Chemosphere 262 (2021) 127785

Contents lists available at ScienceDirect

Chemosphere

journal homepage: www.elsevier.com/locate/chemosphere

The pest-specific effects of glyphosate on functional response of a wolf spider

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HIGHLIGHTS

- Spiders are beneficial predators in crops.
- Spider feeding behavior is affected by pesticides.
- We evaluated the effect of glyphosate of wolf spiders when feeding on different prey.
- Glyphosate affected wolf spider's functional response in a prey-specific way.
- Prey-specific response to glyphosate can affect wolf spider's biocontrol services.

ARTICLE INFO

Article history:
Received 14 May 2020
Received in revised form
19 July 2020
Accepted 20 July 2020
Available online 7 August 2020

Handling Editor: Willie Peijnenburg

Keywords:
Acromyrmex sp.
Anticarsia gemmatalis
Miogryllus sp.
Herbicide
Feeding behavior
Sublethal effect

ABSTRACT

Although glyphosate is widely used for weed pest control, it might have negative side effects on natural enemies. Wolf spiders are one of the most representative predators found on soybean crops in Uruguay, preying on a wide variety of potential pests. However, the sublethal effects that pesticides might have on this group have been poorly explored for South American species. Herein, we explored the sublethal effects of glyphosate on the functional response of the wolf spider *Hogna cf. bivittata* against three potential pest insects, namely ant (*Acromyrmex* sp.), caterpillar (*Anticarsia gemmatalis*), and cricket (*Miogryllus* sp.). We contaminated residually adult females of the species *Hogna cf. bivittata* with glyphosate (Roundup®) and compared their functional response against non-contaminated spiders. We did not observe any mortality during the study. We found that overall *Hogna cf. bivittata* showed a functional response type II against crickets and caterpillars but no functional response to ants. Contaminated spiders killed less ants and caterpillars in comparison to the control group, probably as a consequence of the irritating effects of glyphosate. We did not observe differences in functional response to crickets at the evaluated densities, probably as a consequence of the low capture rate against this prey. Although glyphosate does not specifically target spiders, it might have negative sublethal effects on native predators such as *Hogna cf. bivittata*. Further studies should explore effect of glyphosate on other native predators from South American crops.

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1. Introduction

Worldwide, glyphosate is one of the most frequently used pesticides for controlling weed pests in several economically important crops (Vila-Aiub et al., 2008). This pesticide is used in many South American countries in which the production of some economically important crops, such as soybean, demands use of a high-level glyphosate for weed prevention (Christoffoleti et al.,

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https://doi.org/10.1016/j.chemosphere.2020.127785
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2008). Glyphosate can have highly negative effects on the environment and human health; however, there are only a limited number of studies that have evaluated the potential impact of glyphosate on other facets of pest control, such as reduction of insect pests by their natural enemies in South America (López et al., 2012).

Negative agrochemical effects on natural enemies have been traditionally measured mainly by lethal effects. However, agrochemicals can also cause various sublethal effects (Desneux et al., 2007), which can have comparable impact on the lethal effects of pest suppression caused by natural enemies (Desneux et al., 2007; Pekár, 2012). For example, pesticides have been shown to cause a reduction in oviposition rate in some parasitoid species (Fangupo et al., 2018). Pesticides can also reduce the capture rate and alter prey selection in generalist insect and spider predators (Pasquet et al., 2016; Petcharad et al., 2018; Zhang et al., 2015). These negative effects caused by pesticides on natural enemies can even increase crop damage by pests (Bommarco et al., 2011; Furlong et al., 2004). Glyphosate and glyphosate-based herbicides were observed to have negative (Benamú et al., 2010; Evans et al., 2010; Korenko et al., 2016; Leccia et al., 2016; Niedobová et al., 2019; Schneider et al., 2009; Wrinn et al., 2012), neutral (Michalková and Pekár, 2009), or stimulating effects (Svobodová et al., 2018) on natural arthropod enemies of insect pests, suggesting species/taxon- and trait-specific responses even in closely related species (Rittman et al., 2013).

Spiders cause a significant reduction in pests on a global scale (Michalko et al., 2019), and as a consequence, are excellent models for evaluating the effect of glyphosate on generalist predators (Benamú et al., 2010; Evans et al., 2010; Wrinn et al., 2012). Wolf spiders (Araneae, Lycosidae) are dominant predators in various crops in which they occur on soil and at lower vegetation in which they can come directly into contact with glyphosate (Benamú et al., 2017; Samu and Csaba, 2002). Wolf spiders lead to a reduction in pests and improve crop performance in various agroecosystems (Birkhofer et al., 2008; Oraze and Grigarick, 1989; Snyder and Wise, 2001; Suenaga and Hamamura, 2015), including soybean (Hlivko and Rypstra, 2003).

Functional response of predator to prey is a widely used characteristic to evaluate the potential of natural enemies to regulate pests, since it is related to the per capita number of prey killed at different prey densities during a certain time period (Benhadi Marín et al., 2019). Several functional response types have been identified (Jeschke et al., 2004), but there are three basic types (type I-III) (Juliano, 2001). In predators with the type I functional response, the number of killed prey increases linearly with increasing prey density and the predators kill a constant proportion of prey until their satiation; type II functional response is characterized by an asymptotic increase in number of killed prey and the proportion of killed prey decreases with increasing prey density (Holling, 1965; Juliano, 2001). This type is common in arthropod predators including spiders (Riechert and Lockley, 1984). The type III functional response follows a sigmoidal shape where there is an initial increase followed by a decrease in the proportion of killed prey as prey density increases (Holling, 1965; Juliano, 2001).

Glyphosate can cause a reduction in the predatory activity of wolf spiders (Korenko et al., 2016; Niedobová et al., 2019). Most studies investigating the effects of glyphosate on predatory activities use only one constant non-pest prey density. However, the densities of pests fluctuate across space and time (Ewald et al., 2015). Moreover, one recent study pointed out that the effects of a pesticide on predatory activity of a generalist predator can be prey-specific, and the predatory activity can decrease, increase, or show no significant changes depending on the prey (Petcharad et al., 2018). Therefore, it is more useful to investigate the effects of pesticides on predators' functional responses to the changing densities of various pests as this type of investigation may yield a better mechanistic explanation for pest suppression patterns observed in the field (Benhadi Marín et al., 2018; Pekár et al., 2015). However, there is no such study concerning glyphosate.

Glyphosate may theoretically change the capture rate and type of functional response in a pest-specific manner (Deng et al., 2007; Michalko and Košulič, 2016). Glyphosate may also cause irritating effects, and the affected spiders can then perform only wasteful killing, thus minimizing handling time (Deng et al., 2007). This would lead to a change from an asymptotical or sigmoid increase in killed prey along the lines of prey density to a linear increase in killed prey (Michalko and Košulič, 2016), id est from a type II or III functional response to type I (Holling, 1965).

In this study, we investigated the effects of glyphosate on the functional responses of the agrobiont wolf spider *Hogna cf. bivittata* to densities of soybean insect pests. *Hogna cf. bivittata* is common in soybean crops in Uruguay, therefore we evaluated its feeding rate against three soybean pests, namely cricket *Miogryllus* sp., selected based on field observations and the caterpillar *Anticarsia gemmatalis,* and the ant *Acromyrmex* sp. which are common pests in local soybean crops (Ribeiro et al., 2008) These three pests differ in their nutritional content, level of danger, locomotion, and escape capabilities (Greeney et al., 2012; Lease and Wolf, 2011; Líznarová; Pekár, 2013). We expected that glyphosate will reduce capture rate of *Hogna cf. bivittata* but it will alter the functional response of *Hogna cf. bivittata* in a prey-specific manner. Specifically, the effect of glyphosate will be more pronounced in a difficult prey that requires more effort to subdue it than in an easy prey.

2. Material and methods

2.1. Specimen collection and hunger standardization

We collected 150 adult females of the species *Hogna cf. bivittata*(mean size±SD: 13 ±4 mm) found in native forests from San José, Uruguay (34°19′08.8″S, 56°43′13.5″W). Spiders were transferred to the laboratory and housed individually in Petri dishes (60 × 15 mm) containing a small piece of wet cotton to keep moisture inside the cage. We kept the cages in room with constant humidity (70 ± 10%), temperature (25 ± 5 °C), and photoperiod (14 L: 10 D) to simulate the natural conditions from the sampling locality.

To standardize the hunger level, all the spiders were fed sequentially with juvenile individuals of the cockroach *Blaptica dubia* during 1 h, when the spider stopped accepting prey, it was considered satiated. The hunger standardization procedure lasted only one day following similar studies focused on wolf spiders feeding behavior (García et al., Accepted). Spiders were starved during two weeks after feeding, before starting the experiments. All spiders spent the same time on Petri dishes (16 days), before starting experiments.

2.2. Effect of glyphosate on spider feeding rate

To evaluate the effect of the glyphosate on the functional response, we randomly assigned 150 spiders without replacement to experimental groups based on treatment (control, glyphosate)/prey type (ant, caterpillar, cricket; see later)/prey density. Five spiders were used for each prey density, we kept the predator:prey body size ratio as similar as possible between treatments to avoid possible bias.

For the spider contamination, we used the residual toxicity method suggested by Řezáč et al. (2010). A filter paper (10 × 10 cm) was submerged into a glyphosate solution, with a concentration of 280 mg/L a.i. (100% field dosage) since it is commonly used in soybean crops in the region (Catacora Vargas et al., 2012). The filter paper was left to dry (30 min) and later rolled in a test tube (15 × 1.5 cm), each single spider was placed inside the tube for 30 min. For the control group the same procedure was repeated but individuals were exposed to distilled water, which is a solvent for glyphosate. After contamination, individuals were transferred to a glass container (19 × 10 × 6 cm) 30 min before starting the experiments to allow the spider to habituate.

We used ant (*Acromyrmex* sp., mean size ± SD: 6 ± 3 mm), caterpillar (*Anticarsia gemmatalis,* mean size ± SD: 17 ± 4 mm), and cricket (*Miogryllus* sp., mean size ± SD: 15 ± 3 mm). Prey were selected based on preliminary field records in the case of crickets, which were observed feeding on soybean seedlings (Lacava *pers obs*), and have been reported as pests for other crops such as grapes (Bournier, 1977). Caterpillars and ants were selected, as these have been suggested as pest for soybean crops in Uruguay (Ribeiro et al., 2008). We also used as a criteria preliminary observations, where adult females of *Hogna cf. bivittata* were observed preying on the selected pests (Lacava *pers. Obs.*). The three pests were tested separately. To avoid bias due to prey size differences, we selected prey with body length up to two times the spider's prosoma length, except for ants that measured about half of the spider's prosoma length. We offered one of the five prey densities to each spider, namely 1, 3, 5, 10, and 15 prey. Each prey item was assigned to treatment/density/spider randomly without replacement. Overall, we used five replications for each prey species and its corresponding density and treatment. The experiment run for 4 h. To ensure constant prey density (Juliano, 2001), we checked for dead prey every 15 min and we replaced the dead prey for living one.

2.3. Data analysis

All analyses were performed within the R environment (R Development Core Team, 2019). We determined the type of functional response (type I-III) by evaluating the relationship between the prey density and the proportion of killed prey (Juliano, 2001). We applied the generalized linear models (GLMs) with quasibinomial error structure and logit link (GLM-qb) as the data were underdispersed (Pekar and Brabec, 2016). The linear predictor of the initial model was of cubic regression type as it can provide a good fit for the type III functional response (Juliano, 2001). The type of functional response was then determined by the significance and slope of the linear term (Juliano, 2001). Type I is determined by non-significant linear term, while types II and III are determined by a significant negative and positive linear term, respectively. Since an experimental treatment can change the type of functional response we analyzed the type for each group separately (Juliano, 2001).

If the linear term was significantly negative we modelled it according to the formula (Holling, 1965):

$$N_e = \frac{aNT}{(1 + aNT_h)}$$

Where N_e, N, a, T, and T_h are number of killed prey, prey density, search efficiency, total time, and handling time (prey capture and ingestion), respectively. We used the linearized form of the formula by inversely transforming the prey density and by using a GLM with gamma error structure and inverse link (GLM-g) (Pekár and Brabec, 2016). To compare the capture rate between the experimental groups we incorporated the effect of treatment into the model (Juliano, 2001). We estimated the search efficiency a according to the relationship $a = 1/\beta T$, where β is the estimate of slope. Th was estimated according to the relationship $T_h = \alpha T$, where α is the intercept (Pekár and Brabec, 2016). As a and Th were estimated from the data, they contain all their sub-components (Holling, 1965). However, as the time of experiments was relatively short while the ingestion takes more time (Sebrie et al., 1991, 1994; Pasquet and Leborgne, 1997), the handling time is most likely composed mainly from prey capture. T was 15 min as the period when we checked for the dead prey.

3. Results

We did not observe any mortality throughout the short-term course of the study. However, we observed that contaminated individuals constantly groomed legs and pedipalps after exposure. The functional response of *Hogna cf. bivittata* to crickets was of type II in control (GLM-qb, $F_{1,23} = 53.6$, $P < 0.001$; Table 1) as well as in the glyphosate contaminated group (GLM-qb, $F_{1,23} = 29.5$, $P < 0.001$; Table 1). The number of killed crickets increased with prey density (GLM-g, $F_{1,48} = 7.90$, $P = 0.007$; Fig. 1) but the capture rate was similar between the two treatments (GLM-g, $F_{1,48} = 0.39$, $P = 0.54$). The estimated asymptote of killed crickets was 0.19 and 0.18 per 15 min in the control and glyphosate treatment, respectively.

For caterpillars, the functional response was of type II in both treatments (Table 1). In all treatments the number of killed prey increased with density (GLM-g, $F_{1,47} = 35.03$, $P < 0.001$). The glyphosate contaminated spiders killed fewer caterpillars than control spiders, which was due to higher handling time (GLM-g, $F_{1,48} = 10.32$, $P = 0.002$; Table 1; Fig. 2). The estimated asymptote of killed caterpillars was 0.33 and 0.53 per 15 min in contaminated and control group, respectively.

The proportion of killed ants decreased with prey density in the control group (GLM-qb, $F_{1,22} = 28.9$, $P < 0.001$; Table 1) and glyphosate contaminated group (GLM-qb, $F_{1,19} = 57.4$, $P < 0.001$; Table 1). On the other hand, the number of killed ants did not increase with prey density in both treatment groups (GLM-g, $F_{1,42} = 0.02$, $P = 0.88$). This means that there was no functional response to ant densities. However, number of killed ants was lower in the contaminated than the control group (GLM-g, $F_{1,43} = 8.09$, $P = 0.007$; Table 1; Fig. 3).

4. Discussion

Here we investigated how the glyphosate affects the functional response of *Hogna cf. bivittata* to three important insect pests of soybean, namely cricket *Miogryllus* sp., caterpillar *A. gemmatalis,* and ant *Acromyrmex* sp. We did not observe any mortality, which is in line with results showing that glyphosate has a minimal immediate lethal effect (e.g., Michalková and Pekár, 2009; Leccia et al., 2016). The application of glyphosate affected the *Hogna cf.*

Table 1
Parameter estimates (SE) of functional responses of the spider *Hogna cf. bivittata* after contamination by glyphosate or exposure to water as a control to three pests. The significantly negative linear term (β) from a quasibinomial model along with stated search efficiency (a) from a gamma model indicates the functional response of type II. Number of killed ants did not depend on prey density indicated by the dash. T_h is for the handling time. The parameters were estimated for total time T = 15 min and area of 728 cm^2. Comparisons are made between contaminated and control group for each prey type. Different letters, indicate significant differences.

Prey	Treatment	B	T_h	a
Cricket	Glyphosate	−0.12 (0.022)	5.2 $(0.86)^a$	0.16 $(0.369)^a$
	Control	−0.16 (0.022)	5.5 $(0.80)^a$	0.36 $(0.478)^a$
Caterpillar	Glyphosate	−0.76 (0.172)	3.1 $(0.40)^a$	0.30 $(0.816)^a$
	Control	−0.26 (0.074)	1.8 $(0.28)^b$	0.21 $(0.889)^a$
Ant	Glyphosate	−0.59 (0.103)	6.9 $(0.83)^a$	–
	Control	−0.58 (0.133)	4.3 $(0.48)^b$	–

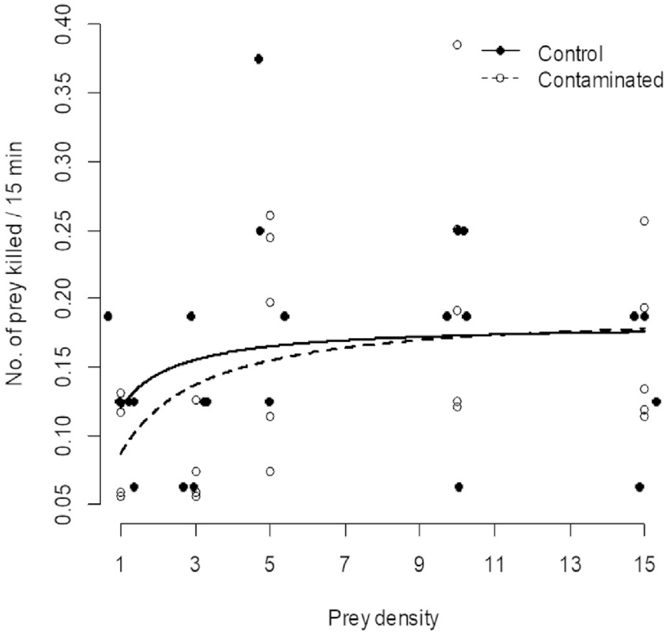

Fig. 1. Functional response of the spider *Hogna cf. bivittata* after contamination with glyphosate or treated by water control to density of crickets *Miogryllus* sp. Estimated relationships are displayed. Small noise in data along x-axis was added to show the data structure. The estimated parameters are shown in Table 1.

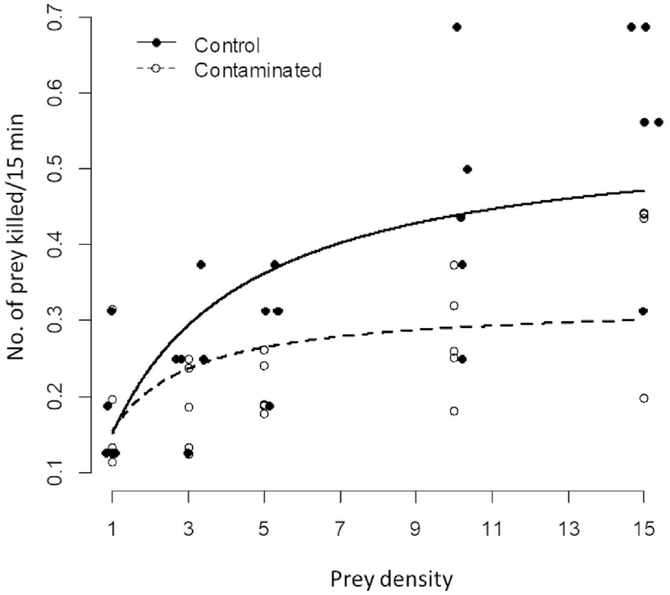

Fig. 2. Functional response of the spider *Hogna cf. bivittata* after contamination with glyphosate or treated by water control to density of caterpillars *Anticarsia gemmatalis*. Estimated relationships are displayed. Small noise in data along x-axis was added to show the data structure. The estimated parameters are shown in Table 1.

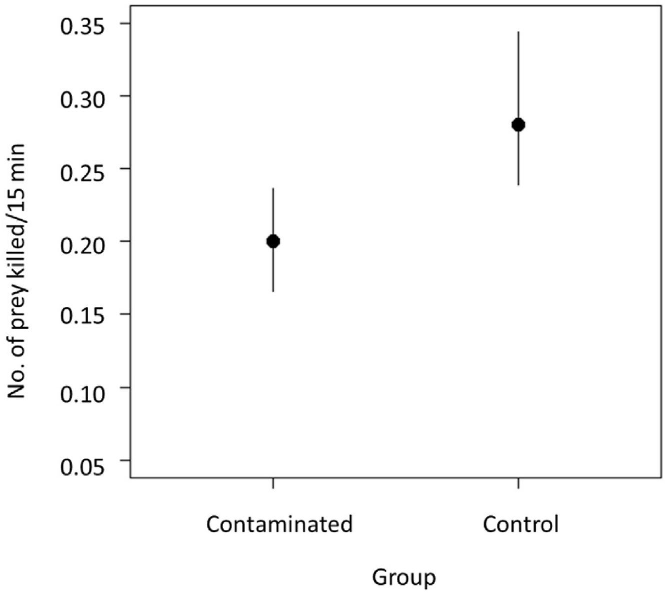

Fig. 3. Comparison of number of killed ants *Acromyrmex* sp. by the spider *Hogna cf. bivittata* after contamination by glyphosate or exposure to water control. The points are means and the lines are 95% confidence intervals.

bivittata's functional response in a pest-specific way. The glyphosate application reduced the capture rate of caterpillars and ants. But the capture rate of crickets was similar between spiders from glyphosate and control groups. Our results agree with Petcharad et al. (2018), who showed that the effects of pesticides can be prey-specific.

Surprisingly, the capture rate of crickets by *Hogna cf. bivittata* was similar in the glyphosate and control treatments. We observed that crickets exhibited highly effective defense as they avoided a spider's attack by jumping and kicking. This might explain the low capture rate on this prey type. It is likely that the low capture rates of crickets prevented the detection of differences between the treatments. In addition, experience with prey can also affect the capture success in spiders (Jakob and Long, 2016). However, we are unaware whether the spiders captured crickets in the field and therefore we cannot say whether experience with crickets might affect the capture success of *Hogna cf. bivittata*.

The reduced capture rate of caterpillars by the glyphosate exposed *Hogna cf. bivittata* was caused by increased handling time while the search efficacy was similar. This suggests a minimal effect of glyphosate on the factors that compose search efficacy, specifically, relative spider and caterpillar locomotion speed, spider reaction area, and killing success rate (Holling, 1965). On the other hand, glyphosate influenced one or more components of handling time, namely time spend by watching, subduing, and consuming prey (Holling, 1965). Rittman et al. (2013) observed that glyphosate does not affect the time when the wolf spider *Pardosa milvina* notices the cricket, time when she initiates the attack, or killing success rate of a single cricket. But, the *Pardosa* exposed to glyphosate invests more in subduing the crickets as it takes more pounces than the unexposed spiders (Rittman et al., 2013). As the experiments were short-term (4 h) and the ingestion time is longer (Sebrie et al., 1991, 1994; Pasquet and Leborgne, 1997), we assume that the observed difference was not caused by the differences in digestion pause of the spiders. Therefore, the lower capture rate of *Hogna cf. bivittata* might be connected to the subduing capacity. We observed that caterpillars struggled more when captured than crickets and ants, which might increase the differences in prey paralysation between glyphosate and control groups.

Glyphosate also reduced the capture rate of ants. However, we did not find a significant relationship between the consumption rate and the prey density. Lycosids rarely prey on ants as they are dangerous (Cushing, 2012; Líznarová and Pekár, 2013; Michalková and Pekár, 2009). The lack of relationship between density and consumed prey might be explained by the fact that ants use group defence (Hölldobler and Wilson, 1990). The reduced searching time at higher ant density can be compensated by the increased time spend by avoiding and defending against ant retaliation (Líznarová and Pekár, 2013). We observed that contaminated spiders spend more time grooming legs and pedipalps. We hypothesize that this might influence the searching time and the number of prey consumed. The intensified cleaning due to pesticde apllication have been reported in different insecticides in other natural enemies such as coccinelids and spiders (Wiles and Jepson, 1994; Niedobová et al., 2016).

The effect of herbicides on spider-prey relationship and food-web dynamics in agroecosystems is often assumed to be indirect through changes in vegetation structure (e.g., Staudacher et al., 2018). However, glyphosate can affect the feeding rate in a prey-specific way within a spider species and the response to glyphosate to a specific prey type might differ among spider species (Behrend and Rypstra, 2018; Rittman et al., 2013). Moreover, glyphosate can affect spider behaviour and life-history parameters across several instars (Behrend and Rypstra, 2018; Benamú et al., 2010; Evans et al., 2010). Since glyphosate may inhibit cholinesterase transmission in crayfished affecting nervous system and altering key functions as feeding (Banaee et al., 2019), further studies should explore if something similar occurs in spider affecting their feeding behavior. Therefore, the application of glyphosate can directly affect the strength and connections within the food-webs and consequently the food-web dynamics and biocontrol services provided by spiders.

Our results have implication for biological control. *Hogna cf. bivittata* have the potential to contribute to pest limitation, especially of the caterpillars but also crickets in soybean crops because the capture rates increased with the pests' densities. Indeed, other wolf spider species have been shown to be an effective predator of a Noctuidae caterpillar pests of cotton (Rendon et al., 2016). However, the suppression potential of *Hogna cf. bivittata* for ants is minimal as the capture rate did not change with ant density.

In conclusion, we found a pest specific short-term effect of glyphosate on the functional response of the wolf spider *Hogna cf. bivittata*. Glyphosate did not affect capture rate of crickets significantly but it reduced capture rate of caterpillars and ants. Our results therefore agree with other studies showing that glyphosate can reduce the biocontrol potential of natural enemies (Benamú et al., 2010; Korenko et al., 2016; Niedobová et al., 2019; Stecca et al., 2016). However, the pest-specific effect on capture rate of *Hogna cf. bivittata* suggests that the application of glyphosate may affect the biocontrol services, not only through reduced overall capture rate but also through the restructured food-web architecture. Our results are therefore in line with those of Petcharad et al. (2018) and illustrate the necessity to investigate the pest-specific response of natural enemies to pesticides if we are to understand the effect of pesticides on biocontrol services. Further studies should explore the effect of glyphosate and other pesticides on food webs where spiders are a representative group of predators.

CRediT author statement

Mariángeles Lacava: Conceptualization, Methodology, Investigation, Data curation, Writing original draft, Resources. Luis Fernando García: Conceptualization, Methodology, Data curation, Formal analysis, Writing original draft, Writing - Review & Editing. Carmen Viera: Conceptualization, Methodology, Writing - Review & Editing, Resources, Project administration, Funding acquisition. Supervision. Radek Michalko. Formal analysis, Data curation, Software, Visualization, Writing original draft, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The Uruguayan Research Grant Agency (ANII: POS_NAC_2011_1_3687 and SNI) and the Sectorial Committee for Scientific Research supported M.L. LFG and CV. RM was supported by the grant no. QK1910296 NAZV provided by the Ministry of Agriculture of the Czech Republic – National Agency for Agricultural Research. We are also indebted to Martín Santana, Ramiro Tambasco and Marcelo Ottati, for their help on laboratory observations. Oscar Lacava, Edgardo Roland and Esteban Arostegui kindly helped us with logistic support. We thank Marco Benamú for his comments on a previous version of this project. We are indebted to Luis Piaccentini for his help on spider identification and the anonymous reviewers whose comments helped us to improve this manuscript.

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