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The Effect of Light Intensity on Wolf Spider Foraging

A Thesis Presented

by

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To the Keck Science Department

of

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The Effect of Light Intensity on Wolf Spider Foraging

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Light is of primary importance to most living organisms and most of the Earth's natural processes. However, with rapidly expanding urbanization, humans have substantially impacted light metrics through the increase of artificial light. Artificial light pollution has been found to have a variety of behavioral and physiological effects on different organisms. However, less is understood about how light impacts community-scale interactions between different trophic levels. Here, we examined the influence of light exposure on nocturnal wolf spider (*Schizocosa myccocki*) foraging and interaction with red runner cockroach prey (*Blatta lateralis*). Of equal interest as the study developed became the relationship between predator body size and predation success. Through automated image-based tracking of predator-prey interactions, we quantified various aspects of foraging performance. In our analysis, we sought to differentiate between the effects of predator and prey size variance and the effects of light treatment. We found that, when foraging under brighter artificial light conditions, spiders saw a stunted latency to first movement but increased detection distance of prey. Body mass of spider and predator-prey body size ratio also played a role in predicting foraging behavior and success. Smaller body-size ratio was found to be correlated with a greater average velocity throughout the trial, and less likelihood of capture success. Understanding both the stunting and exploitative effects of artificial light on nocturnal foragers builds an important bridge between the effects of light pollution on individual organisms and larger, community-level effects between species and their interactions.

INTRODUCTION:

Anthropogenic changes to light levels have become an increasingly prevalent concern in ecology and biology, with light pollution now impacting nearly half of the United States land cover (Davies et al. 2013, Falchi et al. 2016). Artificial light has led to a wide variety of ecological disturbances in organisms, ranging from mammals to crustaceans to birds. Studies have confirmed adverse changes in behavior, migration patterns, prey choice, sleep patterns, and nest siting due to exposure to artificial light (Fraser & Metcalfe, 1997; Gal et al., 1999; Navara & Nelson, 2007; Stone et al., 2009; Titulaer et al., 2013; Raap et al., 2015; Manfrin et al., 2018). Understanding light pollution's ecological effects is increasingly important at the organismal level.

Ecological changes due to light are also present at the community level. In opposition to these disturbances, some predators have been able to exploit artificial light at night (ALAN) in interspecific interactions for their own foraging benefits. Bats spend more time around street lights, consuming the insects that are attracted to these lights (Rydell, 1992). Fish experienced altered prey assemblages, but much higher rates of predation under artificially lit conditions that nearly resembled daytime predation levels (Bolton et al., 2017). Studies focusing on the trophic impacts of light on arachnids are relatively uncommon, however, exploitation of light for increased predation has been a proven effect of ALAN. Nocturnal web-weaving spiders captured significantly more prey at webs that were placed near LED lights, but diurnal spiders are also able to reap predation benefits from ALAN (Frank, 2009; Willmott et al., 2019).

The ecological effects of light intensity vary widely, demonstrating that organisms respond differently to anthropogenic changes, whether through altered individual behavior or interspecific interactions. As urbanization increases, it is increasingly crucial to garner a picture of the varied impacts that artificial light continues to have on community interactions.

Wolf spiders (Family Lycosidae, Figure 1) are nocturnal, non-web-building, generalist arthropods that typically employ a sit-and-wait predation strategy (Wagner & Wise, 1997). Wolf spiders provide important ecosystem services to grassland and wetland habitats, including pest control (Rendon et al., 2018). Although there is variation between individual species, wolf spiders often depend upon vision for hunting, locomotion, and courtship (Clemente et al., 2010). Wolf spiders are visually sensitive to prey movement, independent of vibratory stimulus, as they were responsive to videos of cricket movement when actual crickets were not present (Persons & Uetz, 1997). It was therefore hypothesized that wolf spiders will be sensitive to changes in light intensity in their interactions with prey because visual perception is an important part of sensing modality in foraging.



Figure 1: Model predator *Schizocosa myczkoeki*

Besides environmental factors, there are many physical traits that affect a feeding relationship. Optimal foraging theory often assumes that foraging behavior is constrained by certain fixed morphological and physical traits (Pyke 1984). The nature of these static traits often leads to one of the largest determinants in predation success: the difference in size of the predator and its prey, or the predator-prey body-size ratio (Nakazawa et al., 2013). Predators are limited in the size range of prey they can attack, as much larger prey

cannot be subdued, whereas smaller prey would not return enough energy on the energetic investment of predation (Radloff & Du Toit, 2004; Van de Walle & Logghe, 2023). Although this ratio can vary significantly between different habitat types, invertebrate predators typically demonstrate a lower body-size ratio than vertebrates (Brose et al., 2006). How much body-size ratio impacts predation outcome also depends on the predator's predation strategy, whether that be active hunting or sit-and-wait predation (Petchey et al., 2008).

While a specific focus on spiders in body-size ratio research thus far is rare, body-size ratios have been proven important in predicting the trophic interactions of arthropods (Van de Walle & Logghe, 2023). It is often difficult to measure specific body-size ratios of each predation event during observational or *in situ* studies, due to the constraints of trying to predict or interrupt an interaction once it has already begun (Nakazawa et al., 2013). Our study, therefore, was designed to determine the components of this value before each foraging trial took place. This was done to elucidate differences between how light impacts foraging and how predator-prey body-size ratios impact foraging.

Quantifying animal behavior is a vital part of ecological research. Automated image-based tracking is a helpful method when quantifying movement from a recorded experimental video. Noldus EthoVision XT allows for the examination of encounters between multiple subjects, which can easily provide significant information about individual behavior along with interactions (Noldus et al., 2001).

In the present study, foraging performance of a light-sensitive nocturnal predator under varying light conditions was quantified through a behavioral analysis. Through analysis of experimental behavioral trials, it was confirmed that brighter lux treatment significantly lengthened the latency to first movement, along with the detection distance. A lower predator-prey body-size ratio, along with lower spider mass, led to shorter latency to first movement and a greater average velocity throughout the trial. Through a closer examination of these results, the impacts of light disruption on a nocturnal predator, predator-prey body-size ratio cut-offs, and wider impacts within a food web are discussed.

METHODS:

1. Collection and Husbandry

214 *Schizocosa myccocki* wolf spiders were collected from a forested wetland in Alton, Illinois (38°57'N 90°16'W) through headlamp collection. Spiders were collected in July 2023 and housed individually for two days after collection at the National Great Rivers Research and Education Center. After collection, spiders were stored in individual plastic cups with small holes in the lid for a standard 36 hours at 23°C and starved until trials. Ambient light conditions during storage were simulated, with spiders being exposed to 12 hours of light and 12 hours of dark.

12 hours after collection, spiders were measured for body size. Measurements of mass in g were taken using an electronic balance. Spiders were photographed against a gridded background to determine abdomen and carapace widths. Measurements of body size metrics were taken in ImageJ.

Red runner cockroach (*Blatta lateralis*, Figure 2) nymphs were purchased and stored at ambient temperature of 23°C and a 12-hour alternating light-dark cycle. They were maintained with damp paper towels, which were changed every 3 days, and food flakes that were distributed throughout the enclosure.



Figure 2: Model prey *Blatta lateralis*

Cockroach masses in g were taken on an electronic balance before the cockroach entered the arena for each trial.

2. Experimental Trials

Light conditions were set at 0, 0.01, 1, and 1000 Lux. These conditions were selected to simulate values across the spectrum of visual light for wolf spiders. 1000 lux was selected as near-daylight conditions, while 1 lux and 0.01 lux simulated moonlight and cloudy moonlight, respectively. Treatments were chosen to simulate a spectrum of values rather than specific values that may be experienced environmentally. A linear behavioral response was expected, and a wide range of values would therefore allow guided assumptions about behavioral responses to be made about conditions that were not tested but still represented within this scale of values. Lighting was created by hanging a metallic hooded overhead lamp above each arena. Specific intensities were simulated by layering filter paper over each light and measured using an Extech SDL400 Light Meter.

Circular plastic arenas with a radius of 13.25 cm were coated in a layer of fluon to keep insects inside and placed within climate chambers (Figure 3). Chambers were utilized to control for temperature (23°C) and humidity (65%), with lux intensity being the only variable factor between each chamber. Arenas were placed atop glass sheets that sat on infrared light squares so that videos of trials could be captured using infrared light at 0 Lux. Between trials, a thin paper was replaced beneath the arena to control for possible pheromone defenses emitted by cockroaches and silk or egg sacs left by the spiders.

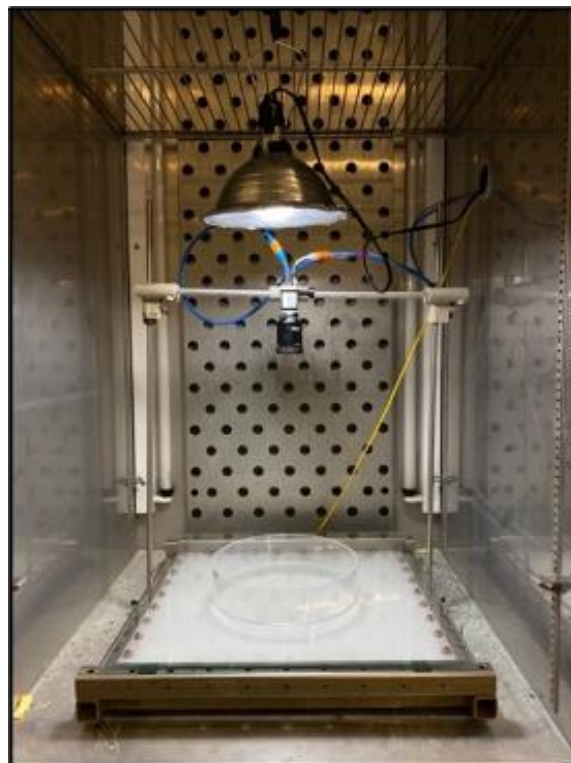


Figure 3: Experimental trial design, including light with designated lux intensity from overhead lamp, camera, and arena

Spiders and cockroaches were introduced to the arena simultaneously and given a 10-minute acclimation period. The two subjects were kept separate during acclimation. The cockroach had a range of the outer area of the arena, while the spider was housed in the center of the arena within a circular piece of plastic piping in a radius of 5.5 cm. After 10 minutes of acclimation, the plastic piping was lifted so the organisms could encounter one another. Trials were concluded when the cockroach had been sufficiently captured, which was defined as being subdued by the spider for more than 5 seconds, or after 10 minutes had passed without capture. After the trial, spiders were preserved individually in ethanol.

3. Automated Image-Based Tracking

Videos of the encounters were captured using StreamPix software. To prepare for further analysis, videos were trimmed to the period between the beginning of the trial, or the lifting of the plastic piping, and ended at the capture as defined above. By trimming the videos to the period of interest, the tracking was standardized between videos. Video data was saved with both spatial and temporal resolutions, which allowed for analysis using EthoVision XT tracking



Figure 4: Example movement paths of predator and prey within tracked video

software. Spatial data is detected by separating a darker foreground subject from a lighter background. Once the position of the subject has been detected in one frame, the program then uses the longer image sequence to define the position of each subject between frames and trajectories through time (Figure 4).

Here, automated image-based tracking allowed us to identify variables of predation success to quantify differences between encounters under different light treatments. EthoVision produced the X and

Y coordinates of each subject for every frame of an experimental video. EthoVision was also used to perform simple calculations such as *average velocity* and *total distance moved*, along with creating a graphical representation of each subject's path throughout the trial (Figure 5). EthoVision tracking also provided the *latency to movement* or the time length in seconds between the beginning of the trial and the spider's first movement. The variable *time to capture* was defined as the time length in seconds of the video clip of each trial because clips were trimmed precisely from the beginning of the trial to the final capture.

Trial	Subject	Velocity	Distance moved
		Center-point	Center-point
		Mean cm/s	Total cm
Trial 1	Subject 1	0.4295	8.2076
	Subject 2	0.8749	16.3018
Trial 2	Subject 1	2.0209	14.3830
	Subject 2	2.6558	18.9014
Trial 3	Subject 1	1.4660	53.0462
	Subject 2	0.7795	28.1423
Trial 4	Subject 1	2.1664	620.4662
	Subject 2	3.2127	722.0310

Figure 5: Distance and Time table of variables calculated by EthoVision (Trials 1-4 pictured, Trials 1-202 calculated)

4. Behavioral Analysis

After tracking the subjects' behavior from the beginning of the trial through to capture, a specific behavioral analysis was conducted concerning the attack period. This was defined as the period between when the spider oriented towards the cockroach and when it captured the cockroach. Using EthoVision's output of X and Y coordinates for both subjects, 5 variables were quantified during this analysis:

1. *Detection distance*: how far, in centimeters, are the two subjects from one another when the spider orients towards the cockroach
2. *Attack duration*: The duration of attack, from detection to capture, in seconds
3. *Attack speed*: The average velocity of the spider during the period from detection to capture, in centimeters per second
4. *Number of capture attempts*: How many strikes the spider performed to capture the cockroach
5. *Capture success*: Whether or not the spider captured the cockroach

5. Statistical Analysis

All analyses were performed using RStudio Statistical Software (v6.2, R Core Team 2023). Data were cleaned and sorted into light treatments (packages *dplyr* and *tidyr*, Wickham H. et al., 2023). Exploratory data analysis for associations between response variables was undertaken, but no significant associations were found (package *corrplot*, Wei, T. et al., 2021). Numerical variables were assessed using Box-Cox Method and transformed using the most effective power transformation to fit assumptions of normality and homoscedasticity. Seven linear models were fit to assess statistical differences between lux treatments and continuous behavioral variables. Models accounted for 3 predictors: lux treatment, spider mass, and predator-prey body-size ratio. Lux was treated as a continuous numerical variable because responses were found to be linear. Energetic state was originally included in models but was found to have no significant effect on any response variables and was therefore removed from predictions. All derived p-values were adjusted using the Benjamini-Hochberg Procedure because 13 total tests were performed and adjustments were necessary to control for the false positive discovery rate (p.adjust, package *base*). Fisher's

exact test was performed to assess associations between light treatment and capture success. In examining the impacts of body-size ratio on capture attempts and capture success, generalized linear models were fit. A binomial model was used for modeling capture success.

RESULTS:

Lux exposure

Light treatment was found to have a significant effect on both behavioral and foraging variables. Exposure to higher levels of lux led to a significant increase in the spider's latency to first movement, with the lowest latency to first movement under the 0 lux condition ($F = 23.66$, $p = 0.0001092$). Detection distance was also found to significantly increase under the brightest light condition ($F = 15.08$, $p = 0.002205$). Results of all continuous behavioral variables in response to lux and body-size ratio and spider mass as covariates are displayed in Table 1.

Table 1: Effects of lux on behavioral response variables, with covariates body-size ratio and spider mass included

Behavioral Response by Predictor	F Statistic	Probability	P-adjusted
<i>A. Latency to first movement</i>			
Lux	23.66	5.200×10^{-6}	0.0001092***
Body-size ratio	1.230	0.3200	0.5339
Spider mass	1.023	0.3130	0.5339
<i>B. Time to capture</i>			
Lux	1.988	0.164	0.4305
Body-size ratio	0.05300	0.0272	0.0952
Spider mass	6.466	0.0118	0.04956*
<i>C. Average velocity</i>			
Lux	2.061	0.3199	0.5339
Body-size ratio	11.52	0.0008860	0.006202**
Spider mass	6.994	0.002795	0.0147*
<i>D. Total distance travelled</i>			
Lux	0.1910	0.6200	0.7035
Body-size ratio	0.4600	0.3300	0.5339
Spider mass	0.5130	0.4750	0.6932
<i>E. Detection distance</i>			
Lux	15.08	0.0002100	0.002205**
Body-size ratio	0.4820	0.9053	0.90527
Spider mass	0.4000	0.5281	0.6932
<i>F. Attack duration</i>			
Lux	4.121	0.05230	0.1569
Body-size ratio	0.6710	0.3305	0.5339
Spider mass	0.4020	0.5271	0.6932
<i>E. Attack velocity</i>			
Lux	0.2610	0.6500	0.7035
Body-size ratio	0.2530	0.6700	0.7035
Spider mass	0.1890	0.6650	0.7035

Asterisks indicate significant effects

There were 8 occurrences of no capture under the 1000 lux condition, 6 under the 1 lux and 0.01 lux condition, and 5 occurrences under the 0 lux condition. While there was variation between treatments, there was no significant difference between capture success under each differing light treatment ($df = 3$, $p = 0.88$).

Body size and predation

Both the spider's body size and the predator-prey body-size ratio had effects on spider performance during foraging trials. Spider mass was significantly correlated with time to capture ($F = 6.466$, $p = 0.04956$), with larger spiders taking longer to initially move. Predator-prey body-size ratio yielded further significance over foraging response and outcome. Smaller body-size ratios led to higher average velocities throughout the entire trial ($F = 11.52$, $p = 0.006202$). It was also a significant predictor of capture attempts ($df = 195$, $p = 0.0001600$). Finally, body-size ratio strongly predicted capture success ($z\text{-value} = 3.187$, $p = 0.001440$, Figure 6).

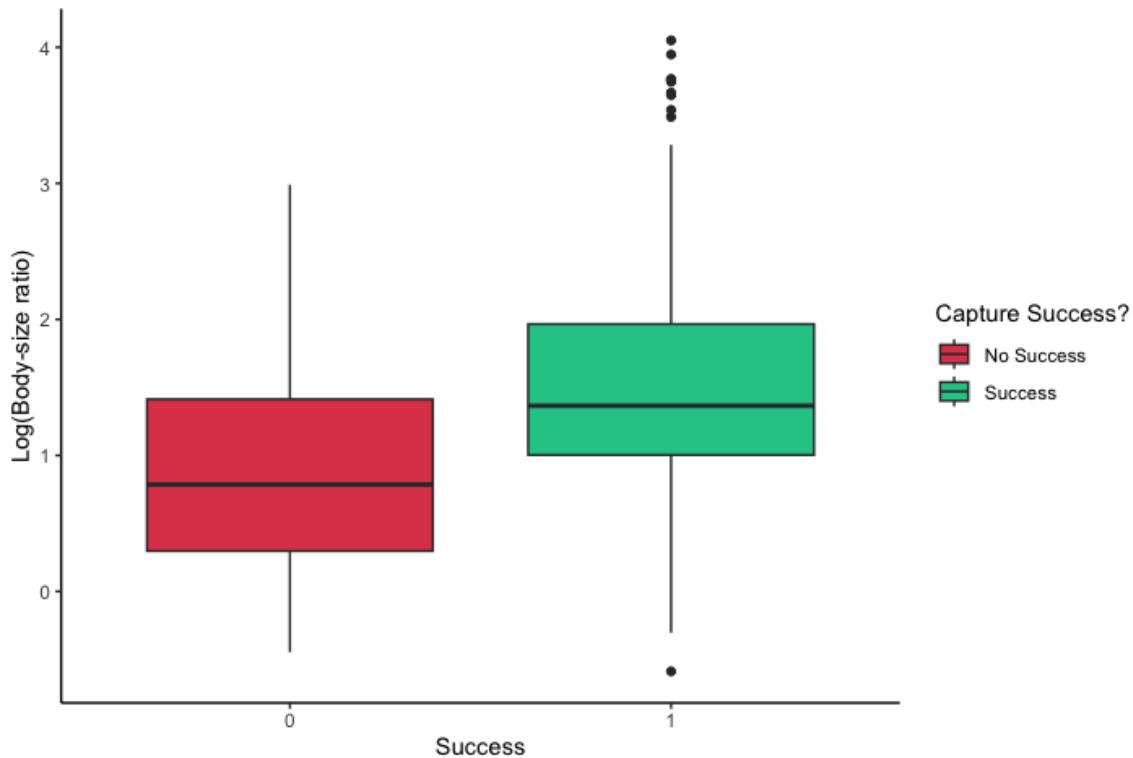


Figure 6: Boxplot of capture success by log body size ratio. Black lines inside boxes indicate medians, lines stretching from boxes indicate 95% confidence intervals, black dots indicate outliers

DISCUSSION

Light

Exposure to greater lux concentrations had clear effects on wolf spider foraging. Spiders under the 1000 lux conditions took the longest to start moving during trials (Figure 7), suggesting that this exposure to bright light may be disrupting their movement or sensing in some way. This provides evidence that the locomotion of nocturnal spiders is lessened under conditions of brighter light. Generally, literature on predation under ALAN points to increased predation under brighter conditions (Rydell, 1992; Frank, 2009; Bolton et al., 2017; Willmott et al., 2019). However, nocturnal wolf spiders are more subject to disruption by ALAN rather than exploitation of the resource.

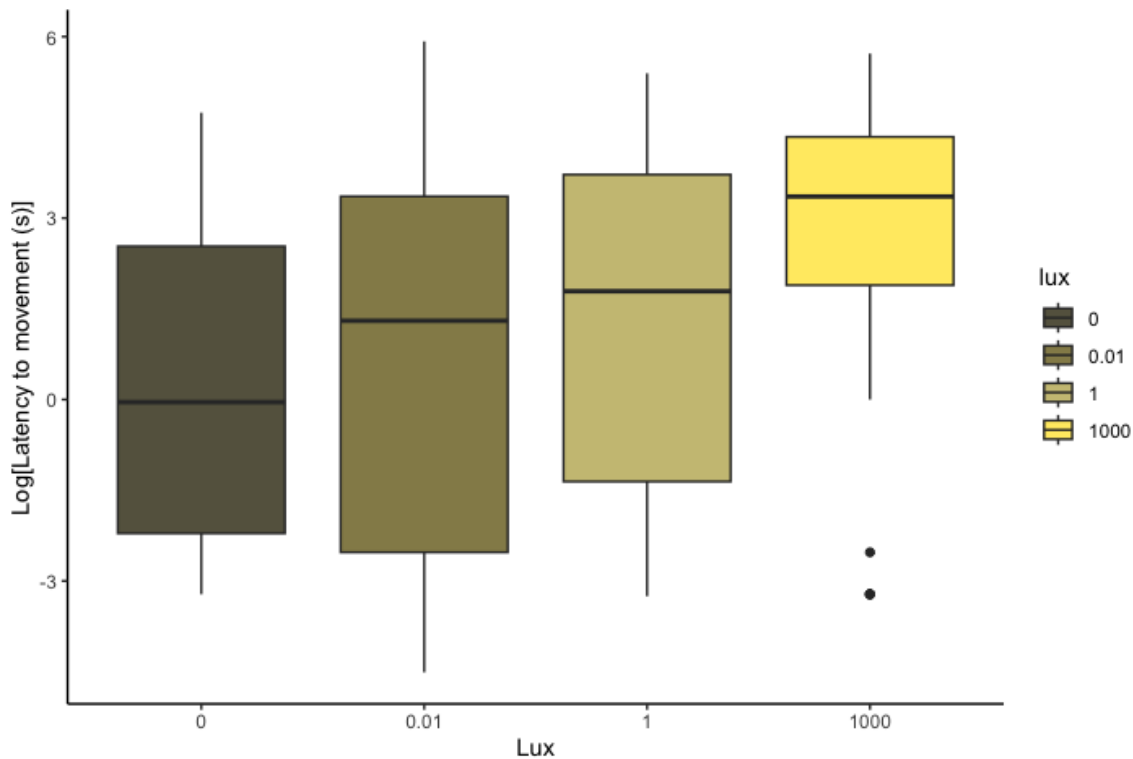


Figure 7: Boxplot of latency to first movement by lux treatment. Black lines within boxes indicate medians, lines extending from boxes indicate 95% confidence intervals, and black dots indicate outliers

Rather than increased foraging, wolf spiders saw decreased behavior under the brightest light condition. It seems that light mainly impacts wolf spiders by disrupting their own behavior rather than the outcome of a predatory interaction. Two recent studies have noted this decreased locomotion under ALAN in aquatic organisms including reef corals and freshwater shredders, but understanding of this effect of artificial light is rapidly expanding (Czarnecka et al., 2022; Mardones et al., 2023).

While our study did not focus on examining any physiological responses to light in wolf spiders, we hypothesize that increased stress could explain longer latency to movement under brighter conditions. To further examine the source of this behavior, it would be interesting to measure stress indicators in wolf spiders, such as Hsp70-positive cell counts, under differing light conditions (Wilczek, 2005). It is confirmed here that ALAN alters the behavior of wolf spiders themselves, which could lead to other negative impacts on their survival, growth, or reproduction because of increased stress. However, it would

take further experimentation to confirm this hypothesis and fully understand the physiological response to ALAN in wolf spiders.

Interestingly, capture success did not differ between significantly light treatments. Prior to the study, we expected more captures under brighter light due to increased reliance on visual sensing. Our work did find increased detection distances demonstrated under increased light (Figure 8, $p = 0.002205$). This implies that wolf spiders, like jumping spiders and other diurnal species, rely on visual detection of prey, which has been confirmed by previous studies of wolf spiders (Persons & Uetz, 1997; Clemente et al. 2010). However, increased visual cues didn't necessarily increase their likelihood of capturing this visually sensed prey. This result implies a multimodality of prey sensing in wolf spiders, and although visual sensing is involved, it is not the main sensory modality that wolf spiders depend on to sense prey. We therefore believe wolf spiders primarily utilize vibratory sensing even in the presence of increased light. Female wolf spiders have been previously noted to be responsive to vibratory cues emitted by male spiders during courtship, and a similar mechanism is likely employed for prey sensing (Wu & Elias, 2013).

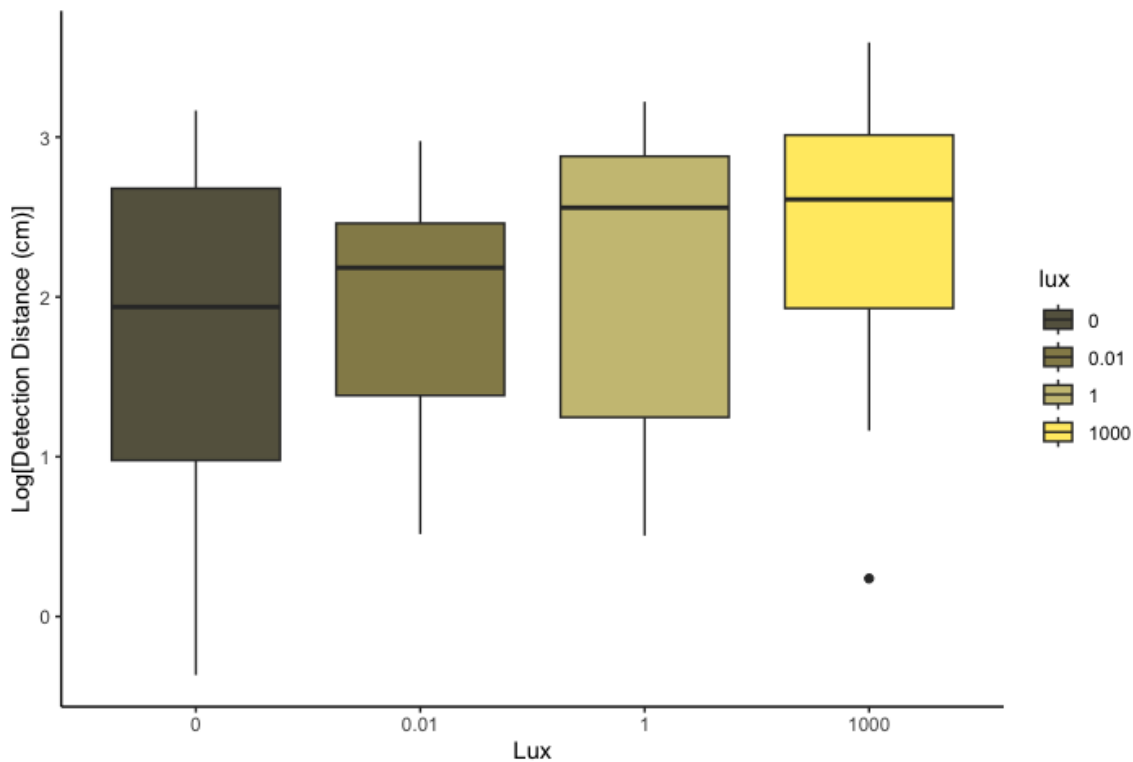


Figure 8: Boxplot of detection distance by lux treatment. Black lines within boxes indicate medians, lines extending from boxes indicate 95% confidence intervals, and black dots indicate outliers

Body size, ratios, and energetic state

This study's dataset represents a wide range of wolf spider body sizes, although all were collected from the same study area. Correlation between a smaller predator-prey body-size ratio and greater average velocity (Figure 9) shows that spiders likely had to spend a greater amount of time in active pursuit when their prey item was larger. Higher average velocities throughout trials with lower body-size ratios provides direct evidence of the energetic trade-off associated with a smaller predator-prey body-size ratio.

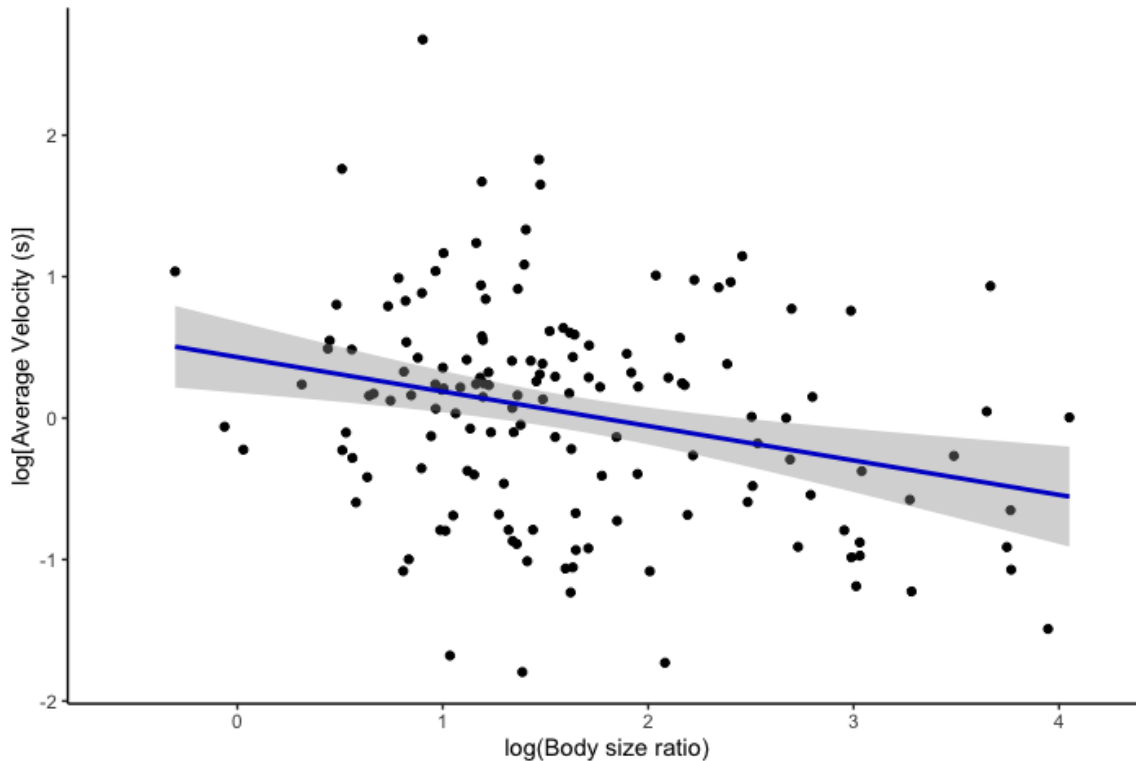


Figure 9: Scatterplot of log predator-prey body-size ratio versus log average velocity throughout trial ($m = -0.2434$, 95% CIs displayed in shaded grey)

Energetic state was found to have no effect on foraging performance. We expected that spiders at a lower energetic state, or with a smaller carapace-to-abdomen ratio, were expected to be more motivated to hunt and capture prey (Lyon et al., 2018). Spiders at a higher energetic state would be less motivated to assert the energy necessary to capture prey. However, the lack of correlation aligns with previous results that found no direct impact of energetic state on wolf spider foraging, rather that the interaction between spider body mass and spider body rotations played a larger role in performance than the energetic state (DeLong et al., 2021). Although not addressed in this study, it would be interesting to further examine whether rotational locomotion is relied on more heavily under certain environmental conditions. Overall, the body-size ratio between predator and prey proved to be a more reliable predictor for foraging outcome than the spider's energetic state.

Wolf spiders were collected between the end of June and the end of July 2023. This period represents a time of significant variation in the life history of wolf spiders (Punzo, 2006). After mating during autumn, females overwinter and produce an egg sac at the end of May to early June. Older females typically die after this egg sac hatches in late June. Throughout July, we overwhelmingly collected newborn and very small wolf spiders, where we had been collecting older and larger female spiders at the same site in June. Although this size variation in predators brought new questions for analysis concerning

predator-prey body-size ratios, it also introduced significant variation and noise to our dataset. If this study were to be repeated, it would be helpful to conduct field collection of spiders during August to standardize body size and life history stage among predators and isolate the question of light even further.

Our study was only able to examine behavioral effects caused by light, but semi-urban organisms are also increasingly disrupted by both chemical and noise pollution along with ALAN (Ellis, 2011). Compounding impacts of these altered environmental conditions is poorly understood, as most studies are only able to examine the disruption caused by one type of pollution (Halfwerk & Slabbekoorn, 2015; McMahon et al., 2017). However, to fully understand wolf spiders in a changing world, examining the interactions between these different types of pollution on behavior and stress is necessary. It is rapidly becoming essential to understand the way anthropogenically modified environmental conditions work separately and interact with one another to disrupt organisms.

CONCLUSION

ALAN has long been understood as a mechanism of increasing predation viability by extending the period of predation for visual predators. Our study, however, confirms that nocturnal, visual wolf spiders showed disrupted locomotion under ALAN conditions. Although increased light allowed for spiders to a greater reliance on visual sensing of prey, this did not necessarily correlate with higher or faster rates of prey capture. Of interest for further studies is a deeper dive into the mechanistic approach that wolf spiders take to foraging, including whether they rely on vibratory sensing or visual sensing of prey under different light conditions. Furthermore, the effects of light on wolf spiders may not be limited to only behavioral effects and an adverse stress response to increased light could be present. Continuing to examine the impact of high light intensity on wolf spider's functioning, whether that be behavioral or physiological, is of high importance to assess the full range of impacts caused by light on nocturnal species.

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