptively settled in another. From a conservation point of view, these results are worrying in that a single novel ecological cue can cause severe behavioural maladaptation for an entire suite of species. Conversely, this result also illustrates that interventions to eliminate this specific multispecies ecological trap can efficiently target the elimination of a single misleading cue via a number of practical and inexpensive methods (Horváth et al., 2009, 2010). To contextualize our results, future research assessing the susceptibility of species to ecological traps might examine how a more taxonomically diverse range of species responds to similar sources of ecological novelty, but exposing animals to a more diverse set of environmental cues.

DATA ACCESSIBILITY

Data are available via Dyrad (<https://doi.org/10.5061/dryad.nq3s6>).

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