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Observational Learning in the Jumping Spider *Phidippus audax*

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OBSERVATIONAL LEARNING IN THE JUMPING SPIDER *PHIDIPPUS AUDAX*

By

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OBSERVATIONAL LEARNING IN THE JUMPING SPIDER *PHIDIPPUS AUDAX*

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Observational learning is a complex form of learning most frequently studied in social vertebrates. However, evidence for social learning exists in several invertebrate species Evidence of invertebrate observational learning also exists, though to a lesser extent. This study addresses observational learning in a jumping spider (*Phidippus audax*) through video playback. My results suggest that while observational learning is occurring, the exact mechanism in use remains unclear. Spiders that saw a conspecific satiate itself on a prey item readily attacked a similar prey item when exposed to a live prey item. However, spiders exposed to a conspecific rejecting or in the absence of a prey item were much more cautious when exposed to a live prey item. While virtually all spiders did eventually attack, a significant increase was found in the latency to the attack. No other groups demonstrated deviated from the behavior of the control group. My data suggest that observational learning may be present in a more diverse array of taxa than is held in traditional views of social learning, including highly asocial invertebrates such as spiders.

ACKNOWLEDGEMENTS

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Chapter 1: Introduction

Animal learning has been a major focus of researchers for more than a century. In spite of the amount of work done on the subject, learning in non-humans remains a relevant topic to both the modern researcher and the layman. Animal learning may be broadly defined as a persistent change from the normal or instinctive behavior of an animal in response to a stimulus. Like the definition, the field of animal learning is also broad in scope, and no single area of learning research can successfully account for all known types of learning. Learning about the quality of food resources, for example, can directly affect an animal's fitness by altering amount of energy it has available for reproduction (Egas, Norde, and Sabelis 2003). However, research on food acquisition may not inform us about the animal's mate choice preferences, nor how they are learned.

The types of animal learning under scrutiny by the scientific community vary greatly depending upon which topic is currently considered the most interesting. Learning plasticity (van Praag *et al.* 1999), contextual learning (Skow & Jakob 2005), and social learning (Chivers & Ferrari 2014) are just a few examples of the types of animal learning that have been popular in the literature. Many types of animal learning have become increasingly specialized over recent decades as individual researchers have continued to narrow their experimental focus. However, social learning has remained relatively broad. Social learning, or the ability to learn from another animal, has been well established in several animal groups. Taxa including fishes (Arai *et al*. 2007, Thonhauser *et al.* 2013), birds (Zentall *et al*. 1996, Midford *et al*. 2000), and mammals (Galef & Laland 2005, Galef *et al*. 2008, Jaeggi *et al*. 2010) all demonstrate at least some ability to learn about their environment through another organism (for a review see Gariépy *et al.* 2014)*.*

As an example, norway rats (*Rattus norvegicus*), are well known for their ability to learn about novel food sources by smelling the breath of a conspecific who has recently fed (Galef and Stein 1985). Rats that smell food on the breath of a conspecific are much more likely to feed on that same food source than an alternative, but equally nutritious food source. However, smelling the food in conjunction with the presence of a conspecific is insufficient for

developing a preference. Instead the smell (and in some instances taste) must come from the conspecific to have the greatest effect (Galef and Stein 1985). In effect, the rats are learning which foods to eat based solely on the chemical cues present on a conspecific.

Like the rats, several bird species are known to use the presence of conspecifics and heterospecifics as a food cues (Krebs 1973). Unlike the rats, some birds learn not only what to forage on, but also how to access that food resource. New Caledonian Crows (*Corvus moneduloides*), for example, learn how to access novel food sources by watching other birds forage. New Caledonian Crows stand out from other birds for their ability to fashion tools from local plant resources. This skill is naturally developed if the birds are isolated from conspecifics. However, if they observe a demonstrator creating and using tools, the observers learn how to fashion tools much more quickly (Kenward *et al.* 2006). Thus, the crows learn how to forage more efficiently, as well as how to craft tools by observing the behavior of a conspecific.

Social learning in crows and rats seems to rely on demonstrators that are familiar with the task required of the observer during their respective experiments (*i.e.* which food is safe and how to access it). However, a knowledgeable demonstrator is not required for social learning to occur, and sometimes a well-trained demonstrator can even be a hindrance. Guppies (*Poecilia reticulata*), for example, utilize shoal members to help them locate novel food sources (Swaney *et al.* 2001). Interestingly, observers that are shoaling with a well-trained demonstrator often take longer to learn the route to a food source than those following less experienced shoal members. The increase in learning time is likely because more well-trained fish swim to the food source faster (and therefore leave the observers behind) than those that are still perfecting the route at a slower pace (Swaney *et al.* 2001). As with the previous examples, observer guppies benefited directly from the experience of the demonstrators.

All of the previous examples, and indeed most of the work in social learning, use vertebrates as the study organism. This pattern begs the question of whether the ability for social learning exists within invertebrate taxa. If so, is the ability as widespread and as varied in what can be learned? While relatively little work has been conducted on non-vertebrate

species, there is evidence to suggest that they can learn socially and in a variety of ways (for a review see Leadbeater & Chittka 2007).

Social learning experimentation on insects, for example, encompasses aspects of learning as disparate as local enhancement of a shelter in cockroaches (Lihoreau & Rivault 2011), to ants teaching conspecifics new routes to food sources (Franks & Richardson 2006). Studies on social learning in non-insect invertebrates are even less common than those on insects. One such study of social learning in a non-insect invertebrate is that of Fiorito and Scotto (1992). In their study, demonstrator octopods (*Octopus vulgarus*) were first trained to attack a colored ball for a food reward. Observer *O. vulgaris* were subsequently exposed to demonstrators in the presence of two colored balls, and allowed to watch the conspecific demonstrators attack the ball they had been trained to attack. Fiorito and Scotto found that the observer *O. vulgaris* were more likely to attack the same color of ball they saw a conspecific attack, even if that observer had a pre-existing preference for the other color of ball. The preference in the observers for the same color of ball clearly demonstrates that *O. vulgarus* can learn socially, while also supporting the hypothesis that social learning in invertebrates is not limited to highly social insects.

Salticids (jumping spiders) represent another non-insect invertebrate group that has the potential for social learning. They are characterized by their large, well developed anterior medial eyes, a cursorial hunting style, and a tendency to explore their environment thoroughly. They are in many respects, as Harland and Jackson (2000) have said "… like tiny eight-legged cats (pg 1)." Instead of spinning a web and waiting for prey to come to them, salticids actively forage for arthropods approximately matching their body size. This foraging behavior is mediated through their exceptional vision, which has a spatial resolution and chromatic sensitivity similar to humans (Harland and Jackson 2000). While their exceptional vision (especially for a spider) is thought to only be present in the anterior medial eyes, the other three pairs of eyes serve as highly sensitive movement detectors. Salticids can detect a moving object from virtually any angle through the integration of information received by each set of eyes. Thus, even if the spider is focused on one point in space with the anterior medial eyes,

movement detected by the other sets of eyes will cause the spider to immediately reorient itself to the direction from which the movement was detected (Forester 1982).

Salticids usually explore their environment to find food rather than waiting for it to come to them. During their foraging bouts, salticids cover relatively large areas, wandering as far as several meters per day in search of prey (Hoefler & Jakob 2006). Once a potential prey item has been located, salticids begin a sequence of attack behaviors (described in Chapter 2) that are highly stereotyped. In other words, the attack behaviors follow the same sequence of movements regardless of the demonstrator performing them. The behaviors of salticids when they reject an unpalatable prey item are also stereotyped. Furthermore, when a rejection occurs, it is often visible to observers, such as conspecifics, as attacks usually occur outside of a nest (Adams pers. obs.). The probability of encounters with hunting conspecifics, and therefore opportunities for social learning, is even higher when the spiders' foraging bouts occur in areas with a high density population.

Although salticids are not known for living in dense populations, I have observed some populations that are uncharacteristically dense (e.g. several per square meter), particularly along ecotones (Adams pers. obs.). Typically these aggregations are centered on ephemeral food resources, such as swarming insect alates. However, they can also form if a microhabitat is particularly attractive to prey items and results in an almost continuous food supply (Adams, pers. obs.). In both cases, salticids can be found oriented towards each other and appear focused on the conspecific until it moves out of sight or a closer stimulus evokes a response. The presence of a conspecific appears to be very important aspect of a salticid's local environment. During a preliminary study, I discovered that salticids will pay more attention to a conspecific than to a fast-moving, brightly colored food item even when food deprived (Adams, unpublished data). My unpublished data suggest that a conspecific's presence is a more salient stimulus than a potential prey item, and can greatly influence the behavior of one or both spiders.

The ability to learn is well established in several species of salticid (Jackson and Cross 2011). *Phidippus princeps*, for instance, can visually differentiate between contexts, and will

learn to avoid aposematic prey items if exposed to them in a familiar, but not in a novel, context (Skow and Jakob 2005). Some salticids, such as *Cyrba algerina*, can discriminate between different prey types and will vary their foraging strategy based on the identity of the prey (Jackson and Li 1998). The *Portia* species group also exhibits a sensitivity to prey type and demonstrates trial-and-error learning in their prey capture behaviors (Jackson 1992). However, much like *Phidippus*, *Portia* begin the trial-and-error process anew each time they are placed into a new context or encounter a new prey item. The fact that multiple genera of salticid treat novel contexts as entirely new situations, regardless of other factors such as prey appearance/familiarity, further reinforces the importance of context in salticid learning.

Salticid behavioral flexibility seems to become more pronounced with age and suggests that the ability to learn develops throughout the spider's lifetime (Edwards and Jackson 1994). Indeed, the lifetime foraging success of salticids may be largely influenced by visual learning within the context of their local environment. Therefore, the dense aggregations of salticids mentioned above could create an ideal context for social learning in salticids.

Social learning seems even more likely when their acute vision, natural curiosity, interest in conspecifics, and penchant for learning are considered. However, social learning in jumping spiders has been entirely unexplored except for an anecdotal report by Jackson *et al*. (2008). During a field study in Africa, these authors encountered aggregations of salticids stealing dead prey items from columns of foraging ants. They also found that the smaller salticids were more likely to exhibit this unique prey snatching behavior than their larger counterparts. Interestingly, the size of the animal was a factor for multiple species even though a variety of species and age groups were found in close proximity to each other. While alternative explanations exist, this anecdote strongly implies that the younger spiders learned this hunting technique from their older counterparts (i.e. through social learning).

The purpose of the research described here was to explore a salticid's ability to learn about potential prey items by observing the foraging behavior of conspecifics. My study builds on the evidence already presented and takes advantage of the natural foraging behaviors of

salticids. The combination of their adaptive traits, learning abilities, and predilection for watching a conspecific, strongly suggests that salticids have the capacity for social learning.

The increased time spent watching a conspecific suggests just how salient the presence of a conspecific is to this species. Even though these spiders are remarkably adaptable as hunters, many salticid foraging behaviors are highly stereotyped. Deviations from the stereotyped attack sequence can be measured and analyzed for changes based on exposure to experimental stimuli. Using this paradigm, I asked the following question: Can a salticid learn about the palatability of an aposematic prey item from observing a conspecific interact with that prey item? The present set of studies were the first to test for social learning in salticids. Furthermore, this study represents one of only a handful of social learning studies that utilize non-social organisms (those that typically avoid contact with conspecifics) as study subjects.

Chapter 2: General Methods

Salticids

Phidippus audax Hentz 1845 is a large (approximately 1 cm in length), heavy-bodied salticid that occurs throughout the continental United States of America. Spiders used in this experiment were collected as juveniles through visual searches, sweep nets, and custom shelters from two locations. The first location was a private residence in Lancaster County Nebraska, USA. The second location was Cedar Point Biological Station in Keith County Nebraksa, USA.

In the lab, spiders were housed individually in acrylic cages (Amac Plastics 760C, 5x5x7 cm). The sides of the cages were wrapped in masking tape to prevent salticids from visually interacting. Water was provided *ad libitum* via a cotton wick inserted into the bottom of the cage. As a source of food, each spider was offered a single cricket, matched to their body size, once a week. All spiders were maintained within a temperature range of 23-26°C and a 12:12 light/dark cycle.

Prey Items

Oncopeltus fasciatus, common milkweed bugs, were held in two 10-gallon terraria. One inch of dirt lined the bottom of each terrarium and dried corn husks were provided as egg-laying substrate. Milkweed bugs are aposematic hemipterans that are bright orange and black. Under natural conditions, milkweed bugs sequester toxins when feeding on Milkweed plants (*Asclepias sp.*), rendering the insects unpalatable to most predators (Berenbaum & Miliczky 1984). However, if reared on sunflower seeds, milkweed bugs retain their warning coloration but are palatable to many predators, including *P. audax* (pers. obs.). All prey items had access to water and sunflower seeds *ad libitum*. Milkweed bugs are sympatric with *P. audax* and I have observed *P. audax* attack them in nature.

Viewing Chamber and Observer Vial

A viewing chamber was created to facilitate delivery of the training stimulus to the observer spiders. The chamber consisted of an observer vial, an iPhone 4, and a four-dram, clear glass vial (the observer vial) that was used to restrain the observing spider during video playback (Figure 1). Each spider was isolated in the bottom centimeter of the vial by a cork. The cork prevented any vertical climbing, but allowed the spider to move freely and face any direction on the horizontal plane. The vial was positioned approximately 10 cm from the video stimuli. The iPhone screen and the vial were visually isolated from the rest of the room by a plain, white paper cylinder (24x21 cm). The cylinder created a nearly featureless arena for the observing spider, making the video the only salient stimulus.
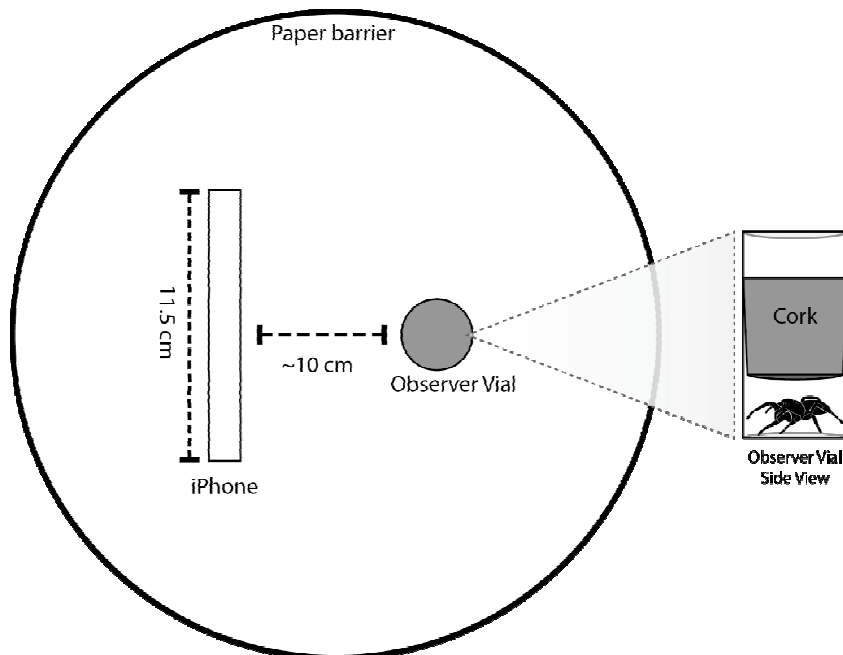

Figure 1: The observation chamber. Spiders were placed in the observer vial during training stimulus presentations. The vial was ~10 cm from the screen displaying the training videos. The iPhone and the observer vial were surrounded on all sides by a white paper barrier to block visual distractions caused by other stimuli.

Filming and Testing Arena

Both test trials and filmed training trials were conducted within the same arena (Figure 2). Using the same arena maintained the context established by the training videos during the test trials. The arena was designed to deliver an electric shock to a demonstrator spider (during the filming of the rejection training stimuli) precisely as it made contact with the prey item. The arena was created from a clear acrylic box (19.1x13.5x10 cm) with a snug fitting lid. A flat piece of Perspex (19x13.4 cm) with a 1.5 mm hole drilled into it approximately 15 cm from one end, centered left to right, was covered with metallic tape and mounted 1 cm from the top of the box. An electrophoresis machine (Thermo Electron Corporation, model EC250-90) supplied the shock (40 V, 10 mA) serving as the aversive stimulus in the rejection treatment videos. To deliver the electric shock, two alligator clips were hot glued to the underside of the Perspex platform. One was connected to a small piece of tinfoil placed under the metal tape at the end of the platform by the hole. The other clip was mounted directly under the drilled hole and held the insect pin used to tether the prey item in place. Both clips were connected to insulated wires that led out of the arena. Each clip formed half of an open circuit (Figure 2), that was closed by the spider's body when it pounced on the prey item. During the Acceptance treatment videos, the electrophoresis machine was powered off. Finally, during test trials, the electrophoresis machine was completely disconnected from the arena.
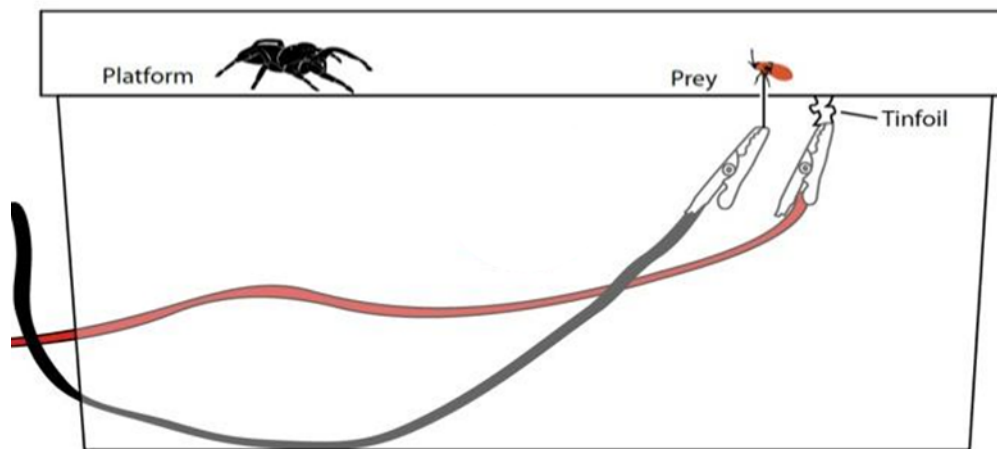
Figure 2: The filming and testing arena. This arena was designed to deliver an electric shock 40 V, 10 mA) to the spider immediately upon contact with the prey during the filming of the training videos. Shock delivery was achieved by creating an open circuit, where one half of the circuit was connected to each clip. The spider closed the circuit with its body when it made contact with the prey item and the floor simultaneously. The same arena was used for testing the observer spiders in order to maintain contextual continuity with the training videos. During the test trials however, the electricity was turned off and the electrophoresis machine that provided the shock was disconnected.

Training Videos

Evidence suggests that salticids do not distinguish between live, animated, or recorded (*i.e.* video playback) models, though they are sensitive to anatomical aberrations in the models (Harland & Jackson 2002). If video playback techniques are efficacious in experiments on predation and mate choice (Woo & Rieucau 2011), then it follows that they should be effective in experiments on learning as well. Therefore, video playback was used to present a foraging conspecific (the training stimulus) to the experimental spiders.

The training videos were created using iMovie (vers. 8.0) and were shown in 640x480 resolution on an iPhone 4 screen. All videos were shot from a lateral angle, approximately perpendicular to the stimulus and from the viewpoint of an observing spider about 30 cm away from the stimulus. The filming angle and distance from the camera created videos that approximated the actual size of both the predator and the prey item when viewed from the

observer vial approximately 10 cm away from the iPhone screen. A total of 10 video segments (each featuring a unique demonstrator) were created: five of a conspecific accepting the prey item and five of a conspecific rejecting the prey item.

All 10 video segments began with a spider wandering into view. The attack sequence began with the spider orienting its body towards the prey item so that its anterior medial eyes were aligned with the prey item, (Figure 1). The anterior medial eyes are used to examine objects in detail and are located at the very center of the animals face. Since those eyes are centered on the "face" of the animal, it was relatively easy to determine where the animal was looking at any given time. Once the prey item had been visually examined, the spider slowly crawled towards the prey item. When the spider was within 1-2 body lengths of the prey item, it positioned its fourth set of legs for pouncing and then leapt onto the prey item. If the prey item was palatable, the spider subdued it and began feeding. If the prey item was unpalatable, the spider exhibited distinctive rejection behaviors consisting of releasing the prey item, raising its front pair of legs over and in front of its body, and quickly backing 1-2 body lengths away from the prey item. After a few seconds of examination, the spider walked away from the rejected prey item and continued exploring the arena.

During the five rejection segments, the demonstrator spider received an electric shock (40 V, 10 mA) upon contact with the prey item; this shock resulted in the spider directing the aforementioned rejection behaviors at the prey item. During the five acceptance segments, no shock was applied and the spider began to feed on the prey item after attacking it. Approximately three to five seconds after an attack occurred, all segments faded to black over a period of two seconds.

The video segments were combined into 10, three-minute long video compilations. Each video compilation was created by grouping all the rejection segments together or all the acceptance segments together in a unique presentation sequence. Segment presentation order was determined using a Latin Square design which counterbalanced effects of the segment presentation sequence and repeated use of the same video segments. Once each video compilation was properly ordered, 12 s of black screen were inserted between each 30 s clip in

order to temporally separate the foraging events from each other, and to create an inter-trial interval.

Observations Recorded

  An example of the behavioral sequence observed during a typical trial can be found in Figure 3. The recorded behaviors were broken into two categories, those involved in the exploration of the arena (Arena exploration) and those involved in the attack (Attack sequence).

Arena exploration: Upon entering the arena, the spiders began to visually examine its environment. Operationally, this behavior occurred anytime a spider was not exhibiting the attack sequence, grooming, or remaining still for more than approximately five seconds. Generally, spiders were wandering around the arena as they explored it.
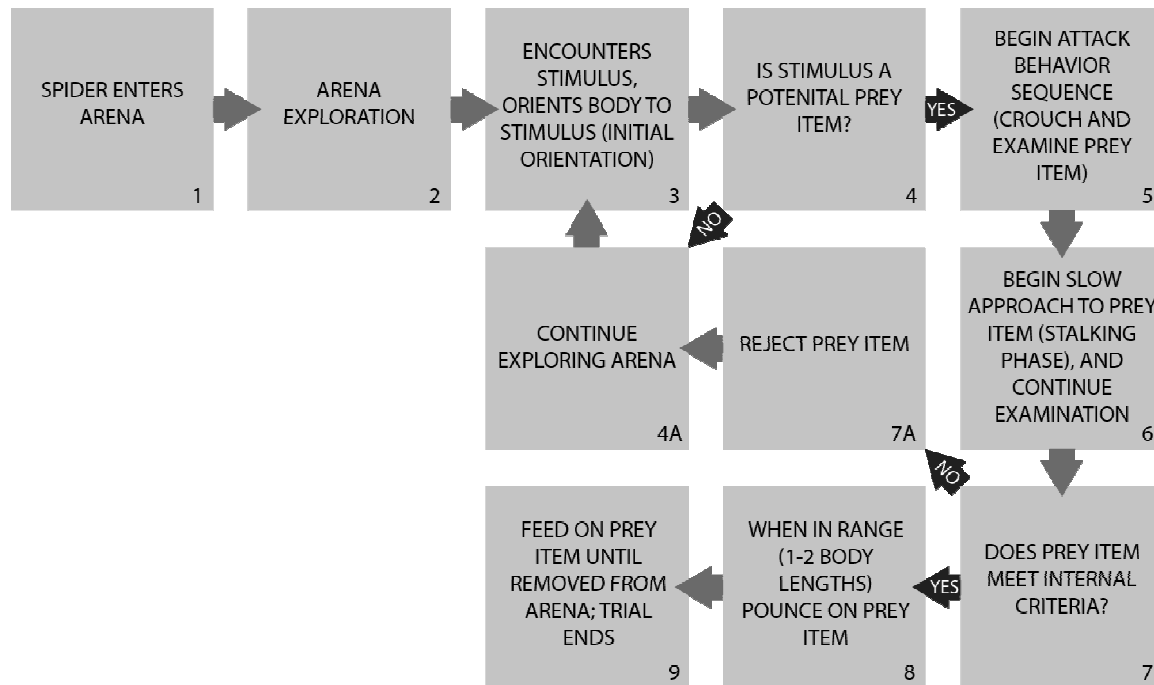
Figure 3: The behavioral sequence of an observer spider during a typical trial. Acceptance treatment spiders on average did not deviate from the most direct path to prey capture (steps 1-9). The Rejection treatment spiders, in contrast, often made one or more detours (*e.g.* step 4A) prior to attacking the prey item.

Attack sequence: The attack sequence was broken into six parts: orientation, observation, crouching, stalking, pouncing, and feeding.

- *Orientation*: The spider rotated its body so that the anterior medial eyes faced the stimulus and then ceased moving. This orientation behavior was stereotyped and only occurred when the spider detected a stimulus as indicated by a cessation of movement.

- *Examination*: The spider remained oriented to the stimulus and scanned it with the anterior medial eyes. No motion, apart from the eye movements, occurred.

- *Crouching*: The spider pulled its legs close to its body, lowering itself as close to the substrate as possible in a single, fluid motion.

- *Stalking*: The spider began a slow, leg-by-leg walk towards the prey item until it was one to two body lengths away from the prey item.

- *Pouncing*: The spider leapt onto the prey item.

- *Feeding*: The spider restrained the prey item with its legs and pierced the prey with its chelicerae.

Metrics Recorded

The following metrics were recorded during each trial. All time data were recorded in seconds.

1. Mass: The mass of the spider in grams prior to the beginning of each trial.

2. Number of orientations: The number of times the spider oriented its cephalothorax to the prey item during a trail.

3. Time oriented to prey: The time the spider spent with its cephalothorax oriented to the prey item during a trial. This was the summation of all the time a spider was oriented to the prey item across the various orientation periods throughout the entire trial.

4. Time oriented to prey prior to attack: The time a spider spent oriented to the prey item during the final orientation prior to the attack.

5. Latency to attack: The time between the final orientation and the attack (i.e. the total trial time minus the time prior to orienting to the prey for the last time).

Data Analysis

All non-latency data were analyzed using ANOVAs or their non-parametric equivalent. Latency data were analyzed using the Cox Proportional Hazards model of survival analysis (Cox 1972). The Cox model (survival package in R vers. 3.0.3) was chosen because three of the

individuals in the Rejection treatment did not attack within the imposed time constraints, but did accept a cricket after the trial. The Cox model specifically accounts for the forced termination of those trials (known as type 1 censoring) through the estimated hazard constant and the event indicator. Because the hazard rate is estimated, and assumed to be initially equal, any difference between failure times is assumed to be the result of the explanatory co-variables (e.g. treatment, demographic info, etc.). In addition, the non-normal distribution of the data does not violate the semi-parametric state of the model.

Where multiple comparisons were needed, the data analyses were corrected using the Tukey HSD method. The Cox Proportional Hazards method ("survival" package in R vers. 3.0.3) was used for metrics containing latency (time until event) data. All other data were analyzed using Generalized Liner Models or ANOVAs. Metrics were first analyzed for an overall effect of treatment, and then examined for between treatment differences if warranted. All statistical tests used an alpha of 0.05.

Methods specific to Experiment One

Spiders (*n* = 53) were randomly divided into two groups: those that viewed videos of a conspecific successfully capturing the prey item (Acceptance treatment), and those that viewed videos of a conspecific rejecting the prey item (Rejection treatment). Each spider was placed into the observer vial and given 5 min to acclimate. Because the experiment used a one-trial learning design, spiders were only allowed to watch one of the five video compilations that corresponded to their treatment. Each video was used equally often. After viewing a video, spiders were transferred to a 10 mL plastic syringe. The syringe was placed into the viewing chamber to maintain context with the training environment while the spiders were given a five minute resting period. During the resting period, a milkweed bug of similar size to the spider was tethered to the arena floor. This milkweed bug served as the prey item for the test trial, and each bug was only used for one trial. Following the resting period, spiders were inserted

into the arena via the syringe for the test trial. Test trials continued until either the spider attacked the tethered milkweed bug or 10 min had elapsed, whichever occurred first. At the end of each trial, spiders and milkweed bugs were immediately returned to their home cage and the entire arena was cleaned with 95% EtOH to remove any potential cues for other spiders.

Methods specific to Experiment Two

The spiders (n = 100) were pseudo-randomly divided into five groups by choosing a spider haphazardly and assigning it to a treatment condition. Trials were ordered so that one spider of each treatment was tested before any treatment repetition occurred. The treatments were tested in the following order: Prey Only, Acceptance, Pin, Rejection, and Spider Only. A trial began when a spider was placed into the viewing chamber, and given five minutes to acclimate to the confinement. The spider was then shown a video based on the assigned treatment condition. After viewing a treatment video, the spider was given a five minute resting period in a 10 mL plastic syringe. During the rest period, a milkweed bug of similar size to the spider was pinned to the floor of the arena. Following the rest period, the spider was placed into the arena for a test trial. Test trials lasted until the spider attacked the pinned prey item or 10 min had elapsed, whichever came first. At the end of each trial, spiders were immediately returned to their home cage and the entire arena was cleaned with 95% EtOH. If a spider failed to attack, it was offered a cricket in its home cage. If the spider did not begin to feed on the cricket within approximately ten minutes, the data point was not used in the analyses.

In Experiment 1, three animals in the Rejection treatment failed to attack, but then accepted a cricket in their home cage. This did not occur during the second experiment, eliminating the need for statistical testing that could account for censored data. Therefore, all data were analyzed using ANOVAs or their non-parametric equivalent. Statistical significance was declared at $p < 0.05$.

Chapter 3: Experiment 1

Results

At the beginning of each set of trials, I measured spider mass as a proxy of fitness (Table 1). Spiders did not differ between treatments in terms of mass (ANOVA, F = 0.408, df = 1,38, *p* = 0.527). All trials began with the spider entering the arena. Once inside, the spiders began an exploration step that lasted until they located the prey item. When the prey item was located, the spiders oriented their cephalothorax towards the prey item so that the prey item was visible to their anterior medial eyes. After the spiders had oriented themselves to the prey item, they spent a variable amount of time visually examining the prey item before the decision to attack was made. The amount of time spent examining the prey item immediately prior to attacking did not differ between treatments (Cox PH Likelihood ratio test = 3.03, df = 1, p = 0.082, Figure 4).

Table 1: Statistical comparisons of video the treatments. The behavior of the spiders in the Acceptance treatment significantly differed from the behavior of the Rejection treatment spiders. The metrics recorded during each trial are reported as means ± standard error of the mean.

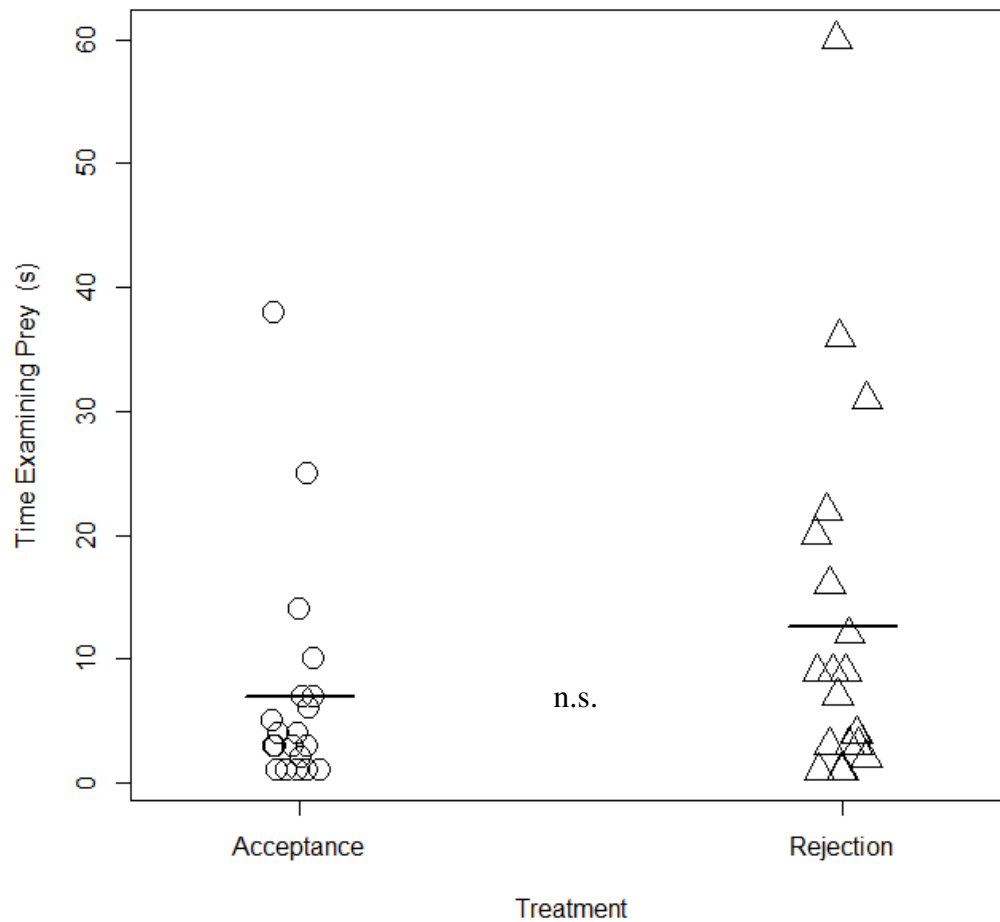| Metric	Acceptance (*n* = 20)	Rejection (*n* = 20)	*p* Value	Analysis Used
Number of orientations	**1.10 ± 0.10**	**2.65 ± 0.56**	**0.002**	Wilcoxon
Total time oriented to prey (s)	**30.15 ± 6.51**	**61.55 ± 10.51**	**0.006**	CoxPH
Time oriented prior to attack (s)	6.95 ± 2.07	12.65 ± 3.36	0.082	CoxPH
Latency to Attack (s)	**28.05 ± 1.48**	**71.60 ± 5.37**	**0.035**	CoxPH
Mass of spider (g)	0.058 ± 0.006	0.054 ± 0.005	0.73	Wilcoxon

Figure 4: Time examining prey in Experiment 1. Spiders that were exposed to a rejection of the prey item did not differ from the spiders that saw the prey item accepted (*p*=0.082). Bars are the average amount of time spent oriented to the prey item prior to making an attack.

Spiders exposed to the conspecific accepting the prey item usually attacked the first time they oriented to the prey item (Mean number of orientations prior to attack: x̄ = 1.1 ± 0.10 SEM). However, spiders exposed to the conspecific rejecting the prey item frequently returned to exploring the arena after the initial orientation to the prey item. After further exploration of the arena, most spiders in the Rejection treatment reoriented themselves to the prey item and, on average, attacked the prey after 2.65 ± 0.56 orientations had occurred. This increased number of orientations seen in the Rejection treatment was significantly more than the amount

seen in the Acceptance treatment (Wilcoxon Rank Sum, W = 290.5, p = 0.002, Figure 5). Spiders in the Rejection treatment also spent more total time oriented towards the prey item than spiders that had viewed conspecifics accepting the prey item (Cox PH, β = -1.00, Confidence Interval ($CI_{95\%}$) = -1.71 - (-0.29), p = 0.006, Figure 6).

Figure 5: Number of Orientations to prey item prior to attacking in Experiment 1. Spiders that were exposed to a rejection of the prey item required significantly more orientations prior to attacking than did spiders that saw the prey item accepted (p = 0.002). Bars are the average number of orientations to the prey item prior to making an attack.

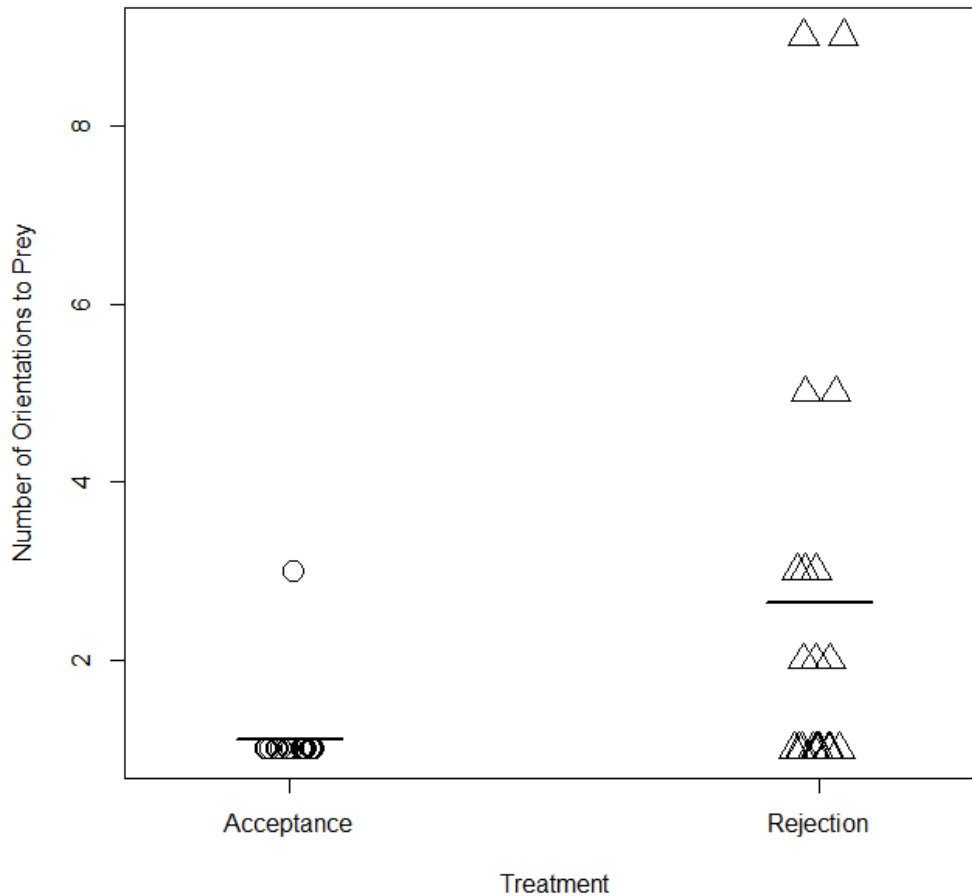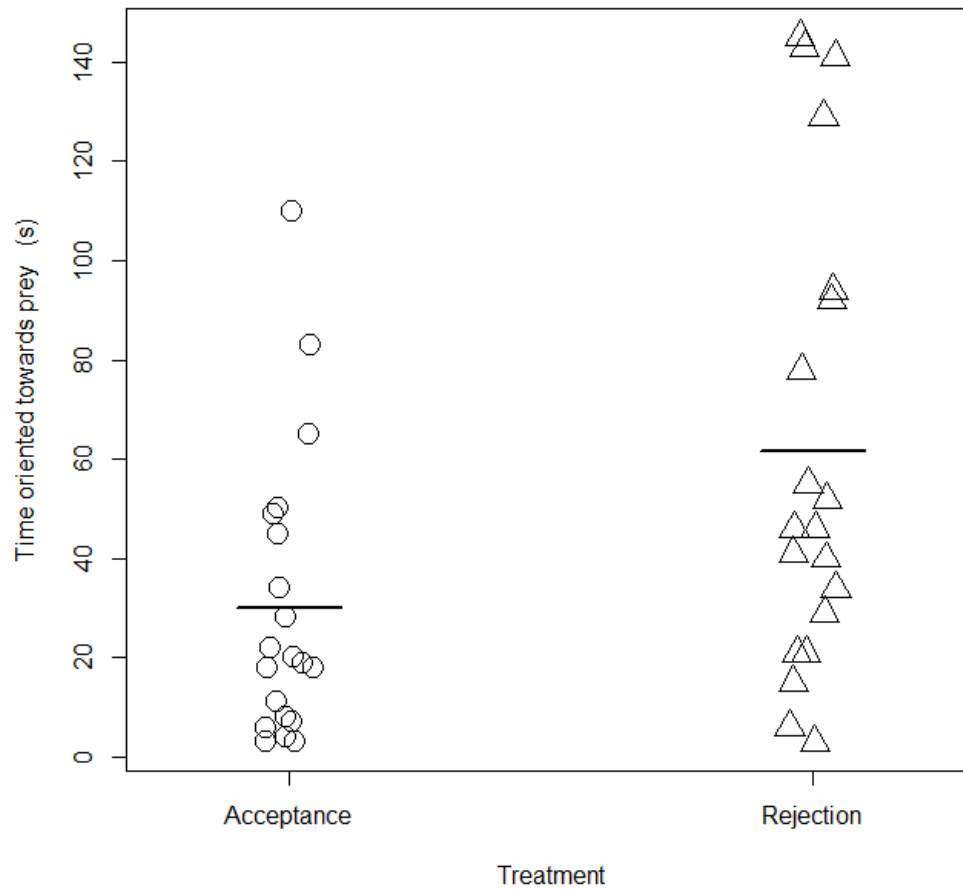Figure 6: The total time the spiders spent oriented to the prey item prior to attacking in Experiment 1. Spiders that were exposed to a rejection of the prey item spent significantly more time oriented to the prey item prior to attacking when compared to spiders that saw the prey item accepted (p = 0.006). Bars are the average total time a spider spent oriented to the prey item prior to making an attack.

After the examination step, the spiders crouched and stalked the prey item prior to attacking. Spiders that were exposed to conspecifics rejecting the prey item took significantly more time to attack (= 71.60 s) than spiders that were exposed to conspecifics accepting the prey item (= 23.95 s, Cox PH, β = -0.73, CI$_{95\%}$ = -1.41 - (-0.05), p = 0.035, Figures 7 and 8).
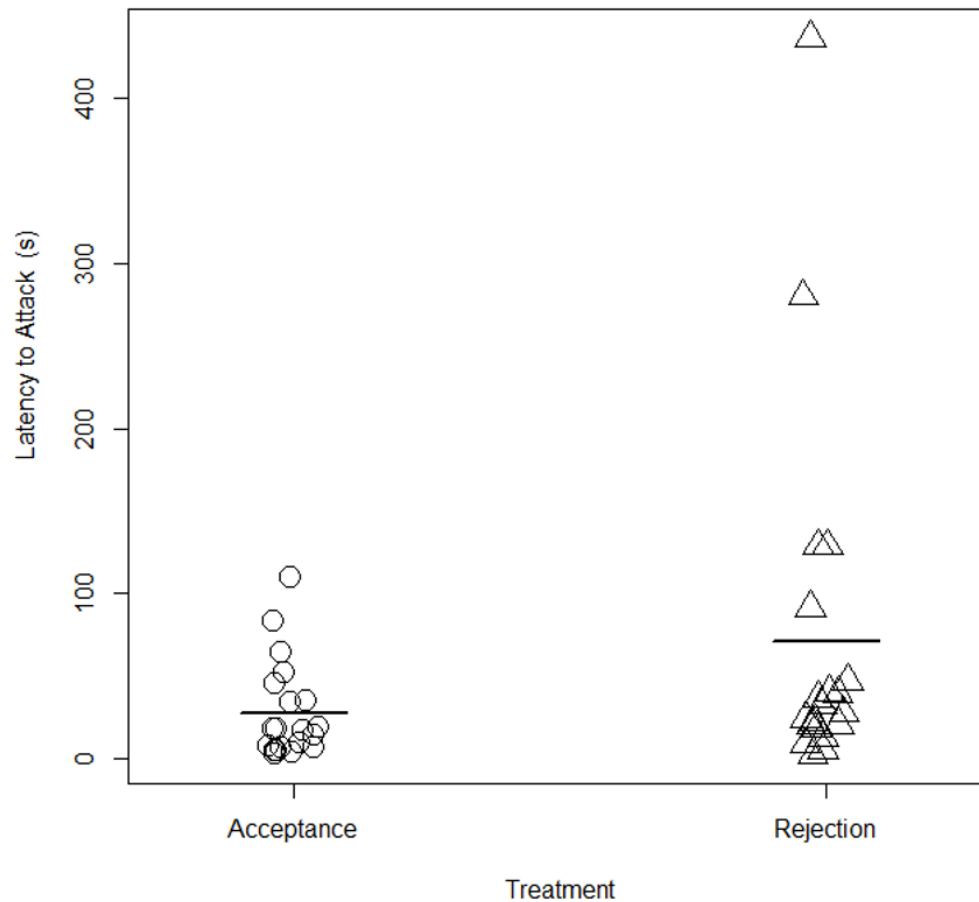

Figure 7: The total time required for a spider to attack the prey item after orienting to it for the final time in Experiment 1. Spiders that were exposed to a rejection of the prey item required significantly more time to attack the prey item prior when compared to spiders that saw the prey item accepted (p = 0.035). Bars are the average time a spider required to attack the prey.
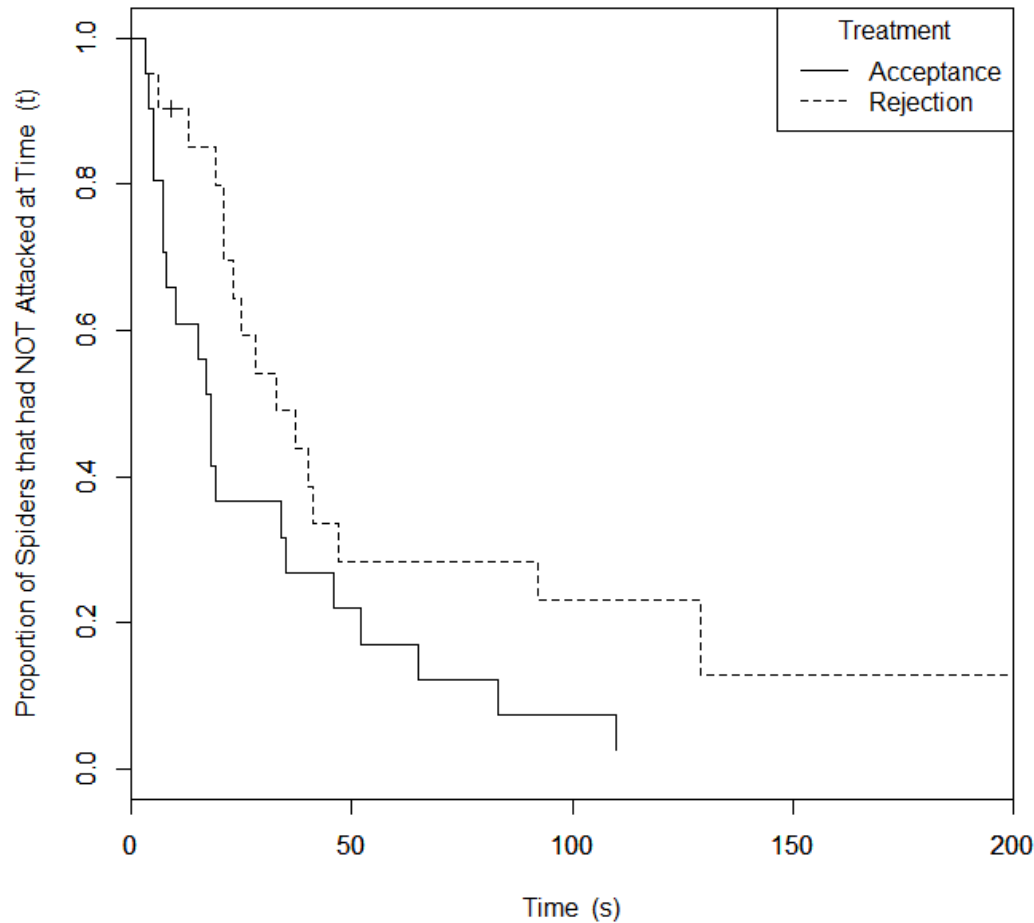
Figure 8: A Kaplan-Meier representation of the hazard rates for each treatment in Experiment 1. Spiders that were exposed to a rejection of the prey item had a lower hazard rate (higher chance of rejecting the prey item) when compared to spiders that saw the prey item accepted (p = 0.035). The lines represent the cumulative average hazard rate across time, where a steeper slope represents an increased chance of the spider attacking the prey item.

No attack occurred during 13 trials (seven in the Rejection treatment and six in the Acceptance treatment). If no attack occurred during the test trial, then the spider was offered a body-size matched cricket in its home cage. If an attack occurred within 10 min of the cricket being presented, the data point was kept and the latency to attack and total time were recorded as 600 s. This occurred three times, all in the Rejection treatment, and resulted in a

final sample size of 20 per treatment. If no attack occurred, the spider was considered unmotivated to feed and was removed from the data set.

Chapter 4: Experiment 2

Rationale

In Experiment 1, *P. audax* were separated into two treatments. Spiders in the Acceptance treatment were exposed to videos of conspecifics attacking and consuming on tethered prey items. Spiders in the Rejection treatment were exposed to videos of conspecifics attacking and immediately rejecting tethered prey items. After exposure to a video, spiders were given the opportunity to hunt a prey item similar to those shown in the training videos. There was a clear difference in the behavior of the spiders that varied with the treatment received. However, the experiment lacked the behavioral baseline provided by a neutral control (*i.e.* a treatment displaying the animal's natural behavior). As a result, I could not determine whether exposure to the training videos in Experiment 1 facilitated or inhibited the observers' attack behaviors, nor if some combination of facilitation and inhibition was present.

The design of Experiment 2 replicated that of Experiment 1 with the addition of three new control treatments. The most important of the new controls was a treatment that served as the behavioral baseline. This treatment video showed the arena in the absence of both conspecific and prey item (Pin treatment). As the baseline, the Pin treatment provided data showing the spiders' behaviors in the absence of any treatment effect aside from exposure to the arena and a video screen. The remaining two new treatments (Conspecific Only and Prey Only) were designed to address additional hypotheses such as the effect of a conspecific's presence. They are described in detail below.

The two types of video compared during Experiment 1 were similar up to the moment when the demonstrator attacked the prey item. Once the attack occurred the demonstrators' responses differed (accepting *vs*. rejecting the prey item). This suggests that something about acceptance *vs*. rejection of the prey item was responsible for the group differences in Experiment 1. Seeing a conspecific reject the prey item may have had an inhibitory effect associated with the possibility of a conspecific's presence. Alternatively, seeing the rejection of the prey item may have created an inhibitory effect towards the prey item. However, these hypotheses are not mutually exclusive and a combination of the two is also possible.

To distinguish between each of these hypotheses, a treatment showing only a conspecific in the absence of a prey item was added (Conspecific Only). If the presence of a conspecific was not inhibitory, then the Conspecific Only treatment should not differ from the baseline control treatment (Pin). If the presence of the conspecific was inhibitory, then the Conspecific Only treatment should produce results similar to the Rejection treatment. If the Conspecific Only and Rejection treatments produced similar behavior in the observers, this would be inconsistent with the hypothesis that viewing the rejection of the prey item caused an increase in attack latency. Alternatively, the Conspecific Only treatment could produce intermediate results, *i.e.* less than the Rejection treatment, but greater than the Pin treatment. This outcome would provide evidence that the rejection of the prey item was inhibitory or evidence of an interaction between the presence of the conspecific and the rejection behaviors.

The Acceptance spiders attack behaviors may have been the result of an excitatory effect caused by seeing conspecifics accept and feed on the prey items. To test whether the conspecifics' acceptance of the prey item had an excitatory effect, a Prey Only treatment was added. If the prey item was excitatory and the presence of a conspecific was neutral or had no effect, then the Acceptance treatment should not differ from the Prey Only treatment. Alternatively, the acceptance of the prey item by the demonstrators could create an excitatory effect, and combine with the presence of an inhibitory conspecific. The resulting interaction could produce results in the Acceptance treatment approximating the results of the Pin treatment. Another possibility is that the prey item was excitatory and the acceptance of the prey item by the conspecific was excitatory. The combined effect of these two excitatory stimuli should produce attack latencies lower than the Prey Only treatment. Finally, the Prey Only treatment allowed the detection of any effects caused by preexposure to the prey item. If a preexposure effect were present, the Prey Only treatment should differ from the Pin treatment, with the direction of the effect determined by whether the prey item was excitatory or inhibitory.

Results

Eight data points were excluded from the data set (final n=92). In seven cases, this exclusion was because the spiders did not meet the criterion described in the methods. In the case of the eighth spider, the animal made an initial orientation to the prey item after 248s, and then went quiescent for the remainder of the trial. It never moved, attempted to interact with the prey item, or demonstrated any other behavior to indicate that the animal was alert or aware of its environment. No other animal demonstrated this lack of behavior in any trial across all treatments.

Spider mass was used as a proxy for fitness. Data were transformed by taking the reciprocal in order to normalize the data distribution. There was no difference across all treatments in terms of spider size as determined by mass (g) at the beginning each day of testing (ANOVA, F = 0.17, df = 4,87, p = 0.953).

The results are presented in the same sequence as the behaviors are seen during a typical trial so as to present a coherent description of what occurred during the test trials. All spiders began their test trial by exploring the arena. Once the spiders located the prey item (indicated by orienting their cephalothorax towards the prey item), they began the attack sequence. The attack sequence began with a visual examination of the prey item, indicated by aligning their anterior medial eyes to the prey item and becoming quiescent. There was no overall difference in the amount of time spiders spent examining the prey item immediately prior to stalking (Cox PH Likelihood ratio test = 6.95, df = 4, p = 0.139, Figure 9).

Figure 9: Time spent examining the prey item immediately prior to attacking in Experiment 2. No difference between any possible pair of treatments was found (p = 0.139).

After examining the prey item, the spiders began the stalk segment of the attack sequence. Occasionally during the stalk segment, a spider would abandon the attack and resume exploring the arena. Eventually, the spider would find the prey item again and reorient to it. Reorientations occurred in all treatments, but there was no difference between treatments in the total number of times the spider oriented to the prey item prior to attacking (ANOVA, F=0.82, df=4,87, p = 0.52, Figure 10).
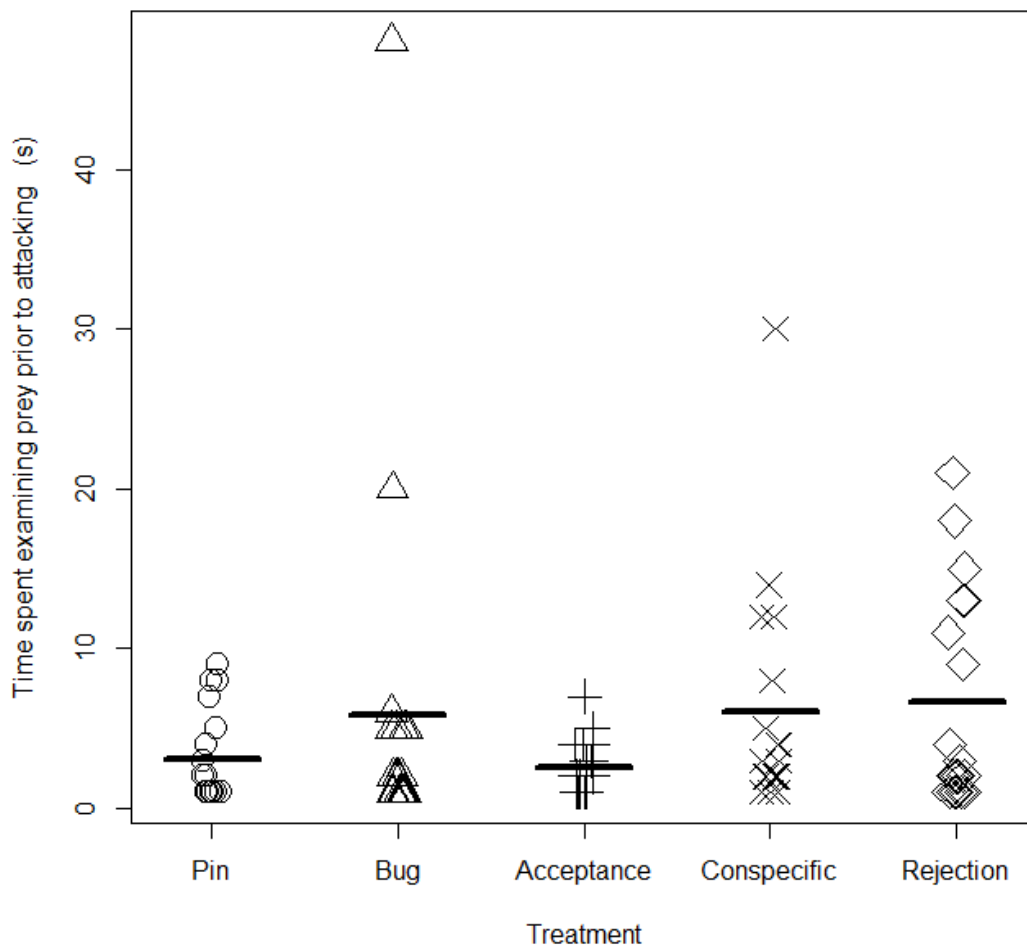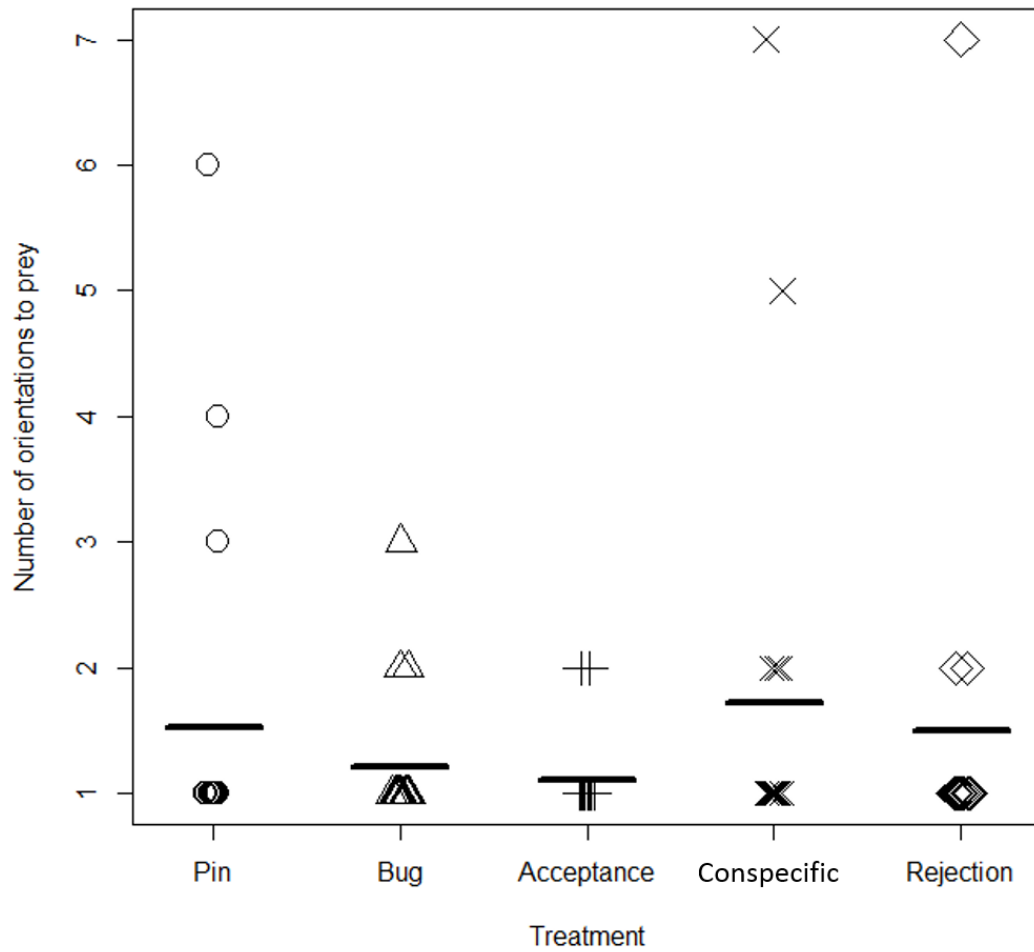
Figure 10: Total number of orientations to the prey item prior to attacking in Experiment 2. No difference between any possible pair of treatments was found (All pairwise comparisons *p*>0.5).

The stalk segment was generally followed by an attack. Attack latency, defined as the time an attack occurred minus the time prior to the spider's final orientation, recorded in seconds, varied between treatments (Cox PH Likelihood ratio test = 16.06, df = 4, *p* = 0.0029, Figure 11). The pairwise comparisons indicated that the subjects in the Rejection treatment had significantly higher mean attack latencies than those in the Pin and Acceptance treatments (z_{pin} = -3.18, p_{pin} = 0.008, & $z_{acceptance}$ = 2.904, $p_{acceptance}$ = 0.020). The Conspecific Only treatment spiders had intermediate attack latencies, but were not significantly different (*z* = 2.45, *p* =

0.069) from the Acceptance treatment spiders. No other differences met criterion for statistical significance (all $p > 0.05$, see Table 2 for the list of comparisons).
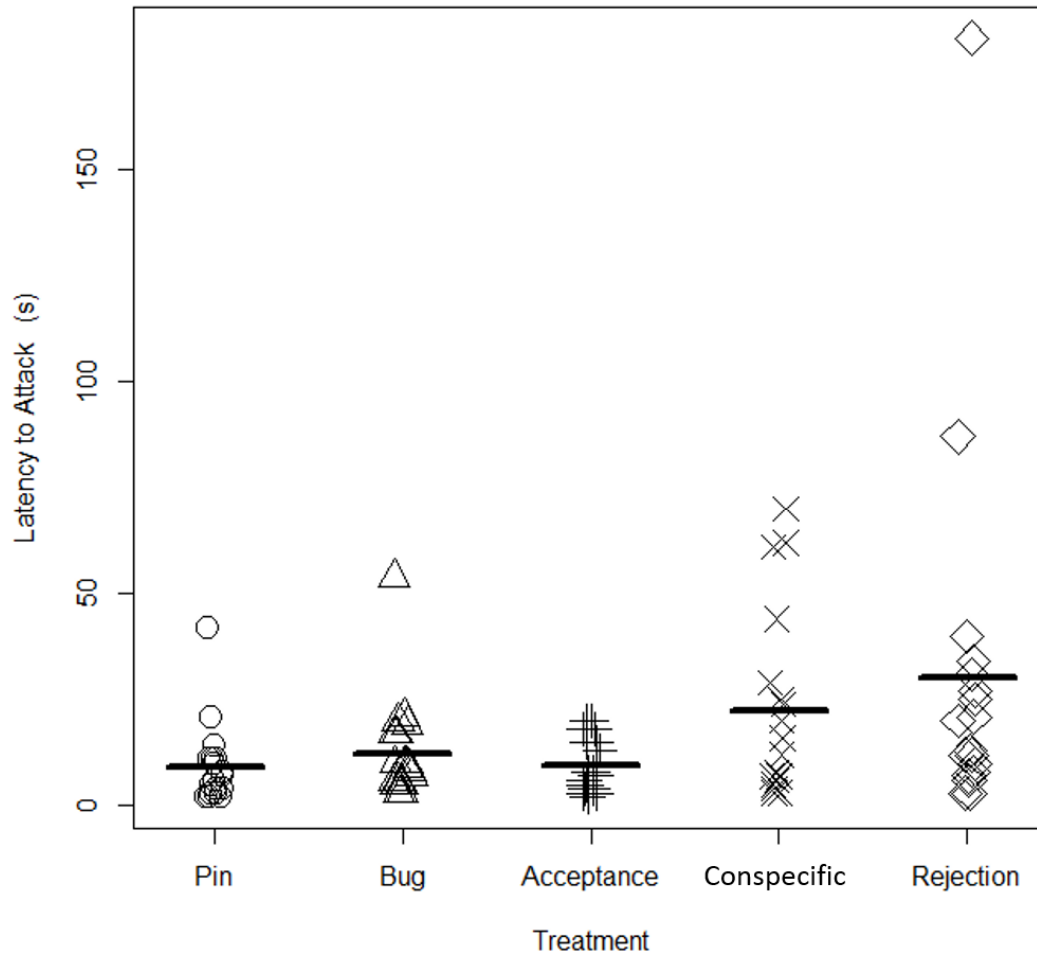
Figure 11: Latency to attack the prey item in Experiment 2. There was an overall effect of treatment ($p = 0.0029$). The Rejection treatment was significantly different from the Acceptance and Pin treatments ($p_{acceptance} = 0.20$, & $p_{pin} = 0.008$). The Conspecific Only treatment was different from the Pin treatment ($p = 0.038$), approaching significance from the Acceptance treatment ($p = 0.069$), but no other differences were found. For a complete list of the pair-wise comparisons made, please see Table 2.

Table 2: Pairwise comparisons tested of the attack latency in Experiment 2. The Tukey HSD method was used to control for alpha inflation due to multiple comparisons and only corrected *p* values are reported. Bolded comparisons are statistically significant.

Comparison	Estimate	Std. Error	z value	*p*
Acceptance *vs.* Pin	-0.063	0.333	-0.190	0.999
Acceptance *vs.* Prey Only	0.247	0.332	0.745	0.912
Acceptance *vs.* Conspecific Only	0.870	0.355	2.449	0.069
Acceptance *vs.* Rejection	**1.053**	**0.363**	**2.904**	**0.020**
Rejection *vs.* Conspecific Only	-0.183	0.345	-0.531	0.973
Rejection *vs.* Prey Only	-0.806	0.350	-2.302	0.144
Rejection *vs.* Pin	**-1.117**	**0.351**	**-3.179**	**0.008**
Conspecific Only *vs.* Prey Only	-0.623	0.341	-1.826	0.358
Conspecific Only *vs.* Pin	**-0.933**	**0.343**	**-2.721**	**0.038**
Prey Only *vs.* Pin	-0.311	0.326	-0.953	0.876

When compared to the results of Experiment 1, average attack latencies of the spiders in the Acceptance and Rejection treatments from Experiment 2 were noticeably shorter ($\bar{x}_{Acceptance}$ = 9.67 ± 1.52 s *vs.* 28.05 ± 6.60 s, and $\bar{x}_{Rejection}$ = 21.12 ± 4.93 s *vs.* 71.60 ± 24.01 s). The lowered average attack latency was found in both populations used during Experiment 2, and no difference in population means was found (Cox PH, $\beta_{Acceptance}$ = 0.602, $CI_{95\%}$ = 0.232 − 1.57, $p_{Acceptance}$ = 0.304, and $\beta_{Rejection}$ = 0.790, $CI_{95\%}$ = 0.300 − 2.08, $p_{Rejection}$ = 0.634).

Chapter 5: General discussion

The goal of this study was to test the hypothesis that spiders exposed to a conspecific accepting a prey item would more readily attack a similar prey item than spiders exposed to conspecific rejecting a prey item. Refinements to the design of Experiment 2 were made based on the data and hypotheses generated from Experiment 1. These refinements included the addition of control treatments. The added treatments were designed to provide baseline (uninfluenced) behaviors, and allow me to address the potential mechanisms of the observed behavioral differences in Experiment 1. The control treatments were as follows: "Prey Only" treatment, showing a prey item in the absence of a conspecific; "Conspecific Only" treatment, showing a conspecific in the absence of a prey item; "Pin" treatment, showing a blank arena, with neither conspecific nor prey item present. Thus, Experiment 2 examined the original hypothesis mentioned above, as well as the hypotheses that resulted from Experiment 1's data (Table 3).

The data from both Experiments 1 and 2 are consistent with my original hypothesis. Spiders that saw a conspecific attack but reject a prey item spent more time examining the prey item, and took longer to attack the prey item than spiders that saw a conspecific attack and consume the prey item. In other words, the Rejection treatment spiders were more reluctant to attack the prey item when compared to the Acceptance treatment spiders. The differences in the responses of the Acceptance *vs*. Rejection and the Conspecific Only *vs.* Pin treatment spiders suggests that observing a conspecific's behavior will influence the observer's future foraging decisions.

Table 3: Predicted outcomes of selected explanatory hypotheses resulting from Experiment 1. Each outcome is shown as a comparison relative to the Pin treatment, which served as the baseline for all other treatments in Experiment 2. This table does not include all possible hypotheses, but instead focuses on those that seemed most likely based on the results of Experiment 1.

	Treatment				
Hypothesis	Pin	Rejection	Acceptance	Conspecific Only	Prey Only
Prey Item Excitatory/Preexposure	0	-	-	0	-
Conspecific Presence Inhibitory	0	+	+	+	0
Rejection of Prey Item Inhibitory	0	+	0	0	0
Acceptance of Prey Item Excitatory	0	0	-	0	0
Conspecific Presence Inhibitory + Rejection of Prey Item Inhibitory	0	+ +	+	+	0
Conspecific Presence Inhibitory + Acceptance of Prey Item Excitatory	0	+	0	+	0

All predictions use the Pin treatment as the baseline.

"+" indicates an increase in average latency relative to the Pin treatment.

"0" indicates that no change is expected from the Pin treatment.

"-" indicates a decrease in average latency relative to the Pin treatment.

Discrepancies between Experiments 1 and 2

The main finding from Experiment 1 was replicated in Experiment 2. That is, spiders in the Rejection treatment took significantly longer to attack the prey item than those in the Acceptance treatment. While the difference between treatments was significant, a significant difference also existed between the two experiments. Spiders in Experiment 2 attacked much sooner than spiders from Experiment 1 ($\bar{x}_{Acceptance}$ = 9.67 ± 1.52s *vs.* 28.05 ± 6.60s, and $\bar{x}_{Rejection}$ = 21.12 ± 4.93s *vs.* 71.60 ± 24.01s). In addition to attacking sooner, the spiders in Experiment 2 also oriented fewer times, on average, prior to attacking.

During Experiment 1, spiders that were exposed to the rejection of the prey item by a conspecific demonstrated an increased number of orientations prior to attacking the prey item

when compared with spiders that saw the prey item accepted. This effect was not replicated in Experiment 2. The average number of orientations prior to attacking in the Rejection treatment of Experiment 1 was 2.65 ± 0.59 ($\bar{x}$ ± SE), whereas in Experiment 2 the Rejection treatment animals oriented an average of 1.53 ± 0.36 times prior to attacking. The number of orientations prior to attacking required by the Rejection treatment spiders in Experiment 2 was not significantly different from any other treatment.

The discrepancies between the two experiments could be explained by several hypotheses, but two seem the most likely and will be discussed here. The most parsimonious explanation is that the extra orientations and increased attack latency recorded in the Rejection treatment of Experiment 1 were artifacts due to experimenter bias when collecting data. However, this is unlikely given that the data were recorded as the trials progressed, and then checked against the video recordings of each trial several weeks later. Few errors were found during the checking process, and those that were found were small in magnitude. Retrospectively collected environmental data, such as average rainfall and average temperature leading up to the field season, also refute the idea of artifacts in the data.

As an alternative explanation, a previously unaccounted for abiotic factor (*e.g.* unusually dry weather) may have affected the spiders' development prior to their being brought into the lab for testing, thereby creating a cohort effect. The lack of variation in the number of orientations, combined with the overall decrease in attack latency across all treatments, suggests that the cohort of spiders used for Experiment 2 may have been under very different selective pressures from the previous cohort. Both populations of *P. audax* (Original and Cedar Point Biological Station) normally have a myriad of food items available to them. However, there was a noticeable decrease in the insect population when the spiders for Experiment 2 were collected during the summer of 2012. This scarcity of prey items was likely due to the lack of rainfall as it was the fourth driest summer on record in Nebraska. Therefore, the spiders used in Experiment 2 may have learned to attack any potential prey items as soon as possible. In contrast, the previous year's cohort of spiders (used in Experiment 1) received an average amount of rainfall and did not face a scarcity of food, as insect prey were abundant.

It could also be the case that due to the scarcity of prey items, strong selective pressure was exerted against cautious hunters, with only the most aggressive hunters left by the time the spiders were collected. Either scenario could result in behaviors similar to that found in Experiment 2: a large decrease in attack latency and fewer orientations prior to attacking. Indeed, the cohort hypothesis is also supported by Carducci and Jakob's (2000) work, which established that the size of the rearing environment affected the cognitive abilities of salticids. If size of the environment affected cognition, then diet which affects mate choice in other spiders (Hebets, Wesson, & Shamble 2008), also seems plausible.

A follow up experiment using spiders reared in the lab under different treatment conditions could provide much needed information regarding this potential cohort effect. For example, as part of the rearing process spiders could be subjected to different feeding regimes where some spiders are fed twice a week and others only every ten days. If a cohort effect caused by a lack of prey was the cause of the differences between Experiment 1 and Experiment 2, the behavior of the spiders that received less food during rearing should be more aggressive (*i.e.* shorter attack latencies and fewer orientations) than those that received more food.

The Role of the Prey Item

The data from Experiment 2 suggest that seeing the prey item, in and of itself, played no role in the subsequent behavior of the observing spiders. Indeed, the behavior of the spiders in the Acceptance treatment was quite stereotyped: with the exception of three spiders, observers always attacked on their first orientation to the prey item, and did so relatively quickly. This pattern is consistent with both lab and field observations of salticid foraging behavior. Furthermore, the Acceptance treatment did not differ from the Pin, or the Prey Only treatments on any metric. The lack of difference between these treatments suggests that the Acceptance videos were not enhancing the prey item's palatability. If the videos had been enhancing the prey item's appeal via the prey item-conspecific interactions, then the Acceptance treatment should have shown a lower attack latency than the Pin treatment.

Alternatively, if a preexposure effect were present, then both the Acceptance and Prey Only treatments should have shown lower attack latencies than the Pin treatment. However, neither of these outcomes were found. It is therefore unlikely that the prey item was the focus of learning during any of the treatments, leaving the conspecific and its behaviors as the only other options.

Prey Acceptance and the Conspecific Demonstrator

My findings suggest that the inhibitory aspects of a conspecific's presence (discussed in the following section) were diminished when the conspecific was seen eating a prey item. By itself the prey item had little or no effect on the observer. However, observing a conspecific successfully attack a prey item had a large effect on the foraging behavior of the observing spiders: Acceptance treatment spiders attacked prey items significantly faster than Rejection treatment spiders (Table 2). Acceptance treatment spiders also attacked faster than the Conspecific Only treatment spiders, though this difference was not quite significant ($p = 0.069$, see Table 2). In contrast to the behavior of the Acceptance treatment spiders, the behavior of the Rejection treatment spiders departed from previously observed foraging behaviors. For example, three Rejection treatment spiders failed to attack the prey item, but accepted a cricket after their test trial.

Prey Rejection and the Role of an Unsatiated Conspecific

There was no difference between the Conspecific Only and Rejection treatments on any metric tested. Seeing a conspecific reject the prey item and seeing a conspecific in the absence of a prey item both resulted in an increased attack latency compared to the other treatments. My original hypothesis held that the Conspecific Only treatment would produce latencies comparable to the Pin treatment, assuming the conspecific's presence was not inhibitory. However, the Conspecific Only attack latencies were significantly higher than the Pin treatment, trending away from the Acceptance treatment, and were not different from the Rejection

treatment latencies. Based on this data pattern, the presence of an unsatiated conspecific was likely inhibitory, and not a neutral control as anticipated.

The measured increase in vigilance seen in the Conspecific Only and Rejection treatments could be the result of the observers being sensitive to the last seen behavior of the conspecifics. Sensitivity to the last seen conspecific behavior (hereafter the vigilant observer hypothesis) explains the Conspecific Only and Rejection treatment data. In both of those treatments, the demonstrator was last seen in the absence of palatable food, and exhibiting foraging behaviors. Previous work on fear in other species (Adolphs 2013) and foraging efficiency as it relates to vigilance (Ferrari, Sih & Chivers 2009), lends credibility to the vigilant observer hypothesis. Generally, the more time an animal spends being vigilant, the less time it can spend foraging.

One way to interpret the increased number of orientations to the prey item in the Rejection treatment spiders is an increase in vigilance. In general, each step in the attack sequence occurred only once during a trial for Acceptance treatment spiders (Table 1). However, in the Rejection treatment trials the repetition of a step or steps frequently occurred due to the observer breaking off and reinitializing the attack at a later time. This break in the attack sequence often occurred after observing the prey item (Figure 3, step 4) or before pouncing on the prey item (Figure 3, step 7). The pattern of repeated orientations to the prey item occurred in approximately 25% of the Rejection treatment spiders, whereas it occurred in only 7.5% of the Acceptance treatment spiders. Viewed collectively, these differences are consistent with the vigilant observer hypothesis, as observers may have been altering their foraging behaviors as a result of seeing a conspecific reject the prey item.

The vigilant observer hypothesis also explains the Acceptance treatment data as those demonstrators were last seen feeding, and were therefore less likely to be a cannibalistic threat to the observer. Unfortunately, the vigilant observer hypothesis also confounds the effect of the last seen conspecific behavior with the effect of context.

Salticids are known to attend to context during learning trials, and will alter their behavior to match the context based on previous experiences (Skow & Jakob 2005). Perhaps

viewing an unsatiated potential predator (the conspecific) in the context of the arena caused an increase in fear or vigilance while foraging (hereafter the dangerous context hypothesis). Like the vigilant observer hypothesis, a context-based increase in fear or vigilance could result in longer attack latencies like those seen in the Conspecific Only and Rejection treatments.

Animals tend to be more vigilant after exposure to a predator (Sih 1992). In addition, animals that have undergone prolonged periods of relative safety from predators, but are then exposed to a predator may react more strongly to the presence of a potential predator (Lima & Bednekoff 1999). This could be the case for spiders in the Rejection treatment, as spiders are normally housed in opaque containers that visually isolate them from the rest of the experimental animals. During training however, spiders are suddenly exposed to several potential predators (*i.e.* the conspecifics in the training videos). As a consequence of this increase in predation risk, the spiders could have been increasing their anti-predator behaviors until they reexamined the arena for the conspecific predators seen in the training videos.

Contextual learning could also result in the shorter attack latencies seen in the Acceptance treatment spiders when compared to other videos featuring a conspecific. Acceptance treatment videos end with the conspecific feeding on the prey item. However, in the testing arena an identical prey item is present but the conspecific is absent. The Acceptance treatment spiders may therefore be perceiving a change in context between the training and testing arenas.

Conclusions

The results of Experiment 1 suggested that seeing a conspecific interact with a prey item caused the observing spiders to alter their foraging behaviors. This finding was replicated in Experiment 2. The data from both experiments ultimately suggested that the change in foraging behaviors was caused by one of three things: the acceptance/rejection of the prey item in the training videos (vigilant observer hypothesis), the presence of the conspecific in the training videos (dangerous context hypothesis), or some combination of the two.

Both the dangerous context and vigilant observer hypotheses are plausible explanations for the effects found in my experiment. Indeed, the two hypotheses may be functioning simultaneously. This conflation requires that any effort to understand the effect of context and the effect of a conspecific's presence must first separate these two components. One way to test these hypotheses would be to use a methodology similar to Skow and Jakob's 2005 study. That is, the context of the training arena shown in the videos would differ in color from the context of the testing arena. A 2x2 between subjects design with same context *vs.* different context as one factor, and videos ending with the conspecific on screen *vs.* the conspecific leaving the arena as the other factor should allow the separation of the dangerous context and the vigilant observer hypotheses. As an additional control, all videos would show the conspecific in the presence of a prey item. The demonstrators would be shown either feeding on the prey item (*e.g.* the Acceptance treatment), or rejecting the prey item (*e.g.* the Rejection treatment). This experimental design should allow for a comparison to the results of Experiments 1 and 2, as well as help disentangle the effect of each hypothesis.

The results of Experiment 1 and Experiment 2 support the idea that salticids are sensitive to the behaviors of conspecifics and can integrate this information into their own foraging decisions (*i.e.* social learning). My work provides the first evidence of social learning in a jumping spider, and is part of a growing number of studies on social learning in invertebrates. My study, and others like it, provides much needed evidence against the common belief that invertebrates are mindless automatons. Indeed, my research highlights the flexibility of salticid learning and hunting behaviors, and paves the way for future work on social learning in arachnids.

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