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Original Article The interface of ecological novelty and behavioral context in the formation of ecological traps

Bruce A. Robertson,^a Desi-Rae Campbell,^a Colyer Durovich,^a Ian Hetterich,^b Julia Les,^a and Gábor Horváth^c

^aDivision of Science, Mathematics and Computing, Bard College, Annandale-on-Hudson, New York 12504, USA, ^bBard College at Simon's Rock, 84 Alford Rd, Great Barrington, MA 01230, USA, and ^cEnvironmental Optics Laboratory, Department of Biological Physics, Physical Institute, ELTE Eötvös Loránd University, H-1117 Budapest, Pázmány sétány 1, Hungary

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Ecological traps occur when rapid environmental change causes animals to actually prefer inferior habitats. Traps increase the likelihood of species extinction, but our understanding of how evolved behavioral algorithms interface with increasingly novel ecosystems to trigger them remains limited. Both polarized and unpolarized light are increasingly common forms of light pollution known to cause maladaptive behavior for both water-seeking and entirely terrestrial insects by maladaptively triggering innate habitat selection and navigation preferences, respectively. We designed a nocturnal, field-based experiment to investigate how diverse nocturnal insect taxa use and contextualize these cues when they are placed in evolutionarily novel proximity, and so test the hypothesis that cues that originally evolved to guide navigation behavior can enhance or hinder the ability of different nocturnal insects to avoid maladaptive behavior within the context of habitat selection. Unpolarized light created more attractive ecological traps, even for aquatic taxa known to use polarized light as their sole habitat selection cue. We found that these cues could, in aquatic taxa, act both additively and synergistically to increase the attraction of ecological traps. While one family showed evidence of partitioning their response to these 2 forms of light within their respective behavioral contexts (navigation, habitat selection), our results indicate that the novel proximity of cues from separate behavioral contexts can act to enhance the attractiveness of ecological traps within a focal context.

Key words: aquatic insect, behavioral, evolutionary trap, habitat selection, light pollution, maladaptation, reaction norm

INTRODUCTION

When confronted with ecological novelty, many species respond adaptively, while others respond incorrectly (Sih et al. 2011). Cases in which rapid environmental change triggers such severe mismatches between perceived and actual habitat quality that animals actually prefer inferior habitats are known as ecological traps (Dwernychuk and Boag 1972; Schlaepfer et al. 2002). For example, artificial night lighting attracts flying insects because its intensity commonly exceeds that of their natural navigational beacon, the moon (Gaston et al. 2013), while the abnormally close and static position in space of night lights elicits attraction and circling behavior (Frank 1988; Longcore and Rich 2004). In this way, night lights draw flying insects away from more suitable habitats to lighted areas where they experience depleted energy stores and

Address correspondence to B.A. Robertson. E-mail: broberts@bard.edu.

© The Author 2017. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com elevated risk of predation (reviewed in Longcore and Rich 2004; Eisenbeis and Hänel 2009; Gaston et al. 2013). Given that ecological traps are increasingly common (Robertson et al. 2013) and can rapidly collapse populations and increase the likelihood of extinction (Delibes et al. 2001; Hawlena et al. 2010; Fletcher et al. 2012; van der Meer et al. 2014; Hale et al. 2015; Kessler et al. 2015) there is an immediate need to better understand the behavioral mechanisms by which ecological novelty interfaces with evolved behavioral rules to form ecological traps, that is if we are to eliminate them where they occur or prevent their creation in the first place (Robertson et al. 2013).

One of clearest examples of an ecological trap is the attraction of aquatic insects to man-made sources of horizontally polarized light. Sunlight becomes horizontally polarized when it reflects off the surface of water bodies and the direction of its electromagnetic vibration changes from random, to one primarily parallel to the surface of the water (horizontal). Emergent aquatic insects use horizontally polarized light as their primary habitat selection cue because of the ability of natural water bodies to horizontally polarize 30–80% of reflected sunlight, and skylight (Horváth 2014). Throughout their evolutionary history, horizontally polarized light has been the most reliable visual cue for locating water (Horváth and Varjú 2004; Horváth 2014). Today, however, the earth is increasingly populated with man-made objects that can easily polarize 95–100% of reflected light (e.g. solar panels: Horváth et al. 2010; glass buildings: Horváth et al. 2009; automobiles: Kriska et al. 2006; asphalt: Kriska et al. 1998). Such artificial polarizers, even vertically oriented (e.g. glass buildings; Kriska et al. 2009), attract day-active insects to sexually display and mate above, then touch down, and preferentially lay eggs on them leading to adult mortality and complete reproductive failure (Kriska et al. 1998, 2006, 2008; Horváth and Varjú 2004; Lerner et al. 2008, 2011; Horváth et al. 2010).

Nocturnally active aquatic insects can also be confronted with polarized light pollution when artificial night lighting is placed in proximity to roads or other artificial polarizers (Horváth et al. 2009). Night-active aquatic insects, then, are attracted to sources of both polarized (Horváth 2014) and unpolarized light (Nowinszky 2003; Nowinszky et al. 2012; Boda et al. 2014; Szaz et al. 2015; Figure 1). Each cue can trigger an ecological trap on its own, but might also interact in the creation of an ecological trap when night lights are placed in close proximity to artificial polarizers (Figure 2a) if insects have not evolved an ability to partition or separate their behavioral responses within their respective navigational and habitat selection contexts. Terrestrial insects, too, may be susceptible to traps driven by a combination of polarized and unpolarized light because they may use both the unpolarized light of the moon (Leuthold et al. 1976; Sotthibandhu and Baker 1979; Ugolini et al. 2003) and the sky polarization pattern (Kovarov and Monchadskiy 1963; Dacke et al. 2003, 2004) as navigational beacons. In this way, artificial night lighting can create ecological traps by placing evolved cues in novel spatial contexts and by presenting cues that have evolved to guide different behaviors in close proximity within the context of one behavior (e.g. habitat selection).

Because both forms of light are attractive stimuli, they may lead to the same behavioral response and so be redundant. Alternatively, animals may have an enhanced behavioral response such that individuals faced with both cues will find a lamp-lit artificial polarizer more attractive than the artificial polarizer alone (e.g. Boda et al. 2014). Antagonism would occur if exposure to both stimuli leads to a reduced behavioral response in the context of habitat selection. This diversity of stimuli-behavioral responses have been well documented within the context of animal communication (reviewed in Partan and Marler 2005; Munoz and Blumstein 2012), but there exists no framework to predict how animals should respond maladaptively and to combinations of stimuli that evolved to guide behavior in separate contexts. Indeed, a wide variation of behavioral responses are theoretically possible, and expected, because taxa vary in their attraction to polarized (Horváth 2014) and unpolarized (Nowinszky 2003) light sources. Ecological traps exist at the nexus of behavioral, ecological and evolutionary sciences, but because they are triggered by maladaptive responses to environmental stimuli a detailed understanding of the mechanisms that create them is fundamental to theory. Historically common types of more narrow-wavelength artificial external lighting such as mercury-vapor and low-pressure sodium lighting are being replaced broad-spectrum light-emitting diodes (LEDs) that insects visual receptors are particularly sensitive to (Gaston et al. 2013), ecological traps formed by new forms light pollution are likely to become



Figure 1

Images of ephemeroptera attracted to sources of polarized and unpolarized light in close proximity. (a) Swarms of mayflies surround LED night lighting and coat the asphalt ground in Minnesota City, WI, USA. (b) Mayflies (Ephoron virgo) attracted to the surfaces of asphalt and an automobile under a street lamp. (c) Mayflies attracted to congregate around street lamps and oviposit on the horizontally polarizing asphalt bridge surface (Szaz et al. 2015). Photos credits: Kelly Gardner (a and b) and György Kriska (c).

more attractive in the future, making these questions relevant to biodiversity conservation.

We conducted a field-based experiment designed to 1) estimate the relative importance of unpolarized versus polarized light in leading families of nocturnally active aquatic and terrestrial insects to settle in ecological traps, and 2) evaluate variation in the specific algorithms species have evolved to guide habitat selection behavior when these cues from 2 separate behavioral contexts are placed in close proximity. Our experiment examines variation in captures of insects in simulated water bodies that vary widely in their ability to polarize reflected light, and under conditions in which they are illuminated such that their unpolarized light source is directly visible from all directions versus shaded such that unpolarized light will only be visible to approaching insects as reflections from the surfaces of simulated water bodies (Figure 2b).



Figure 2

Study sites and elements of experimental design. (a) Night-active aquatic insects can simultaneously experience 2 forms of light pollution from a single artificial light source: (i) unpolarized light can travel directly from a street light to an insect, but (ii) artificial polarizers such as asphalt parking lots can horizontally polarize reflected light and reach flying, water-seeking insects. In this visual representation of the experiment colored squares represent black, grey, and white oil-filled trays which reflect horizontally polarized light with high, moderate and low degrees (d) of polarization, respectively (Figure 3, Supplementary Figure S1, Online Appendix A). One trap of each color is illuminated by a LED (Light-Emitting Diode) that is either shaded and downward-oriented (center) or unshaded and able to emit unpolarized light in almost all directions (apart from behind) (top-right). In the former case, approaching insects will primarily encounter only light reflected from illuminated trays with various degrees of polarization. Unshaded lights will more directly present both polarized and unpolarized light to insects in the vicinity of the trap. (b) Experiments were conducted on the banks of 5 tributaries of the Hudson River (white line) and located in 3 of the 6 shown counties (bordered in black) of southern New York state.

METHODS

Study sites and experimental design

In 2012, we selected sites on 5 different tributaries of the Hudson River in southern New York State, USA (Figure 2c). Study sites were located in sparsely populated areas along heavily forested river corridors. We chose residential properties with lawns extending from the high water line inland at least 60 m to ensure sufficient area for our experiment, and so vegetation would not impede insect lines of sight toward the experiment. Nocturnal lighting was absent within a 200-m radius of the experiment. We captured insects 3 times at each site: 1) May 19th–June 3rd; 2) June 4th–16th; 3) June 19th–25th. Capture sessions lasted 120 min, beginning 30 min after sunset.

We used salad-oil-filled trays painted white, black, and grey to capture insects and assess their relative preference for surfaces varying in their ability to horizontally polarize light and which were associated with shaded or unshaded sources of unpolarized light (Figure 2b). We placed 2 of each of 3 colored tray (black, grey, white) in a row parallel to the riverbank at a distance of 8 m, spaced 0.5-m apart, and centered them upon a $2 \text{ m} \times 9 \text{ m}$ piece of black plastic tarpaulin that acted as a strong polarizer attracting insects to the experiment (Kriska et al. 1998). On the upland side of each tray we placed a table lamp (60W LED bulb, Figure 2b and d), lit at an elevation 0.3 m. One light associated with each tray color was equipped with a cardboard shade that restricted lamplight to illuminating only the tray below it. Paired, unshaded bulbs could be directly viewed from all directions. The experiment began with trays placed in a random color order within rows. We rotated their positions every 20 min within existing shade-treatment, according to a standardized algorithm. After each sampling session, we poured tray contents through fine cheesecloth to separate insects, which we stored in 80% ethanol for later identification to the family level. Biomass is commonly more reflective of the relative importance of the functions played by arthropods in ecological communities than is abundance (Saint-Germain et al. 2007) so we estimated the dry biomass of each individual using family specific length-biomass regressions (Sabo et al. 2002), excluding flightless taxa from analyses.

Physical and optical characteristics of oil-traps

We measured the reflection-polarization characteristics of these trays using imaging polarimetry (Horváth and Varjú 2004) in the red (650 \pm 40 nm = wavelength of maximal sensitivity \pm half bandwidth of the polarimeter detector), green (550 \pm 40 nm) and blue $(450 \pm 40 \text{ nm})$ parts of the spectrum. We visualized patterns for the blue spectral range only (Figure 3) because the red and green spectral ranges were similar. We created black oil-traps (degree of polarization d = 97%) that polarized reflected light more strongly than natural water bodies are capable of (water \approx 30–80%), one representative of a typical river (grey, d = 51%) and one color with a *d*-value less than any natural-occurring object but typical of manmade objects such as bright buildings (white, d = 27%, (Horváth and Varjú 2004; Horváth 2014, Supplementary Figure S1, Online Appendix A). These were maximal *d*-values based upon polarimetric measurements taken in a darkroom with the optical axis of the polarimeter aimed toward the shaded LED and downward at the Brewster angle at which surfaces maximally polarize reflected light $(\Theta_{\text{Brewster}} = \arctan n \approx 56.3^{\circ}$ from the vertical using the refractive index $n \approx 1.5$ of salad oil).

Focal taxa and experimental predictions

We define aquatic insect families as those with a larval or adult lifehistory phase critically dependent on the availability of a freshwater body (Johnson and Triplehorn 2004). We focused our analysis on aquatic insect taxa known to exhibit stronger attraction to sources of horizontally polarized light with greater values of *d*: ephemeroptera (Kriska et al. 1998, 2006; Horváth et al. 2010; Szaz et al. 2015) plecoptera (Horváth 2014), trichoptera (Kriska et al. 2008; Horváth et al. 2010), dolichopodidae (Horváth et al. 2010), ceratopogonidae



Figure 3

The reflection-polarization characteristics of oil-filled black (left), grey (center), and white (right) trays used in the choice experiments in riparian sites in southern New York state, USA, measured by imaging polarimetry in the blue (450 nm) part of the spectrum. Row 1: Color photographs of illuminated trays. Row 2: Patterns of the degree of linear polarization *d*. Darker-colored trays polarized a greater fraction of reflected LED light. Row 3: Patterns of the angle of polarization α . Double-headed arrows show the local direction of polarization of reflected light. At and immediately around the reflection of the LED bulb the reflected light is horizontally polarized, while farther away from the mirror image of the bulb it is non-horizontally (obliquely or vertically) polarized.

(Robertson et al. In review), empididae (Robertson et al. In review), simuliidae (Robertson et al. In review), chironomidae (Robertson et al. In review; Lerner et al. 2008, 2011; Horváth et al. 2011), aquatic coleoptera (Kriska et al. 2006; Boda et al. 2014), corixidae (Kriska et al. 2006). When seeking a suitable oviposition site, these taxa touchdown on the surface (Kriska et al. 2006; Horváth 2014), but will be captured in the oil-traps due to the weak surface tension. If unpolarized light is relatively more important shaping habitat preference than polarized light, we expect more captures in unshaded, than in shaded trays, independent of color. If polarized light is more important, we expect darker-colored oil-traps to capture more insects, independent of shading. If both cues are important in guiding behavior, both patterns should be apparent. We use the relative number of captures among treatment to assess the additive versus synergistic nature of these cues in shaping habitat preference and, therefore, the degree to which both types of light pollution are interpreted within different behavioral contexts (navigation vs. habitat selection) or in tandem.

Whiter objects (e.g. buildings) reflect more unpolarized light than those of darker colors, and polarize less reflected light (Umow 1905). As such, man-made objects will inevitably face a trade-off between their brightness and their ability to polarize reflected light such that strongly polarizing and bright objects or unpolarizing dark objects are extremely uncommon (or even physically impossible). Therefore, differential responses of insects to man-made objects, including the oil-traps in our study, cannot be perfectly attributed to attraction to polarized versus unpolarized light. They will, however, accurately reflect how insects respond to shaded and unshaded LED lights and their reflections from natural or manmade objects of different colors. Matte (rough) surfacing of objects can partially reduce their ability to polarize light independent of its wavelength (Kriska et al. 2006; Horváth et al. 2010; Boda et al. 2014), but we focus on objects with a smoother finish and typical of exterior building paint, asphalt, automobiles, windows and solar panels which are common sources of diurnal polarized light pollution. We used an OceanOptics USB2000+ spectrometer to measure the absolute irradiance $(\mu W/cm^2/nm)$ of among tray colors and shaded versus unshaded trays to assess the role of tray brightness in shaping responses.

Statistical analyses

We examined the effect of 1) light shading (polarized only vs. polarized and unpolarized light) and 2) the degree (percentage) of polarization (d) of tray-reflected light on the abundance of captures for each aquatic insect family using Poisson regression with a logit link function in SPSS (SPSS 2009). Shading and d-value were treated as categorical variables. Because we were interested in longer-term responses of insects to experimental treatments, we combined captures from all three site visits into a single measure of captures per treatment per study site, prior to analysis. Yet, since temporal trends in capture probability have the potential to bias responses to focal variables we tested the effect of Julian sampling date on captures in all models. Where Poisson models were over-dispersed ($\hat{c} >$ 6.0) we fit negative-binomial models. We examined the effects of shading and d on total terrestrial and total aquatic insect biomass using these same methods but with a linear link function. We used pairwise least significant difference tests for post hoc comparisons amongst treatments.

RESULTS

Nocturnal reflection-polarization characteristics of oil-traps

Darker-colored oil-traps horizontally polarized a greater fraction of reflected light under both nocturnal (Figure 3) and diurnal skylit circumstances (Supplementary Figure S1, Online Appendix A), but lamp-lit trays produced unique patterns in the degree and angle of polarization of reflected light. Unreflected LED light was unpolarized (d = 0%), as was the reflected matte white cylindrical shade of all lamps. The mirror image of the bulb and shade and its surrounding reflection in the surface of the oil-traps reflected horizontally polarized light (angle of polarization clockwise from the vertical: $80^\circ < \alpha < 100^\circ$) with high degrees of polarization ($d \ge 72\%$) independent of the oil-trap color, though this circular horizontally polarized area was larger in size in increasingly darker-colored oil-traps (Figure 3). Outside of this area, angle of oil-trap-reflected LED light was more vertically polarized with decreasing degrees (d) of polarization with increasing brightness of the oil-trap color. The maximal degree of polarization for each oil-trap was slightly lower than when measured under clear skies (black: d = 92%; grey: d = 40%; white: d = 15%). White trays were slightly more efficient reflectors of unpolarized LED light, but this effect was minor relative to the reflectivity of the other trays and in relation to the overall brightness of the unshaded LED bulbs (Supplementary Figure S2, Online Appendix A).

Abundance responses of insects to treatments

We captured a total number of 102 229 insects in 118 families (aquatic: n = 63257, 37 families; terrestrial: n = 38972, 81 families). We were able to fit models to 14 families and 1 order (plecoptera) of aquatic insects, and 10 families of terrestrial insects without being over-dispersed (Table 1).

Aquatic taxa exhibited a diverse set of responses to experimental lighting treatments consistent with habitat selection/oviposition behavior that gives differential importance to unpolarized light, polarized light, and to both cues. Five taxa (plectoptera, glossomatridae, heptageniidae, ceratopogonidae, and ephydridae) were captured in higher numbers in traps illuminated by unshaded lights, but captures were unrelated to horizontal polarization (Figure 4a–e). Chironomids and empidids were also captured in higher abundance in unshaded trays, but were also more likely to settle upon the least-polarizing white trays (Figure 4f–g). Captures of simuliids were greater in unshaded

Table 1

Captures and biomass of the 22 insect families and 1 insect order captured during riparian light pollution experiments on 5 rivers in the Hudson River valley, USA, and to which we were able to fit Poisson and negative-binomial models

Taxonomic group	# of captures	Biomass (mg)	% of total biomass
Aquatic	63257	459.66	69.50%
Heptageniidae	40151	300.00	45.36%
Plecoptera	571	60.76	9.19%
Chironomidae	5253	56.07	8.48%
Dolichopodidae	660	18.46	2.79%
Ephydridae	1798	12.23	1.85%
Empididae	278	4.61	0.70%
Caenidae	10153	3.42	0.52%
Simulidae	153	1.07	0.16%
Ceratopogonidae	6904	1.03	0.16%
Corixidae	63	0.89	0.13%
Hydropsychidae	624	0.60	0.09%
Hydrophilidae	391	0.36	0.05%
Polycentropodidae	341	0.08	0.01%
Glossomatridae	179	0.08	0.01%
Terrestrial	40210	201.71	30.50%
Cicadellidae	15055	58.10	8.78%
Nabidae	1386	53.89	8.15%
Scarabidae	700	50.21	7.59%
Miridae	2045	16.76	2.53%
Mycetophilidae	8083	8.21	1.24%
Carabidae	331	7.16	1.08%
Cecidomyiidae	5346	4.89	0.74%
Chrysomelidae	114	1.99	0.30%
Geometridae	171	0.46	0.07%
Tineidae	69	0.04	0.01%

Taxa are organized in descending order of biomass captured relative to the total insect biomass captured throughout the course of the experiment.



Figure 4

Insect responses to experimental variation in the shading of exterior LED lighting and illuminated oil-trap color in riparian areas in southern New York state, USA. The experiment diagrammed in Figure 1b is designed to expose insects to variation in the intensity of unpolarized (shaded to illuminate only oil-traps versus bulb unshaded and directly visible) light and the degree of polarization of light reflected from oil-traps. Darker-colored trays polarized more reflected LED light (Figure 3). Histograms represent the results of Poisson or negative-binomial regressions using oil-trap color (black, grey, or white-colored bars representing trap colors) and whether LED light bulbs were shaded or not to predict captures in different insect taxa with aquatic life-history phases (a–l, water drop symbols) or those with entirely terrestrial life-histories (m–u, leaf symbols). The statistical significance of individual treatments in predicting captures or biomass are indicated (* $P \le 0.05$; ** $P \le 0.01$; *** $P \le 0.001$). Letters indicate differences between mean values in treatment combinations from pairwise LSD post hoc tests with a minimum significance level of $P \le 0.05$, such that bars sharing a same letter cannot be considered as having different mean values.



Figure 4. Continued

trays, but they exhibited a preference for more horizontally polarizing and unshaded trays (Figure 4h). Two families of caddisflies (hydropsychidae and polycentropodidae) and one family of aquatic beetles (hydrophilidae) also preferentially settled in unshaded traps, but were captured at highest abundance in least-polarizing, then most-polarizing, then moderately polarizing traps (Figure 4i–k). Water boatmen (corixidae) exhibited a unique behavioral response in preferentially settling in moderately polarizing oil-traps, especially under unshaded light sources (Figure 4l). Neither long-legged flies (dolichopodidae) nor squaregill mayflies (caenidae) exhibited significant numerical responses to shading or polarization treatments.

Compared to aquatic insect groups, terrestrial insect families exhibited a more narrow range of behavioral responses to experimental treatments, none of which were consistent with horizontally polarized light influencing in habitat selection decisions. Five (chrysomelidae, miridae, tineidae, mycetophilidae, nabidae) of the 10 terrestrial insect families we examined showed preference for settling in traps under unshaded lights, regardless of oil-trap color (Figure 4m–q). Three families (scarabidae, carabidae, cicadellidae) showed preference for unshaded traps in general, but were more attracted to white oil-traps than grey or highly polarizing black ones (Figure 4r–t). Geometrid moths were preferentially attracted to poorly polarizing white traps, but only under unshaded lights (Figure 4u). Gall midges (cecidomyiidae) showed no significant numerical response to any treatment. Julian date was unimportant in explaining variation in captures in all taxa (all P > 0.16).

Biomass responses of insects to treatments

Heptageniid mayflies dominated aquatic captures in terms of both biomass and abundance and 98% of the aquatic insect biomass

were represented by just 4 families and one order (plecoptera) of insects (Table 1). Terrestrial insect families were more evenly represented in captures with respect to biomass (Table 1). Insects of both the aquatic (Figure 5a) and terrestrial (Figure 5b) communities were captured at greater biomass in unshaded oil-traps. Shading LEDs reduced the biomass of aquatic insects captured by 77% (marginal means: unshaded: 39.8 g/trap, SE = 10.5; shaded: 9.3 g/trap, SE = 10.5) and of terrestrial insects by 74% (marginal means: unshaded: 33.5 g/trap, SE = 8.6; shaded: 10.1 g/trap, SE = 2.6). Julian date was unimportant in explaining variation in terrestrial and aquatic biomass of arthropod captures (both P > 0.44).

DISCUSSION

Our results indicate that nocturnally active insets are broadly susceptible to ecological traps created primarily by unpolarized light, that evolution has designed behavioral algorithms that make insects susceptible to traps differently and as a function of their taxonomy and terrestrial versus aquatic habitat preferences. We also show that taxa vary in their ability to correctly respond to polarized and unpolarized light within the behavioral contexts within which the respective cue use evolved.

As predicted, nocturnally illuminated oil-traps of darker color more completely polarized reflected LED light. All oil-traps reflected a signature of horizontally polarized light represented by the circular mirror image of the LED bulbs and its immediate surroundings. The darker the lamp-lit tray, the greater the degree of LED light horizontally polarized and over a larger spatial area around the lamps mirror image. Outside of the mirror image and its annular halo, however, reflected polarized light was dominated by the light component returned from the trap bottom (especially for the white trap), and thus was more vertically oriented (Figure 3). These reflection-polarization patterns are characteristic of those of natural (dark and bright) water bodies when facing toward the sun or moon (reviewed in Horváth 2014). Moreover, because all water-seeking aquatic insects so far tested by science are positively attracted to horizontally polarized light (reviewed in Horváth 2014), the reflection-polarization characteristics of our oil-traps should effectively elicit evolved behavioral preferences for darker or brighter aquatic habitats.

No families of terrestrial insects exhibited patterns of capture consistent with their using upwelling reflected horizontally polarized light as a cue in guiding their navigation and orientation behavior. This suggests that despite documented ability of terrestrial insects to use sky polarization patterns for navigation (Kovarov and Monchadskiy 1963; Dacke et al. 2003, 2004) they were able to avoid ecological traps baited with this cue. Moonlight is only weakly polarized (0-9%, Nowinszky and Puskás 2012) and so the high d of light in our experiment could have triggered a supernormal attraction (sensu Tinbergen 1951) responsible for ecological traps in other cases (prey abundance: Kloskowski 2012; mate size: D'Amore et al. 2009; nest site availability: Mänd et al. 2009). Yet, at least one species (desert locust, Schistocerca gregaria) has evolved the ability to use polarized light to actually avoid water bodies (Shashar et al. 2005). The most common pattern of habitat preference in both terrestrial and aquatic insects was a strong attraction to unshaded and unpolarized LED light sources (Figure 4a-e and m-q), especially in white trays (Figure 4e, o, r, t). Compared to the brightness of a full moon (0.1–0.3 lux, Gaston et al. 2013), the 60-watt LEDs we used were over 2000 times brighter at a distance of 1 m (636 lux) and approximately the brightness of the moon at a distance of ~ 45 m. This and the fact that many widely used light traps designed for the capture of nocturnal flying insects incorporate large and white reflective surfaces like sheets or netting (Nowinszky 2003; Nowinszky and Puskás 2012) suggest a role for the interaction of color and spatial area of a light signal in navigational guidance for both terrestrial and aquatic taxa.

Polarized light increased the attractiveness of ecological traps in less than half of the aquatic insect groups we studied, but in those cases insects used polarized and unpolarized light in guiding their behavior in diverse ways. Black flies (simuliidae) preferentially settled in more highly polarizing, darker traps, but only in front of unshaded light sources, indicating that the d of polarized light is given the most influence in habitat selection. Hydropsychid caddisflies and aquatic scavenger beetles (hydrophilidae) preferred unshaded traps, but avoided intermediate values of polarized light. This pattern suggests that these taxa were acting on preferences for cues separately within the context of either navigational or habitat selection behavior. Polycentropodids exhibited diverging patterns of



Figure 5

Biomass of captures of aquatic (a) and terrestrial (b) insects in response to experimental variation in the shading of exterior LED lighting and illuminated oil-trap color in riparian areas in southern New York state, USA. Both terrestrial and aquatic taxa found traps with direct exposure to unpolarized light (unshaded) more attractive, regardless of the degree of polarization of light they were associated with ($P \le 0.001$). Letters indicate differences between mean values in treatment combinations from pairwise LSD post hoc tests with a minimum significance level of $P \le 0.05$, such that bars sharing a same letter cannot be considered as having different mean values.

preference under different shading conditions, indicating contextdependence in how they used polarized versus unpolarized light tica in guiding behavior. In contrast, corixid bugs (water boatmen) even were captured at highest abundance in grey, especially unshaded trays, suggesting 1) they give equal importance to unpolarized and polarized light, or 2) they prefer intermediate values of d typical of streams with a lighter-colored bottom substrate (e.g. grey stone) (Horváth 2014). Previous tests have shown the latter to be false (Schwind 1991; Kriska et al. 2006) and so we conclude either that corixids have not yet evolved the ability to partition their behavioral responses between the contexts of navigation and habitat selection or that other unexamined cues (e.g. conspecific attraction) might be simultaneously influencing behavioral responses. Collectively,

we found that nocturnally active insect taxa variously were more attracted to brighter sources of unpolarized light, more horizontally polarized light, or combinations of the two, and varied widely in their ability to partition their responses to ecological novelty within relevant behavioral contexts. It is surprising that many aquatic insects did not use the d of

polarized light to guide their habitat selection behavior after dark because no species of aquatic insect ever tested has failed to show this response during the day (reviewed in Horváth 2014). Mosquitos (family Culicidae) use ancillary other cues in locating oviposition sites (e.g. odors of conspecifics, scent of eggs or water vapor) (Bernáth et al. 2012), but taxa we captured were unable to use such cues to avoid the ecological traps we presented them with. In theory, aquatic taxa could have been unready to oviposit and so patterns of capture should have been reflections only of the use of navigational cues. However, adult forms of aquatic insects are typically so short-lived with such a strong driving force to mate and oviposit quickly that experimentally restricting the availability of high-quality oviposition sites can actually lead adults to oviposit in suboptimal habitats (Lerner et al. 2011). That empidids and dolichopodids studied at these same sites exhibited strong preference for more strongly polarizing oil-traps during daytime (Robertson et al. (forthcoming)), but not at night (this study) further underscore the hypothesis that unpolarized light can exhibit dominance over polarized light as a habitat selection cue when artificial night lighting is present.

Previous studies have suggested that aquatic insects are capable of using both the d of polarized light and the intensity of unpolarized light in guiding their habitat selection decisions (Boda et al. 2014; Szaz et al. 2015). Besides exposing a broad taxonomic susceptibility of insects to ecological traps caused by separate forms of light pollution or the interaction of the two, our results break new ground in showing that these 2 different forms of ecological novelty (unpolarized and polarized light pollution) can act to enhance behavioral responses more additively (Figure 4f and g), more synergistically (Figure 4h-j), or even act antagonistically (Figure 4i-k) in triggering maladaptive behavior. Only corixids (Figure 41) appeared to possess a behavioral algorithm that was sufficiently robust to guide them to the grey traps, which were most optically representative of natural water bodies. If these maladaptive behavioral responses to supernormally bright or polarized light were simply a consequence of the degree to which lighting exceeds the relative intensities of these forms of light under natural conditions, the taxa in this study should have responded to treatments in a uniform fashion. Instead, the diversity of responses shown by different taxa indicates that natural selection has not designed a universal algorithm to govern the relative influence of these stimuli in decision making and so species will vary substantially in the degree to which they are susceptible to ecological traps triggered by an identical form of novelty. Our results also indicate that cues that have evolved to guide entirely different behaviors can act together to trigger maladaptation within a single behavioral context (e.g. Burley and Symanski 1998), presumably because selection has not had sufficient opportunity to partition them through the process of natural selection.

Because the strongest behavioral response in both aquatic and terrestrial insects was attraction to unshaded unpolarized lights, we conclude that mitigating and eliminating sources of unpolarized artificial night lighting will have a greater benefit in immunizing the effect of light pollution driven traps on these taxa than efforts attempting to minimize artificial polarizers. In fact, our results indicate that shading night lighting can reduce the biomass of both terrestrial and aquatic insects attracted to artificial light sources by approximately 75%, and will likely have benefits for other species negatively impacted by light pollution (Longcore and Rich 2004; Hölker et al. 2010). More broadly speaking, our research is concerning in that they suggest a single type of ecological novelty has the potential to create ecological traps for a broad range of species, but also heartening in that conservation practitioners may efficiently target their efforts on a focused set of interventions to benefit a diverse range of species.

SUPPLEMENTARY MATERIAL

Supplementary data are available at Behavioral Ecology online.

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