

Western black widow spiders (*Latrodectus hesperus*) remember prey capture location and size, but only alter behavior for prey caught at particular sites

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Abstract

Animals form memories and use them to guide future behaviors. The information stored in memory is selected to include only details that result in adaptive decision-making. Understanding the contents of animal memories can provide insight into an animal's ecology and evolution. In this paper, we use an assay of searching behavior to reveal the contents of West black widow spiders' memory. We provided prey in two major components of black widow webs and then stole the prey to elicit searching behavior. We used search effort, in terms of likelihood of searching and the number of bouts of searching, to determine whether spiders form memories of their prey, and whether their memories include any specific features of their prey. Black widows were significantly more likely to search after experiencing prey theft, which demonstrates the spiders form memories of their prey. Black widows were also more likely to search for relatively larger prey, but this effect depended on the site of prey capture within the web (only for prey snared at the web's gumfooted lines). This indicates that black widows also form memories of the relative size of their prey and its capture location. Further, their natural history helps interpret when these details are stored or used, and when not. Our results underscore the importance of behavioral observations for understanding the contents of animal memories.

KEYWORDS

ecology, memory, searching, spider

1 | INTRODUCTION

Animals make memories about their environment and their movements within it and use the information in these memories to guide subsequent decision-making (Shettleworth, 2010). Food caching animals, for example, possess extraordinary spatial memory that is adaptive in the context of locating stored food (Sherry & Duff, 1996; Smith & Reichman, 1984). The information that an animal stores in memory is a function of the sensory biology and ecology of the animal (Dukas, 2004; Healy & Braithwaite, 2000; Pravosudov & Clayton, 2002; Pravosudov & Roth II, 2013; Shettleworth, 2010). Further, memory formation and retention is energetically expensive, and thus, the information stored in memory is curated adaptively

(Mery & Kawecki, 2002; Placais & Preat, 2013; Shettleworth, 2010; Tello-Ramos et al., 2019). Selection thus favors the formation of memories that lead to adaptive behavior when the memory is later recalled (Shettleworth, 2010). The information stored in memory can also vary between closely related species (Kamil et al., 1994; Platt et al., 1996; Shettleworth, 2010), which means that studying what information an animal stores in memory can give useful insights into the relationship between ecology and the evolution of cognitive abilities.

Web spiders offer interesting opportunities for studying the formation of memories. These spiders build webs with diverse structures in manifold environments and capture an array of arthropod prey (Blackledge et al., 2009; Eberhard, 2020; Foelix, 2011). Web

spiders form memories of their web and its contents and use these memories to guide decision-making. Some remember the overall layout of their web and their position in it (LeGuelte, 1969; Sergi et al., 2021). Some remember the location in the web where they captured prey, and alter their webs to make them better able to capture prey in the web location where past prey captures have occurred (Nakata, 2012). Many web-building spiders also remember the contents of their web, such as the presence of prey, the relative size of captured prey, and even the relative number of captured prey (Kilmer et al., 2018; Kilmer & Rodríguez, 2019; Rodríguez et al., 2013; Rodríguez et al., 2015; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011).

Most of the evidence regarding spider memories of their web and its contents comes from species that build orb webs, which are relatively simple in the sense that they are two-dimensional structures. There are, however, many spiders that build more complex, three-dimensional webs (Eberhard, 2020). Such webs may offer a greater number of features that may afford greater possible detail for memory. However, this may also make it a more challenging for a spider to adaptively represent the relevant aspects necessary to aid navigation and decision-making.

In this study, we analyze the content of memories of captured prey in Western black widow spiders, *Latrodectus hesperus* (Theridiidae). Black widow spiders build three-dimensional cobwebs with distinct components: mainly, a semi-horizontal sheet and vertical gumfooted lines that connect to the substrate (Figure 1). Theridiid cobwebs with their gumfooted lines may have evolved as specializations for capturing terrestrial prey such as ants (Liu et al., 2015), and black widows do primarily capture terrestrial prey which become stuck to the sticky-ended gumfooted lines of their webs (Figure 1) (Benjamin & Zschokke, 2003; Salomon, 2011). However, black widows also capture diverse arthropod prey that vary widely in size (Benjamin & Zschokke, 2003; Blackledge & Zevenbergen, 2007; Salomon, 2011). This includes capturing flying prey on the sheet of their web; such prey, although representing a small percentage of their prey items, are larger on average than the terrestrial prey and might therefore be of relatively high value and importance (Salomon, 2011). We therefore asked whether the memories black widow spiders form of their prey include information about prey size and the location at which the prey was captured.

We used an assay of memory afforded by the natural history and behavior of web spiders (Kilmer et al., 2018; Kilmer & Rodríguez, 2019; LeGuelte, 1969; Rodríguez et al., 2013; Rodríguez et al., 2015; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011). Whenever a prey item is snared in a spider's web, the spider quickly approaches it, every once in a while briefly orientating by tugging on the web to correct its trajectory (Foelix, 2011). A different kind of searching can occur in the absence of a "triggering" stimulus. This searching is prolonged and non-directional (see below), with the spider walking around the web and pulling or plucking on web threads to gain vibrational information (e.g., Movie S1), and occurs whenever the layout of the web is changed in the spider's absence (so the spider seeks to re-orient itself) (LeGuelte, 1969; Sergi

Significance Statement

The information animals store in memory is selected to contain information that supports adaptive decision-making. Understanding the information an animal stores in memory can therefore support conclusions about the ecology of animal. Using an assay of searching behavior, we investigated whether black widow spiders form memories of captured prey, and whether these memories include information about the prey capture location and relative prey size. Black widow spiders remember information about captured prey, but only alter searching behavior when prey are captured at particular sites within the web. These results inform conclusions about the ecology of black widow spiders—particularly conclusions about the relative importance of terrestrial and flying prey capture events.

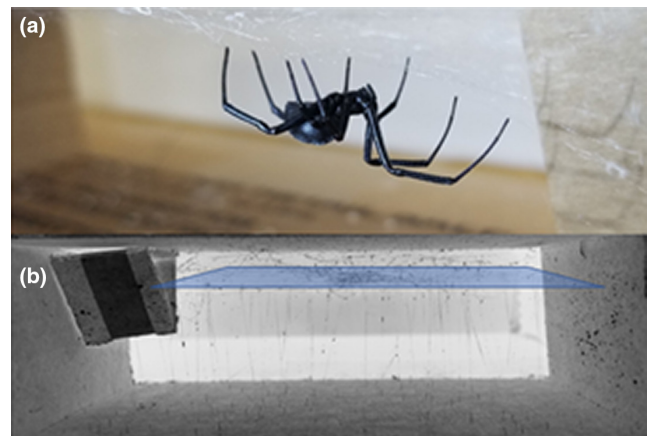


FIGURE 1 Black widow spider and representative web with a sheet and vertical gumfooted lines. Black widow spiders construct space-filling cobwebs (Benjamin & Zschokke, 2003). (a) A female black widow spider in a typical posture on the sheet of her web. (b) Negative image of a black widow web constructed in a cardboard frame. The sheet extends from the retreat to the far side of the frame. The bottom of the sheet forms a two-dimensional plane (blue rectangle inset in b). The gumfooted lines are the primary prey capture structures of black widow webs. Reproduced with permission from Sergi et al., 2021.

et al., 2021), or when an item in the web is removed (so the spiders seeks to re-acquire it) (Kilmer et al., 2018; Kilmer & Rodríguez, 2019; Opell, 2001; Rodríguez et al., 2013; Rodríguez et al., 2015; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011). Consequently, this searching indicates the presence of a memory about the aspect of the web that has been changed. Further, variation in the likelihood of searching and in searching effort can be used to uncover the particular features represented in memory, and whether some features are more important than others (Rodríguez et al., 2013; Rodríguez et al., 2015; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011).

TABLE 1 Control and treatment groups we used to analyze memory of captured prey in black widow spiders

Control or treatment	Treatment name	Description	n
Control	Full feed	Offered cricket. Allowed spiders to consume entire cricket.	10
	Make hole	Cut hole in web sheet with scissors	9
	Sham theft	Offered cricket in sheet. Stole cricket and immediately gave back to spider.	10
Treatment	Sheet	Offered cricket in sheet. Stole cricket.	20
	Gumfooted line	Offered cricket in gumfooted line. Stole cricket.	19

Note: We assigned spiders to one of three control groups or one of two treatment groups to assess whether searching behavior varied according to whether a spider experienced prey capture and subsequent prey theft, and whether searching behavior varied according to site of prey capture.

We used the above searching assay to test two hypotheses about black widow memory. First, we tested the general hypothesis that black widows form some memory of the prey they capture in their webs. This hypothesis predicts that black widows will search for prey that they have captured and subsequently lost.

We then tested the hypothesis that black widows form memories of some specific features of their prey. This hypothesis predicts that black widows will exhibit different searching behavior when features of their captured prey differ. To test this second hypothesis, we tested two more specific hypotheses. First, we tested the hypothesis that black widows form memories of the size of their prey. This hypothesis predicts that black widows will be more likely to search and/or have higher search efforts for larger prey (assuming larger prey are preferable). Second, we tested the hypothesis that black widows form memories of where in the web they captured prey (i.e., sheet versus gumfooted lines; Figure 1). This hypothesis predicts that black widows will be more likely to search and/or focus their search efforts on the area of the web where the prey was captured and lost.

It might be argued that, rather than being indicative of memory, searching is caused by a disturbance on the web or to the disturbance caused when stealing prey. We therefore also tested whether black widow spiders search in response to disturbances similar to theft of prey and whether they engage in searching without any disturbance at all.

2 | METHODS

2.1 | Spider husbandry

We worked with adult female black widow spiders collected from Medford, Oregon, in June 2018 and May 2019. We shipped collected spiders to our laboratory at UWM and maintained them under our laboratory husbandry protocols until we used them in experimental trials. We kept spiders in 473-ml plastic food storage containers that contained a diagonal piece of bamboo garden stake, placed at an angle from the bottom corner of the container to just beneath the lid on the opposite side, that allowed spiders to climb and begin

constructing webs. We fed all spiders one approximately 1.5 cm-long cricket (*Acheta domesticus*) 1 week after being placed in their enclosures and then once every 2 weeks until spiders were used in an experimental trial. We began all trials 3 days after feeding spiders to standardize satiety across all spiders.

2.2 | Experiment setup

We used 40 × 33 × 17 cm plastic boxes for all trials. To provide spiders enough texture to climb the sides of the enclosures, we applied tape horizontally approximately 2 cm below the top edge of the box and along one long side and one short side of the boxes. We also applied vertical strips of tape that extended from the horizontal tape to the floor at approximately 10 cm intervals. We applied petroleum jelly to the interior floor and walls of the region of the box without tape so that spiders could not adhere silk to one-half of the box. Spiders were thus able to construct webs that spanned half of the box and left the other half unobstructed by silk, which allowed us to complete the experimental manipulations without damaging spiders' webs. Spiders built retreats in the corner of the box where the long and short sides meet, against the horizontal tape along the top of the box. The overall structure of the spiders' webs was a triangular sheet that extended along a plain formed by the horizontal tape, with gumfooted lines that descended from the sheet and attached to the plastic bottom of the box, and a retreat in the corner of the web furthest from the edge of the sheet.

2.3 | Experimental and control procedures

To begin each trial, we placed each spider in an experimental enclosure. We then allowed spiders 1 week to construct a web. After the web-building period, we examined each enclosure to determine whether the spider had built a web with a horizontal sheet that spanned the entire area of the box that had tape around the top. We excluded spiders that did not build webs or built webs in only part of the box. We also checked whether spiders had constructed any gumfooted lines (Figure 1).

We randomly assigned spiders to one of our control (full undisturbed feeding, make hole in web, or sham theft of prey) or treatment (provide cricket in gumfooted line, then steal it; or cricket in sheet, then steal it;) conditions (Table 1). The controls served to account for the potential effect of the disturbance involved in experimental trials (involving cricket capture and theft—as spiders often made holes in their web sheet in the process of wrapping a cricket in silk, and spiders might have become scared by the cricket theft). If a spider was assigned to receive a cricket on a gumfooted line, but had not made a gumfooted line, we switched that spider's treatment with the next spider in our random assignment that had made at least one gumfooted line. In each treatment in which we offered a cricket, we used a forceps to hold the cricket against the web and vibrated the cricket to simulate trapped prey (Table 1). In the gumfooted line treatment, we vibrated the cricket against a single gumfooted line. In each treatment in which we stole the cricket, we allowed spiders to wrap crickets in silk, detach it from the web sheet, and begin to carry it back toward their retreat suspended from a silk line attached to the spinnerettes. We then used a forceps to steal crickets from spiders.

To begin each trial, we placed the experimental enclosures in our filming location, with one video camera placed directly above the enclosure looking down (as in Video S1), and one placed near the corner of the box furthest from the spider's retreat looking diagonally down, so the view was as close as possible to looking through the web from front to back (as in Video S1). We filmed all trials using both cameras so that we could observe spider behavior in three dimensions. We filmed all trials for 60 min after completing the experimental manipulation (offer cricket, steal cricket, or make hole) (Table 1), except for our “Full feed” treatment in which we filmed spiders until they had finished eating the cricket (Table 1).

In all trials in which we gave a cricket to a spider, we weighed the cricket before offering it to the spider and again at the conclusion of the trial. After each trial was done, we also weighed each spider. We calculated the mass of each spider by subtracting the difference in cricket mass before and after each trial from the mass of the spider after the trial.

2.4 | Video analysis

We used the videos from each trial to collect behavior data. We used the event logging software Alice2 (J. T. Kilmer, unpublished) to record the times at which spiders exhibited specific behaviors: time to start searching, the total time spent searching, the number of bouts of searching, the length of the between search bout intervals, the total time spent searching the floor of the enclosure, and the number of trips each spider made to the floor of the enclosure. We considered one bout of searching to begin when spiders began to move about and tug web threads and to end when spiders returned to their retreat or remained motionless on the web for 3 min or longer. We also measured handling time, which we defined as the amount of time from when spiders first began

to flick silk at the offered cricket to when they started to bring it back to their retreat.

It was not possible to record data blind because it was not possible to blind observers to treatments while they recorded data from videos.

2.5 | Statistical analysis

Spiders that searched did so in bouts lasting several minutes (see below). We therefore analyzed variation in the following response variables: whether each spider searched, the number of search bouts each spider engaged in, whether each spider searched on the floor, and the number of times each spider searched on the floor. We chose to focus on the number of search bouts, rather than summed search times across bouts because these measures were correlated (number of search bouts and search times: $r = 0.33$, $p = .02$; number of trips to the floor and time on the floor: $r = 0.79$, $p < .001$), and we considered that the numbers of bouts give a better indication of decisions by the spiders to extend search efforts, because each decision to resume searching provided a clear indication that the spiders intended to continue searching, but increased duration of a single bout could merely indicate a spider continuing to do what it had been.

To analyze variation in whether spiders searched, we used logistic regression with a term for treatment or control group and a term for site of prey capture nested within treatment. We pooled controls because the crux of our study was whether spiders searched after experiencing prey theft, and no control spiders experienced prey theft.

We then analyzed the behavior of the spiders in the treatment groups (likelihood of searching, number of search bouts, and number of search bouts on the floor), with logistic regression (binomial and Poisson distribution) with the following explanatory terms: location of prey capture (gumfooted line or sheet), handling time, the ratio of the mass of the cricket mass and mass of the spider (hereafter “relative prey size”), and cricket location \times relative prey size interaction.

In all initial models, we also included the time to start searching (seconds from the end of an experimental manipulation to the beginning of the first search bout) as a covariate, but we removed this from our final models because it was never significant ($p \geq .06$ in all models). We also did not include the cricket location \times handling time and relative prey size \times handling time interactions in the final models, because our hypotheses did not make predictions about these interactions, they were never significant ($p \geq .1$ in all models), and including them reduced our power to detect effects of the variables for which we predicted effects.

3 | RESULTS

Spiders in the treatment groups were 4–5 times more likely to search than spiders in any of the control groups (Tables 2, 3,

Figure 2). No other explanatory variable had a significant effect on the likelihood of searching (site of prey capture, relative prey size, handling time, and site of prey capture x relative prey size interaction; Tables 2, 3).

For spiders in the treatment groups that searched, search effort was not significantly related to any of the explanatory variables (site of prey capture, relative prey size, handling time, cricket location x cricket/spider ratio interaction) (Tables 2, 3; Figure 3). However, spiders were more likely to search the floor for larger prey, and the site of prey capture x relative prey size interaction was marginally significant; no other term was significant (Tables 2, 3; Figure 4). And spiders increased search effort on the floor for

larger prey, but only if that prey was captured in a gumfooted line (Tables 2, 3; Figure 5).

4 | DISCUSSION

We tested the hypothesis that black widow spiders form memories of prey they have captured in their webs. We found that black widows do form memories of captured prey and are much more likely to search about their web after experiencing the theft of a prey item. We also tested the hypothesis that black widows remember certain features of their prey. We found that black widows were more likely

TABLE 2 Description of search effort by black widow spiders

		Spiders in treatment groups	Spiders in control groups
Number of spiders that searched		38 of 39 (97%)	8 of 30 (27%)
For spiders that searched	Search time	10 min (0.5–22 min)	3.5 min (0.25–1)
	Search bouts	2 (1–5)	1.2 (1–2)
	Bout duration	6 min (0.25–19 min)	4 min (0.5–15 min)
Number of spiders that searched on floor		18 of 39 (46%)	3 of 30 (10%)
Spiders that searched on the floor	Time on floor	3 min (0.1–12.5 min)	0.33 min (0.25–0.5 min)
	Trips to floor	4.5 (1–18)	1.7 (1–2)
	Trip duration	0.5 min (0.05–9.5 min)	0.12 min (0.05–0.5 min)

Note: Spiders in treatment groups (center column) were more likely to search (top rows) than spiders in the control groups (right column). Spiders exerted more search effort on the floor after experiencing theft of relatively larger prey (bottom rows).

TABLE 3 Analysis of variation in black widow spider searching behavior

Response	Predictor	Statistic	p-value
Likelihood of searching (all spiders)	Treatment or Control	$\chi^2_1 = 22.95$	<.001
	Site of prey capture	$\chi^2_1 = 1.76$.41
Likelihood of searching (treatment groups only)	Site of prey capture	$\chi^2_1 = 0.28$.60
	Relative prey size	$\chi^2_1 = 1.35$.99
	Handling time	$\chi^2_1 = 0.02$.88
	Site of prey capture x relative prey size	$\chi^2_1 = 8.5e-9$.99
Bouts of searching	Site of prey capture	$z = 0.088$.93
	Relative prey size	$z = 1.26$.21
	Handling time	$z = 0.56$.58
	Site of prey capture x relative prey size	$z = 0.48$.63
Likelihood of searching on floor	Site of prey capture	$z = 1.52$.13
	Relative prey size	$z = 2.01$.045
	Handling time	$z = 0.44$.66
	Site of prey capture x relative prey size	$z = 1.92$.055
Number of trips to floor	Site of prey capture	$z = 1.04$.3
	Relative prey size	$z = 3.71$	<.001
	Handling time	$z = 1.26$.21
	Site of prey capture x relative prey size	$z = 2.09$.036

Note: Significant terms shown in bold.



FIGURE 2 Percent spiders that searched. Spiders were more likely to search about their webs after experiencing prey theft (right two bars) than after experiencing control conditions (left three bars)

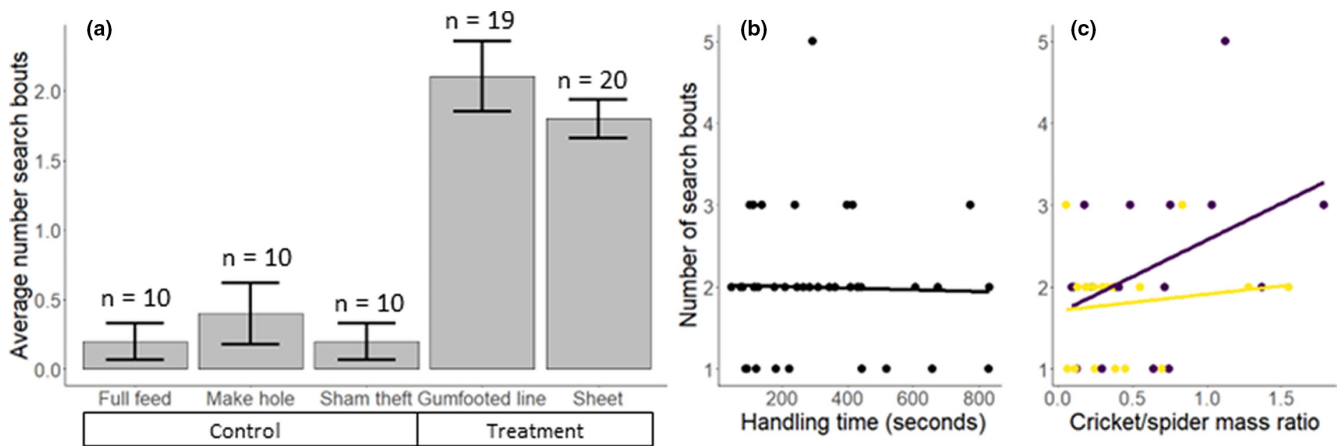


FIGURE 3 Number of searching bouts. (a) Average number (+/- standard error) of search bouts for spiders in control groups (left three bars) and treatment groups (right two bars). Sample sizes shown above bars. (b) Number of search bouts by handling time for spiders in treatment groups. (c) Number of search bouts by relative prey size for spider in treatment groups. Black points are spiders that captured crickets in gumfooted lines, and yellow points are spiders that captured crickets on the web sheet. Lines show slope of relationship for spiders in the gumfooted line (black) and sheet (yellow treatments).

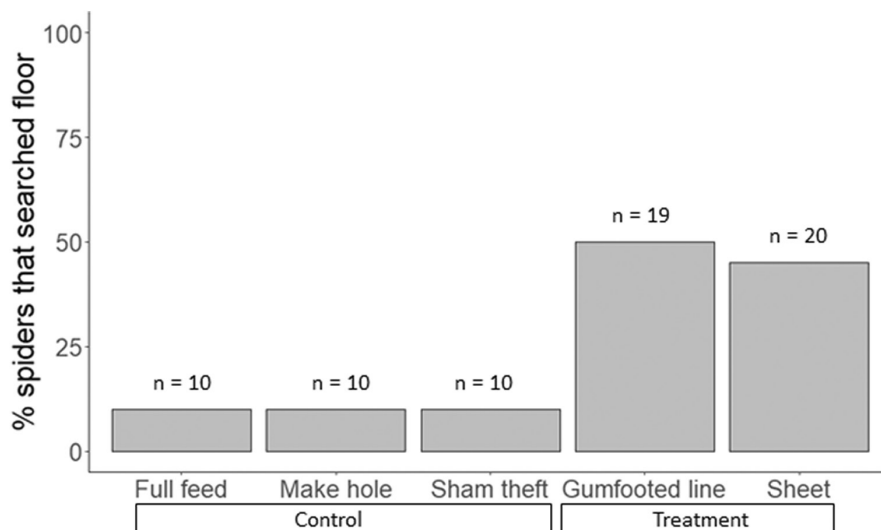


FIGURE 4 Percent spiders that searched floor of enclosure. Spiders were more likely to search the floor of their enclosure after experiencing prey theft (right two bars) than after experiencing control conditions (left three bars).

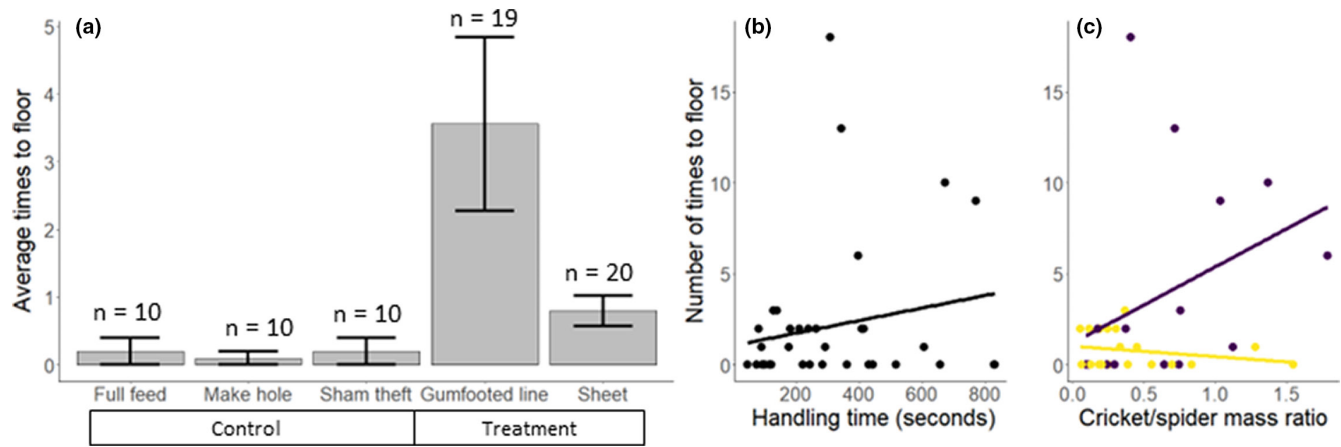


FIGURE 5 Number of trips to floor of enclosure. (a) Average (\pm standard error) number of trips to floor for spiders in control groups (left three bars) and treatment groups (right two bars). Spiders that captured crickets in gumfooted lines made more trips to the floor than spiders in all other groups. (b) Number of trips to floor by handling time for spiders in treatment groups. (c) Number of trips to floor by relative prey size for spiders in treatment groups. Black points are spiders that captured crickets in gumfooted lines, and yellow points are spiders that captured crickets on the web sheet. Lines show slope of relationship for spiders in the gumfooted line (black) and sheet (yellow treatments). Spiders that captured crickets on a gumfooted line made more trips to the floor after capture and theft of larger prey. Spiders that captured crickets in the web sheet did not make more trips to the floor after capture and theft of larger prey.

to search on the floor, and expended more search effort there, when they had captured and lost relatively larger prey they had captured there.

Our findings are in agreement with other studies that show web spiders search for lost prey, revealing memories of the presence of the prey (Kilmer & Rodríguez, 2019; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011). However, our finding that spiders only adjusted their trips to the floor in response to relative prey size when they had captured the prey on in a gumfooted line is novel. We suggest this reflects the ecology of black widow spiders—namely that they capture primarily terrestrial prey on their gumfooted lines (Salomon, 2011). Numerous web spiders have been shown to search longer for larger or more numerous prey (Kilmer & Rodríguez, 2019; Rodríguez et al., 2015; Rodríguez & Gamboa, 2000; Rodríguez & Gloudeman, 2011), but other features of memories of stolen prey are not well researched.

The variation in effort searching the floor according to the interaction between site of prey capture and relative prey size suggests the spiders are adapted to store and use information about relative prey size only when the prey came from their main capture site. However, our results have two potential explanations. (1) Black widows may form memories of prey size and capture location each time they capture prey, but only use the memory of relative prey size to guide behavior when the prey was captured in a gumfooted line. (2) Black widows only form memories of relative prey size when the prey was captured in a gumfooted line. Our experimental design does not allow us to differentiate these two possibilities.

Although our experiment does not allow us to differentiate the above possibilities, our experiment does allow us to rule out alternative explanations for searching behavior. It is conceivable that searching behavior could be a response to disturbance or an attempt to flee from the animal stealing a spider's prey, but we consider

these alternative explanations for searching behavior unlikely. First, we controlled for the effects of disturbance and found clear differences in searching behavior between our control and treatment spiders. Second, the searching behavior described in this paper is distinct from the fleeing or crouching behaviors of disturbed or frightened spiders, as we have described in a prior publication (Sergi et al., 2021).

Our results offer an interesting insight into Western black widow ecology. In the field, black widows capture both terrestrial and flying prey (Salomon, 2011), and some of the flying prey are quite large relative to black widows (e.g., lepidopterans, certain hymenopterans) (Salomon, 2011). Flying prey would presumably become entangled in the sheet, in much the same way we offered crickets to spiders in the sheet in our experiment. However, black widows did not alter their searching behavior in response to differences in relative prey size after capturing prey in the sheet, which suggests that these flying prey capture events could be relatively unimportant in ecological and evolutionary terms.

We used simple experimental manipulations and observations of behavior to reveal the contents of a web spider's memory. Thus, our results underscore the importance of behavioral observations when examining the contents of animal memories. Our experiment and observations of behavior also provided insight into the ecology of the spider and therefore also underscore the importance of the study of memory contents for understanding animal ecology.

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CONFLICT OF INTEREST

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

All data associated with this manuscript are included as supplementary files associated with this manuscript.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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