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Sensory Behavioral Ecology of Prey Capture in Spiders

By

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Abstract

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Animals that engage in active predation need to acquire sufficient sensory information to locate, capture, and overtake their prey. Different types of foraging and prey capture behaviors can require specific types of sensory input. The exact sensory requirements for prey capture depend on hunting strategy, prey defensive behavior and morphology, and habitat characteristics. Within spiders there have been several independent evolutionary enlargements and modifications of eyes, allowing for changes in the visual capabilities of the spider. In these spiders, different pairs of eyes can be responsible for different visual tasks. Vision in spiders – and in all animals – is dependent not only on the properties of the viewer but on the environment as well, particularly on the quality of the ambient light. Spider vision exists alongside other senses, such as vibratory and trichobothria senses, that can be used in prey capture. In this dissertation I studied how spiders use different senses in combination to guide prey capture. To do so, I performed lab prey-capture experiments on wild-caught spiders in which I restricted their access to sensory information, through manipulations to the environment or the spider.

In the first chapter, I found that *Habronattus formosus* jumping spiders never catch a prey insect in complete darkness, and that they are slower to capture in dim light conditions. I then tested how *H. formosus* captures prey under a variety of manipulations. By varying light conditions and substrate, I restricted visual and/or vibratory information and measured its effects on hunting behavior of spiders with two types of insect prey. By doing so I characterized how senses are used together or in isolation in prey capture, and how this sensory usage changes with context, such as different prey. I found that *H. formosus* are more likely to capture flies than crickets, and more likely to capture prey under bright light than dim light. I also found that these spiders caught prey more quickly on flexible substrates than on stiff substrates. This was the first study of actual prey capture performance of *Habronattus* in different sensory environments, and the first to explicitly examine multimodality of prey capture in these spiders.

In the following chapter I studied sensory usage in prey capture across lighting contexts in *H. formosus*, but with a focus on vision. Through selective blindfolding of the enlarged forward-facing principal eyes of these spiders, I tested the role that the specific vision of this pair of eyes plays in prey capture. Using similar methods to those in the preceding chapter, I ran fully crossed behavioral trials measuring prey capture success-rates and speeds of blindfolded and

sham-painted spiders in either bright or dim lighting conditions. I found that blindfolding of the principal eyes of *H. formosus* diminishes prey capture rates, as do dim-light conditions. These spiders also caught prey more slowly under dim or blindfolded manipulations. Furthermore, I found that spiders with occluded principal eyes *never* caught prey in dim light, suggesting that these eyes are necessary for low-light prey capture. This study confirmed and expanded upon previous research documenting the importance of salticid principal eyes in prey capture.

In the final chapter I studied the role of vision from another eye-pair in prey capture, but in flattie spiders (*Selenopis*). Within this family there has been an independent evolutionary eye enlargement of a different pair of eyes, the backwards-facing posterior lateral eyes. Flattie spiders capture prey differently from jumping spiders, ambushing their prey and using a rapid spinning motion to capture prey that is behind or beside them. Using a factorial design, I studied how Selenopid striking behavior changes with different access to visual information. I found no effect of blindfolding of the backwards-facing posterior lateral eyes on the strike dynamics of a flattie spiders. Strike characteristics such as angular and linear speeds of strikes did not change with the occlusion of these large eyes. Unlike *H. formosus*, these spiders did catch prey under dim light when their largest pair of eyes were covered. This was the first behavioral study of vision in Selenopidae, and the first step towards understanding the currently unknown function of their enlarged eyes.

Spiders display an incredible array of sensory abilities. This fact, combined with the diversity of prey capture strategies in spiders and the concomitant diversity of their sensory systems, make this order of arachnids an excellent system for behavioral studies of sensory ecology. Additionally, the way in which spiders subfunctionalize their vision across their pairs of eyes make them particularly well suited for the behavioral study of vision. Despite their small eyes and small brains, spiders can acquire and process the sensory information to perform tasks that can be quite complicated. These stark limitations also make them great subjects of study to move towards an understanding of the sensory ecology of animals overall. Though it's most obvious in the tiny and fascinating world of spiders, we animals are all forced to meet our sensory needs only within what is allowed by the constraints of physics, evolution, development, and ecology.

Dedicated to Mommy

Oski Wow-Wow!

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General Introduction

"Jeepers creepers, where'd ya get those eyes? [...] How'd they get that size?" -Johnny Mercer

There is such thing as too much information. Most readers will be familiar with the frustration of junk email clogging up their inbox. The more discounts and newsletters you receive, the harder it becomes for you to find the emails that actually matter to you. Having a spam filter helps you by restricting the flow of information. This phenomenon is not only restricted to email: in general, it is most useful to maximize *relevant* information, not to have more information overall. This principle is a useful framework for understanding animal senses. An animal is best off if its senses provide it with all the information necessary for its lifestyle, but not with information in excess of its needs. This is known as the concept of matched filters (Warrant, 2016; Wehner, 1987). A sensory system is best when it filters out all unnecessary information while preserving the information that is truly relevant. Just like an email about discounts on sneakers would be relevant to some people and not others, the sensory needs of animals vary and a based on an animal's particular ecology. For example, a sponge can't move and accordingly doesn't have any use for vision. Contrastingly, birds of prey need extremely detailed vision to locate and identify their distant quarry. In general, animals that engage in active predation tend to rely on higher volumes of sensory information. The exact sensory requirements for prey capture depend on hunting strategy, prey defensive behavior and morphology, and habitat characteristics.

The natural world is replete with predators of all sorts. Among these predators, spiders are particularly effective, widespread, and diverse. Every year spiders kill around a half a billion tons of prey (Nyffeler and Birkhofer, 2017). While almost all spiders are devastating predators, the methods of prey capture they employ are wildly different across species of spider. Some spiders use webs, some use traps, some toss their silk, some attract prey with deceptive lures, and some forego webs and actively hunt their prey (Elgar et al., 1996; Harland and Jackson, 2006; Stafstrom, 2017; Wang et al., 2017; Wood et al., 2016). Alongside this diverse predatory behavior is a concomitant variation in sensory systems. Many spiders are near-blind and reliant on vibrations through their webs, others display some of the most impressive vision of all animals (Harland et al., 2012). Such variation is one of many factors that make spiders an excellent subject for the study of sensory ecology, a field that explores the function of animal senses. In my dissertation I study the sensory ecology of prey capture in webless spiders, with a particular emphasis on the role of vision.

Spider eyes are unusual. They are more similar in function to a human eye than they are to the compound eye of an insect (Harland et al., 2012). These "camera-type" eyes have the potential for extremely detailed vision for their size. Interestingly, some (but not all!) of a spider's eyes evolved from simple compound eyes (Land and Nilsson, 2012). This is the only known example of a camera-type eye evolving from a compound eye. The three pairs of eyes that evolved from compound eyes are referred to as "secondary eyes," while the remaining pair are called the "principal eyes" (Land, 1985). The principal eyes and secondary eyes are quite different from each other; they have strikingly different morphology and are connected to entirely different brain areas (Strausfeld and Barth, 1993). In my personal opinion, vision from principal eyes and vision from secondary eyes can reasonably be considered as entirely different senses. Between each pair of eyes, not just between principal and secondary eyes, there can be divergent specialization in form and function. Eyes on the same spider can vary in their size, shape, position, optics, and sensitivity to different colors of light (Nagata et al., 2012; Steinhoff et al., 2020). These eyes can be used for a wide array of behaviors including navigation, mate choice, and of course prey capture (Forster, 1985; Girard et al., 2011; Nørgaard et al., 2007).

Of the many forms a spider eye can take, some are particularly extreme. “Ogre-faced” spiders get their name from their giant eyes that allow them to see prey in deep darkness, in order to target them for attack with nets of silk (Stafstrom et al., 2017). The large size of these eyes endow them with adequate vision even when light is scarce (Stafstrom and Hebets, 2016). Jumping spiders have cartoonishly large eyes as well, but they are used in very different contexts than those of the aforementioned ogre-faced spiders. Jumping spiders are typically active in the daytime, and their largest pair of eyes – the principal eyes - are riddled with features that allow them to see in extremely fine detail (Blest and Price, 1984; Blest et al., 1981). These eyes are elongated into a natural telescope, much like the eyes of a hawk, giving them a narrow field of view with a very high resolution (Williams and Meintyre, 1980). Light collected by these telescopic eyes is focused onto a bizarre retina. These retinae are tiny, shaped like a boomerang, and stacked into four layers like pancakes (Blest and Carter, 1988). Their photoreceptor cells are packed optimally to make resolution as high as possible (Blest, 1985a). Because jumping spiders have eye tubes instead of eyeballs, they move their retinas instead of moving their eyes (Canavesi et al., 2011). The gaze of these telescopic principal eyes is guided by another pair of eyes with a much wider field of view (Jakob et al., 2018). These very different pairs of eyes combine their individual strengths and make a perfect team.

While sensory structures such as the eye affect what information an animal receives, the effects of the environment is equally important (Endler and Basolo, 1998). Consider how hard it is to find keys under your car seat without a flashlight; your eyes are the same, but the light environment restricts your senses. Vision is not the only sense that is affected by environmental factors. Remember how spiders have other senses? They have vision (detects light), hearing (detects airborne vibrations), tremorsense (detects substrate-borne vibrations), trichobothria sense (detects airflow), tactile sense (detects physical objects), maybe even electric field sense (detects electric fields, as you may have guessed) (Barth, 2015; Cerveira et al., 2019; Clarke et al., 2013; Manfredi et al., 2012; Shamble et al., 2016) These senses are affected by environmental factors as well. To envision this, imagine the difference between standing next to a jumping friend on a trampoline versus standing next to a jumping friend on pavement. The trampoline transmits vibrations much better, so even with your eyes closed you can much more easily detect the movement of your friend on a trampoline than on the firm pavement (personal observation).

Spiders use their senses to great effect when capturing prey. An easy example to imagine is a spider feeling the vibrations of an insect caught in its web. However, many spiders do things differently. Actively hunting spiders provide an interesting example, especially when considering vision. Many families of spider known to use vision in prey capture. In addition to the jumping and ogre-faced spiders mentioned above, families such as wolf spiders, crab spiders, and wandering spiders all have been shown to use vision in prey capture. (Defrize et al., 2011; DeVoe et al., 1969; Fenk et al., 2010). Jumping spiders arguably use vision for prey capture in the most impressive ways. They can discriminate types of prey visually and plan attacks accordingly, strategically altering their approach route or their strike targeting (Jackson and Pollard, 1996). They also see color and can use such information to guide their foraging decisions (Vickers and Taylor, 2018). They can even quasi-vampirically feed on vertebrate blood by specifically targeting female mosquitoes that just had a blood meal (Nelson and Jackson, 2012). Other spiders have fascinating prey capture behaviors for which the contributing sensory input remains a mystery to science. Flattie spiders attack prey from all directions by turning at speeds faster than documented in any other animal (Zeng and Crews, 2018). Such spiders must have some sensory information to alert them to the presence of their targeted prey, but scientists do not yet know what types of information they use!

Spiders are incredible predators, and they are vastly diverse. This diversity is reflected in both their predatory strategies and in the senses required to execute these strategies. When multiple sensory streams are necessary for completing a task such as effective predation, it becomes increasingly difficult to study the sensory ecology of these behaviors in their full complexity. This is especially the case when different environmental contexts are considered, as the necessity and availability of different types of sensory information can rapidly change. In this dissertation my aim is to advance our understanding of the sensory ecology of prey capture, using spiders as a convenient and fascinating model.

50 Shades of Prey

Vision and vibratory sense in the prey capture behavior of a jumping spider

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It's quite a Salticid delight
To forage in places so bright
And when light goes away
They never catch prey
But in dimness they still do alright

Introduction

Animals that engage in active stalking as a predation technique need to acquire sufficient sensory information to locate, capture, and overtake their prey (Elliott et al., 1977). The exact sensory requirements for prey capture depend on hunting strategy, prey defensive behavior and morphology, and habitat characteristics (Stevens, 2013). Different types of foraging and prey capture behaviors can require specific types of sensory input (Garamszegi et al., 2002). Because sensory structures and processing are often energetically costly, they are expected to meet but not exceed the needs of the animal possessing them (Warrant, 2016). Active stalking of mobile prey requires a relatively high input of sensory information and thus corresponds to relatively complex sensory structures (Holmes and Gibson, 1983).

Multimodality, the combining of information from more than one sensory channel, can provide greater information content than that of one sensory modality alone (Higham and Hebets, 2013; Partan and Marler, 1999). Multimodal signaling can improve localization of a signal, can serve as an indication of quality, can reduce ambiguity, and can increase memorability (Partan and Marler, 2005; Rowe and Halpin, 2013). Several animal taxa employ multimodality - it has been documented widely especially in its communicative role in informing mate choice (*Lizards* - Martín and López, 2010; *Mantis Shrimp* - Mead and Caldwell, 2011; *Primates* - Rigaill et al., 2013; *Birds* - Taff et al., 2012). Different sensory modalities can also affect the rate at which information is learned (Verzijden and Rosenthal, 2011).

Sensory inputs can also be combined multimodally in the acquisition of food resources, and its usage can vary in relation to the uncertainty of the ecological environment (Munoz and Blumstein, 2012). Trout hunt by combining chemical and lateral line senses, whirligig beetles use visual, tactile, and vibratory information in hunting prey (Kolmes, 1983; Montgomery et al., 2002).The high stakes of active predation behavior can make any advantage important, and multimodality in prey capture may be far more prevalent than what studies have shown to date.

Jumping spiders (family Salticidae) are day active, actively stalking predators (Jackson and Pollard, 1996). They are notable for their extremely high visual spatial acuity, the highest for any eye their size (Blest and Price, 1984). Vision and chemoreception have been shown to interact multimodally in some jumping spiders, informing intraspecific contests as well as color preference of potential prey (Cross et al., 2007; Vickers and Taylor, 2018). Several genera of jumping spiders are also known for their complex multimodal courtship displays, which involve visual dancing and ornamentation alongside substrate-borne vibratory songs (Girard et al., 2011; Jackson, 1977).

The visual and vibratory aspects of courtship displays have been shown to both inform mate choice in several genera of jumping spider, including the speciose North American group *Habronattus* (Elias et al., 2012). Spiders of this genus exhibit complex displays during courtship (Elias et al., 2004; Elias et al., 2005; Elias et al., 2006a). It has even been suggested that the notable diversity of this genus has been driven by sexual selection, a force that acts largely based on the characteristic complex courtship of this genus (Leduc-Robert and Maddison, 2018; Masta and Maddison, 2002). Multimodal courtship displays can provide increased information to potential mates, and *Habronattus* spiders have been shown to prefer novel or complex signals (Elias et al., 2006b; Herberstein et al., 2014).

Though the multimodality of communication is well documented in *Habronattus*, it is not known if multimodal sensory input is used to inform their active hunting behavior. There is limited knowledge of multimodality in invertebrates, and even more so in the context of prey capture and foraging. As such, *Habronattus* provides a valuable opportunity to study the breadth of functions of multimodality within a clade in which it is known to be employed.

This study seeks to test if, and to what extent, the jumping spider *Habronattus formosus* uses visual and vibratory information multimodally for prey capture. Tremorsense, the detection of substrate-borne vibrations, is known to be widespread and important in jumping spider (Gygax, 1977; Huber, 2005). Though it's role in communication is well documented, I know of no studies documenting what role, if any, tremorsense plays in prey capture in Salticids. Tremorsense has been previously hypothesized to play a role in salticid prey capture (Forster, 1982). In this study I investigate if tremorsense is used in prey capture by *Habronattus*, and if it's use is contextually dependent on the availability of visual information, or on the type of prey. I test the hypotheses that tremorsense aids prey capture, and that this sense is more important when visual information is sparse and when prey are difficult to capture. The first hypothesis predicts that prey capture performance will be worse on stiff substrates that poorly transmit vibrations. The second hypothesis predicts that the effects of reduced vibration will be larger in the presence of other challenges such as evasive prey or low-light environments. For example, stiff substrates could reduce prey capture rates under dim light while not changing capture rates under bright light.

In this study I also explore the ability of *Habronattus* to capture prey under reduced light conditions, both dim light and complete darkness. *Habronattus formosus* are observed to be active during daylight hours, especially during bright days (Pers. Obs.). Salticid vision and prey capture are well studied, but very little is known about their ability to catch prey in low light, as these spiders are typically only considered in the context of their observed diurnailty (Cerveira et al., 2019). Cerveira et al. (2019) found that *Cyrba*, a distant Salticid relative of *Habronattus,* was able to detect simulated prey under low light. My study is the first to test the ability of a jumping spider to capture living prey under low-light conditions. I test the hypotheses that *Habronattus* can capture prey under low or absent light, and that prey capture performance is diminished by the visual restriction of reduced light.

Methods

Experimental Design

I conducted a series of lab behavioral experiments testing if, and how quickly, a jumping spider can catch a prey insect under a variety of conditions. To assess the role of vision in prey capture, I conducted experiments under visually restrictive dim light conditions, or under bright light. In these same experiments I tested the role of vibratory sense by running trials on one of two substrates that varied in their vibratory transmission properties. Furthermore, I used two types of prey insect to see if sensory usage in prey capture would vary for prey that differed in visual appearance and movement patterns. To address each of these factors and how they might interact with each other, I used a fully crossed 2 x 2 x 2 experimental design. I varied lighting (bright or dim), vibration (vibration + or vibration -), and prey (fly or cricket), resulting in eight total treatments. Each spider was run in exactly one trial.

Animals

Habronattus formosus jumping spiders (**Fig. 1.1)** were collected at Lake Berryessa, CA from March – June of 2017 and 2018. This species was chosen for this study because they exhibit multimodal courtship displays (visual and vibratory), because they could be collected locally, and because of their relatedness to other *Habronattus* used in previous behavioral studies in the Elias lab.

Individual spiders were housed separately and fed a diet of pinhead - ⅛" *Acheta domesticus* crickets (Ghann's Crickets, Augusta, GA) and flightless *Drosophila* (*D. hydei* and *D. melanogaster*) fed on enriched media (Josh's Frogs, Owasso, MI). Spiders were categorized as "mature male" (striped face and enlarged palps), "mature female" (drab with black epigynum dot), "immature male" (red face), or "immature female" (drab without black epigynum dot) based on naked-eye assessments of their external genitalia and body patterning.

Spiders were unfed for 7-15 days preceding each trial. Prey insects used in the experimental part of the study were flightless *Drosophila hydei* fruit flies ("fly" treatment) and pinhead crickets of similar size ("cricket" treatment). Both the flies and crickets were bred in captivity. Trials were conducted between June - July of 2017 and during June 2018.

Arena

Spiders were placed in an 8-inch diameter, 11-inch tall cylindrical enclosure with interior walls painted matte white. The top of the enclosure was covered with a light and camera fixture (described below). Within this enclosure, I placed a smaller arena constructed from a 4-inch diameter embroidery hoop (**Fig. 1.2)**. The sides of the arena were made from a plastic transparency rubbed with fluon and petroleum jelly to prevent the spiders and prey insects from escaping. The floor of the arena was made of stretched black nylon stocking material (Daiso support panty stocking). In "vibration -" trials (but not in "vibration +") the stocking material was stretched over a convex surface of cement. I verified that the "vibration -" substrate greatly attenuated substrate borne vibrations caused by the prey insects used in the study using a scanning laser vibrometer (Polytec PSV-400) to measure vibration caused by a fly or cricket on cement or nylon, at varying distances from the insect. Separate pieces of nylon were used for male and female spiders.

The enclosure was lit with a downward-facing Radion X15Pro G4 aquarium lighting fixture (Ecotech Marine, Allentown, PA). Each color of LED could be separately controlled, and the settings for each treatment were such that the sidewelling irradiance was 2806.9 $\mu W/cm^2$ in "bright" trials and 4.0 $\mu W/cm^2$ in "dim" trials. These settings were chosen to have varied light intensity while preserving similar spectral form and were a result of experimental validation to find a light intensity at which prey capture would be noticeably impacted. Spectra are shown in **Fig. 1.3**. All trials were recorded with a downward-facing GoPro Hero4 Silver mounted on the lighting fixture (GoPro Inc. San Mateo, CA).

Experimental Procedure

Before each trial the spider was not given any food for 7-15 days. Spiders were placed in the arena with one prey insect, which prior to the trial was covered by a removable plastic exclosure (a transparent square vial lid attached to a piece of string). Immediately after each filming began, I removed the exclosure. Time to capture was recorded as the time in seconds from the removal of exclosure until the spider captured the insect. A capture was defined as an event in which the spider caught and held the insect in its chelicerae. If the spider did not capture the insect within 3 minutes, I recorded the trial as absence of capture. Latency to orient was defined as the time in seconds between the removal of the exclosure and the first instance of the fly orienting its body to face the prey insect. I defined pursuit time as the time in seconds between the first orientation and the capture of the insect. I recorded a total of 240 trials, each with a unique spider. Temperature was measured with an Omega Type K thermocouple and recorded at the beginning of each trial.

Preliminary Experiment

Prior to the main experiment, I conducted a preliminary experiment which differed from the above methods in the following ways: Spiders were unfed for 9-15 days preceding each trial. The top of the arena was covered with a drop cloth of blackout fabric to avoid penetration of any outside light. The floor of the arena was made of stretched tan nylon stocking material, never over cement (equivalent to the “vibration +” treatment above but differing in color). All “dark” trials were recorded with a Samsung Smartcam security camera instead of a GoPro and illuminated only with the camera’s internal infrared lighting. Each of 37 spiders were run - when possible - in all three treatments (bright, dim, and dark) in a randomly determined order. This resulted in n = 36 “bright”, n = 33 “dim”, and n = 35 “dark” trials, (total n= 102), after accounting for incomplete repeated measures due to deaths of the spiders or other errors.

Statistics

Video data were digitized with BORIS (Friard and Gamba, 2016). All data were analyzed with R statistical software (R Core Team, 2014). Capture rate was analyzed as a GLM binomial logistic regression with a model including all treatments and their interactions, as well as the sex of the spider, the temperature in the arena, the number of days since being fed, and the time of day. I analyzed another GLM including the same treatments but using the carapace width of the spider instead of sex; both were not included in the same model due to multicollinearity, as well as the absence of 32 carapace measurements. Time to capture was analyzed as a GLM including all treatments as covariates. Interactions and other parameters were not included in the model, due to the necessarily smaller sample size (time to capture has no value for treatments where no capture occurred). For the preliminary experiment, capture rate was analyzed with a Pearson's Chi-squared text with light treatment. Time to capture was analyzed with a two-sample t-test using light treatment as the independent variable.

Results

Main experiment – Capture rates

In the main experiment, spiders were more likely to catch flies than crickets, catching flies in 80.00% of trials while catching crickets in only 54.17% of trials ($Z_{239} = 3.966$, $p < 0.0001$). Spiders were more likely to catch prey in bright conditions, with a capture rate of 87.50% in bright treatments compared to a 46.67% capture rate under dim light ($Z_{239} = 4.140$, $p < 0.0001$) **Fig.1.4**. The spiders did not capture the prey insect at significantly different rates across substrates; catching prey in 69.17% of vibration+ trials on nylon, while catching prey in 65.00% of vibration- trials on cement ($Z_{239} = 1.162$, $p = 0.2451$). The 26.70% capture rate of crickets in dim light is lower than would be predicted from the combined effects of prey type and light conditions, but this effect was not significant; there were no significant effects of this or any other higher-order interactions between treatments on capture rate.

The capture rate was not significantly affected by the temperature in the arena. Hunger level, the number of days since being fed, also did not predict capture rate, nor did the sex of the spider or the time of day that the experimental trial occurred. Larger spiders (those with a wider carapace) were more likely to catch prey ($Z_{207} = 2.423$, $p = 0.0154$). In this model where carapace width was used as a parameter instead of the sex of the spider, the effects of prey type and light treatment on prey capture rates remained significant ($p < 0.001$).

Main experiment – Time to capture

The spiders caught the prey insects faster on nylon substrates than on cement; i.e. total time to capture in "vibration -" treatments was on average 43.4s, compared to the 35.1s average of "vibration +" treatments ($t_{159} = -2.183$, $p = 0.0305$) **Fig.1.5**. Unlike capture rates, total time to capture did *not* differ significantly in response to light or prey type (light, $t_{159} = -1.507$, $p = 0.1337$; prey, $t_{159} = 0.399$, $p = 0.6906$). Though spiders were more likely to catch prey in bright light and more likely to catch the insect if it was a fly, those spiders that did successfully catch prey did so at similar speeds irrespective of light and prey treatment.

Spiders took longer to orient towards prey under dim light ($t_{68} = 5.256$, $p < 0.0001$) **Fig.1.6**. Latency to orient was not affected by either prey or substrate treatment ($p > 0.1$). After orienting towards the prey insect, spiders spent longer amounts of time pursuing they prey if it was a cricket ($t_{68} = 3.242$, $p= 0.002$) or if the light was dim ($t_{68} = 2.962$, $p= 0.004$). Pursuit time did not differ between substrate treatments ($p > 0.1$).

Preliminary experiment

Spiders in the preliminary experiment *never* caught the prey fly under complete darkness. Anecdotally, spiders left in a dark arena with 10+ flies for over an hour still did not catch a single fly. The capture rates in the preliminary experiment were significantly affected by light level; spiders caught no prey in the dark (0%), almost always caught prey under bright light (97%) and caught prey less frequently (75%) under dim light ($\chi^2 = 73.579$, $p < 0.0001$) **Fig.1.7**. Spiders in the preliminary experiment caught prey more slowly in "dim" treatments than in "bright" treatments ($t_{57} = 6.081$, $p < 0.0001$) **Fig.1.8**. The average time to capture was 19.5s under bright light, compared to 72.3s under dim light. This finding of light level affecting capture speeds differs from the finding of the main experiment, despite using identical bright and dim light treatments and using spiders of the same species.

Discussion

I placed jumping spiders in artificial prey-capture scenarios in which I varied light intensity, prey species, and the vibrational transmissibility of the substrate. Spiders were more likely to catch prey when the arena was brightly lit, or when the prey was a fly rather than a cricket. Successful prey capture never occurred under complete darkness. Though the probability of a successful capture did not differ between substrates, spiders caught prey faster on the more transmissive nylon substrates than on cement. Under dim light there was a longer delay before the spiders oriented towards their prey.

Prey capture occurred less frequently in very low light, but still did occur. This surprising ability for jumping spiders to catch prey under dim light corresponds with the findings of what Cerveira et al. (2019) found while studying *Cyrba*. *Habronattus formosus* spiders in my study were apparently - at least under these experimental conditions - able to make do with diminished visual information. The observed decrease in capture rate under reduced light supports the hypothesis that performance is linked to access to visual information. Though the reduced capture rate appears to be a result of lowered abilities, it may also result from a more general change in behavior type due to light condition. This type of general behavior change is seen in *Argiope aetherea* orb-spinning spiders, which adjust their prey-capture behavior (web building) in response to changes in ambient light intensity (Elgar et al., 1996). Light conditions can change other types of behavior as well, such as how female wolf spiders become more choosey in mate choice decisions while in the dark (Rundus et al., 2011). I observed some apparent behavior changes across light conditions in my experiments, with spiders under dim light spending more time trying to escape the arena. These behavior changes likely contributed to the patterns found in my study.

Some degree of visual input seems to be necessary for prey capture in *H. formosus*, as these spiders never captured prey in the dark. This finding of a 0% prey capture rate for jumping spiders in the dark differs from the results of a study by Taylor et al. (1998) in which Salticids representing 42 species were able to capture house flies in tubes or petri dishes in the absence of visual cues (Taylor et al., 1998). In Taylor et al. (1998) the spiders only struck at prey after making physical contact with it, and they only lunged but never leapt at this prey. Of the 42 species of jumping spider studied by Taylor et al. (1998), none represented the genus *Habronattus*. This stark discrepancy in results could result from differences in experimental design; the larger prey and tighter conditions may have forced contact to occur irrespective of any need for visual information. In other words, vision may only be needed for active prey capture while not being strictly necessary for food acquisition. It may also be the case that *Habronattus* would not catch prey without visual cues under any circumstances. Future studies can replicate the methods of Taylor et al. (1998) using *Habronattus* to determine if this genus truly will never catch prey without using sight. Though the jumping spider *Trite planiceps* uses vision in prey capture, it is still able to successfully capture some prey in the absence of light through tactile cues (Forster, 1979; Forster, 1982).

The spiders caught the flightless flies more often than they caught the crickets. This may be due to differences in the movement/evasion of the insects, different appearance/visibility, or different motivation by the spider to pursue each type of prey. Salticids have been shown to display preferences in prey type, and they distinguish between these prey types visually (Jackson, 2000; Taylor et al., 2014). Some jumping spiders, such as the araneophagous *Portia*, distinguish between types of prey and modify their approach behavior accordingly (Harland and Jackson, 2000). I hypothesized that the spiders would change their sensory strategy in response to different prey species. My results did not support this hypothesis, as the impacts of sensory restriction were not exacerbated when the prey type was more difficult. *H. formosus* may however display such flexibility in natural conditions with types of prey other than flies or crickets.

The spiders caught their prey more quickly, but not with differing frequency, on substrates that better conducted vibrations. This finding is similar the findings of Roberts et al. (2007) in which the jumping spider *Phidippus clarus* responds more quickly to artificial cues of a prey spider when these cues involve vibratory information in addition to visual information (Roberts et al., 2007). Though the frequency of prey capture did not vary across substrates in my study, in natural habitats the slower response on non-vibrating substrates could allow the prey to escape (Mikolajewski et al., 2010). The effect of substrate did not depend on lighting condition – these findings provides evidence against my hypothesis that information from tremorsense can provide redundancy for diminished visual information. Tremorsense may also provide benefits to *Habronattus* outside of courtship and prey capture; Long et al. (2015) showed that vibration can be used as an aversive stimulus for jumping spiders; in principle tremorsense could be used to avoid predators or undesirable prey (Long et al., 2015).

This study occurred in a flat, constrained, homogeneous arena, which was used for the benefit of simplicity in manipulation, but certainly does not reflect that natural environment in which this predator-prey interaction would actually occur (Calisi and Bentley, 2009). Variability and 3D complexity in substrates would cause small-scale variation in visual and vibratory information and could more greatly facilitate hiding or ambushing (Choi et al., 2019; Cooper and Wilson, 2007) Moreover, the prey used (crickets and flightless flies raised as animal feed) have defensive tactics that may differ from those wild prey. Furthermore, I did not account for any effects that these manipulations of light and substrate may have had on the ability of the prey to evade capture by the spider. Field manipulations can be used in the future to investigate the extent to which these sensory restrictions affect jumping spider prey capture in natural environments.

My hypotheses were formed in the context of comparing to the multimodality used by *Habronattus* in courtship communication. I found mixed and inconclusive evidence that prey capture was multimodal in this species. *H. formosus* is, however, only one species out of the more than one hundred that represent *Habronattus* (Maddison, 2015) Furthermore, there is evidence that *Habronattus* species vary in the degree to which multimodality is used in their courtship; in some species either vibration or visual signals determine mating outcomes alone (Damian Elias, Pers. Comm.). Future studies can replicate my methods across species of *Habronattus* that vary in sensory modality of courtship to determine if this variation corresponds with a variation in the multimodality of prey capture.

Habronattus, and jumping spiders in general, are not the only spiders to use multimodal communication in courtship. Wolf spiders (Family: Lycosidae) use both vibratory and visual signals in their courtship displays while varying both lighting and substrate in a manner similar to my study (Hebets et al., 2013; Rundus et al., 2010; Uetz et al., 2013). The vibratory components of these signals travel differently across different natural substrates, and these differences guide wolf spider behavior in the wild (Hebets et al., 2008; Rosenthal et al., 2019). While varying both lighting and substrate in a manner similar to my study, Meza et al. (2020) found that the transmission properties of the substrate did not affect prey capture success for wolf spiders (Meza et al., 2020). They similarly found that the transmission properties of the substrate did not affect prey capture success for these spiders. In fact, the spiders in Meza et al. (2020) caught prey most frequently on sand – the substrate that was the poorest transmitter of vibrations and that led to the lowest number of mating events (Rosenthal et al., 2019). Unlike my findings, this study provides an example from spiders in which the senses used in courtship differ from those used in prey capture.

A major goal of sensory ecology is to find out the adaptive benefits of animal senses to the animals that possess them. Tremorsense was known to have a use in *Habronattus* in the context of courtship, but prior to this study there was no documented function of tremorsense in this group that was relevant to natural (as opposed to sexual) selection. We now finally have evidence that tremorsense may aid survival in this species. Multimodality is clearly present throughout animals and used widely in communication, but we know relatively very little about how it is used in foraging and prey capture. The inherent multi-factorial nature of multimodality makes it more difficult to study than a single sense in isolation, but if we ignore multimodality, we may be missing out large parts of how animals truly conduct themselves in the natural world.

Acknowledgements

This chapter would not be possible without the efforts of Katie Sanko, Monica Sheffer, and Geovanni Zepeda.

Figures

Fig. 1.1. *Habronattus formosus* performing a multimodal courtship display. Spider is facing the camera. Elevated red “knees” are elevated and in focus the center-middle of the picture. “Dance” elements such as this are coordinated with “song” vibration elements that are transmitted through the substrate.

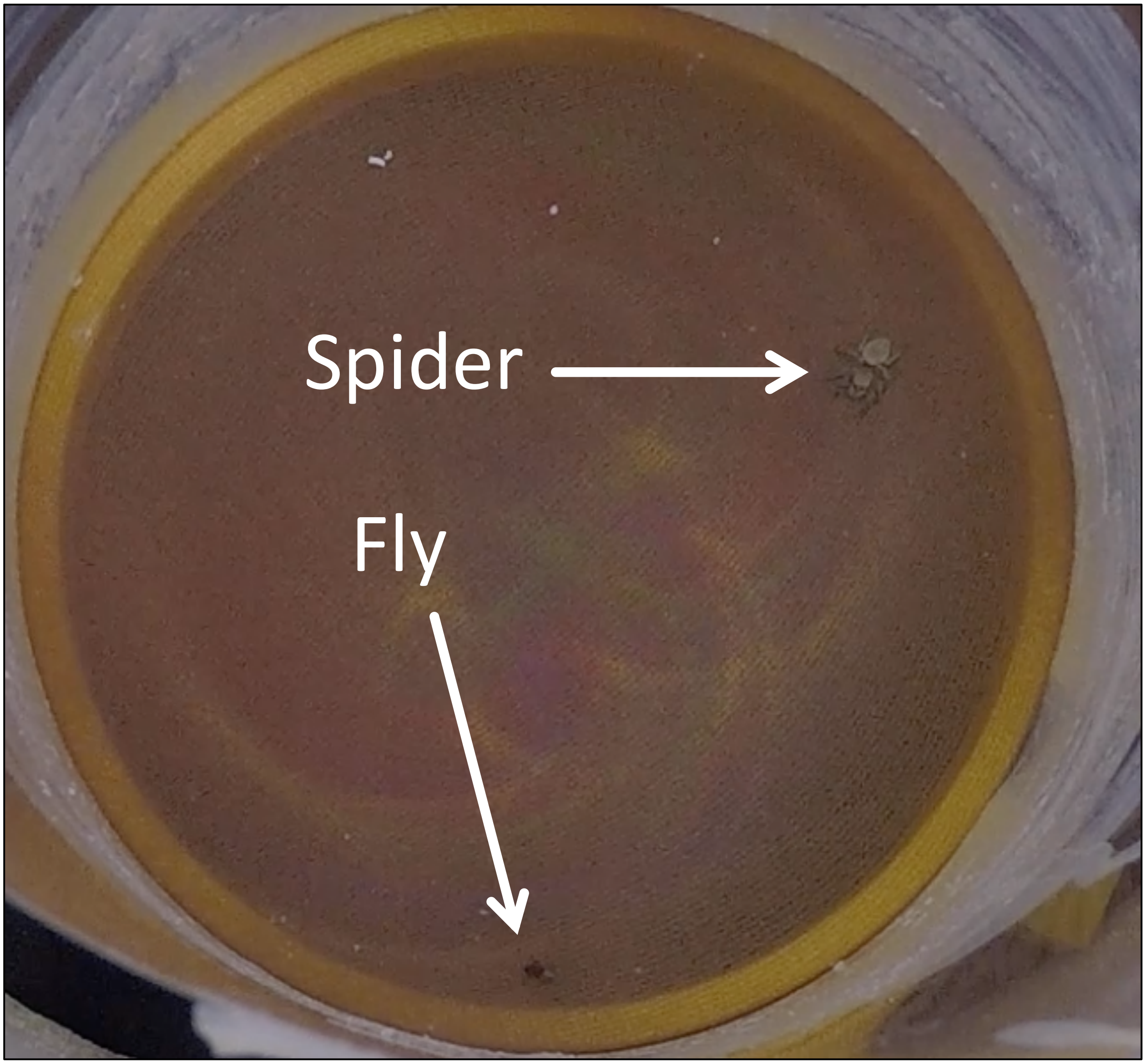

Fig. 1.2. Setup of arena. An adult “female” *H. formosus* is oriented towards the *D. Hydei* flightless fruit fly. Substrate is nylon without cement, and lighting treatment is “bright.” The white flecks on the substrate are fallen pieces of fluon from the wall.

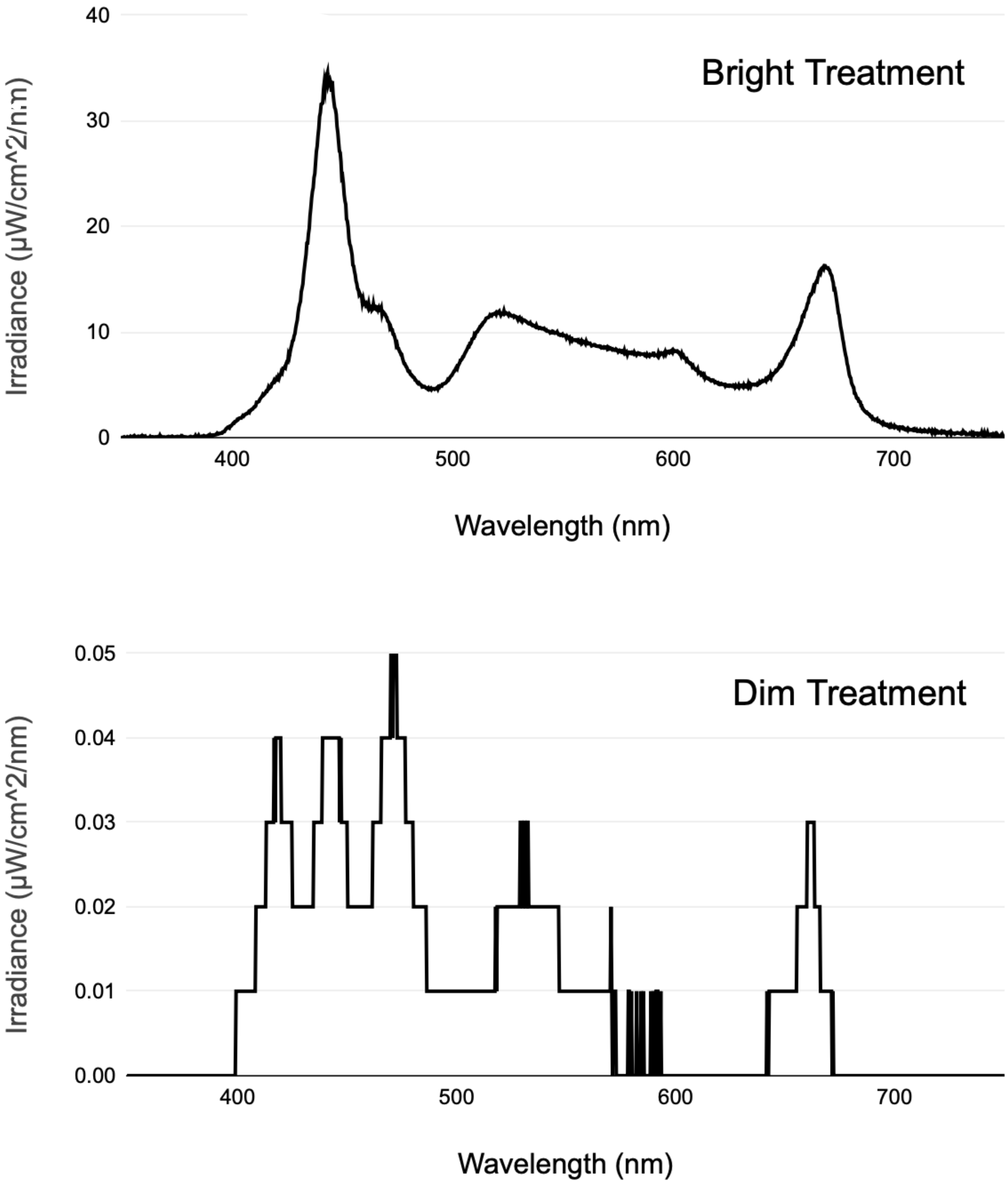

Fig. 1.3. Spectral irradiance (sidewelling) of light treatments. Note difference in vertical axis scales

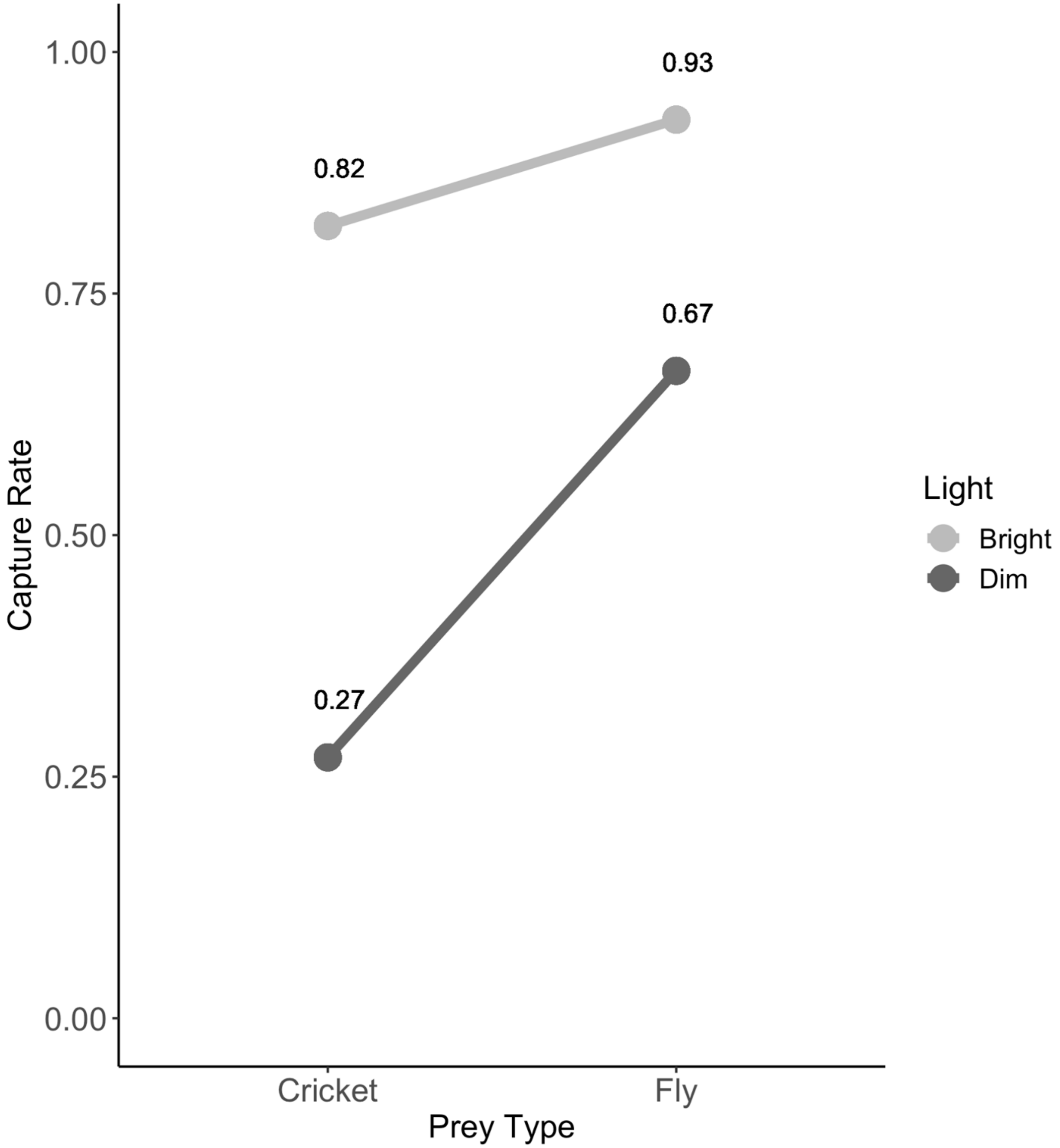

Fig. 1.4. Prey-capture success rates by prey type and light treatment. Vibration treatments are pooled.

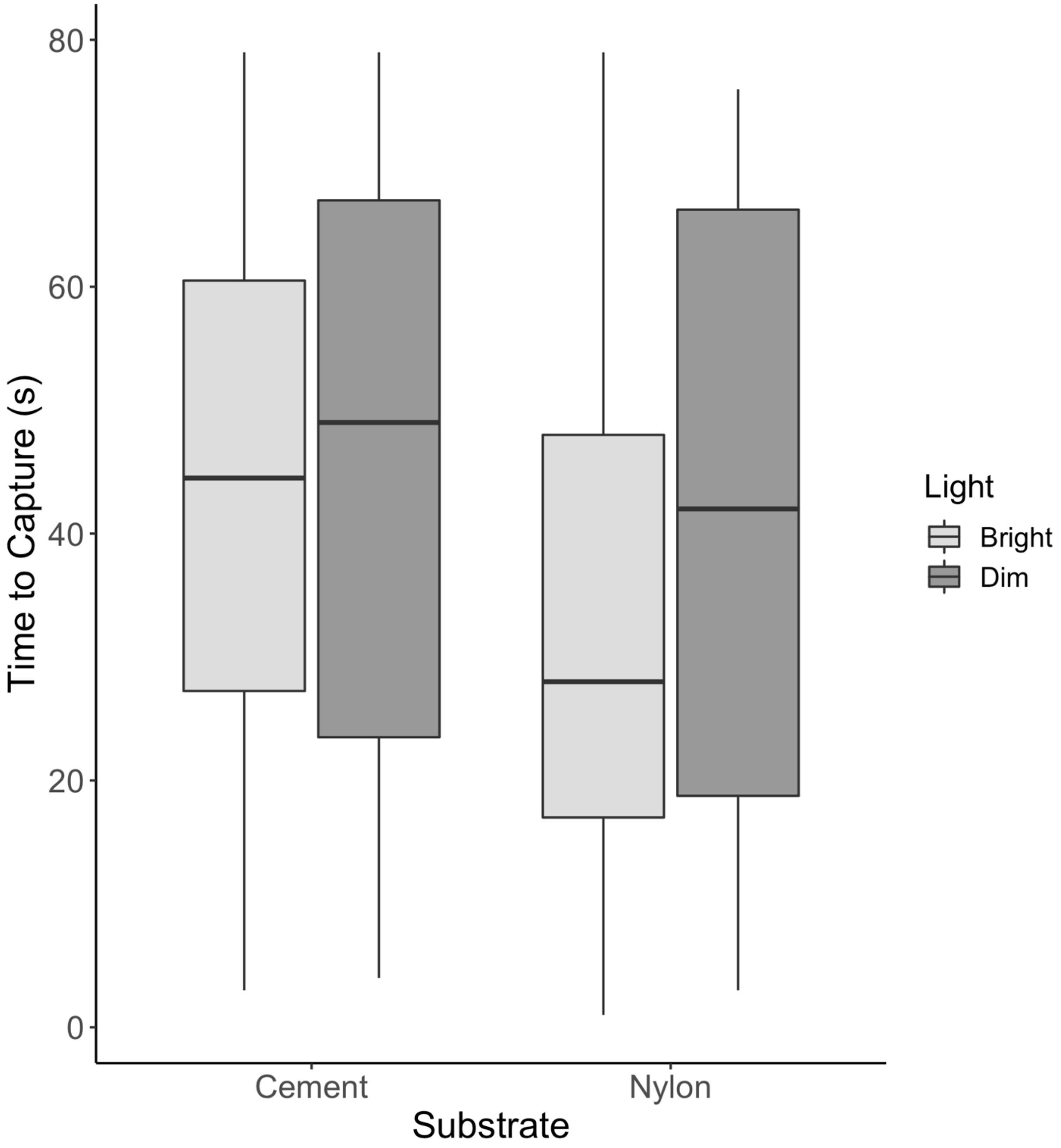

Fig. 1.5. Total time from removal of exclosure until capture. Only defined for successful capture events (n = 133).

(a

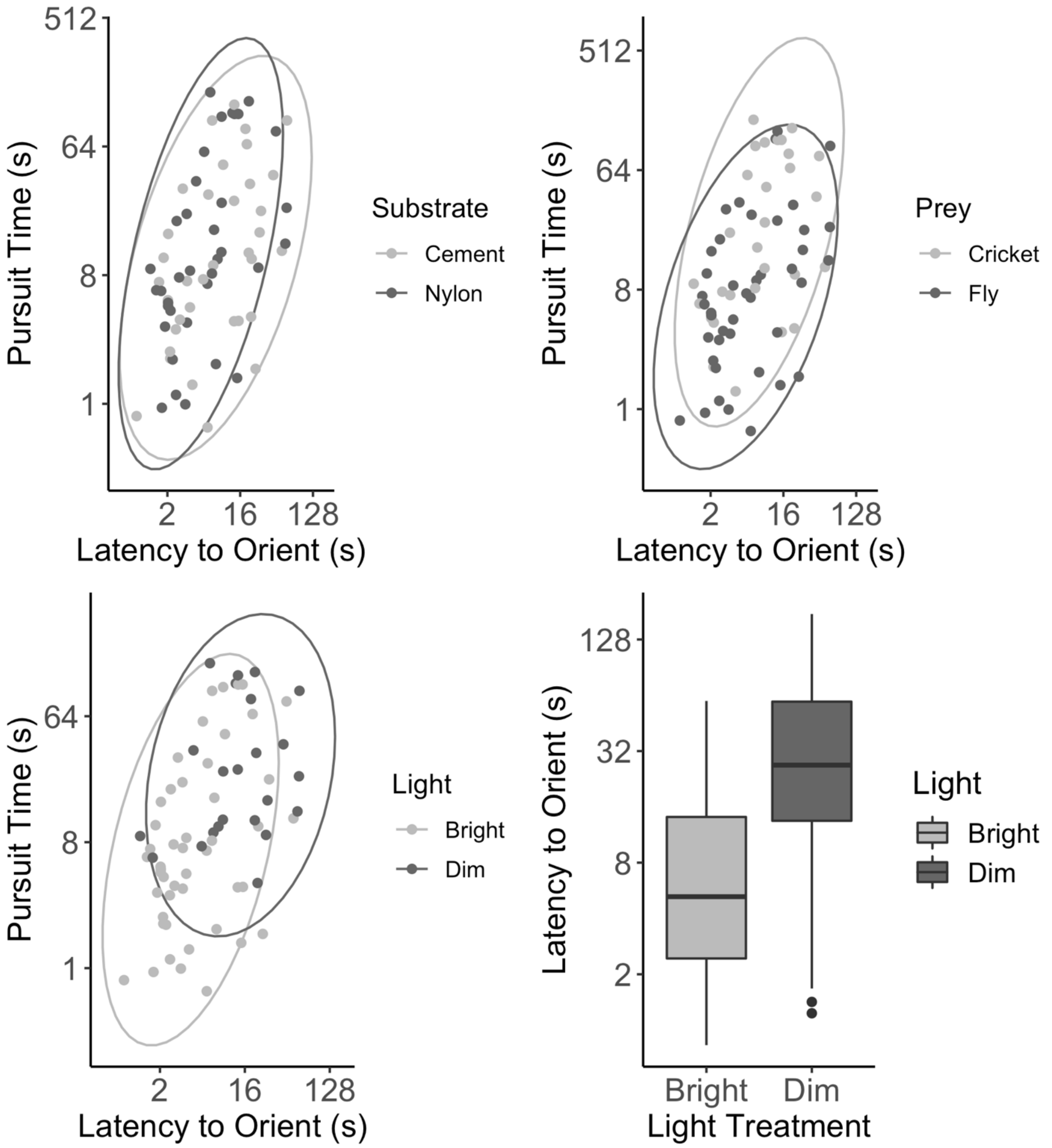

Fig. 1.6. Latency to orient toward prey, across treatments. Latency to orient was defined as the time in seconds between the start of trial and the first time the spider oriented its body to face the prey insect. Pursuit time is the time in seconds between first orientation and successful capture. Ellipses are 2-D 95% confidence intervals. Only light treatment had a significant effect on latency to orient, in which spiders were slower to orient in dim light. Continuous axes are $\log_2$ scaled for visibility.

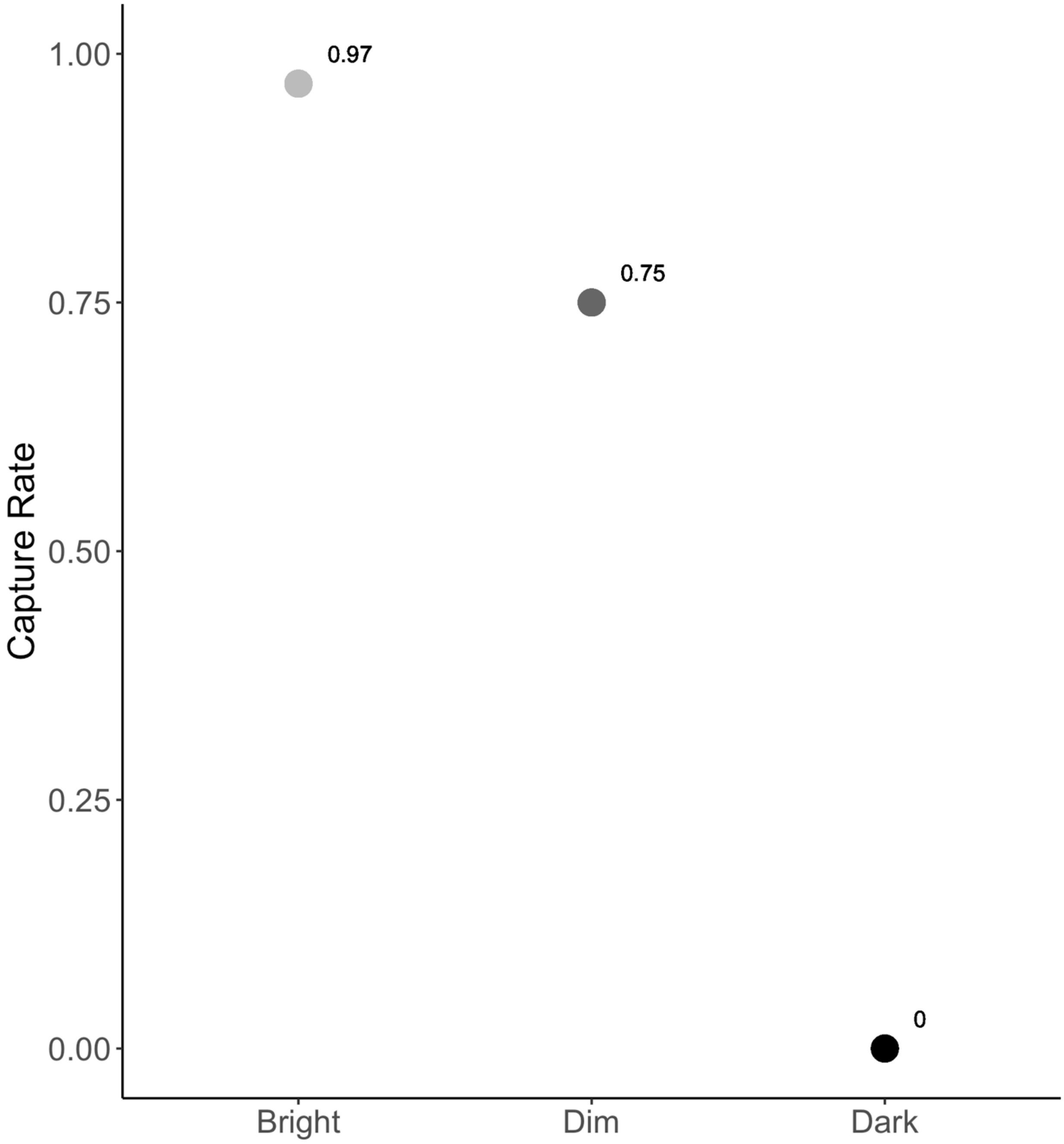

Fig. 1.7. Prey capture rates of flies by jumping spiders, across lighting treatments (including complete darkness) on nylon in preliminary experiment.

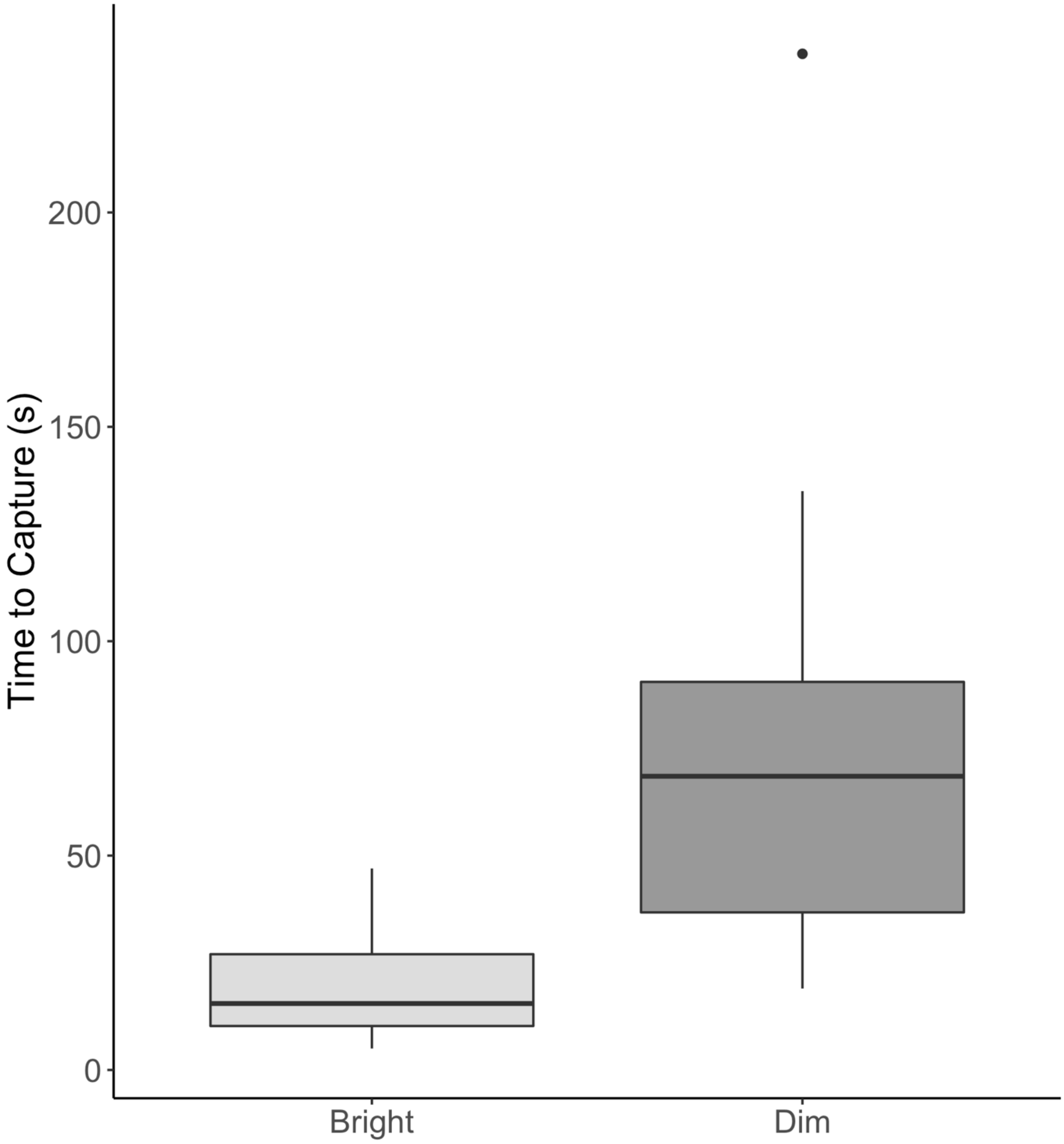

Fig. 1.8 Duration of trials that led to successful capture, from preliminary experiment.

Wide Eyes Shut

Principal eye vision and prey capture in varied light environments

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It turns out that jumpers can see
In lights that are dim as can be
But only by blinding
Did I get the finding
That principal eyes are the key

Introduction

Evolutionary trade-offs can result from physical, developmental, or ecological constraints (Ghalambor et al., 2004). This is exemplified by two fundamental aspects of vision: acuity and sensitivity. Visual acuity is the ability to resolve fine static detail, and sensitivity is the ability to see reliably in low light. For a given eye size, increasing either acuity or sensitivity diminishes the other (Caves et al., 2018; Warrant and McIntyre, 1992). This physical constraint, which is present even in digital photography, results from the increased noise inherent in finer visual sampling (Farrell et al., 2006). The arrival of photons at the eye is an inherently stochastic process, and at low levels of light it becomes increasingly difficult to distinguish true photoreception from the baseline levels of random firing of photoreceptors (Barlow, 1956). Acuity is achieved by splitting incoming light into many distinct and separate points to discern spatial detail, whereas sensitivity requires summation or pooling of sparse signals to increase their reliability in the presence of noise (Warrant, 1999). The importance of the sensitivity/acuity trade-off depends on an animal's environment and natural history, as tasks performed in bright light do not require high sensitivity, and tasks that need only coarse detail do not necessitate high acuity (Land and Fernald, 1992; Nilsson, 2013). For example, fish that live in more complex habitats tend to have higher spatial acuity (Caves et al., 2017). Another example is given by two closely related bees, in which the nocturnal species has relatively higher sensitivity (Frederiksen et al., 2008).

The sensitivity/acuity trade-off can be addressed by either optimizing one factor at the other's expense, by increasing the size of the eye, or having separate eyes for different tasks (Nilsson, 2009; Schmid, 1998). Space for photoreceptors is limited in small eyes, so smaller animals face the sensitivity-acuity trade-off more severely because they may not be able to sustain eyes large enough to perform both functions adequately (Nilsson, 2009). This is particularly striking in arthropods, as they both tend to be small and often rely on visual information (Warrant and McIntyre, 1993). Sometimes arthropods that use vision do not have vision acute enough to perceive details that can be seen by other animals. Colorful cleaner shrimp have vision that is capable of seeing their client fish, but that is not acute enough to see the color patterns of other shrimp (Caves et al., 2016). The aposematic coloration on black widows is visible as a warning to bird predators but cannot be discerned by their insect prey (Brandley et al., 2016).Yet, some arthropods do have commendable spatial acuity – dragonflies have sufficiently acute vision to discern and capture distant prey in flight (Cronin, 2020). Even the small crustaceans known as water fleas have acute eyes that they use in prey capture (Nilsson and Odselius, 1982). Arthropods can also display impressive sensitivity with their small eyes. Nocturnal bees can use neural processing to sum visual inputs to sacrifice visual information in exchange for reliability in low light (Frederiksen et al., 2008). Sophisticated optics can relieve the sensitivity/acuity trade-off somewhat; nocturnal hawkmoths can see both color and reasonable spatial detail in extremely low light because of the particular "superposition" structure of their compound eyes (Kelber et al., 2002; Warrant, 2004).

Though insects and crustaceans can possess incredible visual abilities, this is in spite of the constraints posed by their characteristic compound eyes; the camera type eyes possessed by vertebrates and spiders can achieve higher sensitivity and acuity than compound eyes of the same size (Pinter et al., 2018). It is for this reason that we find within spiders some of the most impressive examples of arthropod vision. For example, nocturnal spiders representing many families have very capable vision in dim light. The night active spider *Cupiennius salei* has a relatively high spatial acuity in dim light as compared to insects (Fenk and Schmid, 2010). *Cupiennius* can use visual cues, alongside airflow and substrate vibrations, to detect and capture prey (Fenk et al., 2010). Spiders can take advantage of their multiple pairs of eyes by specializing different pairs of eyes for different functions (Campione and Schmid, 2014). The nocturnal wandering desert spider *Leucorchestris arenicola* can visually detect local cues to use in navigation at night (Nørgaard et al., 2007). The most impressive sensitivity of any spider eyes is seen in net-casting spiders in the family Dinopidae (Laughlin et al., 1980). Net casting spiders have enormous posterior eyes which allow them to ambush prey under very low light conditions (Stafstrom and Hebets, 2016). These eyes have structural features that increase sensitivity at the expense of acuity, such as a short focal length and large photoreceptors (Blest and Land, 1977).

On the other extreme for spiders, jumping spiders (family: Salticidae) have eyes that can be capable of incredibly high acuity (Blest et al., 1990; Land, 1969a; Land, 1985). Their acuity is not only high in comparison to other spiders, it is higher than any other animal of comparative size (Harland et al., 2012; Land and Nilsson, 2012; Williams and Meintyre, 1980). Jumping spiders use their acute vision in tasks ranging from mate choice to prey capture to aggressive contests to habitat selection (Bednarski et al., 2012; Echeverri et al., 2017; Elias et al., 2008; Harland and Jackson, 2000; Nelson and Jackson, 2012; Tedore and Johnsen, 2016). Jumping spiders have evolved suites of adaptations for high acuity vision at least twice convergently within the family, once in the basal sparteines (the group that contains *Portia*, the spider with the highest documented acuity), and once in the more prevalent and speciose salticoid clade (Blest and Sigmund, 1985; Su et al., 2007).

Jumping spiders have a variety of morphological adaptations that allow for high spatial acuity. These adaptations, which are particularly pronounced the anterior median (principal) eyes, include focusing optics, retinal morphology, and photoreceptor arrangement (Blest and Price, 1984). The lens optics of salticid principal eyes act as a Galilean telescope, focusing light from a narrow field of view in a manner analogous to the foveae of birds of prey (Williams and Meintyre, 1980). Jumping spider principal eyes are thus elongated and cannot be moved without the spider moving its entire head; however, the retinas of the principal eyes are equipped with several muscles which the spiders can use to change the viewing direction of these eyes (Land, 1969b). Jumping spider principal eyes include a narrow, boomerang-shaped retina that is stacked into four tiers (Blest et al., 1990). There are several documented and hypothesized functions for this structure. This tiered retinal arrangement allows jumping spiders to perceive depth by comparing the relative defocus of an image on each retinal tier (Nagata et al., 2012). Retinal tiering allows incoming light of different frequencies to all be in focus despite chromatic aberrations, which could lead to a more focused and detailed image (Blest and Carter, 1987). This retinal tiering captures more light than a single-layered retina would, as such this tiering has also been hypothesized to function in increasing sensitivity (Blest et al., 1981). Retinal tiering has also been hypothesized to be a mechanism for color vision, as chromatic aberrations result in light of varying wavelengths to differ in their relative defocus on each retinal tier (Stubbs and Stubbs, 2016). The structure and arrangement of the photoreceptors of jumping spider principal eyes vary between species. The photoreceptors of the highest acuity species are long and narrow to allow fine spatial resolution, and slightly separated to prevent crosstalk between receptors

(Blest, 1985a; Blest, 1985b; Eakin and Brandenburger, 1971; Harland et al., 2012). However, different photoreceptor arrangements that appear to favor sensitivity are found in some species such as the sparteine *Yaginumanis* (Blest and Sigmund, 1985).

Though often overshadowed by the principal eyes, salticid anterior lateral eyes (ALE's) also have impressive spatial acuity for their size, particularly when detecting motion (Zurek and Nelson, 2012a). ALEs are used to detect the motion of prey, and ALE vision alone is sufficient to elicit stalking behavior (Zurek et al., 2010). The relatively large field of view from the ALEs is also used in conjunction with the principal eyes, guiding the gaze of the principal eyes to allow the tracking of targets (Jakob et al., 2018; Zurek and Nelson, 2012b). The ALE's are important for "chasing" behavior in jumping spiders, while the principal eyes are used in stalking (Forster, 1979).

The apparent adaptations for high acuity in jumping spider eyes, alongside observations of their behavior, have led the scientific community to consider this family to be diurnal (Foelix, 2011; Forster, 1982; Land, 1969a). As a result, the study of dim-light vision in this family has been minimal (Cerveira et al., 2019). Some jumping spiders occupy dimly lit environments such as leaf litter under dense forest canopies, and in a few of these species their eye morphology seems to favor sensitivity over acuity. (Blest, 1983; Blest, 1985b; Cerveira et al., 2019). Moreover, electrophysiological studies show that jumping spider secondary eyes have high sensitivity, at least in comparison to similarly sized compound eyes of insects (Hardie and Duelli, 1978).

The North American jumping spider genus *Habronattus* is thought to be particularly diurnal, favoring sunny habitats. *Habronattus* achieves trichromatic vision through spectral filtering by oil droplets in the principal eyes, and the spectral tuning performed by these droplets greatly reduces the intensity of the light that reaches the filtered photoreceptors (Zurek et al., 2015). Some species of *Habronattus* have been shown to use color information to inform both prey choice and mate choice (Taylor and McGraw, 2013; Taylor et al., 2014). At least some visual functions of *Habronattus* appear to be dependent on bright light, considering the finding that red coloration only affects mate choice under full sunlight (Taylor and McGraw, 2013). Mate choice is an important function in this clade and is thought to have contributed to its notable diversity (Leduc-Robert and Maddison, 2018).

In the previous chapter I found that *Habronattus formosus* depends on light to catch prey, and that it can capture prey under dim light albeit with diminished performance. The adaptations for high acuity and color vision in the principal eyes of *Habronattus* suggest that principal eye function may be particularly impacted by decreased light availability. In the current chapter I test the hypothesis that diminished prey capture under dim light in *H. formosus* results from relatively high light requirements of the principal eyes. To do so I investigated the extent to which principal eye vision is necessary for prey capture *H. formosus*, and how the necessity of these eyes changes across light environments. I conducted a prey capture experiment on wild-caught spiders, varying light levels and selectively occluding principal eyes. If lowered performance under dim light were in fact due to loss of principal eye vision, I would expect the effects of light dimming and principal eye blindfolding to be redundant. Alternately, if principal eyes were indeed used in low-light prey capture I would expect the effects of these treatments to be additive, with a combined effect more extreme than the effect of either manipulation alone.

Methods

Experimental Design

I conducted a series of lab behavioral experiments testing if, and how quickly, a jumping spider can catch a prey insect under different visual restrictions. To test the particular role of principal eye vision in prey capture, half of the spiders had their principal eyes occluded but all secondary eyes revealed, while control spiders had sham painting that covered no eyes. I also varied light level, as in the previous experiment, to see if the importance of principal eye vision was dependent on ambient light. I used a fully crossed 2 x 2 experimental design, varying lighting (bright or dim) and ocular occlusion (blindfold or sham) resulting in four total treatments. With this design I set out to test if (a) principal eyes were necessary or relevant for prey capture in this species in general, (b) the high-acuity adaptations of principal eyes rendered them irrelevant or nonfunctional in low light, or (c) the large size of principal eyes made them important or even necessary for low-light prey capture.

Animals

Habronattus formosus were collected at Lake Berryessa, CA from June of 2018. Individuals were housed separately and fed a diet of pinhead - ⅛" *Acheta domesticus* crickets (Ghann's Crickets, Augusta, GA) and flightless *Drosophila* (*D. hydei* and *D. melanogaster*) fed on enriched media (Josh's Frogs, Owasso, MI). All spiders (n = 40) were anesthetized with CO2 and had Chroma A2 permanent green deep hue heavy body acrylic paint applied to them. Spiders were given at least 24 hours after manipulation to recover before behavioral trials. Control spiders (n=20) had paint applied to the top of the head **Fig. 2.1**, and blindfolded spiders (n-20) had the principle eyes occluded **Fig. 2.1**.

The paint used for blindfolding is nontoxic and opaque. I verified the opacity of the paint by photographing a checkerboard pattern through painted and unpainted *H. formosus* principal eyes. I did so by hanging removed cuticles (painted and unpainted) by a drop of frog Ringer's solution and photographing the pattern as focused by the principal-eye corneas.

Arena

Spiders were placed in an 8-inch diameter, 11-inch tall cylindrical enclosure with interior walls painted matte white. The top of the enclosure was covered with a light and camera fixture (described below). Within this enclosure, I placed a smaller arena constructed from a 4-inch diameter embroidery hoop. The sides of the arena were made from a plastic transparency rubbed with fluon (on the bottom) and petroleum jelly (on the top) to prevent the spiders and prey insects from escaping. The floor of the arena was made of stretched nylon stocking material (Daiso support panty stocking). Separate pieces of nylon were used for male and female spiders.

The enclosure was lit with a downward-facing Radion X15Pro G4 aquarium lighting fixture (Ecotech Marine, Allentown, PA). Each color of LED could be separately controlled, and the luminous intensities for each treatment were either: sidewelling irradiance 2806.9 $\mu W/cm^2$ “bright” or 4.0 $\mu W/cm^2$ “dim”. These settings were chosen to have varied light intensity while preserving similar spectral form. All trials were recorded with a downward-facing GoPro Hero4 Silver mounted on the lighting fixture (GoPro Inc. San Mateo, CA). Arena and lighting details are identical to those in the main experiment described in the preceding chapter, except that the substrate was nylon (without cement) in all treatments.

Experimental Procedure

Spiders were unfed for 7 to 8 days preceding each trial. Prey insects used in the experimental part of the study were flightless *Drosophila hydei* fruit flies. Spiders were placed in the arena with one fly, which prior to the trial was covered by a removable plastic exclosure (a transparent square vial lid attached to a piece of string). Immediately after each filming began, I removed the exclosure. Time from removal of exclosure until the spider captured the insect was recorded, as was the number of jumps made toward the insect and the latency to orient toward the insect. A capture was defined as an event in which the spider caught and held the insect in its chelicerae. If the spider did not capture the insect within 3 minutes, I recorded the trial as absence of capture. Of 40 spiders, most (38) spiders were run in two trials, one bright and one dim (order randomized), eight days apart. Of the remaining two spiders, one was run in trials seven days apart, and one was run in only one trial (bright).

Statistics

Video data were digitized with BORIS behavioral analysis software (Friard and Gamba, 2016). All data were analyzed with R statistical software (R Core Team, 2014). Capture success was analyzed with a logistic regression including the light treatment and blindfold treatment and their interaction. Time to capture was analyzed with a linear regression including the same covariates, except for the interaction between the treatments as there were no values for time to capture for the dim-blindfold treatment.

Results

Capture rates

Spiders were less likely to catch prey when blindfolded, catching prey in 23% of blindfolded trials and 80% of sham trials ($Z_{75} = -2.755$, $p = 0.006$) **Fig. 2.3**. Prey capture occurred in 36% of dim light treatments and in 68% of bright light treatments, but this difference was not statistically significant ($Z_{75} = -1.515$, $p = 0.130$). The interaction between the influence of lighting and blindfolding on capture success was also not statistically significant ($Z_{75} = -0.011$, $p = 0.991$).

Blindfolded spiders *never* caught the prey fly under dim light conditions. This remained true outside of the formal experiment – blindfolded spiders left under dim light with a fly for extended periods of time still did not capture the fly. In a few instances, these blindfolded spiders would go on to catch the fly once the light was brightened or the cover of the arena was removed (allowing in more light).

Time to capture

Blindfolding the spiders and dimming the light each increased the average time to capture the prey insect. Blindfolded spiders were slower to catch prey, taking an average of 81s compared to an average of 49s in sham treatments ($t_{40} = 3.433$, $p = 0.001$). Time to capture was longer under dim light conditions, averaging 71s in dim light and 47s in bright light ($t_{40} = 3.234$, $p = 0.001$) **Fig. 2.4**. Time to capture was undefined for spiders that were both blindfolded and under dim light, as there were no successful captures in this category.

Discussion

Habronattus formosus are observed to be active during daylight hours, especially during bright days (Personal observation). The genus *Habronattus* in general is known for its diurnailty (Taylor and McGraw, 2013). This aspect of their natural history combined with the morphology of their principal eyes led me to hypothesize that the principal eyes would only be important in bright light, but my findings suggest otherwise.

The spiders in my study caught prey more quickly and more frequently under bright light than dim light. For spiders that were not blindfolded, prey capture still occurred under dim light. This finding is consistent with a study on the sparteine jumping spider *Cyrba*, which was able to approach images of prey under low light but did so with diminished accuracy (Cerveira et al., 2019).

Spiders with occluded principal eyes also caught prey less frequently and more slowly, but still were able to do so successfully under bright light conditions. Zurek et al. blindfolded all eyes but the anterior lateral eyes, and these spiders were still able to orient towards prey with their principal eyes occluded (Zurek et al., 2010). These findings suggest that the principal eyes are important for prey capture in jumping spiders, but that they are not strictly necessary for prey capture in sufficiently bright light.

Unlike the merely diminished prey capture rates under each manipulation alone, there were *zero* instances of prey capture from blindfolded spiders in dim light treatments. This result strongly rejects my hypothesis that prey capture impairment in low light is due to principal eyes relying on bright light to function. In contrast, I found that in low light the principal eyes are not only functional but *necessary* for prey capture. It is in fact the other pairs of eyes that appear to cease functioning under low light conditions. Despite their many high acuity adaptations, the principal eyes are critical for visual sensitivity in *H. formosus*. Rather than falling on one end of a sensitivity/acuity spectrum like *Portia* or *Yaginumanis*, it appears that *Habronattus* principal eyes serve a dual function of both high acuity and high sensitivity (Blest and Sigmund, 1985). Such dual function has been documented in other jumping spiders. Maximum acuity and sensitivity are constrained by eye size; the smaller eyes of some juvenile jumping spiders particularly prioritize acuity over sensitivity, and greater sensitivity is only achieved as the spiders develop and their eyes become large enough to gain sensitivity while maintaining acuity (Goté et al., 2019). Size constraints on spiders can drive their morphology in many ways – the brains of some small spiders extend into their legs (Quesada et al., 2011). The sensitivity required to capture prey in the low light conditions of my experiment may be a consequence of the size of the principal eyes, such that despite their adaptations for high acuity they still capture enough photons to see in dim light. Larger eyes in general tend to correlate with higher acuity in animals, as demonstrated in ray-finned fish (Caves et al., 2017).

Though *Habronattus* are thought to be active only in bright environments, it may also be the case that they conduct some prey capture in low light as well. Diurnal jumping spiders from another genus have been observed hunting by artificial lights at night (Frank, 2009). Though artificial light is not a low-light environment, it shows that jumping spiders can conduct active prey capture at night even if they represent a species that is normally day active.

My light manipulations did include ultraviolet (UV) lighting. Jumping spiders have UV-sensitive photoreceptors, and transmission optics that can allow for UV vision (DeVoe, 1975; Hu et al., 2012; Nagata et al., 2012). Behavioral evidence suggests that salticids do use this capability for UV vision (Lim and Li, 2006). Furthermore, there is evidence that UV can be of particular importance in prey capture (Zou et al., 2011). It would be interesting to study what contribution, if any, the UV component had on the effects of light dimming in my experiment.

My study is the first to my knowledge to address the specific use of principal eyes in low light prey capture. That some - but not all - prey capture ability is lost in these spiders when their principal eyes are occluded leaves open the possibility for further, more detailed studies on the way tasks are distributed between pairs of eyes.

Future studies can make interesting comparisons to behaviorally similar but phylogenetically distinct families of spider. For example, lynx spiders (family: Oxyopidae) are also actively stalking predators, but unlike jumping spiders they are observed to be active during both day and night (Nyffeler et al., 1987). Lynx spiders do not have the enlarged principal eyes of jumping spiders, but they are still able to carry out apparently visual prey capture tasks that are quite similar to those of salticids (Muñoz-Cuevas et al., 1998). There is variation in both sensitivity and acuity between species of lynx spider, but very little is known about their vision (Muñoz-Cuevas et al., 1998). Comparison between salticids and oxyopids may be a fruitful avenue of research.

The study of dim-light vision in general provides a fascinating view of vision at the extreme. Cockroaches can detect light at the level of a single photon (Honkanen et al., 2014). Nocturnal bees can achieve some vision at night, but hit a hard limit imposed by constraints from the evolutionary history of their eyes (Kelber et al., 2006). Some nocturnal insects can improve sensitivity by moving slowly and summing visual input over time – analogous to a slow shutter speed in a camera (Warrant and Dacke, 2011). Deep-sea fish have eyes specially adapted to see faint bioluminescence amidst the otherwise utter darkness (Warrant, 2004). An animal's mechanisms for coping with limited sensory information can provide deep insight into natural history and evolution.

Acknowledgements

This chapter would not be possible without the efforts of Lin Yan for deftly painting and helping with trials, and Malcolm Rosenthal for helping verify the opacity of the painting treatment.

Figures

Fig. 2.1 (a). *Habronattus formosus* with sham painting on head, all eyes unobscured.

Fig. 2.1 (b). Blindfold painting on principal eyes. All secondary eyes unobscured.

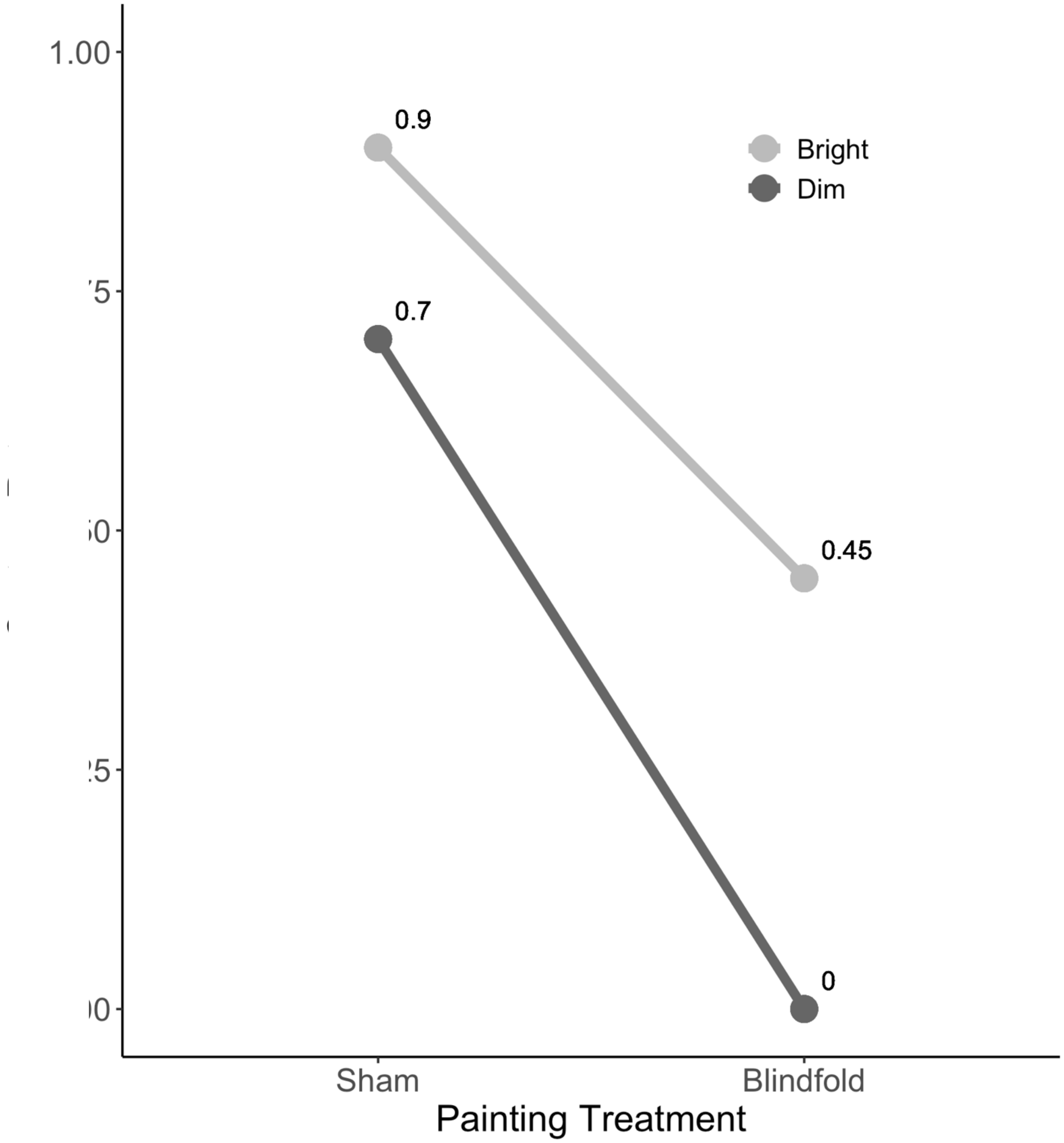

Fig 2.2. Effects of painting treatment and light treatment on prey capture rates. Dim light and blindfolding both make prey capture less likely, and prey capture never occurred with blindfolded spiders under dim light.

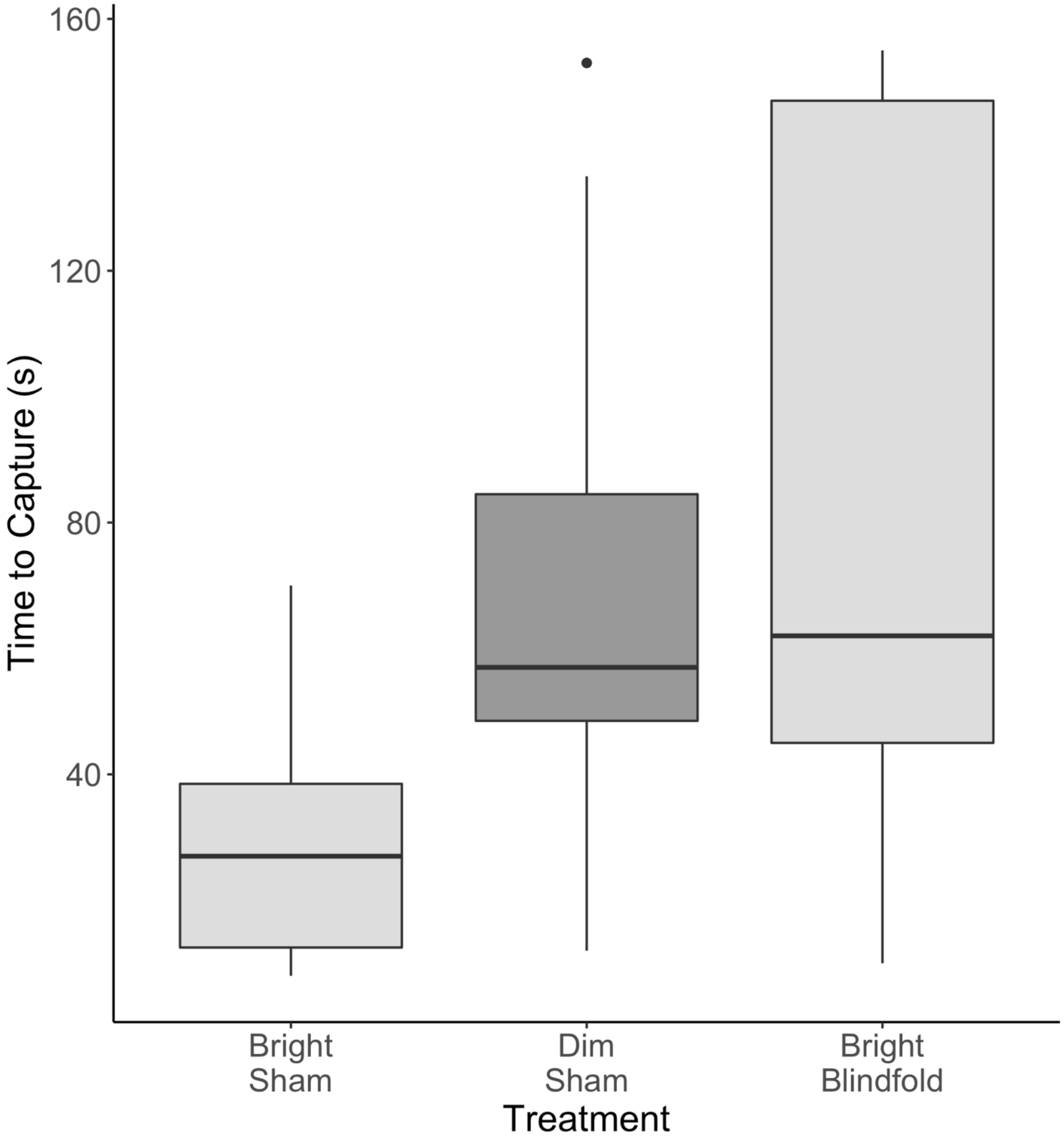

Fig 2.3. Effects of lighting and blindfolding treatments on time to capture prey. Spiders were slower to capture prey when blindfolded or when under dim light.

Your Fore-Eyes Only

Posterior lateral eye vision and strike dynamics in flattie spiders

In collaboration with Sarah Crews

It seems that more often than not
Good vision can cost you a lot
But eyes on a flattie
Are driving me batty
Why is it they got what they got?

Introduction

A predator's prey capture behavior is guided by its sensory capabilities (Lannoo and Lannoo, 1993; Milet-Pinheiro et al., 2016). Animal behavior in general can be limited by what sensory information is available (Warrant, 2016). This principle is particularly well demonstrated in terms of vision, wherein certain physiological thresholds in the eye need to be surpassed to allow an animal to perform a given behavior (Nilsson, 2009). Certain behaviors, such as diel activity patterns and habitat choice, only require simple vision and processing, whereas behaviors such as visual mate-recognition or hunting (visual tracking and identification) can necessitate a more complex eye or sophisticated neural processing of visual information (Gonzalez-Bellido et al., 2016; Sison-Mangus et al., 2006). Environmental conditions can also influence eye demands. For example, eyes requires sufficient photon catch for reliable visual information; in low-light environments, this necessitates adaptations such as larger eyes that gather more photons (Warrant and McIntyre, 1992).

As different behaviors can require visual information, some species have multiple eyes, or parts of eyes, that are specialized for different tasks. In mayflies, the males have an additional pair of upwards-facing eyes used specifically to find mates (Zeil, 1983). In the "four-eyed fish" *Anableps*, the shape of the cornea differs in curvature in order to allow vision both above and below the water (Schwassmann and Kruger, 1965). Dragonflies use their compound eyes for several functions including prey capture (Olberg, 2012), and they also have separate small camera-type eyes (ocelli) that are used in maintaining their orientation while flying (Stange, 1981). In "cockeyed" squid, the left and right eyes are asymmetric, which may be an adaptation for perceiving input from both upwelling and downwelling light environments (Thomas et al., 2017). Pit vipers use their pit organs (which can be considered eyes) for infrared vision that supplements the use of their other eyes in guiding prey capture (Chen et al., 2012).

There are several documented cases of eye evolution throughout spiders. The ancestral state of spiders is small, relatively low-resolution eyes (Fenk et al., 2010), and it has been thought that spiders primarily gather information through other senses such as chemoreception and tremorsense (Barth, 1985; Seyfarth and Barth, 1972). However, some spiders have evolved to rely on vision for capturing prey (Bednarski et al., 2012; Harland and Jackson, 2006). In some of these species there is conspicuous morphological evolution of at least one of their pairs of eyes, including but not limited to enlargement of the eyes. To give a few examples, the anterior median eyes and anterior lateral eyes of jumping spiders are enlarged and have other morphological specializations that allow the vision of these spiders to have color vision/discrimination and incredibly high spatial resolution (Land, 1969a; Zurek et al., 2015). In net casting spiders, the posterior median eyes are greatly enlarged to allow for low-light vision for capturing their prey by ambush at night (Stafstrom and Hebets, 2016).

Within a spider, separate pairs of eyes can differ in morphology, anatomy, and function; the specialized eyes in spiders like those above are very different from the other pairs of eyes (Blest and Land, 1977; Stafstrom et al., 2017; Steinhoff et al., 2020). It is worth noting that, enlarged or not, the anterior median eyes of spiders ancestrally differ in morphology and neural wiring as compared to the other three pairs of eyes (Strausfeld and Barth, 1993). The enlarged eyes of some spiders are hypothesized to be driven by particular visually mediated functions -

such as navigation, courtship, predation - and by their natural history, such as whether the spiders are nocturnal or diurnal (Clemente et al., 2010; Opell, 1988). Though spider eyes have been subject to a considerable amount of research, the function of enlarged eyes in most species is still under question. The purpose of this study is to investigate a potential role of enlarged eyes in prey capture, for a family of spiders whose enlarged eyes have not been studied in a behavioral context.

Flattie spiders (Araneae: Selenopidae) are nocturnal sit-and-wait predators. These spiders do not use webs, and instead ambush their prey (primarily insects) while standing directly on the substrate (Crews, 2011; Crews and Harvey, 2011). Their prey capture ability is extraordinary — they can strike prey approaching from any direction at extreme speeds (Zeng and Crews, 2018). They have been recorded to have one of the fastest angular rotations of any arthropod (Zeng and Crews, 2018). Within Selenopidae, there has been an evolutionary enlargement of one pair of eyes, the posterior lateral eyes (PLEs), which have a lateral and posterior field of view (Zeng and Crews, 2018). Posterior lateral eyes are the largest pair in 96% of the species described (Crews 2011), ranging from 1.29 to 6.15 times the average size of the anterior eyes and from 0.8 to 3.67 times the size of the posterior median eyes. Zeng and Crews hypothesized that a wide field of view from enlarged posterior lateral eyes allowed prey detection from anterior, lateral and posterior directions and thus improved prey finding capabilities. The purpose of our study was to test if and how vision, especially PLE vision, affects the dynamics of the predatory behavior of these spiders.

We performed a lab behavioral study on Selenopid spiders of the genus *Selenopis* in a fully crossed 2 x3 experiment, varying the ambient light level (bright or dim) and eye occlusion (all eyes blindfolded, PLEs blindfolded only, all eyes uncovered). We allowed each spider to capture a prey insect and filmed them with high speed video. For each trial we measured the relative location of the prey with respect to the spider, and the duration of the strike. We hypothesized that diminished vision would impact strike dynamics, making them both slower and more constrained to the front of the spider. The backwards facing position of the PLEs led us to hypothesize that the occlusion of these eyes in particular would reduce the magnitude of rotation in each strike. Due to the conspicuous size of the PLEs, we hypothesized that the effects of PLE-occlusion would be similar to the effects of blindfolding all eyes. Furthermore, because enlarged lateral eyes in other spiders are involved with increased sensitivity in low light, we hypothesized that the effects of PLE occlusion would be particularly severe in dim light.

Methods

Experimental Design

We conducted a series of lab behavioral experiments testing if and how flattie spider strike dynamics change under a variety of conditions. We used a fully crossed experimental design, varying light environment and occlusion of eyes. Under these manipulations we used high speed video to measure the speed and directionality of strikes at prey. Experimental details are given below.

Animals

Spiders from the *Selenopis debilis* group and *Selenopis submaculosus* were collected, housed in plastic vials, and fed every other day; they were fed either fruit flies or crickets depending on availability and spider size. Spiders are identified as being part of the *Selenopis debilis* group rather than to species as species boundaries are unclear in this clade (Crews, 2011). Due to logistical constraints we used two congener species for our study and used individual spiders in multiple trials. All specimens are deposited in the California Academy of Sciences collection. Flightless *Drosophila hydei* flies were used as prey in all experimental trials.

Arena

Spiders, unfed for 3 days preceding each trial, were placed in a 20×30×10 cm tall rectangular box with a white paper bottom and transparent plexiglass sides. Five to 10 flies were then added to the arena and the trial continued until a fly was captured. We recorded the period from strike to capture from above at 700 fps using a high-speed camera (HiSpec1, FasTec Imaging, San Diego, CA, USA). Calibrations for each video were made using Lego® bricks at the start of each date of trials or if the camera was moved during the trials and needed to be re-calibrated. Experiments were conducted from 28 Sep 2017 to 21 Nov 2019.

Experimental Procedure

Trials in "bright" treatments (n= 23) were illuminated with both LED (visual and infrared light) and incandescent light, while "dim" treatments (n = 23) were illuminated only with infrared LED lights and low levels of ambient light. The luminous intensities of sidewelling irradiance with wavelengths between 300nm and 750nm were 4249.9 $\mu W/cm^2$ for the "bright" treatment and 176.7 $\mu W/cm^2$ for the "dim" treatment. Spectra are shown in **Fig. 3.1**.

Spiders in the "PLE-blindfold" treatments (n = 13) had their posterior lateral eyes occluded with opaque, dental silicone (Delikit Light Body, Fast Set 2 VPS Impression Material) **Fig. 3.2(b)**. No eyes but the PLEs were occluded with the silicone. All eyes were occluded for spiders in the "all-blindfold" treatment using the same procedure (n = 14). Spiders in blindfold treatments were anesthetized with CO_2 before the silicone was applied and were given a day to recover before participating in experimental trials. Control spiders **Fig. 3.2(a)** were not blindfolded, handled, or anesthetized (n = 19).

A strike was defined as the interval between the initiation of the spider's movement and the moment its chelicerae made contact with the fly. During some trials the fly was kicked by the spider, and therefore the spider initially missed the fly, but ran after it or started a new strike to catch the fly (and always did so successfully). In these instances, we calculated the strike interval as the maneuvering phase *sensu* Zeng and Crews (2018), which was defined as the (initial) interval during which the spider performs one continuous rotation and finishes with completed deceleration of both translation and rotation.

The distance of the fly at the start of the strike was measured from the spider's center of mass (COM) to the closest part of the fly's body (not including the legs); this was usually the fly's head as the flies that the spiders attacked tended to be walking toward the spider. The COM was based on Zeng and Crews (2018). Measurements were made using ImageJ (Rueden et al., 2017). The angle of the fly at the beginning of the maneuver was made by measuring the angle defined by 3 points: one at the spider COM, one between the anterior median eyes, and one at the nearest part of the fly (excluding the legs).

Statistics

All data were analyzed with R statistical software (R Core Team, 2014). We used multiple linear regression to determine how the duration of a strike, angular and linear speed, and angular and linear position of the fly at strike-initiation were affected by each of the treatments. We did not find any differences between the two species in their behaviors in this study, so we pooled them for analysis. To construct plots of the variables and effects of treatments, we used ggplot2 (Gómez-Rubio, 2017).

To examine correlations between variables and visualize them per treatment, we used corrplot (Wei, 2017) and Hmisc (Harrell, 2019) **Fig. 3.3**. To visualize and analyze angular position and linear distance, we used Python, including the NumPy (Oliphant and Millma, 2006) and SciPy (Virtanen et al., 2020) libraries, to access pandas (McKinney and Team, 2015) and matplotlib (Hunter, 2007).

Results

Directionality

Light condition and eye painting both affected the directionality of the flatties' strike maneuvers. Strikes involved smaller degrees of turning under dim light. Under bright light conditions the prey flies were angularly positioned more towards the back of the spider at strike initiation ($t_{40} = -2.383$, $p = 0.022$). The range of these fly approach angles was smaller in dim light than in bright light (range 171 degrees for bright treatments and 127 degrees for dim treatments). Fly approach angle was also decreased significantly when all eyes were occluded ($t_{40} = -3.700$, $p < 0.001$), but not when only posterior lateral eyes (PLEs) were covered ($t_{40} = -0.082$, $p = 0.934$). These findings suggest that vision is important in Selenopid strike behavior, and that this behavior is not dependent on vision from the large PLEs alone**. Fig3.11** and **Fig3.12** show strike directionality through the distribution of fly positions at strike initiation, grouped by blindfold treatment and light treatment, respectively. The restriction of directionality for all-blind spiders under dim light was less than the sum of effects of these two treatments separately ($t_{40} = 2.354$, $p = 0.023$), suggesting the effects of these two treatments both result from the same mechanism (presumably the removal of vision).

Strike Speed

Strike speed was also affected by experimental manipulations, both in terms of angular speed and the total duration of the strike. Angular speed is fundamentally dependent on strike duration, but both are considered as they show slightly different patterns. Total strike duration was longer for fully blindfolded spiders ($t_{40} = 3.606$, $p < 0.001$), whereas strike duration was not significantly different between PLE-blind spiders and control ($t_{40} = 1.635$, $p = 0.110$). We did not find a difference in strike duration between light treatments, with strike maneuvers taking similar amounts of time in both bright and dim light ($t_{40} = 1.240$, $p = 0.222$).

Angular speed, however, was slower in dim light ($t_{40} = -3.242$, $p = 0.002$). As total duration was not different between light levels, this difference in angular speed must be due to the relatively larger angles turned under bright light. Angular speed was also slower for *both* blindfold conditions; all-blind and PLE-blind treatments both had lower angular speeds relative to unpainted spiders (All-blind $t_{40} = -4.277$ $p < 0.001$; PLE-blind $t_{40} = -2.029$, $p = 0.049$). There was a significant interaction effect on angular speed between light treatment and both PLE-blind treatments ($t_{40} = 2.312$, $p = 0.026$) and all-blind treatments ($t_{40} = 2.173$, $p = 0.036$). This interaction happened in the opposite direction of the manipulations alone, such that the combined effect of dim light and blindfolding slowed down angular speed less than would be predicted from the individual effects.

Discussion

Though the full sensory milieu involved in Selenopid prey capture remains to be explored, our results suggest that vision plays an important role. Reduced visual information affected the way in which flattie spiders struck their prey, slowing strikes and limiting their characteristic 360° angular range. The effects of dim light environments were similar, but not identical, to those of blindfolding the eyes. We found mixed and inconclusive evidence that the large and rear-facing posterior lateral eyes (PLEs) play a special role in directing prey capture behavior.

Zeng and Crews (2018) suggest that the PLEs are integral to flattie spiders' 360° field of view. This led us to hypothesize that the PLEs would be particularly important in guiding strikes towards prey behind the spider. This hypothesis predicted that flies attacked by PLE-blinded spiders would be more anterior to the spider as compared to the prey of spiders without visual occlusion. In other words, we predicted that strike directionality would be restricted for spiders without access to PLE vision. In light of this hypothesis, we were surprised to find that PLE occlusion alone did not affect the angle of attacked prey. This finding was especially surprising considering that the more generalized visual restrictions of dim light or of total blindfolding did in fact reduce have such an effect. In isolation, these results seem to suggest that PLE vision is not important in striking posteriorly positioned prey. However, we did find that spiders turned around more slowly when their PLEs were blindfolded, supporting our original hypothesis about the relative importance of the PLEs. The hypothetical special role of PLE vision thus remains a subject for potential future study.

While the role of PLE vision in particular in prey capture is not fully resolved, we did find convincing evidence that vision in general plays an important role. Blindfolding of all eyes reduced strike speed and restricted strike directionality. Dim light conditions also restricted strike directionality but had a more complex effect on strike speed. Angular (turning) speed was slower under dim light, but the total durations of strikes were not statistically different between dim and bright light conditions. This disparity is best explained by considering that dimly lit spiders struck at flies that were relatively towards their anterior, so quick turning speeds would be less relevant for catching this prey.

That both blindfolding and light dimming affected strike dynamics in similar ways supports the hypothesis that vision is used in prey capture by flatties. However, we also discovered that vision is not strictly necessary for flattie prey capture; blindfolded spiders under dim light were still able to catch prey despite the lack of visual information. Other senses then are likely also involved in detecting and locating the prey, such as tactile senses or detection of airflow with trichobothria (Reissland and Görner, 1985). The tactile hair sensilla of spiders are sensitive to touch and can alert the spider to the presence of a prey fly when the two animals make physical contact (Barth, 2015). Trichobothria can detect prey by bending in response to changes in airflow caused by the prey's motion (Humphrey and Barth, 2007). Though it would be more difficult to test, the role of these senses in flattie prey capture could provide a very interesting topic of investigation.

Flattie spiders are thought to be primarily nocturnal sit-and-wait predators, so dim light treatments may be more indicative of their natural prey-capture conditions (Crews and Harvey, 2011; Zeng and Crews, 2018). Considering previous findings on these spiders' great aptitude for capturing prey that approach from behind, our findings of restricted strike directionality under dim light provide an interesting contrast. In theory, being able to strike prey from any possible angle should increase the total area in which prey can be captured, potentially maximizing hunting effectiveness. It may be that nocturnal lighting conditions in nature are sufficiently bright often enough to still allow the use of vision in prey capture by flatties (Johnsen et al., 2006).

This study tested for effects of visual restriction on the manner and specifics of a strike, but we did not test for what effects if any, vision or PLE usage has on the probability of prey capture success. While the reduction of speed and directionality under manipulated conditions may be indicative of diminished prey capture performance, further studies are needed to determine if this is truly the case. Furthermore, we still do not know if vision is the primary sense used to guide prey capture in flattie spiders; other senses such as trichobothria, tactile, or vibratory senses may later be found to be as or more important than vision (Barth, 2015; Forster, 1982; Reissland and Görner, 1985; Shamble et al., 2016). Flatties may be similar to the wandering spider *Cupiennius salei*, whose prey capture behavior relies more heavily on detecting substrate vibrations and airflow than it does on vision (Fenk et al., 2010).

This experiment is the first to examine how vision in Selenopid spiders, including PLE vision specifically, can be used to guide their behavior. Yet, very much of the mystery of the enlarged PLEs remains unsolved and unaddressed. The findings of multiple non-effects of blindfolding PLEs alone suggest that either these eyes are used for something other than prey capture, are employed in prey capture in a way that we did not measure, or they are non-adaptive structures. For example, some dung beetle eyes are specialized for navigating using the dim light of the Milky Way (Dacke et al., 2013; Foster et al., 2017). As another example, the eyes of some blowflies are specifically structured to detect potential mates (Van Hateren et al., 1989). It may be that these spiders use vision in some instances but not others, like tiger beetles which are typically visual but become blind during rapid movement (Riggins and Hoback, 2005). The other three pairs of eyes may also provide robustness to different conditions, filling in for the PLEs when they are occluded. This would be similar to how fish can use vision as a backup sense when increased levels of dissolved CO_2 remove their ability to communicate chemically (Lönnstedt et al., 2013).

Future studies can address other potential functions of the PLEs, either for other aspects of prey capture or for other behaviors such as predator avoidance, mate choice, or habitat choice. Studies can also assess the costs of these eyes - large eyes tend to be costly tissues that can be lost with disuse (Porter and Sumner-Rooney, 2018). The concept of matched filters, that sensory abilities are tuned to the type of information necessary for an animal, predicts that these eyes would not persist if they were not relevant to the sensory needs of the spider (Warrant, 2016). Animal sensory morphology is often linked strongly with behavior, but it is not yet broadly known how strong or ubiquitous this matching is throughout animals (von der Emde and Warrant, 2015). We know of many examples where the animal world seems finely tuned to its sensory needs, but the ubiquity of this pattern remains to be further explored. While perfectly tuned animal senses provide striking examples of evolution at its finest and most beautiful, the study of animal behavior frequently exposes the fact that evolution does not always produce the perfection we might expect.

Acknowledgements

This work would not be possible without the Bob Full lab and CiBER.

Figures

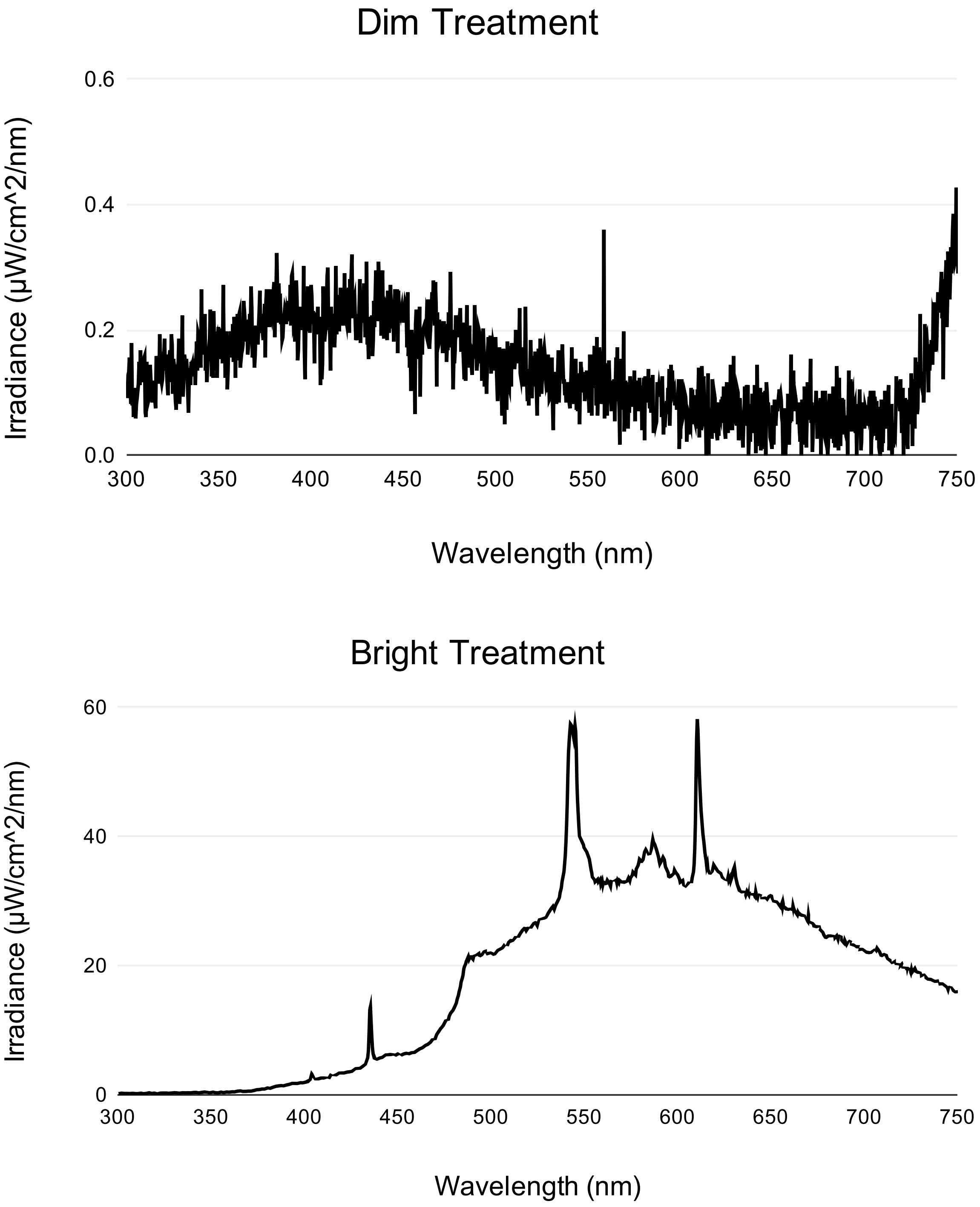

Fig. 3.1. Downwelling irradiance (µW/cm^2/nm) of light treatments. Infrared light is standard across treatments (for filming) and is not believed to be visible to spiders. Spectral shape is not preserved across treatments. Note vertical axis – the scale for the bright treatment is 100x the scale for the dim treatment.

Fig. 3.2 (a). *Selenopis debilis* gp. species with posterior lateral eye (PLE) visible (red arrow points to right PLE). Photo credit Yu Zeng. Adapted from (Knight, 2018).

Fig. 3.2 (b). *Selenopis debilis* gp. species with posterior lateral eyes (PLEs) covered with dental silicone (red arrows point to orange dots).

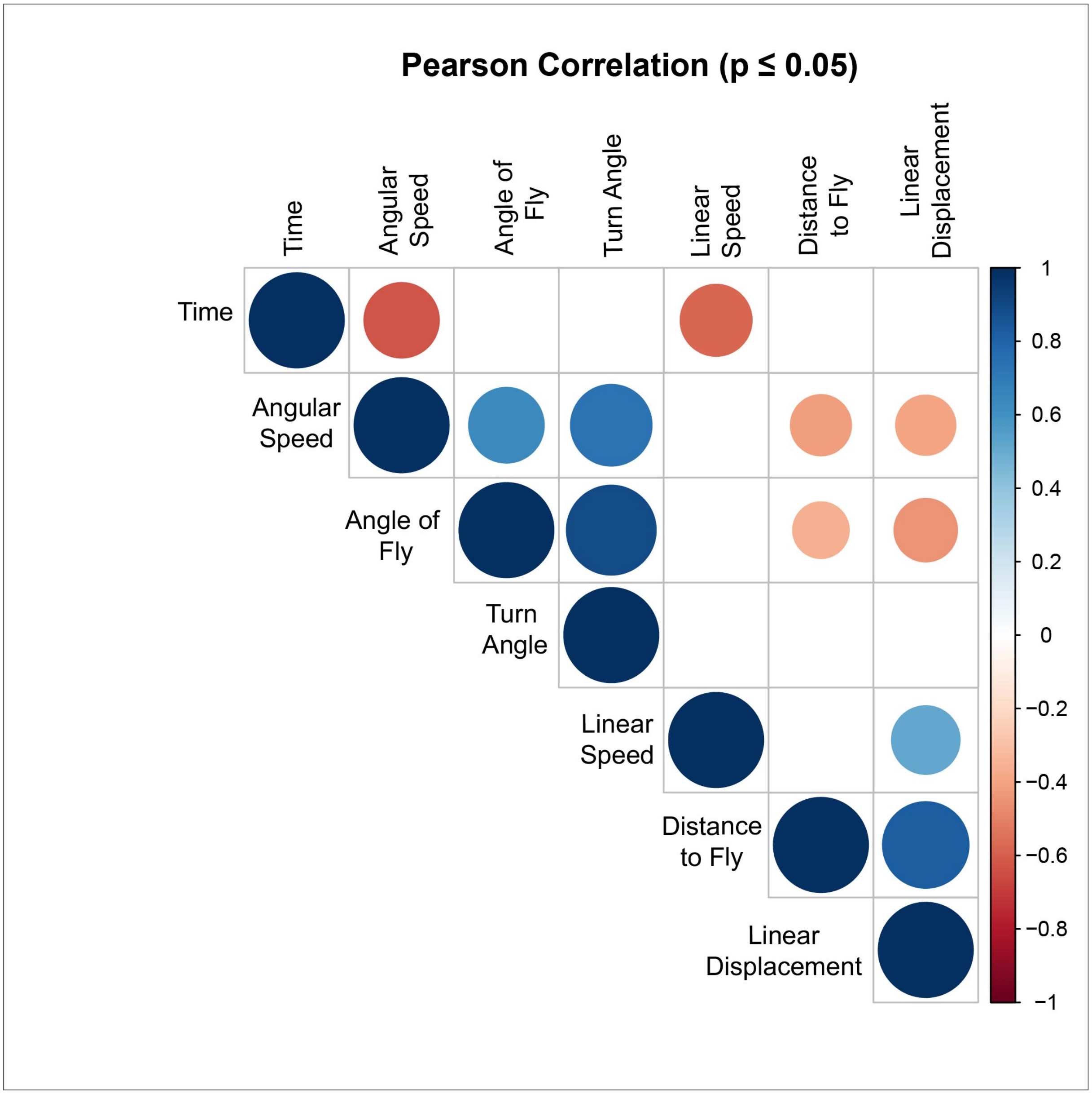

Fig. 3.3 Pearson correlations between measured variables. Only those with statistically significant (p≤0.05) linear regressions are shown.

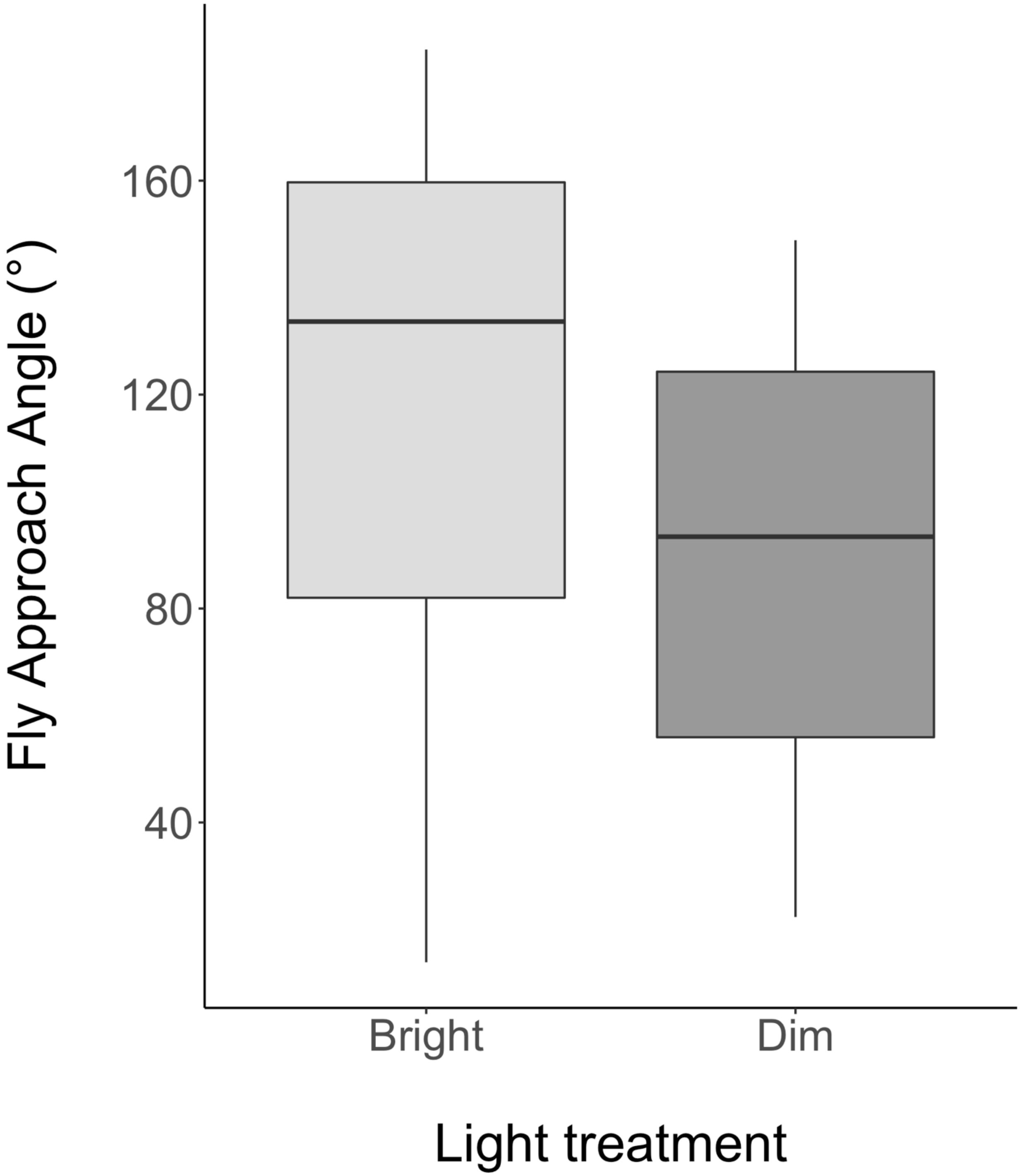

Fig. 3.4 Angle of fly relative to spider at beginning of strike, grouped by light treatment. A 0-degree angle means the fly is directly in front of the spider, and a 180-degree angle means the fly is directly behind the spider.

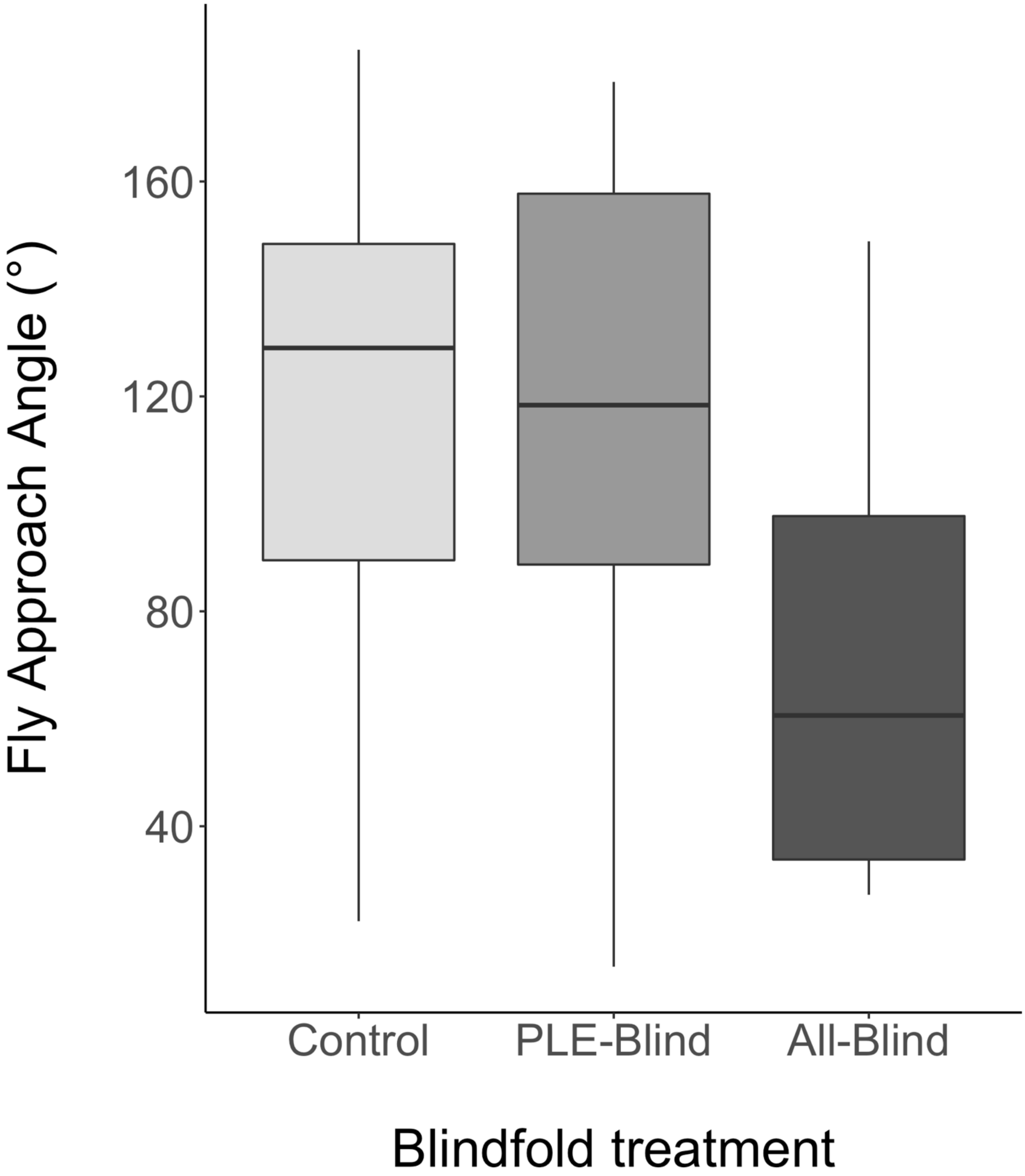

Fig. 3.5 Angle of fly relative to spider at beginning of strike, by painting treatment. A 0-degree angle means the fly is directly in front of the spider, and a 180-degree angle means the fly is directly behind the spider.

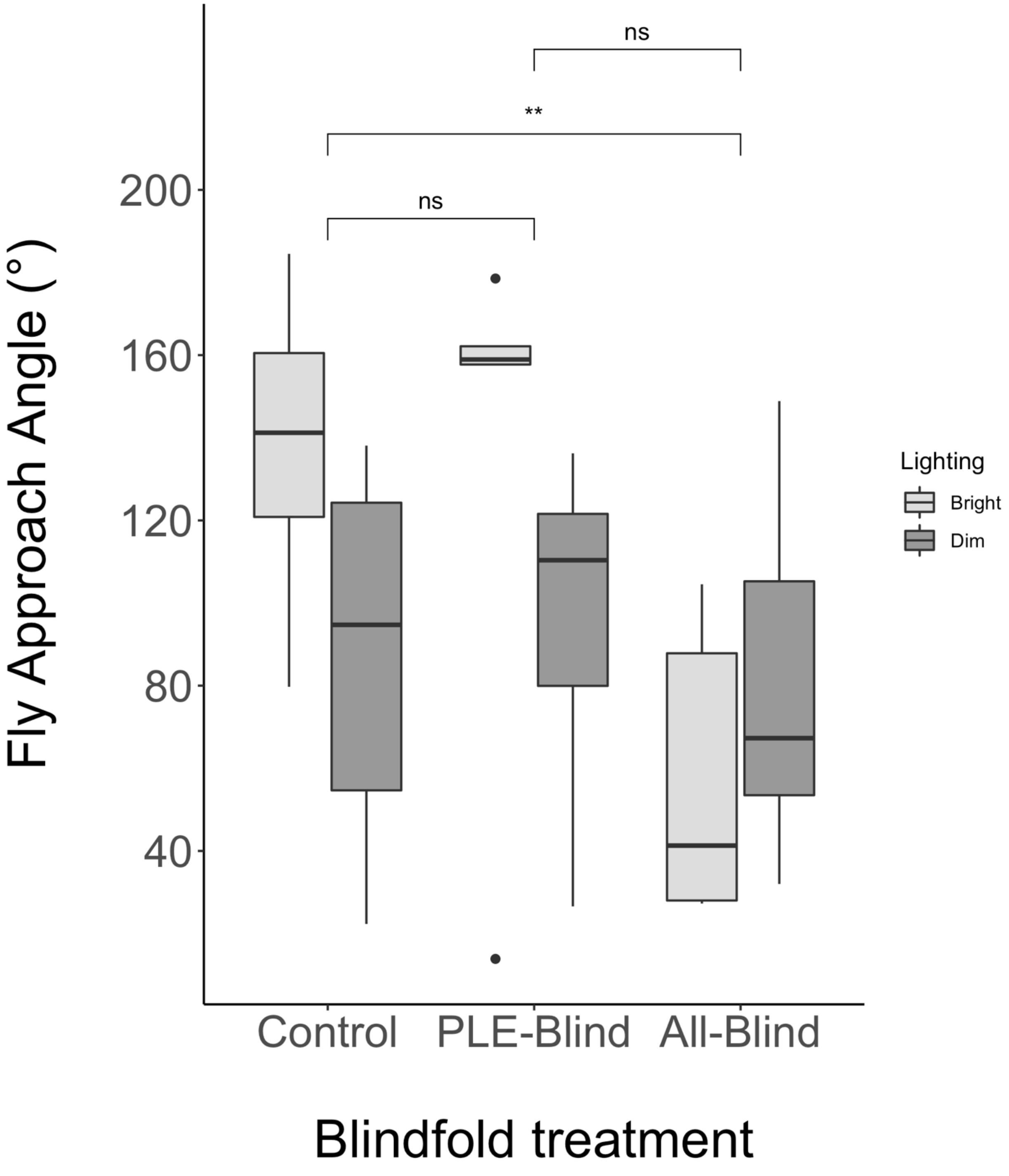

Fig. 3.6 Angle of fly relative to spider at beginning of strike, by both light and painting treatment. A 0-degree angle means the fly is directly in front of the spider, and a 180-degree angle means the fly is directly behind the spider.

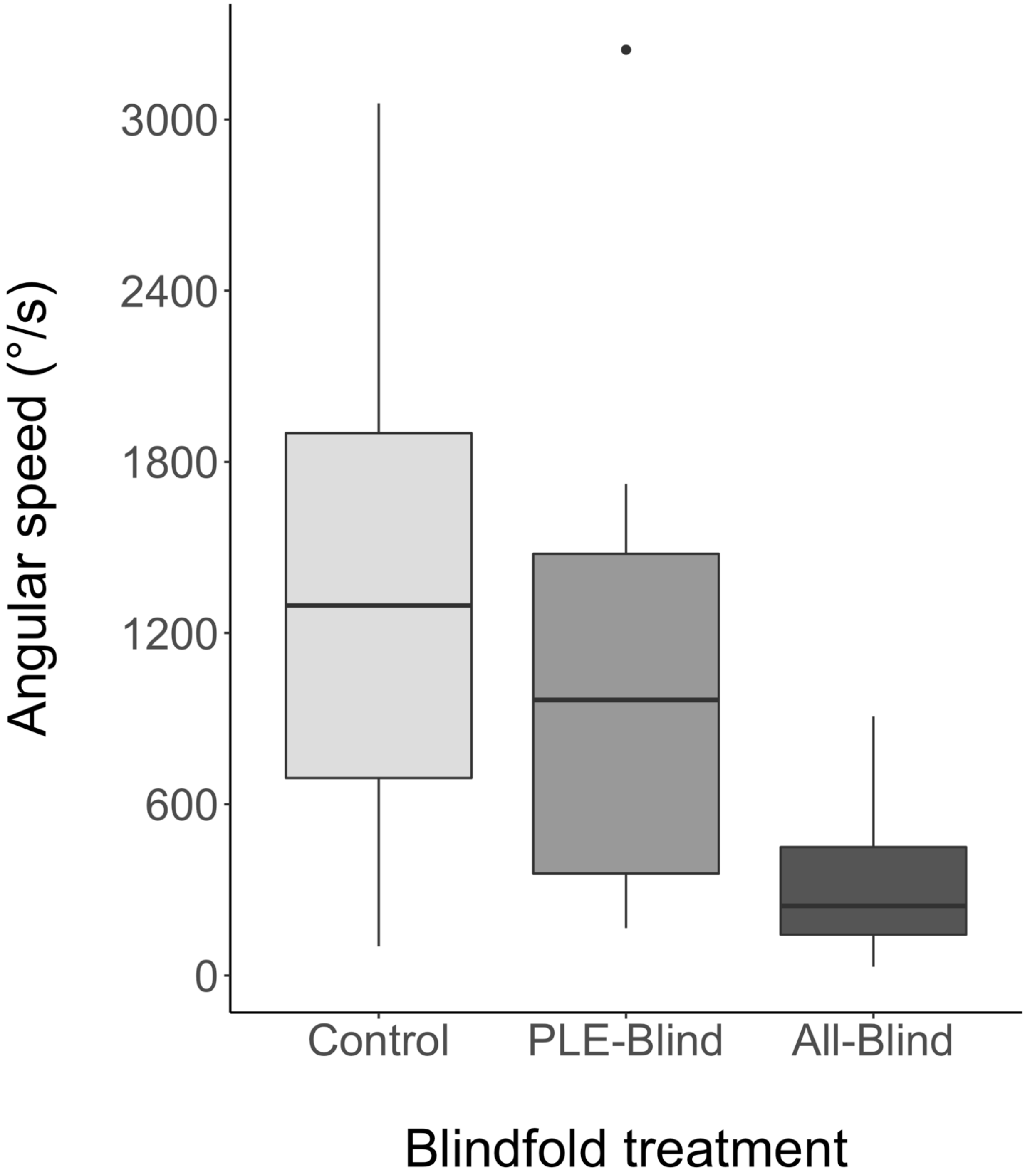

Fig. 3.7 Angular speed of spider during strike maneuver, grouped by blindfolding treatment.

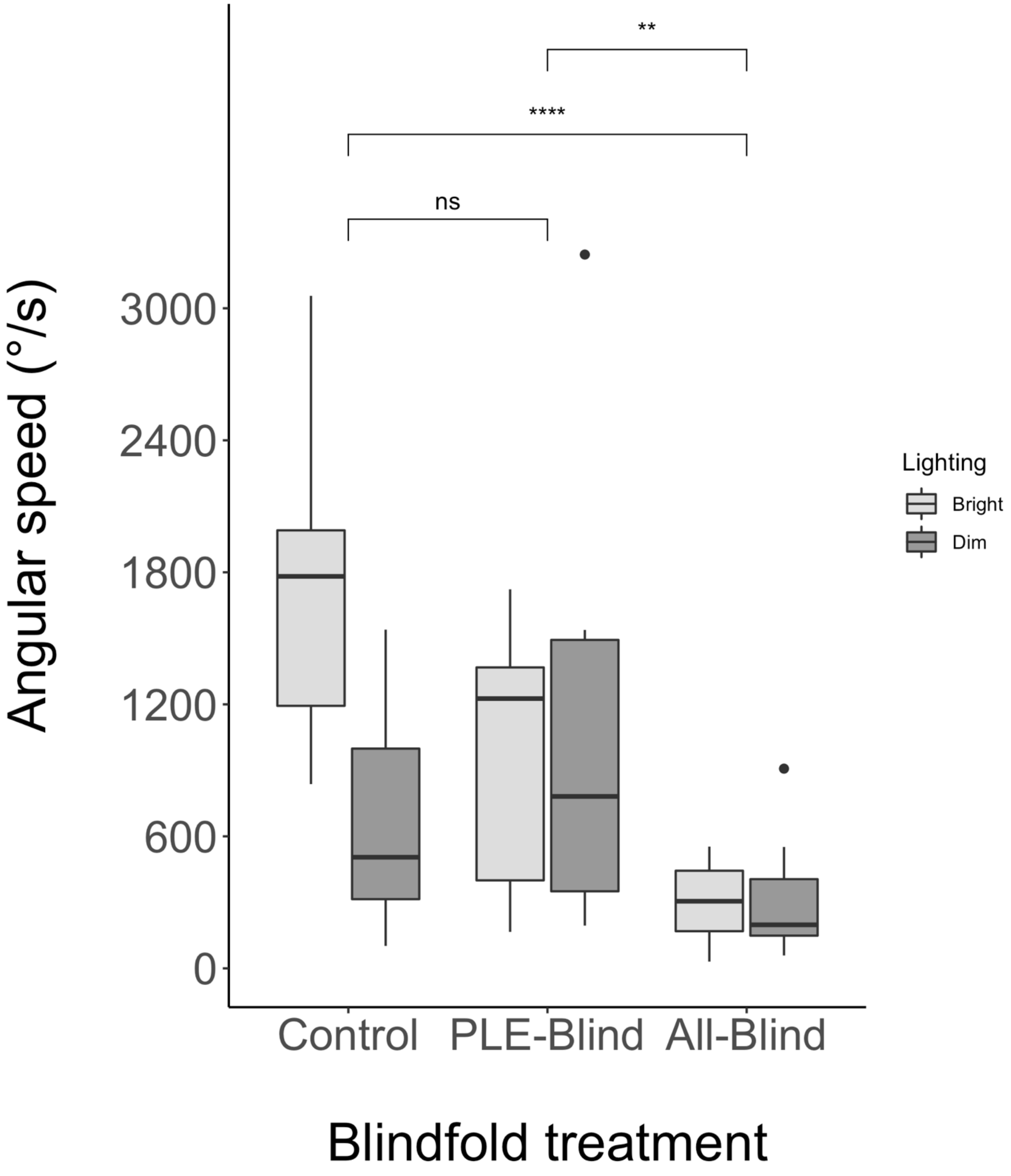

Fig. 3.8 Angular speed of spider during strike maneuver, grouped by light and blindfolding treatment.

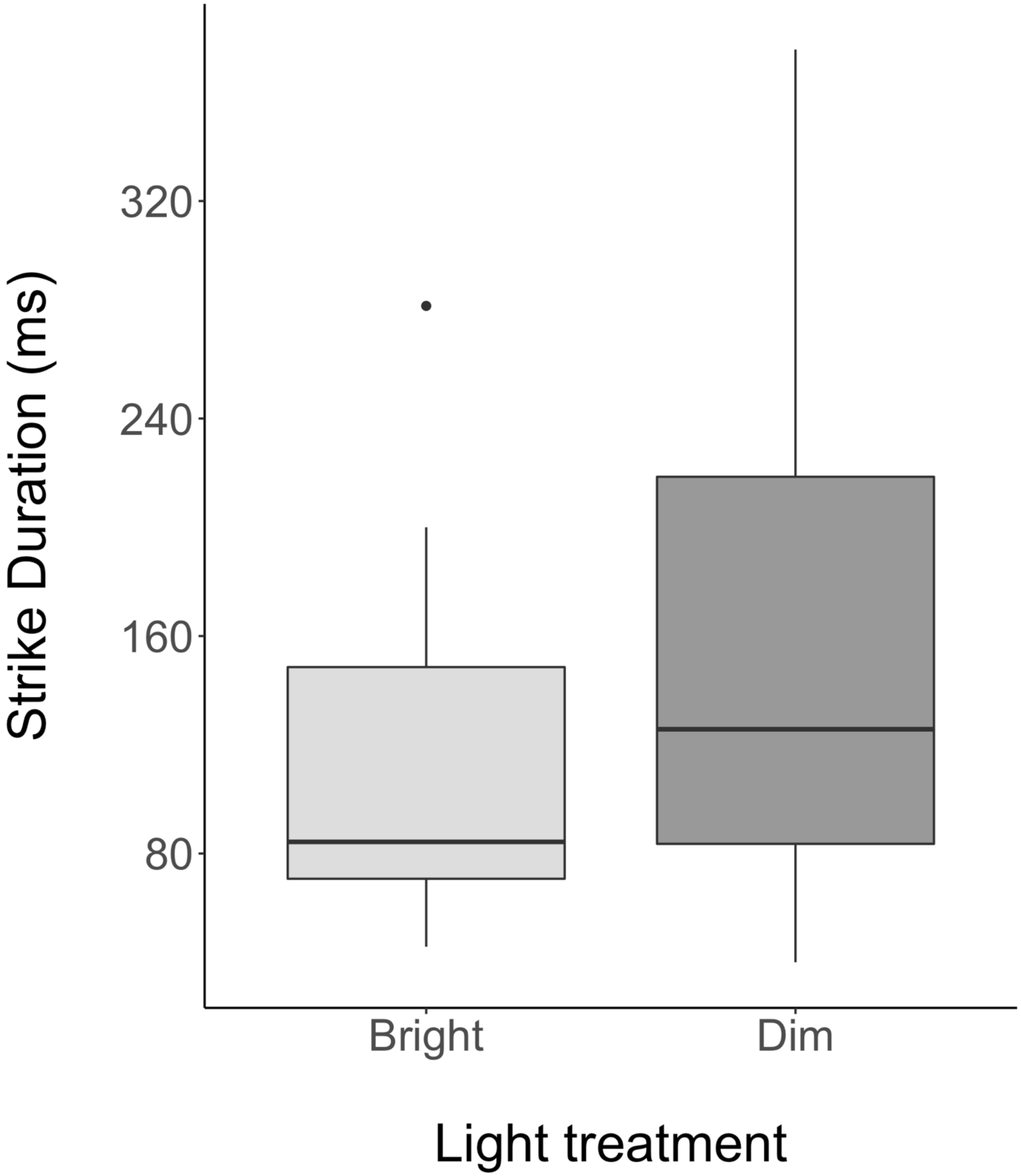

Fig. 3.9 Duration of strike maneuver. Grouped by light treatment.

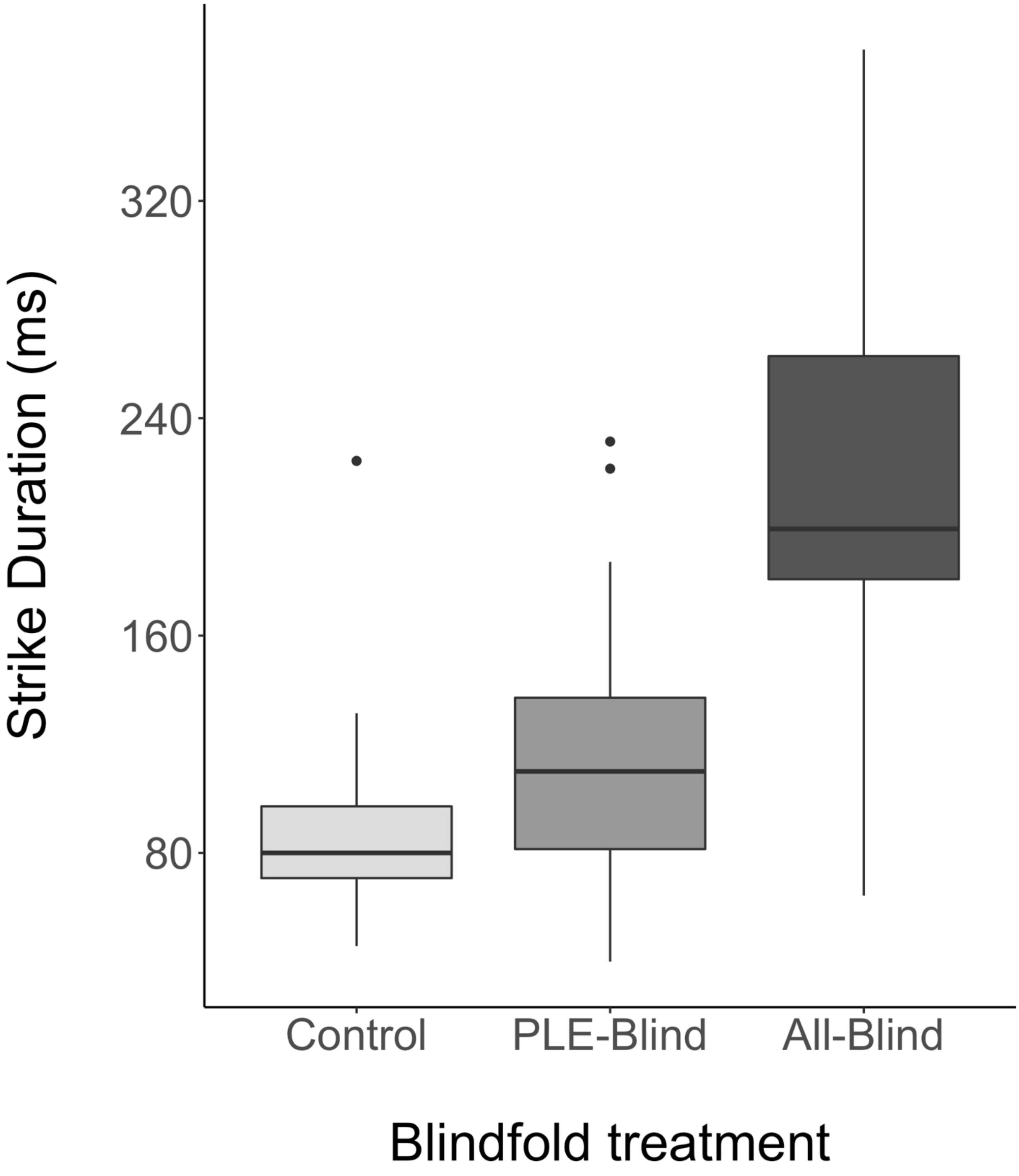

Fig. 3.10 Duration of strike maneuver. Grouped by blindfold treatment.

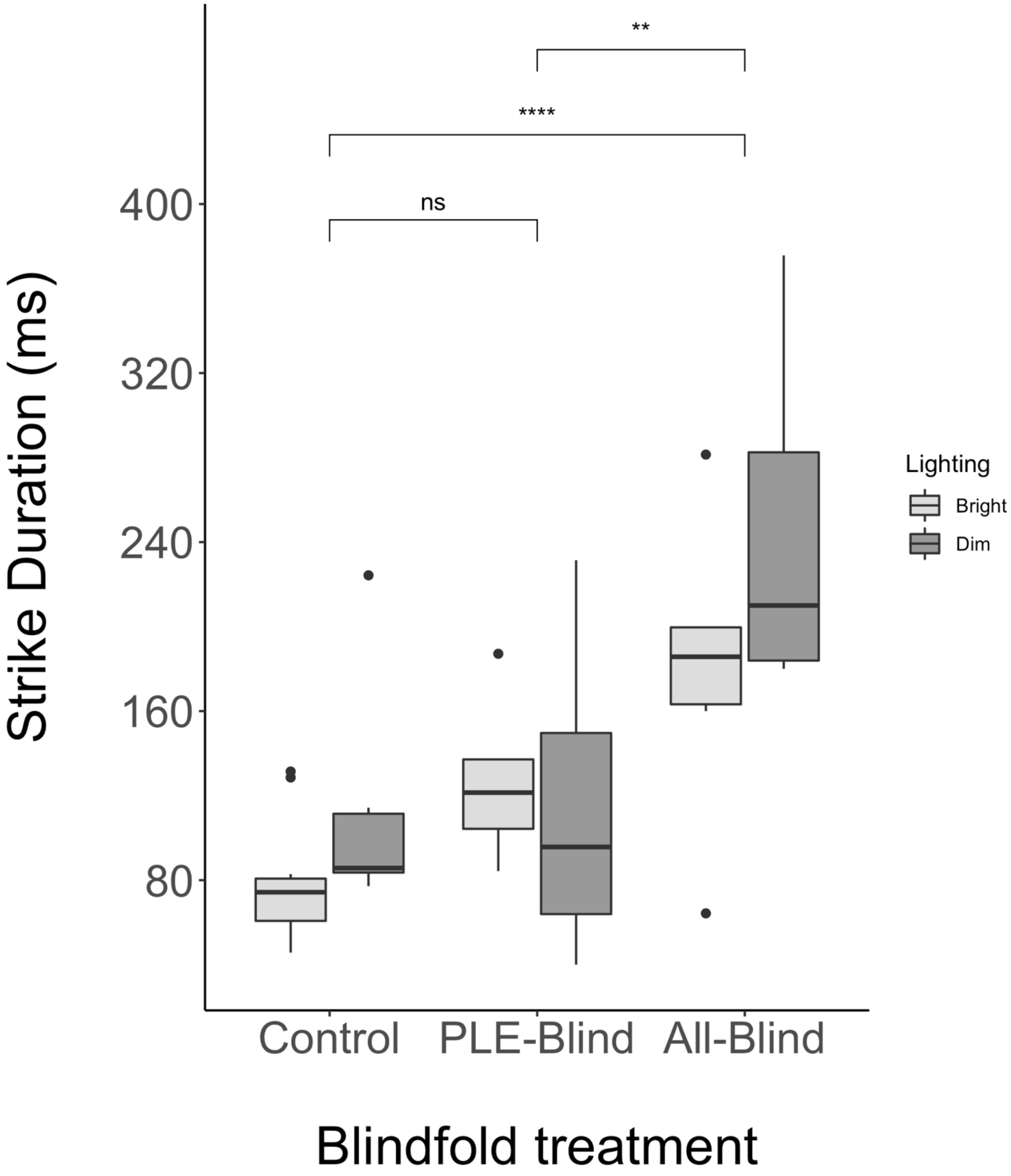

Fig. 3.11 Duration of strike maneuver, by light and blindfold treatment.

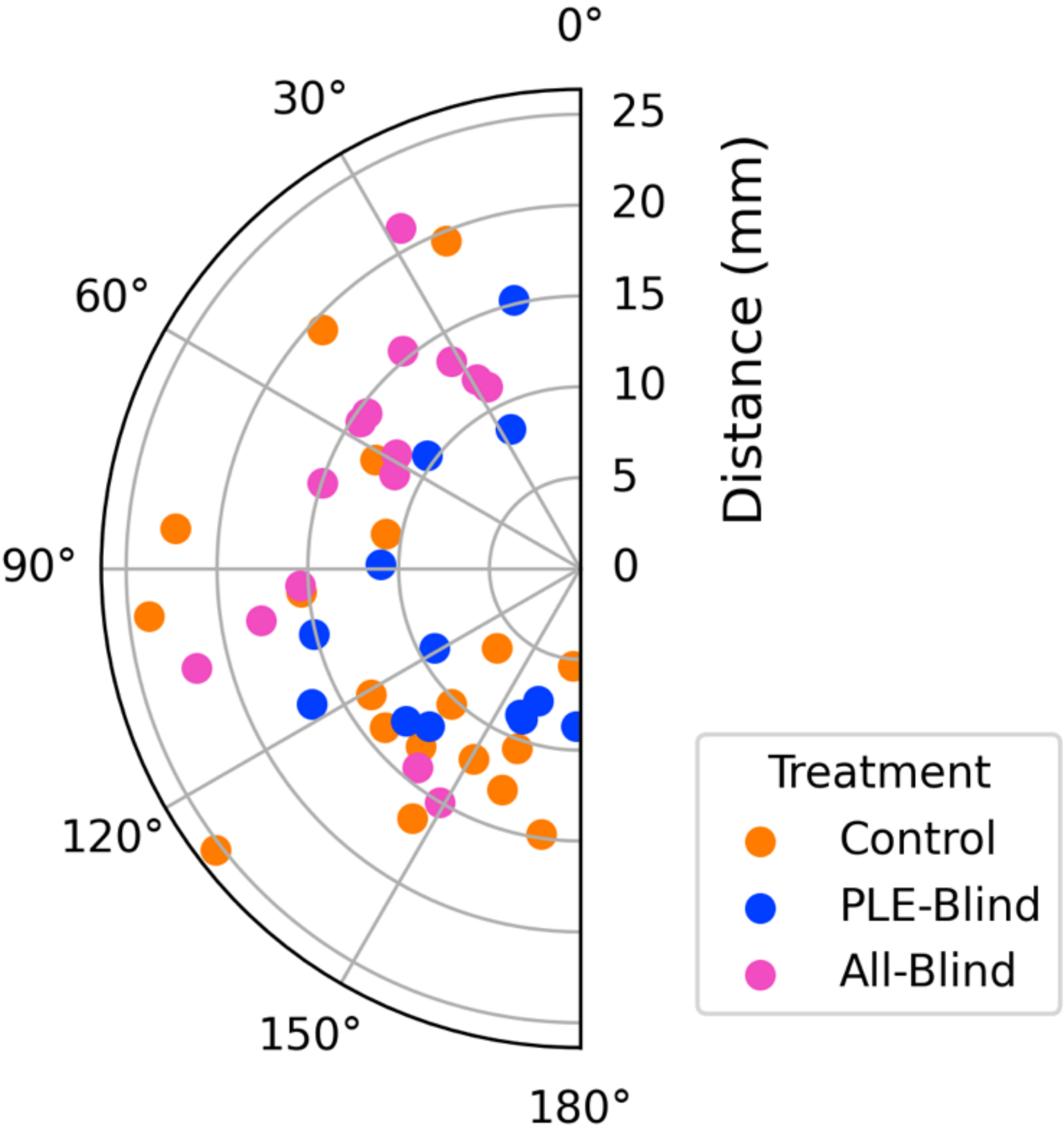

Fig. 3.12 Relative position of the fly to the spider at initiation of strike, including distance and angle. Grouped by painting treatment.

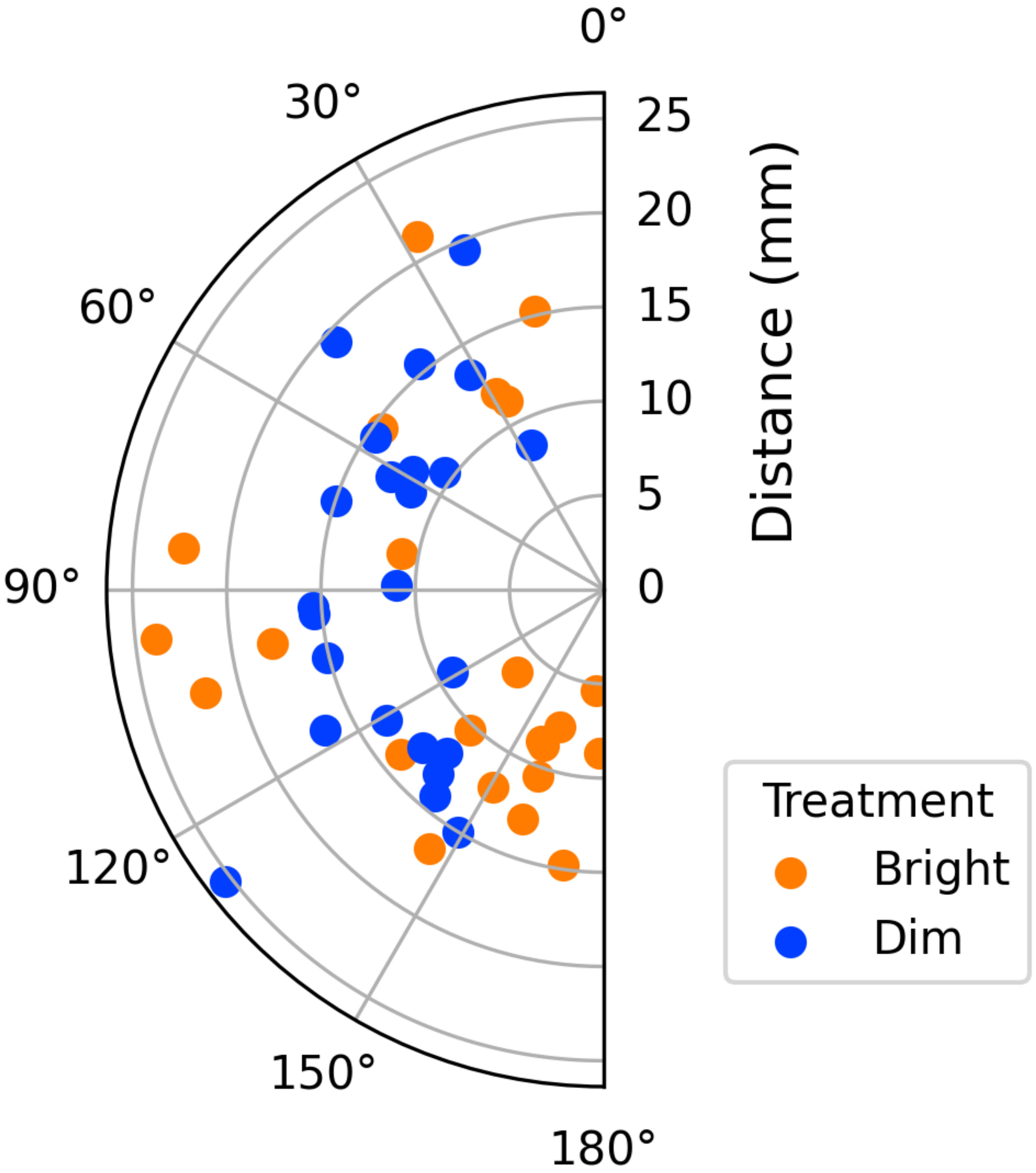

Fig. 3.13 Relative position of the fly to the spider at initiation of strike, including distance and angle. Grouped by light treatment.

	Duration	Speed (linear)	Speed (rotational)	Approach angle	Distance to fly
Light (Dim)	33.28	-1.49	-983.80***	-48.55**	3.70*
	(26.85)	(2.26)	(303.43)	(20.37)	(1.97)
PLE blindfolded	49.12	-10.87***	-689.11**	-1.88	-3.50
	(30.05)	(2.53)	(339.61)	(22.80)	(2.21)
All blindfolded	101.79***	-7.77***	-1,364.28***	-79.24***	3.10
	(28.23)	(2.38)	(319.00)	(21.42)	(2.07)
Light by PLE-blindfold	-43.71	10.10***	1,095.24**	11.23	-1.56
	(41.91)	(3.53)	(473.67)	(31.80)	(3.08)
Light by All-blindfold	26.66	-1.51	997.51**	72.54**	-6.14**
	(40.63)	(3.42)	(459.13)	(30.82)	(2.98)
Intercept	77.74***	16.22***	1,665.61***	136.12***	13.32***
	(16.30)	(1.37)	(184.18)	(12.36)	(1.20)

*p<0.1; **p<0.05; ***p<0.01

Table. 3.1 Linear model coefficients and significance values for experimental manipulations.

Conclusion

Beside the more readily apparent themes of spiders, prey capture and light conditions, a more subtle theme pervades all of the above studies: surprise. In each of the above chapters are results that differed greatly from my predictions, ranging from simply unexpected to borderline shocking. I was in near disbelief upon discovering that *Habronattus formosus* jumping spiders would never catch a prey insect in complete darkness. Further, given my notions about their diurnality, I was also surprised to see that these spiders could hunt in such dim light. When I designed the experiment in Chapter 2, I thought that principal eyes might only be important in bright-light prey capture but not in dim light; my findings were almost the exact opposite of my expectations. All of these experiences with *H. formosus* set me up for even further surprise, as the Selenopids' largest pair of eyes did not seem to have the function I thought it would.

Before getting into specifics of how my research fits into the broader context of sensory behavioral ecology, I want to comment on what it reinforced to me more generally: **Despite our informed guesses, we barely have any idea about how animals work.** I myself am often lulled into a false sense of complacency, thinking that we can easily extrapolate findings from a small subset of animals, or that we can make safe assumptions from our understanding of how things are supposed to work. While our understanding of nature can grow broader, more useful and more robust with each study we conduct, we should not lose sight of the very stark reality that animal behavior is far more complicated than we will ever fully understand. I am far from the first person to put forward this well-known idea, but I mention it now to give weight to the personal understanding and internalization of this concept which I gained through the experience of conducting this research.

So then what broader conclusions, if any, can be drawn from my findings? I believe that most of all my research provides one more point of evidence that we should verify our assumptions through actual behavioral experiments. Most animals will not abide by the laws of nature we think we have discovered. The elegant patterns that have been found throughout the history of biology often end up being far more limited in scope than those searching for general patterns would hope. This could either be because we haven't searched widely enough yet, or because these laws are nonexistent or ever-changing. If we ever find out the answer to this meta-question, I'm confident it will be well after my lifetime.

In particular my findings show that apparently specialized structures or species can have more generalist function than they would seem to. The telescopic principal eyes of jumping spiders have so many characteristics associated with highly acute vision, many of which are at the direct expense of sensitivity, and yet these very eyes are required for prey capture to occur in dim light. And on a larger scale, the day-active jumping spiders who possess these eyes are surprisingly able to see and capture prey in conditions vastly darker than the bright sunlight in which they are most often found. Furthermore, the enlarged and backwards-facing eyes of flattie spiders turned out not to be key to the visual component of guiding strikes behind the spider.

For me, at least, it is more fun to formulate hypotheses than to actually test them. The process of storytelling is much easier than the often-monotonous grind of getting to the bottom of a scientific question. This being said, whenever I get over my reluctance to do a necessary but boring-seeming part of an experiment, more often than not I am rewarded with unexpected results more interesting than anything I had been setting out to test. The whole scope of this dissertation is actually the result of a fortunate failure; I began studying prey capture as a backup once my spiders refused to mate in the lab!

If anyone reading this dissertation is planning on following in my footsteps, I have a few pieces of advice. They are as follows:

- Don't collect jumping spiders with an aspirator. They die from it a lot.
- If you have a good collecting day and there are tons of spiders out, don't leave (even if you're hungry). You might not get another day like that all season.
- Bring swimming clothes whenever you go collecting.
- Be formal when setting up preliminary experiments. That can turn pilot data into real data.
- Read a lot about how light works before you try and do any experiments with light. I was saying above how animals don't behave like you think they would - light puts animals to shame in that regard. Get comfortable using a radiospectrometer.
- Set up experiments in such a way that it's easy to redo, so that if something gets knocked over or if the video doesn't record you don't lose the whole data point.
- Set up your hypotheses and experiments so that they'll be interesting no matter what the results are.
- Don't use the "sex" of your spider in your analyses unless there's a meaningful scientific rationale to do so, you can state that rationale explicitly, and it's related to the question you're trying to answer.
- Write down your methods section on the same day (or before) you conduct your experiments. It makes your life so much easier later.
- Think about how many individuals your experiments will need to have adequate sample sizes for your questions, and make sure that you'll actually be able to catch that many (and factor in that many may die before you get to experiment on them).
- Let yourself feel sad about collecting. Sometimes it's worth it, but it's always a sad thing to have to take an animal out of its habitat.
- If you're arachnophobic you can do exposure therapy on yourself. It really works, and I did it successfully!

Last of all, if you're thinking about studying spiders you should do it. Spiders display an incredible array of sensory abilities. This fact, combined with the diversity of prey capture strategies in spiders and the concomitant diversity of their sensory systems, make this order of arachnids an excellent system for behavioral studies of sensory ecology. Additionally, the way in which spiders subfunctionalize their vision across their pairs of eyes make them particularly well suited for the behavioral study of vision. Despite their small eyes and small brains, spiders are able to acquire and process the sensory information to perform tasks that can be quite complicated. These stark limitations also make them great subjects of study to move towards an understanding of the sensory ecology of animals overall. Though it’s most obvious in the tiny and fascinating world of spiders, we animals are all forced to meet our sensory needs only within what is allowed by the constraints of physics, evolution, development, and ecology.

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