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Functionally redundant multimodal predator cues elicit changes in prey foraging behavior

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Abstract

Many prey species can assess the risk of predation from information acquired through different sensory systems. For many animals, this information is detected with sensory organs specialized for visual (sight) or chemical (smell or taste) stimuli. It is unclear; however, whether information acquired through multiple sensory systems is functionally redundant or interchangeable, especially if the message is the same. Here, we assess prey response to unimodal visual and chemical cues as well as multimodal (visual + chemical) cues. We specifically test if a foraging individual shows a stronger behavioral response to risk when they can perceive that risk through multimodal versus unimodal cues. To do this, we measured the functional response (prey abundance–foraging rate relationship) of *Tibellus oblongus* spiders foraging on midges while exposing them to visual stimuli, chemical stimuli, or a combination of both visual and chemical stimuli from potential predators. We then determined if the spider’s functional response for the multimodal treatment differed more strongly from a control treatment than from

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either unimodal treatment. We found that under any simulated predation risk (multimodal and both unimodal), *T. oblongus* spiders showed longer handling times than in control groups without risk. However, we saw no elevated anti-predator response in the multimodal treatment, suggesting that information from visual and chemical modalities is interchangeable and sufficient to indicate reliably predation risk.

Keywords: anti-predator behavior, functional response, multimodal signaling, predation risk, risk sensitive foraging.

Introduction

Finding food is essential for survival and reproduction. Heterotrophic organisms consume other organisms or non-living organic matter to procure nutrients and energy. However, the action of searching for and obtaining food (for both herbivores and predators) can expose foragers to predation risk. Therefore, many species must find a way to balance the need for food and the need for safety (McNamara and Houston 1987; Lima and Dill 1990).

Natural selection has generated a variety of strategies that animal foragers use to successfully forage and avoid predation. When faced with predation risk, foragers may modify how they forage, where and when they forage, or even what they select as food (Urban and Richardson 2015). For example, elk (*Cervus canadensis*) have abandoned some foraging habitats to escape wolves re-introduced into Yellowstone National Park (Creel et al. 2005). In orb weaving spiders (*Cyclosa turbinata*), females foraged less and avoided bold foraging behavior when predators were in proximity (Watts et al. 2018). In Black Sea crustaceans, foragers selected more easily captured rotifers in the presence of predatory fish cues (Lehtiniemi and Linden 2006). In other situations, foragers may hide or flee to minimize the risk. For example, Blackcaps (*Sylvia atricapilla*) and European Robins (*Erithacus rubecula*) change flight patterns when presented with simulated attacking predators (Kullberg et al. 1996; Lind et al. 1999). Overall, many organisms are known to change from a foraging pattern that involves searching to maximize energy gain to a foraging pattern with a lower rate of energy gain but that allows for greater safety from predators (Brown and Kotler 2004), resulting in lowering the overall foraging rate.

A reduction in foraging rate due to predation risk must be mediated by a change in the functional response, or the relationships between

prey density and predation/foraging rate (Solomon 1949; Holling 1959). Most commonly, foraging increases with prey abundance but asymptotes when the number of prey captured limits additional searching by imposing a time cost, known as handling time. This standard functional response model is the Type II, Holling disc equation:

$$f_{pc} = \frac{aR}{1 + aRh} \quad (1)$$

In this model, f_{pc} is the per capita foraging rate of the predator (number of resources acquired per time per predator), a is the space clearance rate (space cleared of prey per time per predator), R is the resource density (resources per space), and h is handling time (time per resource). Space clearance rate describes how quickly a predator can remove prey from a given space, while handling time describes the loss in search time associated with the acquisition and/or consumption of an individual resource item. Any change in the time budget of a forager (i.e., time allocated to searching) will be reflected in a change in the handling time, and any change in foraging behaviors, including decisions to attack or searching behavior, will be reflected in the space clearance rate (DeLong 2021). Therefore, discerning changes in the functional response in response to predation risk can provide information about whether and how foragers modify their foraging in response to risk (Urban et al. 2020).

Foragers can detect risk by gathering information from the environment using a variety of sensory systems or modalities. In addition to the familiar sensory modalities of vision and hearing, information about predation risk can be collected through the detection of chemical stimuli (taste or smell), substrate-borne vibrations, electrical currents, thermal gradients, and even air particle movement stimuli (Bradbury and Vehrencamp 1998). Many species may use combinations of stimuli to gather environmental information. It is unclear, however, whether detecting risk through different modalities generates different perceptions of the magnitude of risk. Moreover, it is unclear if detection of predation risk through more than one modality suggests greater risk to the organism or if information gathered through multiple modalities is functionally redundant, providing similar information.

If information gathered through different modalities leads foragers to perceive different levels of risk, then we predict that functional

response parameters will differ for foragers experiencing different types of predator stimuli. For example, a forager might perceive more imminent risk if they can see a predator rather than just detecting chemical stimuli that indicate the predator is in the area. In addition, multimodal cues might be non-additive or additive. If, for example, stimuli detected across sensory modalities are interpreted similarly in terms of predation risk (e.g., are redundant and overlapping in terms of their content), functional response parameters should be similar in scenarios with single sensory stimuli and multimodal sensory stimuli. If multimodal information is additive, on the other hand, we expect a greater change in the functional response with multiple sources of predator information (multimodal stimuli) versus a single source (unimodal stimulus).

In this study, we tested whether different forms of information about predation risk, in terms of unimodal visual, unimodal chemical, or multimodal visual + chemical stimuli, elicited different, functionally redundant/interchangeable, or additive responses in the slender crab spider, *Tibellus oblongus* Walckenaer, 1802.

Tibellus oblongus is found throughout the United States in grassy habitats and may be predated by larger predators, including larger spiders (Fritz and Morse 1985). To test the response of *T. oblongus* to unimodal versus multimodal predatory cues, we exposed individuals to the visual and/or chemical stimuli from a potential predator, the large wolf spider *Hogna baltimoriana* Keyserling 1877. During exposure to these different risk conditions, we measured the functional response of *T. oblongus* foraging on midges (*Chironomidae*). We predicted that (1) *T. oblongus* would show reduced foraging activity and a lower functional response with predation risk than without it, (2) that exposure to visual stimuli would reduce the functional response more than the reduction elicited by chemical stimuli, due to the immediacy of the risk when predators are in close proximity, and (3) that exposure to multimodal information would reduce the functional response to a greater degree than exposure to either unimodal stimulus. A lowered functional response caused by a reduced space clearance rate would imply changes to predatory searching behavior, while increases in handling time would indicate modifications in prey processing behaviors.

Methods

Collection and maintenance

We collected *T. oblongus* between 0800 and 1400 h by sweep netting in grassy vegetation around Lake Ogallala, Nebraska, USA (41°07'26.40" N–101°43'5.99" W) at the University of Nebraska's Cedar Point Biological Station (CPBS) beginning in early June of 2019. We housed spiders individually in 120 mL square plastic containers with a dampened 1.5" × 3/8" cotton roll (3D Dental, Euclid, OH, USA) to provide moisture. We did not feed spiders after capture, and we kept spiders unfed for approximately 36 h to standardize hunger and increase motivation to hunt during trials. We determined sex and maturity where possible, but some individuals were immature, making it impossible to determine their sex. *Tibellus oblongus* spiders weighed 23.2 mg on average (± 12.1 SD). Preliminary analyses indicated that our measure of size—body mass—would not help us understand differences among treatments and thus we proceeded without considering it further. We collected *H. baltimoriana* from the same locations, housed them in the same type of containers used for *T. oblongus*, and fed them midges. We collected midges to serve as prey shortly before trials commenced using an aspirator from a light trap near the laboratory space. Midges were approximately 0.5 cm in length.

Foraging trials

To estimate the functional response, we conducted foraging trials in arenas created from 25-cm diameter circular plastic domes (the lid of a food display container) placed over a clean sheet of standard printer paper. The dome cover had a small opening in the top for adding prey. We manipulated the presence and absence of predator stimuli in the visual and chemical sensory modalities in the following manner. In visual stimulus trials, we placed a single *H. baltimoriana* in the center of the arena underneath a clear plastic 50-mm diameter Petri dish. This allowed the *H. baltimoriana* to be detectable throughout the foraging trial to the foraging *T. oblongus* spider. This setup limited the motion of the *H. baltimoriana* spider, reducing the potential for vibratory stimuli to be generated, but some vibration signals could have been produced. In chemical

stimulus trials, we allowed a *H. baltimoriana* spider to walk along the base paper, laying silk, and depositing feces for approximately 6 h prior to the commencement of foraging trials. We removed this spider shortly before the trial began. This treatment ensured that the *H. baltimoriana* chemical stimuli were readily detectable through the arena during the trial even though the *H. baltimoriana* was no longer in the arena. In the multimodal stimulus trials, we included both a pre-treated paper floor and a spider under a Petri dish. We also had a control treatment in which foraging trials had clean paper floors and Petri dishes without *H. baltimoriana* present, thus not having any stimuli from predators. Thus, we had four treatment groups in total, two unimodal and one multimodal—(1) control, (2) visual, (3) chemical, and (4) visual + chemical. We used *H. baltimoriana* spiders multiple times each for visual and chemical trials.

To generate functional response curves, we used five midge densities (3, 5, 10, 15, and 20 in number) and replicated each density five times for each of the four treatments. We used each individual *T. oblongus* in only one foraging trial in the experiment. We randomly distributed individual spiders to each treatment without regard to age or body size, but we distributed male and female spiders equally across each treatment to facilitate analysis of how sex affects anti-predator behavior. There were therefore 200 separate foraging trials (five prey levels \times four treatments \times two sexes \times five replicates). We ran trials in the evening, in low light in the laboratory after dusk when all three species are active in their natural habitats (FGS pers. obs). Trials lasted 15 min, at which point we removed the *T. oblongus* spider and counted the number of the midges killed.

Analysis

We used a bootstrapping approach to fit functional responses, obtain parameter estimates, and assess differences in functional response parameters between control, visual, chemical, and visual + chemical treatments. To do this, we sampled with replacement each data set 500 times and fit a functional response model to each bootstrapped data set. We did not replace prey as they were consumed during the experiment, so we used the Lambert *W* version of the Roger's Random Predator equation (Royama 1971; Rogers 1972; Bolker 2011):

$$R_e = R_o - \frac{W(ahR_o e^{-a(30-hR_o)})}{ah} \quad (2)$$

where a and h are as in Equation 1, t is the time duration of trials (15 min), R_e is the number of midges eaten, R_o is the number of midges offered, and W is the Lambert W function. We fit Equation 2 to each of our datasets separated by treatment. There was no indication of a sigmoidal shape in the data, so we only fit the type II model (Equation 2). We used nonlinear least squares regression in MATLAB 2021a for all fits. Each fit gave us estimates of a and h , and we used the median and 2.5 and 97.5 percentiles to get the estimate and 95% confidence intervals on each parameter for each treatment.

To compare the curves among treatments (control, visual, chemical, visual + chemical), we calculated the difference between all bootstrapped estimates for each parameter between each treatment. Then we used the distribution of those differences to assess significance, with the percentile at which the distribution crossed zero equal to the p -value. For example, we took all estimates of handling time from the control treatment and subtracted all pairwise estimates of handling time for the visual treatment, giving 250 000 possible differences (i.e., each of the 500 bootstrapped estimates of the control parameter subtracted from each of the 500 bootstrapped estimates of the treatment parameter). The distribution of differences shows the chance of one parameter being larger than the other because it shows the proportion of differences that are positive or negative (DeLong 2021). For example, if 96% of the differences are positive, then we can conclude that the difference is positive with $p = 0.04$. We did this for each contrast to determine significance of differences between all pairs of treatments. Functional response foraging trials will be archived in the online database FoRAGE (Uiterwaal et al. 2022).

Results

Functional responses were broadly similar and type II in all treatments (**Figure 1** and **Table 1**). Space clearance rate did not differ among treatments (**Table 2** and **Figure 2**), as bootstrapped contrasts among all treatment levels indicated p -values all exceeded 0.1 (Table 2). In

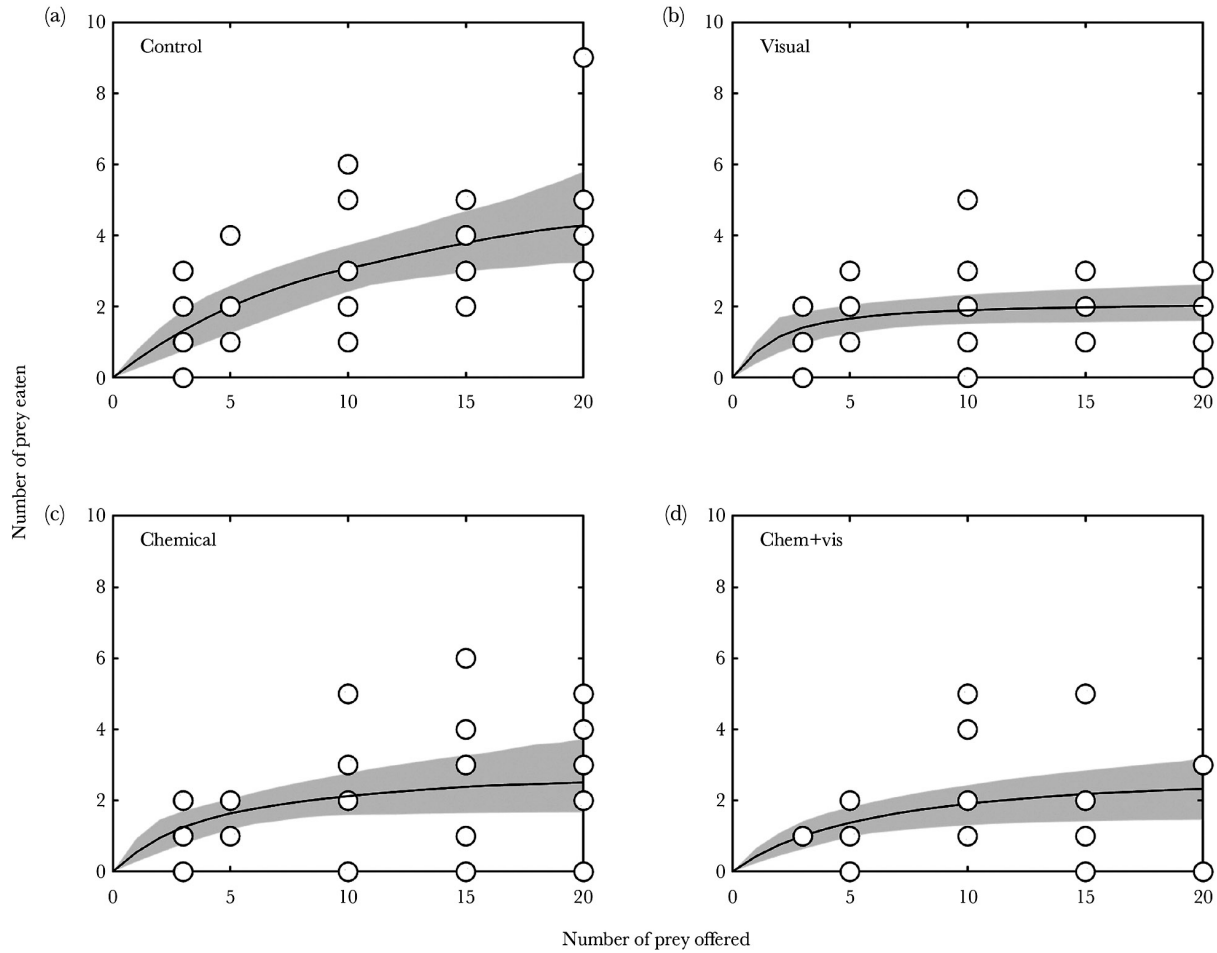


Figure 1 Functional responses of *Tibellus oblongus* spiders foraging on midges under four different scenarios presenting predation risk through different signaling modalities. Spiders foraged (A) without risk (control), (B) with a larger wolf spider (*Hogna baltimoriana*) visible but contained nearby, (C) with the chemical residue of a wolf spider that had walked across the foraging arena floor, or (D) with both the chemical and visual modalities. Open circles are observations, black lines are median fitted functional response, and gray shaded areas are the 95% confidence limits of the fit.

Table 1 Fitted parameters of the Holling disc equation (Equation 1) to foraging trial data for *Tibellus oblongus* foraging on midges. Data are means with 95% confidence intervals estimated from 500 bootstraps. The mean of R^2 values across bootstraps is shown

| Treatment | Space clearance rate, α | Handling time, h | Mean R^2 |
|-------------------|--------------------------------|--------------------------------------|------------|
| Control | 0.049 (0.019 to 0.12) | 2.31 (1.1×10^{-7} to 3.92) | 0.38 |
| Chemical | 0.064 (0.023 to 0.35) | 5.11 (1.92 to 8.7) | 0.12 |
| Visual | 0.13 (0.040 to 1.19) | 7.01 (4.6 to 9.23) | 0.07 |
| Visual + chemical | 0.045 (0.019 to 0.11) | 5.19 (2.27 to 9.22) | 0.16 |

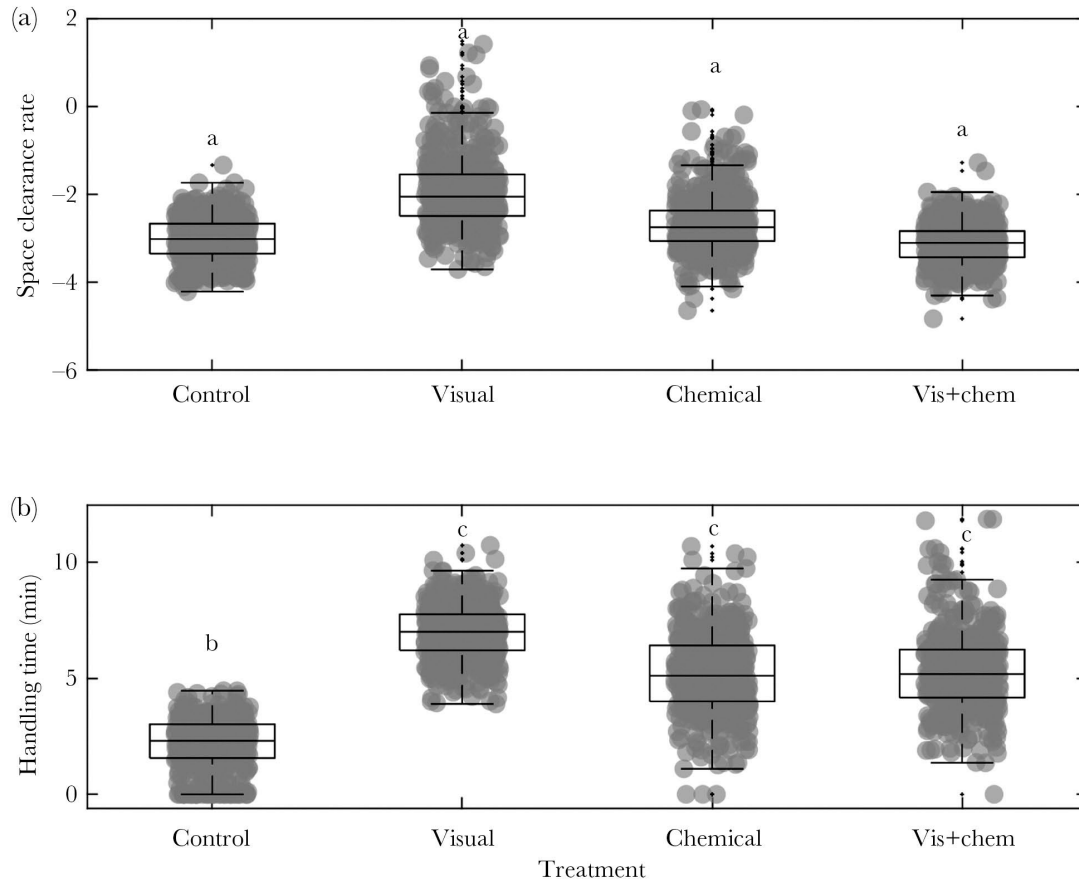


Figure 2 Estimated functional response parameters for *T. oblongus* spiders foraging on midges in different risk scenarios. Spiders foraged (A) without risk (control), (B) with a larger wolf spider (*H. baltimoriana*) visible but contained nearby, (C) with the chemical residue of a wolf spider that had walked across the foraging arena floor, or (D) with both the chemical and visual modalities. Box plots show median and inner 50% of parameter estimates. Lower case letters indicate significant differences between estimates.

Table 2 *P*-values for all pairwise differences for space clearance rate (*a*) and handling time (*h*).

| | | <i>a</i> | | | |
|----------|-------------------|-------------------|---------------|-----------------|--------------------------|
| | | <i>Control</i> | <i>Visual</i> | <i>Chemical</i> | <i>Visual + chemical</i> |
| <i>h</i> | Control | | 0.10 | 0.32 | 0.55 |
| | Visual | <0.0001 | | 0.78 | 0.74 |
| | Chemical | 0.06 | 0.83 | | 0.74 |
| | Visual + chemical | 0.04 | 0.49 | 0.84 | |

Note: Differences in bold are considered significant.

contrast, handling time was higher for all risk treatments (both unimodal and multimodal) than for the control treatment (Table 2 and Figure 2). The handling time in the unimodal chemical treatment versus the control treatment was marginally significant ($p = 0.06$), while the unimodal visual versus control and multimodal visual + chemical versus control contrasts were significant ($p < 0.05$; Table 2). The handling time in the unimodal visual treatment did not differ from that in the unimodal chemical treatment (Table 2). Most importantly, the multimodal visual plus chemical treatment did not differ from the unimodal treatments (Figure 2).

Discussion

Generally, prey are under selection for effective means of detecting potential predators. Many species use an amalgamation of sensory systems such as vision, olfaction, and hearing to detect the presence of predators and thus assess predation risk. But it is unclear whether information gathered from modality-specific predator stimuli is detected and interpreted similarly, or if prey may detect and interpret modality-specific stimuli differently in terms of perceived predation risk. Our results show that *T. oblongus* detect predators when presented with visual and substrate-borne chemical stimuli and respond in a similar way (reducing their functional response, prediction 1) regardless of the modality through which that information about risk originated.

Perhaps surprisingly, the change in the functional response was similar for the unimodal visual and chemical stimuli. This contradicts our second prediction that visual stimuli would have had a larger effect because it might signal a more immediate risk. This lack of a difference between visual and chemical stimuli is even more surprising given the possibility that there were some *H. baltimoriana* vibratory stimuli present in the visual treatment. In other words, our visual stimuli may have been slightly bimodal (visual + substrate-borne vibratory), although our observations suggest that substrate-borne vibratory stimuli were minimized.

One interpretation for our observed similarity in response to unimodal visual and chemical predator stimuli is that for the forager it does not pay to evaluate the magnitude of risk, as errors in assessment could

be lethal. If true, foragers should respond with equal strength to a predator cue in any modality. Alternatively, our assumption of visual cues indicating a more immediate predator risk may be wrong in this system. For example, the active space, or area where the cues are detectable, of visual and chemical stimuli may actually be similar for *T. oblongus*, thus representing equal distance and threat from a predator. *Tibellus oblongus* occurs in grassy fields in a vertically heterogeneous environment. This signaling environment may restrict the active range of visual predator cues, making them no more informative of imminent danger than chemical cues.

Moreover, we did not find support for an additive effect of predator stimuli (prediction 3). The foraging response we observed was not more pronounced when receiving both visual and chemical stimuli relative to either stimulus alone. Although these results indicate that *T. oblongus* can perceive predation risk through stimuli received across multiple sensory systems, the results also indicate that these multimodal stimuli are interchangeable. The visual and chemical predator stimuli appear functionally redundant in terms of perceived predation risk, at least with respect to driving behavioral changes that alter the functional response. Within our field collection site, *T. oblongus* is abundant but occurs alongside many larger spider species, birds, and predatory insects, about which it would be beneficial to collect information. If the spiders can smell their predator, needing to see them is unnecessary, and vice versa, but environmental conditions that allow the transmission of visual or chemical stimuli may be highly unpredictable, favoring the ability to use either sense as necessary (Partan 2013). Notably, our study only evaluated the interaction of two sensory modalities, and other modalities (e.g., vibratory detection, nearfield soundwaves, and magnetoreception) might provide a different quality or type of information that could alter the way foragers respond to predation risk.

The difference in functional responses between risk and control treatments was due to differences in the handling time. Thus, *T. oblongus* altered their time budget in response to risk. Handling times estimated through functional responses include all of the time costs associated with processing prey that cut into additional searching time. Our direct observations of spiders during the experiments indicate that *T. oblongus* spiders held on to captured midges for longer in the risk treatments than in the control treatments. Thus, one possible explanation

for the longer handling times is that when faced with risk, it is advantageous to more thoroughly consume prey that has been captured rather than search for more prey and risk encounters with predators. The behavioral mechanism driving the difference in functional response may then be longer processing in safer locations, even if processing prey for longer yields diminishing returns (Cook and Cockrell 1978; Okuyama 2012). Alternatively, it may be that the spiders were paying more attention to potential predators in their surroundings rather than their food, increasing the time it takes to process the prey. The lack of any difference in space clearance rate (i.e., the initial slope of the functional response, a) suggests no behavioral modifications of searching patterns, velocities, or hunting styles when faced with risk, or, alternatively, a set of changes that canceled out in their effect on the estimated parameter.

Finally, our results indicate that the foraging rate of *T. oblongus* spiders at higher prey densities in the risk groups was roughly half that of the control groups, suggesting that risk greatly reduces energy intake and potential fecundity of *Tibellus* spiders. This possibility indicates that the population dynamics of *Tibellus* could be altered by the risk-induced changes in the functional response. This is because predation risk can not only impact population dynamics through direct killing but also by reducing energy uptake and therefore reproduction and survival (Zanette et al. 2011). Our results, therefore, suggest strong potential for behavioral responses to predation risk to alter the abundance and dynamics of species throughout food webs via changes in the functional response (de Ruiter et al. 1995; Creel et al. 2007). Future work building off these findings would benefit from directly assessing fitness costs of altered foraging behavior.

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Data Availability Analyses reported in this article can be reproduced using the data provided by Shogren et al. (2022).

Conflict of interest The authors declare that they have no conflicts of interest.

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