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Eristalis tenax Movement Behavior in Response to Light, Temperature, and Food

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ERISTALIS TENAX MOVEMENT BEHAVIOR IN RESPONSE TO LIGHT, TEMPERATURE, AND FOOD

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Drone flies, *Eristalis tenax* (Diptera: Syrphidae), are important generalist pollinators and visit flowers globally that range widely in color. The flies' photoreceptors allow them to sense light wavelengths between 300-600 nm and *E. tenax* exhibit a positive phototactic response. To understand the effects of light on *E. tenax* movement, we conducted two-choice behavioral tests to determine their phototactic response to different wavelengths of light across the spectrum (ultraviolet to red light, plus full spectrum white light). The drone flies moved most and quickest toward sunlight, with almost twice the percentage of flies moving toward sunlight than toward black and purple light (short wavelength sources), which elicited the second strongest phototactic responses. *Eristalis tenax* moved minimally toward green and red light sources. When increasing air temperature by 6°C, the percent of *E. tenax* moving toward fluorescent white light increased by a factor of four. They also moved toward a food source in light but not dark conditions. Our findings may be useful for managing *E. tenax* populations in the lab or for increasing crop pollination.

***Keywords*:** *Eristalis tenax*, drone fly, hoverfly, light response, phototaxis, wavelengths

INTRODUCTION

More than 105 crops grown globally are aided by insect pollinators, and non-bee pollinators contribute to ~US$1.2 billion in production (Rader et al. 2020). Flies (Diptera) are often the second major order contributing to pollination after bees (Hymenoptera) (Larson et al. 2001; Klein et al. 2007; Rader et al. 2020) with Syrphid flies (Syrphidae) noted as one of the most important non-bee pollinator families (Larson et al. 2001; Doyle et al. 2020; Rader et al. 2020). Because bee populations are in decline (IPBES 2016; LeBuhn and Luna 2021), non-bee pollinators such as Syrphid flies may be even more important for future pollination services. *Eristalis tenax* (Diptera: Syrphidae), drone flies, are recognized as important contributors to pollination globally (Klein et al. 2007; Howlett et al. 2013; Stavert et al. 2018; Rader et al. 2020) and are similar to honeybees (*Apis mellifera*) in size (Buckton 1895, p. 8) and pollination behaviors (Golding et al. 2001; Rader et al. 2009; Chisausky et al. 2020; Broussard et al. 2022). *Eristalis tenax* are generalist pollinators and use a wide range of plants throughout the year (Irvin et al. 1999). In agricultural areas, *E. tenax* increases pollination percentage (Stavert et al. 2018) and percent seed set by plants (Jarlan et al. 1997; Perez-Banon et al. 2007). Living on every continent except Antarctica (Global Biodiversity Information Facility 2023) and in environments from islands (Pérez-Bañón et al. 2007) to mountains (Gomez and Zamora 1999), *E. tenax* encounter a wide variety of plant species with variable flower shapes, sizes and colors.

Researchers have found *E. tenax* on flowers of many different colors including white, red, pink, yellow, green, blue, and purple (Haslett 1989; de Buck 1990; Zoller et al. 2002;

Nordström et al. 2017; An et al. 2018; Neimann et al. 2018). De Buck (1990) observed *E. tenax* on ~150 plant species in the field, ~73% categorized as having white-yellow-green flowers and 27% with red-blue. Haslett (1989) found *E. tenax* selecting blue and red flowers more than their proportion in the environment. *Eristalis tenax* are able to discriminate between flower colors (Isle 1949). In simulation studies, *E. tenax* tended to prefer yellow over green or red (An et al. 2018; Lunau et al. 2018; Neimann et al. 2018). They also preferred bright over dark colors and were influenced by ultraviolet (UV) light (An et al. 2018; Neimann et al. 2018).

Color choice is possible because *E. tenax* have photoreceptors that are able to sense between 300-600 nm (Lunau 2014); their receptors are most sensitive to light at 350 nm (UV), 450 nm (blue), and 520 nm (green) (Horridge et al. 1975). A study on houseflies (*Musca*) found no photoreceptor for red wavelengths but suggested visual pigments would allow response to red light (Goldsmith 1965). When presented color stimuli, *E. tenax* were able to discriminate color similarly as bees, were able to distinguish yellow and blue from gray, and landed on yellow more often than blue (Hannah et al. 2019). Experiments assessing a probiscis extension response found *E. tenax* responded positively to green and yellow light (550 nm), had minimal or no response to violet/blue (440 nm), were not affected by red light, and did not extend their proboscis toward UV sources (Lunau and Wacht 1994; Dinkel and Lunau 2001).

Flies show a phototactic response, moving toward or away from a light source (Kevan 1979; Gorostiza et al. 2016; Schmid et al. 2017; Nicholas et al. 2018; Schnaitmann et al. 2020). When placed in a choice chamber, the greatest positive phototactic response by six arctic fly species was toward UV and violet light, with a smaller percentage moving toward blue light; green and yellow light elicited a lesser phototactic response (Kevan 1979). Broad spectrum tests on Hessian flies (*Mayetiola destructor*) found females moved toward green light most and blue second, with low response to amber and red light. Males moved toward green and blue equally and did not respond to amber or red light (Schmid et al. 2017). *Mayetiola destructor* responded more to lower end green light (502-525 nm) and higher intensity light, while responding least to white light (Schmid et al. 2017).

Because *E. tenax* are able to sense across the light spectrum, have been found on flowers from both ends of the light spectrum, and showed proboscis extension responses that differed from flower color choice, we did not hypothesize specific phototactic responses. Response to light can be tied to a number of physiological and behavioral responses that address evolutionary needs such as foraging and reproduction (Kim et al. 2019). For example, *E. tenax* use floral guides to help them find flowers and locate pollen/nectar (Dinkel and Lunau 2001). They also use polarized sky-light to navigate (Wellington and Fitzpatrick 1981). Migratory hoverflies, *Scaeva pyrastri* and *Scaeva selenitica*, use the sun as their primary cue for orientation (Massy et al. 2021). *Drosophila* females move away from UV light when laying eggs but toward UV light when not ready for oviposition (Schnaitmann et al. 2020). To learn more about how light affects movement of *E. tenax*, we conducted phototactic response experiments using two-choice behavioral tests and compared movement toward lights that span the light spectrum (UV to red, plus full spectrum white light). To the best of our knowledge, this is the first two-choice phototactic response experiment conducted on *Eristalis tenax*.

MATERIALS & METHODS

Study species - Eristalis tenax

Eristalis tenax (Diptera: Syrphidae) is a honeybee mimic found worldwide (Buckton 1895, p. 8, 75-76; GBIF 2023), feeds on nectar and pollen (Buckton 1895, p. 26; Gilbert 1985), and has been highlighted as an important pollinator species (Klein et al. 2007; Howlett et al. 2013; Stavert et al. 2018; Rader et al. 2020). Adults are active diurnally (D'Amen et al. 2013; Howlett et al. 2013; Stavert et al. 2018) when temperatures are between 5-30°C, foraging most when temperatures are 18-26°C (Howlett et al. 2013). Under constant temperature (25°C) and light conditions (12:12 Light:Dark), researchers found the average life expectancy for adults was 23.4 days and the maximum 72 days (Campoy et al. 2020). When managing populations by manipulating temperatures to simulate hibernation conditions (cold storage), researchers were able to extend *E. tenax* lifespan to seven months (Thyselius and Nordström 2016). In our study, individuals housed at 22.5±1.4°C lived longer than six months. Sex of adults can be determined by looking at their eyes; male eyes touch one another at the front while female eyes do not touch one another (Irvin et al. 1999).

Larvae collection

Female *E. tenax* lay eggs in wet areas with high nutrient content, often considered polluted, including manure pits on farms (Buckton 1895, p. 75; Altincieck and Vilcinskas 2007; Basley et al. 2018; Hirsch et al. 2020). In the third week of April 2021 and 2022, we collected *E. tenax* larvae from manure pits at a dairy farm in northwest Georgia, U.S.A. We used Nicholas et al. (2018) rearing methods as a guide for rearing larvae to adults.

Adult fly rearing/housing

During the time we conducted our experiments, we housed adult flies in the net insect rearing cages and provided food via cotton balls saturated with spring water, drizzled with organic honey, and sprinkled with natural bee pollen (Nicholas et al. 2018). We found it necessary to change the food approximately every two days to avoid mold. In 2021, we originally housed the adult fly cages in a greenhouse (5 – 13 May). While in the greenhouse, flies were exposed to the outside temperature which measured between 9–28.3°C. Because plant management in the greenhouse included pesticide use, we moved the flies to a laboratory room to avoid potential pesticide overspray into the fly cages during plant care. Inside the laboratory, we placed the flies next to a window to receive natural light. The lab room temperature was under university management and consistently remained between 22.5±1.4°C. In 2022, we housed adult flies in the lab, at the same window location, for the entire study.

Every few days we moved the flies into new clean cages using phototaxis. When moving flies between cages, we connected the sleeve opening of an empty clean cage to a cage containing flies and then covered the occupied cage with a black-out cover, preventing light from entering the cage. We exposed the clean cage to light, typically sunlight when weather permitted us to change cages outside. Flies moved from the

occupied darkened cage to the lit receiving cage. When flies did not move independently, we manually moved them to the clean cage.

Testing E. tenax movement responses to light, food, and temperature

We conducted experiments using *E. tenax* born in two different years, 2021 and 2022. Both years, we separated the adult flies into four cages, to use as replicates for the experimental trials. We created our groups using the phototaxis response described above, attaching cages together and covering one with a black-out cover. Separating flies into groups while using phototaxis resulted in two trial cages with flies that moved first and two trial cages with flies that responded less quickly. We did not observe replicate creation, moving first or not, affecting fly movement response when conducting our experiments. We attempted to get even numbers of flies in each replicate by counting them as they moved from one cage to the next but were not able to get the same number of flies in every cage. In 2021, we used 76 *E. tenax*, in trial cages containing 22, 21, 17, and 16 flies. In 2022, we used 161 *E. tenax* in cages containing 46, 40, 39, and 36 flies. We did not control for sex within each cage. The overall sex ratio for our experimental population was near 50/50 each year.

In 2021, we ran trials from 24 June to 1 September when flies were ~51 to 120 days old. When running our control trials on 1 September 2021, only 38 flies were still alive, limiting our control trials to two replicates (n = 23 and 15 flies) instead of the four replicates we used for the experimental trials. In 2022, we ran trials from 13 May to 12 June when flies were ~13 to 43 days old. Only five flies died across the 2022 trial period, allowing us to use four replicates for all 2022 experimental trials. We conducted all experiments between 0800-1800 hrs.

We assessed *E. tenax* movement under different conditions by connecting the sleeve opening of an *E. tenax* occupied cage to the sleeve opening of an empty net insect cage and counting the number of flies that moved from the starting cage (occupied) to the receiving cage (unoccupied at start).

Phototaxis experiments

To assess *E. tenax* response to light wavelengths across the light spectrum, we covered the starting cage with a black-out cover (covered cage), leaving only the sleeve opening to the receiving cage exposed to control or experimental light (Figure 1). During trials with exposure to light, we counted how many flies moved into the lit receiving cage during 1-minute intervals for 30 minutes. We only counted flies as having moved into the receiving cage if they passed through the connected sleeves and completely into the receiving cage.

We assessed responses across the light spectrum, from ultraviolet to red light, and also full spectrum light (Table I). We conducted all artificial light experiments in rooms with no windows or light exposure other than the experimental lighting. We used LED black, purple, blue, green, red, and full spectrum white light bulbs placed within an aluminum work lamp shade that we sat on the top of the net insect cage (Figure 1). The LED bulbs were 4.5 watts, except the black (7.5 watts) and white light (9 watts) bulbs. We also tested *E. tenax* response to full spectrum fluorescent white light, typical in office and lab ceiling installation, and to sunlight; we conducted the sunlight trials outdoors. Additionally, we ran two control experiments, one where the starting and receiving cages were uncovered

and exposed to fluorescent white light and a second experiment with the starting and receiving cages, and sleeve connection, all covered (zero-light environment). For zero-light trials, we were only able to count the total number of flies that moved when the 30-minute trial ended.

Because light intensity could influence fly behavioral responses (Dinkel and Lunau 2001; Schmid et al. 2017), prior to conducting our experiments we measured the light intensity of our experimental lights using a Vernier light sensor. We took two measurements, one with the light sensor at the edge of the cage aimed into the lit cage and a second measurement from the center of the lit cage with the sensor aimed straight up at the experimental light, providing minimum (edge of the cage) and maximum (aimed at the light) intensity measurements (Table II). Differing experimental light conditions, sunlight, overhead fluorescent, and LED lighting, prevented us from controlling light intensity.

To avoid effects of moving flies from where they were housed to where we conducted the experiment, we waited for the flies to settle back to their typical state of no to low movement before starting the experiment, typically taking 2-5 minutes. In 2021, but not in 2022, we removed food from the occupied cage prior to starting the light experiment. We measured temperature for each trial (Table III).

Figure 1. Our phototaxis experiment setup. The covered cage on the left is occupied with *Eristalis tenax* (starting cage) and the empty cage with experimental lighting on the right is the receiving cage. The two cages are connected via sleeve openings that are clipped together. The pictured experimental environment is white LED light.

Food and temperature experiments

We conducted two additional experiments in 2022 to assess the effects of food and temperature on *E. tenax* movement behavior. To assess the effects of food availability on *E. tenax* movement, we removed the flies' food source from their housing cage one hour prior to conducting a movement trial when we counted individuals moving into a

receiving cage that contained their regular food source. We ran the food experiment under the same two light conditions as our control experiments, one with the starting and receiving cages, and their connecting sleeves, receiving zero light and one with the starting and receiving cages both exposed to fluorescent white light (overhead room lights).

To assess the effects of temperature, we used electric space heaters to raise the temperature in our experimental room from 18.9°C to 25°C prior to bringing flies into the experimental room. We then re-ran the fluorescent white light phototactic experiment (starting cage covered with a black-out cover and receiving cage exposed to fluorescent white overhead lighting).

Analyses

Because cages had different numbers of individuals, we used the percent of individuals that moved as our data for statistical analyses. We used program R (R Core Team 2023) to run non-parametric Kruskal-Wallis tests to assess differences in the percent movement response data, which had unequal variances. To determine differences among experimental light types, we ran pairwise comparisons using Wilcoxon rank sum exact tests with a Benjamini-Hochberg correction, subject to fewer false negatives (Benjamini and Hochberg 1995). We used the aforementioned analyses to address two types of responses 1) the percent of flies that moved to a receiving cage over 30-minutes and 2) the percent of flies that moved to a receiving cage during the first trial minute (quickest response). When assessing movement over the full 30-minutes, we pooled data between years, giving us eight replicates per light type except for White LED and Black LED (four replicates each), which we only tested in 2022. This analysis included variation between years within the analysis. To compare the quickest movement toward experimental light (first trial minute), we analyzed 2021 and 2022 data separately (four replicates for each light source), assessing within year variation. We considered p-values of ≤0.05 statistically significant. We assessed effects of temperature increase on percent of fly movement by determining averages and 95% confidence intervals from the replicates and assessing the confidence intervals. Overlapping 95% confidence intervals indicate no statistical difference.

Table I. Light wavelength (nm) peaks recorded for light sources used during *Eristalis tenax* phototaxis trials conducted in 2021 and 2022. Purple light peaked at two different wavelengths. We measured wavelength using a Vernier emissions spectrometer.

Sunlight	White LED	White Fluorescent	Black LED	Purple LED	Blue LED	Green LED	Red LED
350 to 616 trailed to 817	418 to 698	366 to 708	398	451 and 624	455	521	655

Table II. Light intensity (lux) measured at the cage entrance, minimum, and pointing at the light, maximum, when conducting *Eristalis tenax* phototaxis trials for specific light sources during 2021 and 2022 experimental trials. We did not conduct white light LED or black light LED experiments in 2021.

	Sunlight		White Fluorescent		White LED	
Year	min	max	min	max	min	max
2021	11000	57000	255	419	n/a	n/a
2022	13200	65500	82	234	610	6842

Table II. cont'd

	Black LED		Purple LED		Blue LED		Green LED		Red LED	
Year	min	max	min	max	min	max	min	max	min	max
2021	n/a	n/a	380	6000	393	7530	340	5972	261	1920
2022	217	2489	271	6130	280	6700	254	6300	98	1988

Table III. Temperature (degrees Celsius) during 2021 and 2022 trials assessing *Eristalis tenax* movement toward specific light sources.

Year	Sunlight	White LED	White Fluorescent	Black LED	Purple LED	Blue LED	Green LED	Red LED
2021	23.35	n/a	21.1	n/a	22.2	20.85	20.85	20.85
2022	22.75	19.4	18.9	18.9	19.4	18.9	18.9	18.9

RESULTS

Eristalis tenax moved toward sunlight most (Figure 2; Table IV). Percent movement to sunlit receiving cages was almost double the movement to black light receiving cages, which elicited the second strongest phototactic response (Figure 2). Movement into the shorter frequency wavelength receiving cages (black light and purple) was at least three times greater than movement into the longer frequency receiving cages (green and red; Figures 2 and 3). Response to specific light types was typically apparent in the first minute of the trial (Figure 3). In 2022, flies moved quickest to sunlight (Figure 3; Table VI). Purple elicited the second quickest response compared to white, green, and red light (Figure 3; Table VI). While showing a similar response to light type between years (Figure 3), the pairwise tests were not significant for the first minute responses in 2021 (Table V). Increasing the temperature from 18.9° C to 25° C led to nearly four times greater percentage of *E. tenax* moving to a lit receiving cage ($10.1 \pm 3.3\%$ (95% CI)$_{18.9^{\circ}C\ condition}$ vs. $37.8 \pm 9.8\%$ (95% CI)$_{25^{\circ}C\ condition;}$ fluorescent white light trials).

For the zero-light control experiment, no flies moved in 2021 (n=2 replicates); in 2022, one fly (2.6%) moved in one replicate and zero flies moved in the other three replicates. For the full light exposure control experiment, zero flies moved to a receiving cage in either 2021 (n=2 replicates) or in 2022 (n=4 replicates).

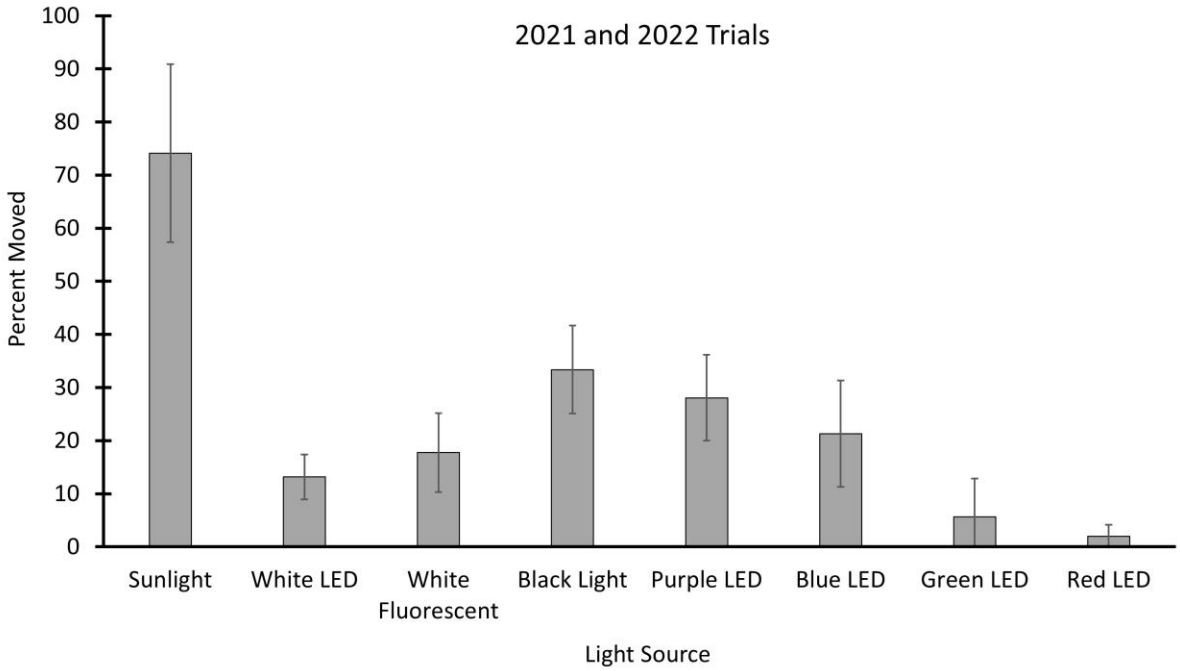

Figure 2. Average percentage of drone flies (*Eristalis tenax*) that moved from a covered starting cage connected to a receiving cage lit with a specific color from the light spectrum during 30-minute trials. We conducted trials with flies reared from larvae captured in two breeding seasons, 2021 and 2022. Error bars represent 95% confidence intervals. Averages and confidence intervals are calculated from eight replicates, 4 in 2021 and 4 in 2022, except white LED and black light (4 replicates) because they were only tested in 2022. Kruskal-Wallis chi-squared = 40.68, df = 7, p-value < 0.001. We present pairwise comparisons in Table IV.

Table IV. Pairwise comparisons using Wilcoxon rank sum exact test with Benjamini and Hochberg corrected p-values corresponding to the average percentage of drone flies (*Eristalis tenax*) that moved from a covered starting cage connected to a receiving cage lit with a specific color from the light spectrum during 30-minute trials shown in Figure 2. Bold numbers represent significant differences.

	Sunlight	White LED	White Fluorescent	Black LED	Purple LED	Blue LED	Green LED
White LED	**0.01**						
White Fluor	**<0.01**	0.76					
Black LED	**0.03**	**0.04**	**0.04**				
Purple LED	**<0.01**	**0.04**	0.15	0.34			
Blue LED	**<0.01**	0.61	0.88	0.27	0.34		
Green LED	**<0.01**	0.07	**0.02**	**0.02**	**0.02**	**0.02**	
Red LED	**<0.01**	**0.02**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.61

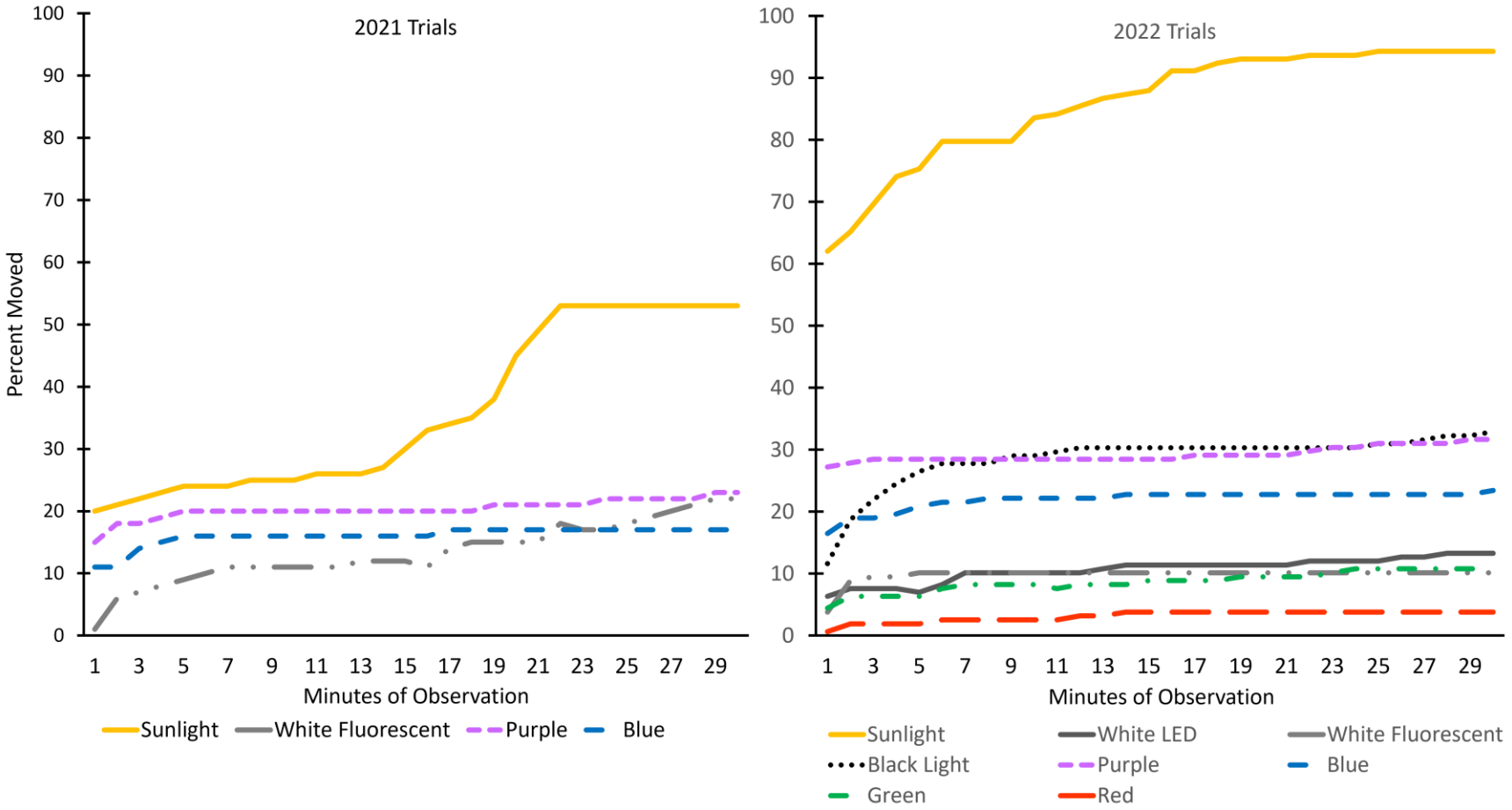

Figure 3. Cumulative percentage of drone flies (*Eristalis tenax*) from four replicates in each 2021 and 2022 that moved from a covered starting cage connected to a receiving cage lit with a specific color from the light spectrum during 30-minute trials. We conducted trials with flies reared in two breeding seasons, 2021 and 2022. In 2021, no flies moved toward receiving cages lit with green or red light. In 2022, we added white LED and black light trials. Percent response in the first minute (quickest response) differed among experimental light types - 2021: Kruskal-Wallis chi-squared = 16.46, df = 5, p-value < 0.01; 2022: Kruskal-Wallis chi-squared = 25.45, df = 7, p-value < 0.001. We present pairwise comparisons in Tables V and VI.

Table V. Pairwise comparisons using Wilcoxon rank sum exact test with Benjamini and Hochberg corrected p-values corresponding to the percentage of drone flies (*Eristalis tenax*) that moved from a covered starting cage connected to a receiving cage lit with a specific color from the light spectrum during the first minute of 30-minute trials in 2021. No flies moved to a receiving cage during the 2021 red and green LED light trials.

	Sunlight	White Fluorescent	Purple LED	Blue LED	Green LED
White Fluor	0.09				
Purple LED	0.86	0.10			
Blue LED	0.74	0.19	0.73		
Green LED	0.09	0.58	0.09	0.12	
Red LED	0.09	0.58	0.09	0.12	

Table VI. Pairwise comparisons using Wilcoxon rank sum exact test with Benjamini and Hochberg corrected p-values corresponding to the percentage of drone flies (*Eristalis tenax*) that moved from a covered starting cage connected to a receiving cage lit with a specific color from the light spectrum during the first minute of 30-minute trials in 2022. Bold numbers represent significant differences.

	Sunlight	White LED	White Fluorescent	Black LED	Purple LED	Blue LED	Green LED
White LED	**0.05**						
White Fluor	**0.05**	0.41					
Black LED	**0.05**	0.30	**0.05**				
Purple LED	**0.05**	**0.05**	**0.05**	0.17			
Blue LED	**0.05**	0.13	**0.05**	0.77	0.30		
Green LED	**0.05**	0.38	0.77	0.17	0.07	0.20	
Red LED	**0.05**	**0.05**	0.17	**0.05**	**0.05**	**0.05**	0.33

When assessing *E. tenax* response to a food source in 2022, no flies moved to a receiving cage containing food when there was zero light available, even when extending the experimental time to 60-minutes. When the starting and receiving cages were both exposed to fluorescent white light for 30-minutes, no flies moved in two replicates; 4.9% and 11.4% moved to receiving cages with food in the other two replicates. After 60 minutes, flies had moved to a receiving cage containing food in three of the four replicates (7.7%, 28.6%, and 29.3% moved).

DISCUSSION

We studied phototactic responses by *E. tenax,* a pollinating fly species, to better understand the behavior of these flies relative to light in their environment. When exposed to a variety of wavelengths across the light spectrum, *E. tenax* moved in different percentages and at different rates across the spectrum; the highest percentage moved

toward sunlight and shorter light frequencies, black, purple, and blue (Figures 2 and 3). We observed higher percentages of *E. tenax* moving when we elevated room temperature. Additionally, *E. tenax* moved toward a food source when light was present but not when light was absent.

Eristalis tenax response to different wavelengths of light

Our control experiments, either zero-light or fluorescent white light, resulted in flies not changing cages (exception, one fly moved during a zero-light trial). When provided an opportunity to move from a covered to a lit cage, *E. tenax* moved most when exposed to sunlight; an average of 75% of flies moved to a sunlit cage (Figure 2). The next highest percentage of flies moved into receiving cages lit with shorter light wavelengths that were in or near the UV spectrum (black light and purple, ~30%; Figure 2). Trials in 2021 and 2022 had similar results (Figure 3). Response to sunlight produced the highest percentage of movement by the flies in both years, with most flies having moved to the lit receiving cage by minute 23-25 of a 30-minute trial (Figure 3). For all light wavelength experiments other than sunlight, most movement occurred during the first 5 minutes of the 30-minute trials (Figure 3). Some flies moving and others not suggests some *E. tenax* have a greater phototactic response than others. Exploring morphological and physiological correlates to *E. tenax* phototactic response may give us insight into ecological adaptations for individuals who responded more or less to light stimuli. *Eristalis tenax* responded least to red light, only around 3% moved into a lit receiving cage (Figures 2 and 3). This corresponds with other research that found *E. tenax* responded less to green and red light (An et al. 2018; Lunau et al. 2018; Neimann et al. 2018) and that *E. tenax*'s visual spectrum is 300-600 nm (Lunau 2014); our red light wavelength peak was at 655 nm (Table I).

There were some notable differences in results between the two study years. In 2022, a higher percentage of flies moved toward sunlight than in 2021 (Figure 3). One difference between the 2021 and 2022 sunlight trials was that it was partly cloudy in 2021 and was sunny in 2022, resulting in five times greater light intensity during the 2022 sunlight trials (Table II). Another difference was that in 2021, flies exposed to fluorescent white light continued to move during the 30-minute trial resulting in ~20 percent moving to the lit receiving cage, whereas in 2022 no flies moved after the first 5 minutes of the trial and only 10% of flies moved into receiving cages lit by fluorescent white light (Figure 3). One explanation for continued movement in 2021 is that the experimental room was two degrees warmer (Table III), which may have made the flies more active, as seen in our temperature experiment. Another difference between the years was the flies' response to green and red light. In 2021, no flies moved toward green or red light while in 2022 a low percentage moved to green and red lit receiving cages (Figure 3). One potential explanation for a higher percentage of movement in 2022 (Figure 3) is that the density of flies in the 2022 trial cages was higher. Effects of density on movement would be interesting to assess in future experiments. Another potential explanation is that the flies were younger when we conducted the experiments in 2022. In both 2021 and 2022, we captured larvae in the third week of April. In 2022, we completed all the experiments between 13 May to 12 June when the flies were ~13 to 43 days old. In 2021, we started trials on 24 June and completed the control trials on 1 September; the flies would have been about 3 times older in 2021 (~51 to 120 days old) when we conducted the

experiments, well past the average 23 day lifespan for *E. tenax* raised under constant temperature (Campoy et al. 2020). Older flies tend to be less active (Thyselius and Nordström 2016; JDL personal observation). For an *E. tenax* population that lived seven months and were reared using cold storage, the highest activity was when the flies were one to two months old; their activity decreased during months three to seven (Thyselius and Nordström 2016). Our 2021 flies were in the three to four months old range, potentially when their activity was decreasing. A phototaxis study on *Drosophila* found individuals with damaged wings decreased their phototactic response (Gorostiza et al. 2016). We noticed some wing deterioration in our oldest flies, which may also have contributed to the lower response percentage in 2021. While the difference in fly age in 2021 and 2022 may have accounted for percent movement differing between years, the relative movement toward specific wavelengths remained consistent (Figure 3) suggesting age may affect movement rate but not response to wavelength. Responding consistently to specific light wavelengths throughout the lifetime would be adaptive if phototaxis is correlated to foraging.

Light intensity has mixed effects on E. tenax phototactic response

Previous research found *E. tenax* moving toward higher intensity light (Dinkel and Lunau 2001) and preferring brighter colored flowers (An et al. 2018; Neimann et al. 2018). We observed *E. tenax* exhibiting more flying behavior when exposed to sunlight (personal observations). In 2022, when sunlight intensity was five times greater than during our 2021 trials (Table II), almost all of the flies moved to the sunlight cage versus 50% in 2021 (Figure 3). The temperature for each sunlight experiment was within 0.6°C of one another, the higher temperature in 2021 (Table III). Increasing temperature corresponded to increased movement in our temperature experiment. However, during the cooler sunlight trial in 2022, twice the percentage of *E. tenax* moved than during the 2021 sunlight trial (Figure 3). In 2022, flies responded more quickly as well, steadily moving to the sunlit cage through the 22-minute mark when 94% of the flies had moved to the lit receiving cage. In the 2021 trials, 27% moved during the first 15 minutes and 26% more moved between minutes 15-22 (Figure 3), potentially corresponding to when there was more or less cloud cover during the experiment. We cannot discount other factors that may have influenced this result such as fly age, or environmental conditions such as humidity or wind.

While sunlight intensity seemed to affect *E. tenax's* phototactic response, we did not see light intensity affecting movement during our artificial light experiments. In our artificial light experiments, flies moved most toward black light (Figure 2). Black light had about one-third the light intensity of purple, blue, white LED, and green lights (Table II). However, flies moved significantly less to green and LED white light (Figure 2) even though their intensities were ~3 times greater than that of black light (Table II). Fluorescent white light had the lowest intensity (Table II). Even though fluorescent white light was around 22 times less intense than blue light (Table II), both light experiments had similar percentages of fly phototactic response (Figure 2). When considering artificial light intensity, our movement results suggest that light wavelength may be more important than light intensity relative to *E. tenax* movement response. Future research looking at the interaction of light wavelengths and intensity under controlled

environments could add more to our understanding and provide insight into fly movement under different light conditions in nature.

Eristalis tenax phototactic response increased with increased temperature

The temperatures we used during our experiments (19-25°C) fall within the temperature range researchers observed *E. tenax* foraging most actively in nature (18-26°C; Howlett et al. 2013). While within a natural foraging temperature range, heating the trial room 6°C increased movement almost four times (10.1 ± 3.3% $_{18.9^{\circ}C\ condition}$ vs. 37.8 ± 9.8% (95% CI)$_{25^{\circ}C\ condition;}$ fluorescent white light trials). The phototactic response to fluorescent white light in a heated room (~38% moved) was more than the percentage that moved during our black and purple light experiments under the typical room temperature conditions (~32%). This result is noteworthy because the flies' phototactic response to black and purple light was second only to sunlight (Figure 2), yet a higher percentage of flies moved under white fluorescent light when we raised the temperature 6°C. Temperature, therefore, appears to play a role in *E. tenax* movement behavior. In our experiments, flies moved more at the higher end of their active foraging temperature (25°C vs. 19°C). *E. tenax* forage less when temperatures are 30°C or greater (Jarlan et al. 1997; Howlett et al. 2013). Perhaps 25°C may be a "Goldilocks temperature" relative to efficient movement, not too hot and not too cold. Research into foraging efficiency across a range of temperatures would help determine temperatures at which *E. tenax* forage optimally.

Given the change in movement we observed from our temperature study, could temperature have affected our light trial results? When conducting our sunlight trials, the outdoor temperature was about 3°C higher than within the trial rooms for both 2021 and 2022 trials (Table III). The higher temperature outside may have contributed to a higher percentage of flies moving during the sunlight trials than the artificial light trials. Conversely, the trial room we used in 2022 was about 2°C cooler than the one we used in 2021 (Table II), but a higher percentage of flies moved in 2022 than in 2021 (Figure 3). Perhaps phototactic response is not affected by a 2-4°C temperature difference, or, fly age affected behavior more than temperature.

Eristalis tenax move toward food in light but not in dark environments

When conducting our food experimental trials, we used the same light conditions as in our control experiments, 1) the starting and receiving cages in a zero-light environment and 2) the starting and receiving cages within a fluorescent white light environment. No flies moved to the receiving cage with food when in the zero-light environment, comparable to movement during the zero-light control trials. While no flies moved in the light experiment control trials, during the food experiment, *E. tenax* moved to receiving cages (with food) when in the fluorescent white light environment. An average of 4% of flies moved into cages with food during the first 30 minutes, suggesting the flies were attracted to the food. These food trials resulted in a higher percentage of flies moving than during green or red light phototaxis trials (Figure 2), indicating food elicits a stronger positive response than some light wavelengths. When continuing the in-light food experiment for an additional 30 minutes (60 minutes total), an average of 16.5 % of the flies moved to cages with food. Sixteen and a half percent moving to a receiving cage is similar to the percentage of flies that moved during the white light phototaxis trials, which

had no food in the receiving cage (Figure 2). Moving to food when there is light corresponds to *E. tenax* being diurnal (D'Amen et al. 2013; Thyselius and Nordström 2016) and foraging most between 1000-1600 hrs (Stavert et al. 2018). We do not know whether the flies in our experiment detected food visually or chemically, as the food source provided could have been visible through the net cage. We also did not control for local enhancement (Thorpe 1963, p. 134), where individuals are attracted to a location with other individuals. Conducting additional experiments would increase our understanding of how *E. tenax* locate food sources.

Research implications

In our study, *E. tenax*'s strongest phototactic response was to sunlight and then shorter wavelength LED light, 398-455 nm (Figures 2 and 3, Table I). Why do *E. tenax* have a positive phototactic response? There are numerous ways organisms can use light to improve survival and reproduction (Kim et al. 2019). For example, flowers absorb and reflect UV in a way that create patterns that insects can see that humans do not (Primack 1982). *Eristalis tenax* exhibit innate responses for landing on specific flower colors (An et al. 2018; Neiman et al. 2018) and proboscis extension (Lunau et al. 2018), suggesting *E. tenax* use light wavelength for foraging cues. A positive phototaxis response for short wavelength light may help the flies detect and navigate to flowers that reflect UV light. After detecting the flower, nectar guides that absorb UV light help *E. tenax* locate a food source (Lunau and Wacht 1994; Dinkel and Lunau 2001; Neimann et al. 2018). Some flowers change colors when the nectaries are empty, providing additional cues for pollinators (Weiss 1991; Furukawa et al. 2022). Because *E. tenax* are active during light hours (Thyselius and Nordström 2016), sunlight may provide cues for diurnal activities (D'Amen et al. 2013; Howlett et al. 2013; Stavert et al. 2018) and orientation/navigation (Wellington and Fitzpatrick 1981; Massy et al. 2021). We observed more hovering when sun was shining on the cages, similar to research noting hovering in sunshine patches more than in shade (Dyakova et al. 2019). Because female *E. tenax* oviposit near water (Buckton 1895, p. 26; Altinciecek and Vilcinskas 2007; Basley et al. 2018; Hirsch et al. 2020), polarized sunlight reflecting off of water may help them locate appropriate habitat. A phototactic response could play a role in each of these examples.

When working with *E. tenax* in a lab setting, it appears that researchers could minimize disturbance by using red light when prepping cages for experiments. If not able to use sunlight for moving flies between cages, we recommend using black or purple LED lights. Why white light, LED or fluorescent, did not elicit as strong of phototactic response as sunlight (Figures 2 and 3) is unclear. There was a tendency for a higher percentage of flies to move toward fluorescent than LED white light, even though fluorescent light had the lowest light intensity (Table II). Fluorescent white light did peak further in the UV range than the white LED bulbs (Table I), which may explain the increased phototactic response to fluorescent white light. To determine which UV range *E. tenax* move toward most, it would be useful to conduct additional experiments assessing effects of smaller wavelength intervals in the UV range.

With the decline of bees and many species of pollinators (IPBES 2016; LeBuhn and Luna 2021), the importance of all pollinator species is likely to be more critical in the future. *Eristalis tenax* are currently important global pollinators (Klein et al. 2007; Howlett et al. 2013; Stavert et al. 2018; Rader et al. 2020) and visit many varieties of

species with flower colors that span the light spectrum (Haslett 1989; de Buck 1990; Zoller et al. 2002; Nordström et al. 2017; An et al. 2018; Neimann et al. 2018). They also disperse widely (Francuski et al. 2013), move relatively far between plants when foraging (Gomez and Zamora 1999), and increase pollination in agricultural settings (Stavert et al. 2018). Farmers may be able to take advantage of *E. tenax*'s generalist pollination and dispersal behavior by trying to attract them to their fields. One suggestion for attracting and keeping flies near crops needing pollination is to leave uncut strips within the crops that contain flowering plants (Rader et al. 2020). Using a variety of species that flower at different times throughout the year would help keep *E. tenax* and other pollinators in the area of crops. Farmers might also try attracting *E. tenax* using a supernormal stimulus (Tinbergen and Perdeck 1950) by placing large simulated flowers that reflect UV light around or within their crops. Coupling supernormal flowers with pollinator strips may attract and keep pollinators in the area and increase the chance of crop pollination. Researchers found increasing the number of *E. tenax* resulted in greater crop production (Jarlan et al. 1997; Pérez-Bañón et al. 2017; Liu et al. 2020). Taking advantage of *E. tenax* and other pollinators' response to light cues may be one way to address the decline in bees and help maintain pollinator ecological services.

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