Glyphosate-Based Herbicide Has Contrasting Effects on Prey Capture by Two Co-Occurring Wolf Spider Species

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Abstract Anthropogenic substances have the potential to affect animal behavior either because they present a novel stimulus or because they interfere with natural chemical communication pathways. Such shifts can alter the dynamic between predators and potential prey, which might affect population success as well as the strength of food web linkages. We examined the foraging of two wolf spiders, *Tigrosa helluo* and *Pardosa milvina* (Araneae, Lycosidae), that are abundant in agroecosystems where they are routinely exposed to herbicides. We tested the hypothesis that the presence of a commercial formulation of a glyphosate-based herbicide would affect the prey capture behavior of these two wolf spiders. We tested the larger *Tigrosa* foraging on *Pardosa* or crickets (*Acheta domesticus*) and the smaller *Pardosa* foraging on crickets. *Tigrosa* subdued crickets more quickly and with fewer lunges than it took them to capture *Pardosa*. The presence of herbicide allowed *Tigrosa* to orient toward and capture both prey species more quickly but it did not affect the number of lunges required to subdue either prey. Herbicide did not affect the timing of prey capture for *Pardosa* but it did cause them to use more lunges in the process. Thus, herbicide had contrasting effects on foraging behavior of these two agrobiont predators, which means that it could shift the direction and strength of food web linkages in complex ways.

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Introduction

Chemical application is one of the primary ways that humans attempt to manage undesirable aspects of their landscape (Myers 1996; Nash 2008; Pimentel 2002). While it is accepted that these substances will be toxic to target species, the sublethal effects on animal behavior during or after exposure generally are underappreciated (Desneux et al. 2007; Sih et al. 2010, 2011; Tuomainen and Candolin 2011). Anthropogenic compounds present a novel stimulus and, as such, may cause changes in the activity patterns of organisms (Desneux et al. 2007). In addition, such chemcials can serve as "info-disruptors" that interfere with accurate signal detection and interpretation for non-target species (Klaschka 2008; Lürling and Scheffer 2007). When animals behave in inappropriate or maladaptive ways, either because of a direct response to a novel stimulus or through info-disruption, unintended consequences may emerge at the population or community level (Relyea and Hoverman 2006; Rohr et al. 2006).

Predation is a key feature of any food web and, hence, is a fundamental driver of population and community dynamics. In addition, the interactions between predators and potential prey often are mediated by using chemical information (Apfelbach et al. 2005; Burks and Lodge 2002), and so the addition of anthropogenic substances is likely to affect that dynamic. For example, nutrient addition and the resultant changes in pH impair the ability of two species of freshwater snail to detect and respond appropriately to predators (Turner and Chislock 2010), while sublethal amounts of insecticide reduce the ability of the parasitoid wasp, *Leptopilina boulardi*, to find prey (Komeza et al. 2001). Additionally, very low levels of two different contaminants have opposite effects on the behaviors that copepods use to escape

predators (Gutierrez et al. 2012). Thus, when anthropogenic chemicals are introduced into habitats, it is difficult to predict how they will affect predator–prey interactions and, as a consequence, what effects they might have on the food web.

With the adoption of genetically-modified herbicide-resistant crops, glyphosate-based herbicides (e.g., Roundup®) are sprayed routinely and repeatedly in urban, suburban, and agricultural systems (Baylis 2000; Lundgren et al. 2009; Woodburn 2000). Standard toxicity tests suggest that these herbicides are safe for animals (Giesy et al. 2000; Pan 1996), but recent studies reveal a variety of potentially problematic effects on both vertebrates and invertebrates (Evans et al. 2010; Howe et al. 2004; Relyea 2005). Specifically, evidence is mounting that commercial formulations of glyphosate-based herbicides alter the activity and affect the reproductive success of several species of terrestrial arthropod predators including species that play important roles in the ecosystems where they would be exposed (reviewed in Pekár 2012; see also Griesinger et al. 2011; Schneider et al. 2009; Wrinn et al. 2012). The goal of this study was to determine if these herbicides influenced the prey capture behavior of two wolf spider species: *Tigrosa helluo* and *Pardosa milvina* (Araneae, Lycosidae). We selected these species because they use chemical information to navigate their environment but persist in agroecosystems where they are regularly exposed to herbicides. We hypothesized that the presence of herbicide would alter predator–prey dynamics by changing the timing of prey capture and/or the effort expended in the prey capture process.

Methods and Materials

Study System We examined the effects of herbicide on prey capture by the large wolf spider, *Tigrosa helluo* (formerly *Hogna helluo* see Brady 2012), foraging on the smaller wolf spider, *Pardosa milvina* or on immature European house crickets, *Acheta domesticus* (Orthoptera, Gryllidae). We also documented capture behavior of *Pardosa* foraging on the same species of crickets. These wolf spiders are among the most common ground dwelling predatory arthropods in agroecosystems of eastern North America (Marshall et al. 2002). While wolf spiders in general make extensive use of combinations of visual, vibratory, and chemical senses (Barth 2002), both of these spider species use chemical information to detect prey (Hoefler et al. 2002; Persons and Rypstra 2000), and both prey species use similar cues to detect predators (Hoefler et al. 2012; Persons et al. 2001). Additionally, both of the spider predators change aspects of their activity when they encounter a surface treated with a commercial formulation of a glyphosate-based herbicide (Evans et al. 2010). While *Pardosa* does not avoid patches where herbicide is applied, individuals representing this species alter more aspects of their behavior when they are on herbicide treated

areas than do those from *Tigrosa* (Evans et al. 2010). On the other hand, the response of *Pardosa* to *Tigrosa* cues is so strong that any shifts in activity induced by herbicide are not detectable when it is sprayed on top of *Tigrosa* cues (Wrinn et al. 2012). While not tested exhaustively, there is no evidence that herbicide alters the activity of house crickets (K.M. Wrinn unpublished data).

Collection and Maintenance We collected spiders from soybean and corn fields at the Miami University Ecology Research Center (Oxford, Butler County, Ohio, USA). The spiders were housed individually in cylindrical plastic containers with 2–3 cm of moistened peat moss-soil mixture covering the bottom. The containers for *Pardosa milvina* had bottoms that were 8 cm diam and sides 5 cm tall. Floors of the containers housing the larger *Tigrosa helluo* were 12 cm diam, and sides were 8 cm tall. Spiders were fed two crickets, each approximately ¼ the size of the spider, weekly. All spiders were used as experimental predators 1 week after a routine feeding. Crickets used as prey for spider cultures and in experiments were selected from populations that were housed communally in large rectangular plastic bins (26×46×21 cm) with water and commercial dog food available *ad libitum*.

Herbicide Preparation We obtained a commercial formulation of herbicide (Buccaneer Plus ®, Monsanto, St. Louis, MO, USA) containing 41 % (480 g/l) glyphosate (N-(phosphonomethyl)glycine) isopropylamine salt and 59 % other ingredients, including a polyethoxylated tallowamine (POEA) surfactant. We diluted this formulation with distilled water to a concentration of 2.5 % (12 g/l of the glyphosate salt) for use in our experiment (as in Evans et al. 2010). The herbicide was applied to five filter paper discs, each 4 cm in diameter, at a rate equivalent to 12 ml/m^2, which is within the recommended range for field application (9.35–18.7 ml/m^2). An equivalent volume of distilled water was applied to control discs. Discs were sprayed and arranged in a regular pattern on the bottom of the experimental arena just before the trials (Fig. 1). Since herbicide is applied to the agricultural fields when the plants are 10–20 cm tall, some of it is intercepted by leaves before it hits the ground. As a result, spiders on the soil surface typically encounter patches of herbicide soaking into the soil surrounded by untreated areas where natural cues remained intact. Here, we attempted to mimic the scenario in which an area in the spider's home range that was previously occupied by a predator is sprayed with herbicide, which lands on the ground in discrete patches.

Experimental Procedure Only subadult and adult female spiders were used in experiments since the foraging behavior of males is limited (Walker and Rypstra 2002). We paired prey with predators prior to experimentation with a desired ratio of prey to predator mass of 0.4, which would be well within the
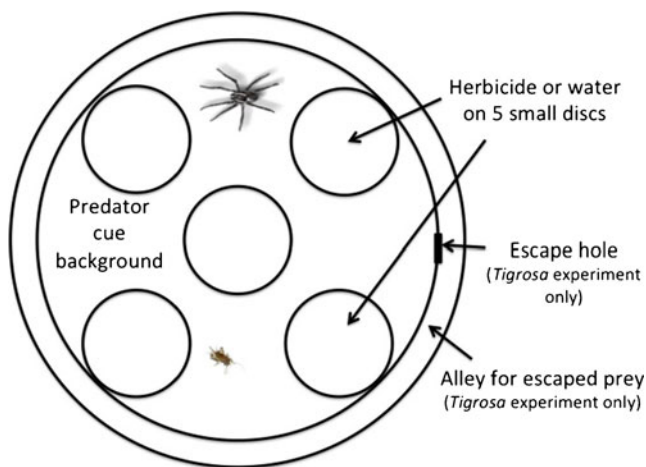
Fig. 1 Diagram showing the arena used in studies. Filter paper covering the entire floor (15 cm diam) of the arena contained predator cues and five discs (each 4 cm diam) were used to present herbicide (or water for controls). Only trials with *Tigrosa* included a prey escape hole

range of prey both *Tigrosa* and *Pardosa* could easily handle (Rypstra and Samu 2005). Experiments were conducted in circular plastic arenas (15 cm diam., 10 cm high) with a Plaster of Paris base. For trials with *Tigrosa* as the predator, a 1 cm hole was cut in the side of the arena at the level of the floor, which allowed prey to escape. We closed the hole during acclimation periods by covering it with a small piece of paper. During trials, this arena was set inside a larger container to trap any escaping prey. Because escape rates were low and not related to treatments, we did not include the escape hole in the experiment where *Pardosa* was the predator.

Because our aim was to determine whether herbicide interfered with predation either by causing shifts in behavior directly or by interfering with predator cues, we included predator cues in all trials. We did not include prey cues and, as a result, the predators had to rely on information (visual, vibratory, as well as chemical) that they gathered during the experiment to execute a successful capture. We collected chemotactile cues (silk, feces, and other excreta) by enclosing the *Tigrosa* or *Pardosa* for 24 h in a 15 cm cylindrical container with a disc of filter paper covering the bottom. A moist cotton ball or dental wick was positioned on the side or top of the container so that water was available to the spider throughout the cue deposition period. Just prior to a trial, the water source was removed and the cue spider was sequestered under a 1 cm opaque vial while we placed five discs of filter paper that had been dampened with herbicide or water on top of the predator cues (Fig. 1). The predator vial was shifted so that the animal was in contact with the herbicide (or water) patches as well as its own cues. A prey item (either *Pardosa* or cricket) was released and allowed to move freely throughout the container for a 5 min. acclimation period. We verified that the prey animal moved throughout the arena in a fashion that allowed it to come in contact with both

predator cues and herbicide or water patches prior to testing. We then corralled the prey item under a second vial and positioned the predator and prey on opposite sides of the arena and released them simultaneously.

Each trial was recorded using a camera mounted directly over the arena with a connection to a video recorder located in a separate room. We monitored their interactions for 15 min or until the prey was captured. Upon review of the recordings, we recorded data as follows: time of the first orientation toward prey, time of the first attack, number of lunges the predator made at the prey item, incidence of prey capture or escape, and time to prey capture.

Statistical Analyses We verified that the prey to predator ratio was similar across treatments using one-way ANOVA. For the *Tigrosa* experiment, we allowed the crickets or *Pardosa* to escape and compared the number of escapes in the presence of herbicide or water using log linear analysis. Trials in which the prey escaped were excluded from subsequent analyses. For both experiments, we achieved normality by square root-transforming the time it took for the predator to orient toward the prey, the time between orientation and the first attack, and the time from the first attack to capture. Since we recorded three aspects of prey capture from the same individuals, we used a multivariate analysis of variance with repeated measures to test for treatment effects. When the MANOVA revealed a significant difference, we followed that analysis with two way ANOVAs with herbicide presence and prey type as factors in the *Tigrosa* experiment or with one-way ANOVAs with herbicide as the factor in the *Pardosa* experiment. Finally, we categorized each prey capture event as requiring one, two, or three or more lunges and used log linear analyses to examine the effects of herbicide in both experiments and prey type in the *Tigrosa* experiment on these frequencies.

Results

Out of a total of 37 trials where *Tigrosa* was tested with *Pardosa*, only five *Pardosa* escaped, and in 37 trials only nine crickets left through the escape hole. There were no differences in the frequency of escape across treatments ($X^2_4 = 1.72$, $P = 0.790$). Our efforts to standardize the prey to predator size ratio across treatments were successful for both *Tigrosa* ($F = 0.34$; $P = 0.56$) and *Pardosa* experiments ($F = 0.99$, $P = 0.33$) with an overall mean of 0.41 ± 0.03.

Both prey type and herbicide affected *Tigrosa* predation (MANOVA, Wilk's lambda, $F_4 = 3.27$, $P = 0.015$). Overall, *Tigrosa* was slower in orienting toward and preying on *Pardosa* than crickets but the presence of herbicide hastened the detection of both prey types (Table 1; Fig. 2). Once *Tigrosa* oriented toward the prey, the first attack followed quickly and was not

Table 1 Average (± S.E.) for the time it took the predators to attack once they had oriented toward the prey item and the time it took them to capture the prey after the initial attack

Predator	Prey	N	Herbicide	Orient to 1st attack (s)	1st attack to predation (s)
Tigrosa	Cricket	14	No	12.9±8.2	120.2±54.1
Tigrosa	Cricket	14	Yes	0.3±0.2	0.2±0.1
Tigrosa	*Pardosa*	16	No	15.1±13.4	200.3±64.6
Tigrosa	*Pardosa*	16	Yes	13.9±13.7	59.6±33.1
Pardosa	Cricket	11	No	0.1±5.4	1.7±1.2
Pardosa	Cricket	11	Yes	1.3±1.3	1.3±0.8

affected by prey type or herbicide (Tables 1 and 2). While the time between that first attack and when the prey item was captured was not significantly different between the two prey types, it was shorter when herbicide was included in the arena (Tables 1 and 2). Herbicide did not affect the number of lunges that *Tigrosa* used to capture prey (X^2_1 = 1.53, P= 0.215), however, *Tigrosa* usually was able to capture crickets with one lunge, whereas it often took three or more to capture *Pardosa* (X^2_1 = 5.05, P= 0.025) (Fig. 3).

Herbicide did not affect the timing of predation by *Pardosa* (MANOVA, Wilk's lambda, F_2= 0.70, P= 0.508; Fig. 2). However, herbicide altered the nature of the predatory event; *Pardosa* was more likely to take three or more lunges in their attempts to capture crickets when herbicide was included in the arena (X^2_1 = 4.74, P= 0.030) (Fig. 3).

Discussion

Clearly the presence of glyphosate affects the predatory interactions of both *Tigrosa* and *Pardosa*; interestingly, it affects
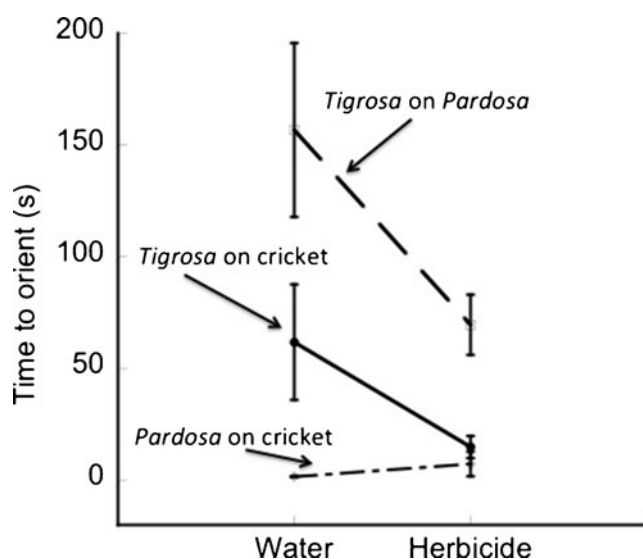
Fig. 2 The time (average ± standard error) that it took the predators to orient toward each prey type tested in the presence of herbicide or distilled water

these two wolf spider species differently. *Tigrosa* detected and subdued both prey types more quickly when herbicide was present, while the timing of predation by *Pardosa* was unaffected. However, herbicide seemed to make prey capture more onerous for *Pardosa* in that they needed more lunges to subdue their cricket prey. The contrasting effects of herbicide on predation by *Pardosa* and *Tigrosa* are consistent with previous studies demonstrating that herbicide influenced the activity of these two predators differently (Evans et al. 2010). In addition, this study verifies that herbicide application may potentially have substantial but unpredictable effects on food web linkages in agroecosystems.

This study verifies that a commercial formulation of glyphosate-based herbicide acts as an info-disruptor and interferes with the efficacy of the responses made by the prey species studied here to predator signals. The large *Tigrosa* benefited from anthropogenic interference even though the design biased the information provided in the arena toward its prey. Both prey species are known to react to substrate-borne cues from predators (Hoefler et al 2012; Persons et al 2001), yet, in this study, adding patches of herbicide reduced survival even when the predator cues were present (Fig. 2). This result is surprising in that Wrinn et al. (2012) found that the response of *Pardosa* to *Tigrosa* cues overwhelmed any effect of herbicide on overall general activity and emigration from a treated arena. In fact, *Pardosa* were less likely to emigrate from areas where herbicide was presented along with *Tigrosa* cues (only 40 % emigrated in comparison to a 60 % emigration rate in trials with just *Tigrosa* cues) (Wrinn et al. 2012). Our data suggest that their reluctance to leave likely renders them vulnerable to predation, and verifies that herbicide disrupts the adaptive reactions of *Pardosa*. We speculate that glyphosate affects the ability of crickets to accurately interpret predation risk in a similar manner.

While *Tigrosa* uses similar types of chemical information to locate and select prey (Persons and Rypstra 2000), in these studies, we did not include prey cues in the arenas. As a result, *Tigrosa* had to rely primarily on visual and vibratory stimuli to detect prey with only the chemicals emitted by the prey during the course of our staged interaction. This result suggests that herbicide could benefit *Tigrosa* even more in natural predator–prey situations. Chemical communication is a primitive and fairly generalized signaling mode (Dicke and Takken 2006; Wyatt 2003) but it is flexible because it can function in environments where vision is limited and vibratory stimuli might be attenuated (Aquiloni et al. 2009; Hebets and Papaj 2005; Partan and Marler 1999). It may be that herbicide effects are diminished when animals encounter one another in environments that allow them to emphasize different sensory modalities.

It seems likely that *Tigrosa* success in the presence of herbicide is due to shifts in prey responses to the chemical information available. Evans et al. (2010) found that *Tigrosa* activity was subtly affected by herbicide; the time they spent in non-locomotory restlessness (i.e., rotational movement that displaced

Table 2 Results of separate ANOVAs revealing the effects of herbicide and prey type on the time it took *Tigrosa* to orient, attack and ultimately capture prey items. None of the interactions between herbicide and prey type were significant and were eliminated from the models

Behavior		df	F-ratio	P
Time to orient	Model	2	7.94	<0.001
	Herbicide	1		0.006
	Prey type	1		0.008
Orient to 1st attack	Model	2	0.45	0.643
	Herbicide	1		0.550
	Prey type	1		0.470
1st attack to predation	Model	2	5.23	0.008
	Herbicide	1		0.006
	Prey type	1		0.135

them less than one body length) increased, while the distance travelled, time spent walking, and speed were all unchanged when exposed to herbicide. It is possible that frequent shifts in orientation helped *Tigrosa* detect prey more quickly, but it is generally thought that the visual systems of wolf spiders are designed to detect motion from a stationary position (Persons and Uetz 1997; Rovner 1991, 1993). Since a previous study revealed that on herbicide-treated surfaces, *Pardosa* spends less time walking and covers less distance than on untreated surfaces (Evans et al. 2010), we might have expected that *Pardosa* would be less susceptible to predation from *Tigrosa* when herbicide was present. However, while *Pardosa* do not avoid entering herbicide treated regions, they move faster once they are there (Evans et al. 2010) whereas they slow down on predator cues (Persons et al. 2001). Since *Tigrosa* detected *Pardosa* more quickly when herbicide was present, we can conclude that the speed of the prey is an important component in *Tigrosa* predatory success and not just the overall activity level as suggested by past studies (Persons and Uetz 1997; Persons 1999).

The susceptibility of crickets to *Tigrosa* predation is consistent with previous studies of these three species. *Tigrosa* attacks crickets across a larger size range much faster than they do other wolf spiders (Rypstra and Samu 2005). Intraguild predation among wolf spiders is common and, as a result, it exerts strong selective pressures on communities of generalist predators (Schmitz 2007; Wise 2006). In this case, *Pardosa* respond to cues from *Tigrosa* in a dramatic and situation-specific manner, suggesting a long evolutionary history between these coexisting predators (Persons et al. 2001; Persons and Rypstra 2001). On the other hand, herbicide had similar effects on the susceptibility of both *Pardosa* and crickets to *Tigrosa* predation even though *Pardosa* were from populations inhabiting fields that had been treated with commercial herbicides for more than 10 years, while crickets were obtained from commercial cultures where exposure to any herbicides would have been minimal. Thus, we have no evidence that *Pardosa* populations have adapted to the selective pressure of regular chemical application to the agricultural fields in a way that would help them when attacked by *Tigrosa* in the presence of herbicide.

It is less clear from the available data why *Pardosa* required more lunges to capture crickets in the presence of herbicide. Since total capture times are the same for water and herbicide treatments, it is possible that, when *Pardosa* moves more quickly overall, it strikes at the cricket prey with increased speed at a cost of accuracy. On the other hand, *Pardosa* predation was completed very quickly in our trials, and it would be difficult for us to detect small differences in the timing of various components of the predatory process. In addition, little is known about any behavioral differences displayed by house crickets in the presence of herbicide. We do know that the mean ratio of prey to predator that we used is much closer to the maximum size threshold for *Pardosa* than it is for *Tigrosa* (Rypstra and Samu 2005). It may be that the presence of a novel chemical stimulus was sufficient to disrupt the process for prey in this size range, and that we might see a similar disruption for *Tigrosa*
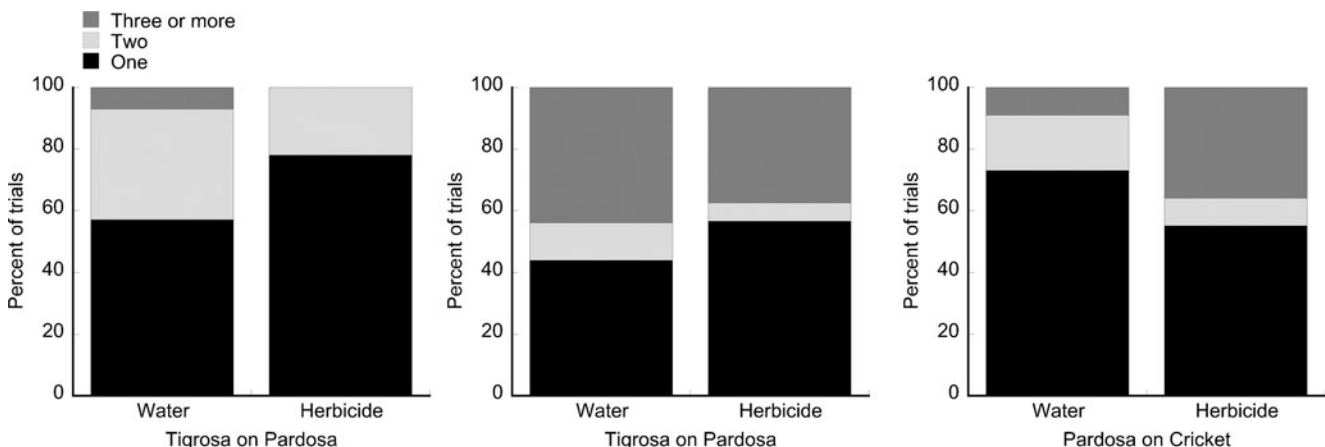

Fig. 3 Proportion of trials in which the predators used one, two, or three or more lunges to capture each prey type in the presence of herbicide or distilled water

foraging on larger prey items that are closer to the upper size limit.

Ecological studies suggest that *Tigrosa* is a strong competitor limited by colonization ability whereas *Pardosa* is an active colonizer constrained by competition (Marshall et al. 2000, 2006). The studies of the effect of herbicide on these two species that have been conducted thus far imply that early applications of glyphosate-based compounds would delay the establishment and reduce the success of *Pardosa,* an important predator in agroecosystems (Evans et al. 2010; Wrinn et al. 2012, this study). Since herbicides are applied to control vegetation, the primary impacts on the arthropod community are through shifts in plant abundance and diversity (Bell et al. 2002; Haughton et al. 1999, 2001, 2003; Roy et al. 2003). A reduction in vegetation reduces plant-dwelling predators, which might increase the importance of epigeal carnivores, such as wolf spiders, in biological control efforts. Here, we showed that *Tigrosa,* the large predator, receives some foraging advantages, whereas the success of the more common *Pardosa* may be compromised. A more detailed understanding of herbicide effects on species interactions may reveal how herbicides affect the development of the agricultural community and, more specifically, how the effects of herbicide on capture success might percolate through the food web. This information can inform decisions about application timing and frequency in integrated pest management programs.

The ecology of information is an emerging field that explores the ecological occurrence and consequences of animal communication (Dall et al. 2010; Schmidt et al. 2010). Here, we presented evidence that one common predator is winner and the other a loser when olfactory landscape is interrupted by herbicide. Hence, the chemically noisy environment created by standard management practices has strong selective implications for animals living in agricultural or garden systems (Desneux et al. 2007; Lane et al. 2011). The extent to which ubiquitous anthropogenic influences affect the efficacy of information flow demands that basic research programs explicitly incorporate the potential for info-disruption influences on their study subjects.

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