



Experimental assessment of trophic ecology in a generalist spider predator: Implications for biocontrol in Uruguayan crops

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Abstract

Conservative biological control promotes the use of native natural enemies to limit the size and growth of pest populations. Although spiders constitute one of the most important groups of native predators in several crops, their trophic ecology remains largely unknown, especially for several generalist taxa. In laboratory, we assessed the predatory behaviour of a wandering spider (the wolf spider *Lycosa thorelli* (Keyserling, 1877) against several arthropods varying in size and trophic positions, all found in South American soybean and rice crops. As prey we used the bug *Piezodorus guildinii* (Westwood, 1837) as well as larvae and adults of the moth *Spodoptera frugiperda* (Smith, 1797), both being considered important pests in Uruguayan crops. We also used several non-pest arthropods as prey, sarcophagid flies, carabid beetles and wolf spiders. All prey were attacked in more or less high, although not statistically differing, proportions. However, carabids were not consumed, and bugs were consumed in significantly lower proportions than flies. A negative correlation was found between prey size and acceptance rate. Immobilization times were longer against larvae when compared to moths and flies, while predatory sequences were longer for bugs when compared to flies, moths and spiders. In addition, we found a positive effect of prey size on predatory sequence length and complexity. Our results confirm the ability of spiders to attack and feed upon prey with different morphologies, included well-defended arthropods, and their potential use as natural enemies of several pests in South American crops.

KEYWORDS

behavioural sequence, biological control, conditional prey acceptance, rice, soybean, wolf spider

1 | INTRODUCTION

Conservative biological control (CBC) has received increasing attention in the recent years as an alternative method to other kinds

of pest management as it uses native natural enemies to control pests (Straub, Finke, & Snyder, 2008). Some advantages of CBC include, for example, preventing the use of pesticides or the introduction of foreign natural enemies, both being associated with

potential environmental risks (Barratt, Howarth, Withers, Kean, & Ridley, 2010; Van Lenteren & Bueno, 2003). CBC has been extensively studied in some regions (e.g. North America, Europe); however, this approach has been poorly explored in other megadiverse regions like developing countries where the potential use of native fauna remains largely unknown (Wyckhuys et al., 2013). Although generalist predators are one of the main groups used in CBC (Symondson, Sunderland, & Greenstone, 2002) and their role has often been considered controversial (Snyder & Ives, 2001; Traugott, Bell, Raso, Sint, & Symondson, 2012), recent evidence suggests this group may suppress effectively some pests found in several crops (Messelink et al., 2014).

Knowledge on fundamental trophic niche is essential when evaluating the potential role of a generalist predator as a biological control agent (Macé, Ebeling, Eisenhauer, Cesarz, & Scheu, 2019), since it reveals the prey spectrum that might be consumed, as well as potential ecological interactions between predators and other animals present in crops (Snyder & Wise, 2001). For example, trophic niche might reveal the consumption on some pests, as well as possible disruptive effects of predators when feeding on other natural enemies (Snyder & Ives, 2001). Fundamental trophic niche can be studied in predators by evaluating some prey traits such as type and size (Pekár, García, & Viera, 2017), providing also relevant information about particular adaptations of a predator for consuming certain prey types (Pekár & Toft, 2015). This importantly includes predatory versatility, which reflects the ability of a predator to use alternative strategies and to feed upon different prey types depending on their local abundance (Líznarová, Sentenská, García, Pekár, & Viera, 2013). Despite the importance of studying fundamental trophic niche, to our knowledge this aspect has been poorly explored in relevant groups of native predators occurring in crops from South America.

Spiders are considered one of the most abundant and diversified groups of predatory arthropods in several crops (Michalko, Pekár, & Entling, 2019). Despite their generalist habits, they are also considered a focal group for CBC (Wyckhuys et al., 2013). In a few cases, generalist spiders have been shown to be effective biological control agents in some crops such as rice and wheat fields (Michalko, Pekár, Dul'a, & Entling, 2019). Recent evidence has also shown an inverse relationship between spider abundance and diversity and pest densities (Michalko, Pekár, Dul'a, et al., 2019). Similarly, crop performance has shown to be also enhanced by high densities and diversities of natural enemies (Marliac, Penvern, Barbier, Lescourret, & Capowiez, 2015; Simon, Bouvier, Debras, & Sauphanor, 2010). In addition, recent studies suggest that spiders found in crops can attack different pest stages or species by using alternative foraging methods (Cotes et al., 2018). Despite their importance, the role of spiders as biological control agents has been explored mostly in temperate regions, and the trophic ecology of neotropical spider species is still poorly known (Pekár et al., 2017), which is also true for species found in crops (Benamú, Lacava, García, Santana, & Viera, 2017).

Although several studies analysed the effect of spiders on pest populations, few evaluated the feeding behaviour and prey choice of spiders originating from crops (Hayes & Lockley, 1990; Michalko &

Pekár, 2015; Nyffeler & Benz, 1988; Roach, 1987; Toft, 2005). Like it occurs in other in other generalist predators, understanding the trophic ecology of spiders is crucial when evaluating their potential role as biocontrol agent of a pest species or group of pests. Study of prey acceptance in *Philodromus* spiders, for example, made possible to establish this group of spiders had a higher consumption on pests when compared to beneficial arthropods found in fruit orchards (Michalko & Pekár, 2015). In addition, generalist predators often exhibit alternative predatory strategies, which allow them to consume prey with various defensive mechanisms (Pekár & Toft, 2015), this being particularly important as alternative predatory strategies might allow predators to capture different pest species or even different developmental stages of a given pest species. However, to our knowledge, only few studies have evaluated the role that alternative prey capture strategy plays for arthropod predators which might act as potential biocontrol agents, with only some documented cases for generalist predators such as ants and spiders (see Alderweireldt, 1994; Kenne, Schatz, Durand, & Dejean, 2000).

Wolf spiders (Lycosidae) are predominant native predators in several temperate crops (Djoudi et al., 2018; Samu & Szinetár, 2002), and this is also the case for Uruguay and surrounding countries, where they are locally abundant in, for example rice, alfalfa and soybean fields (Armendano & González, 2010; Bao et al., 2018; Liljesthrom, Minervino, Castro, & Gonzalez, 2002). On top of their local abundance, wolf spiders are known for having high predation rates and multiple feeding behaviours against some insects (Kuusk, Cassel-Lundhagen, Kvarnheden, & Ekbom, 2008; Samu & Biró, 1993). Despite being a diversified group of generalist predators, their role as potential biological control agents in agroecosystems has been studied mostly in Europe and USA (Birkhofer et al., 2008; Kuusk & Ekbom, 2010; Macé et al., 2019; Mathirajan & Regupathy, 2003; Radermacher, Hartke, Villareal, & Scheu, 2020; Snyder & Wise, 2001), to our knowledge little is known about their predatory versatility, and how this parameter is linked with its ability to capture different prey, including pests.

The aim of this paper was to evaluate the trophic ecology of *Lycosa thorelli* (Keyserling, 1877), a wolf spider commonly found in crops from Uruguay (e.g. rice and soybean: Bao et al., 2018, L. F. García, pers. obs., respectively), and the feeding behaviour upon several arthropods including predators, decomposers and the two major crop pests *Spodoptera frugiperda* and *Piezodorus guildinii*. We hypothesized that, because of the wide diet found in other wolf spider species (Kuusk & Ekbom, 2010; Radermacher et al., 2020), *L. thorelli* would have an euryphagous diet too, attacking and consuming all offered arthropods (including the well-defended prey such as other wolf spider species); yet, rejecting stink bugs because of their chemical defences. Since wolf spiders are one of the most abundant predators in crops of the South American region, but poorly studied compared to other groups such as insects, this study also aims at better understanding the general feeding ecology of this wolf spider species, by assessing the influence of both prey type and size on sequence length and acceptance probability, as well as the whole predatory sequence for all prey types. To our knowledge, this is

thus the first study to evaluate the predatory versatility in lycosid spiders against potential prey that play different ecological roles in crops, working as a baseline to show the role of these spiders in agroecosystems.

2 | MATERIAL AND METHODS

2.1 | Specimen sampling

A total of 89 adult females of *Lycosa thorelli* (mean body length \pm standard error: 1.04 ± 0.02 cm) were collected in grasslands and natural fields of Uruguay (Department of Treinta y Tres, $33^{\circ}13'59''$ S, $54^{\circ}22'59''$ W) between September and December 2018. Spiders were sampled at night by two collectors using headlamps. According to preliminary observations, spiders are found in the soil during day, and in high numbers on plants and grass at night.

Once collected, spiders were transferred to the entomology laboratory from CURE-Treinta y Tres and individualized in Petri dishes (diameter: 9.5 cm, height: 2 cm). Humidity ($60 \pm 10\%$), temperature ($25 \pm 5^{\circ}\text{C}$) and photoperiod (14:10 hr L:D) were kept in similar conditions as those recorded on the sampling locality.

2.2 | Prey selection

Prey were selected based on their ecological role on rice and other local crops, which are rotated with rice and soybeans, for example. We selected carabid beetles (cf. *Bembidion* sp. of the same morphospecies and the wolf spider species *Lycosa inornata* (Blackwall, 1862) as other natural predators in soybean and rice fields (Bao et al., 2018, L F. García, pers. obs.). As potential pests, we selected last instar larvae and adults of the moth *Spodoptera frugiperda* (Smith, 1797). We also used adult specimens of the bug *Piezodorus guildinii* (Westwood, 1837). In addition, we also used flesh flies as prey (Sarcophagidae: cf. *Oxysarcodexia* sp.), since these were locally abundant on the same localities where spiders and the other prey were collected and also, because these flies act mainly as decomposers (Xavier, Barbosa, Barbosa, & Queiroz, 2015), representing another ecologically important role besides predators and pests. We collected a different number of individuals for each prey species based on their availability in the field (Table 1). Individuals were sampled using sweep nets

in soybean fields from the localities of Treinta y Tres and Paysandú (Uruguay), between October and December 2018.

All individuals were measured using software ImageJ (Schneider, Rasband, & Eliceiri, 2012), and full body length was measured for both spiders and their prey (see Table 1).

2.3 | Feeding behaviour experiments

Until one week before starting the experiments, spiders were fed ad libitum offering them one *Tenebrio molitor* (Linnaeus, 1758) larvae until the spider did not accept more prey. Afterwards, all spiders were not fed during one week.

After the starvation period, one selected prey was randomly offered to one spider only once, following a randomized design. Therefore, we used as many spiders as prey offered ($n = 114$). For each experiment, we measured several parameters, that is the attack occurrence, consumption, immobilization time and the complete predatory sequence. All experiments were recorded with a surveillance and a Canon vixia camera, so the immobilization time and predatory sequence could be assessed after the experiment. Observations were made in Petri dishes, following similar studies about feeding behaviour in other wolf spider species (Korenko, Saska, Kysilková, Řezáč, & Heneberg, 2019; Samu, 1993; Samu & Biró, 1993). Each prey was considered as attacked when the spider grasped the prey and tried to bite it. Consumption was noted if, after an attack, the prey was consumed. Both attack and consumption were measured during 10 min. If the prey was not consumed or attacked during the selected time interval, it was considered as rejected or not attacked, respectively. If prey was not accepted, we offered a *T. molitor* larvae as prey to discard the possibility prey was rejected for other reasons than spider hunger level.

Prey attack was compared between prey using a generalized linear model (GLM), with a binomial distribution (GLM-b) since data did not present under/overdispersal (Pekár & Brabec, 2016), using the attack as the response variable, while the ratio of the prey to the spider's body length and prey species was used as explanatory fixed variables. Consumption rate for the different prey was also compared using a GLM with a binomial distribution since data did not present under/overdispersal. In this model, we used prey consumption as the response variable, while prey type and prey:predator size ratio were used as explanatory variables. Since prey consumption

TABLE 1 Common and scientific names, ecological role, size and number of individuals used (N) of different prey types offered to adult females of *Lycosa thorelli*

Common name	Scientific name	Ecological role	Size in cm (mean \pm SE)	N
Carabid beetles	cf. <i>Bembidion</i> sp.	Predator	1.03 ± 0.05	10
Flesh fly	cf. <i>Oxysarcodexia</i> sp	Detritivore	0.81 ± 0.04	20
Larva (caterpillar)	<i>Spodoptera frugiperda</i>	Pest	2.13 ± 0.15	20
Moth	<i>Spodoptera frugiperda</i>	Pest	1.29 ± 0.04	25
Stinky bug	<i>Piezodorus guildinii</i>	Pest	0.73 ± 0.02	23
Wolf spider	<i>Lycosa inornata</i>	Predator	0.91 ± 0.04	16

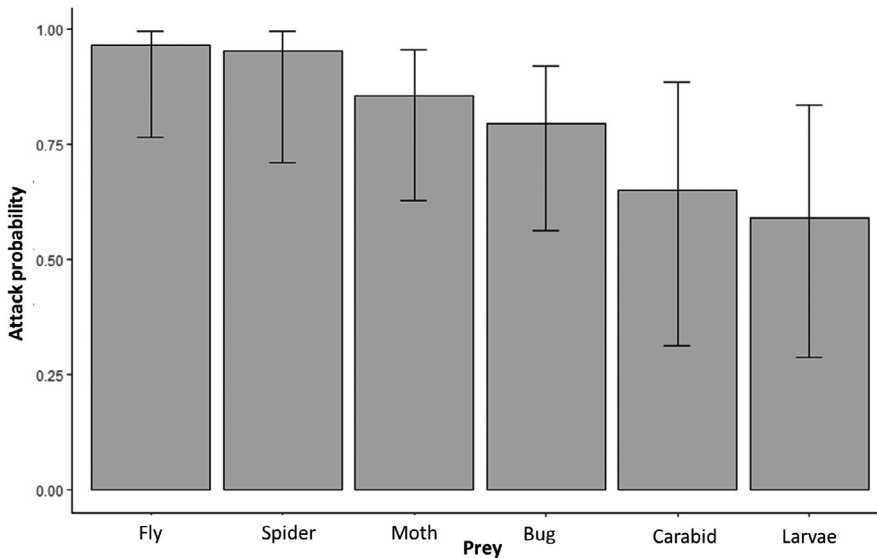


FIGURE 1 Attack probability of *Lycosa thorelli* against bugs (*Piezodorus guildinii*), spiders (*Lycosa inornata*), moths (*Spodoptera frugiperda*), caterpillars (*Spodoptera frugiperda*), carabid beetles (cf. *Bembidion* sp.) and flies (cf. *Oxysarcodexia* sp.). Bars represent means, lines are 95% confidence intervals, both estimated using a binomial GLM

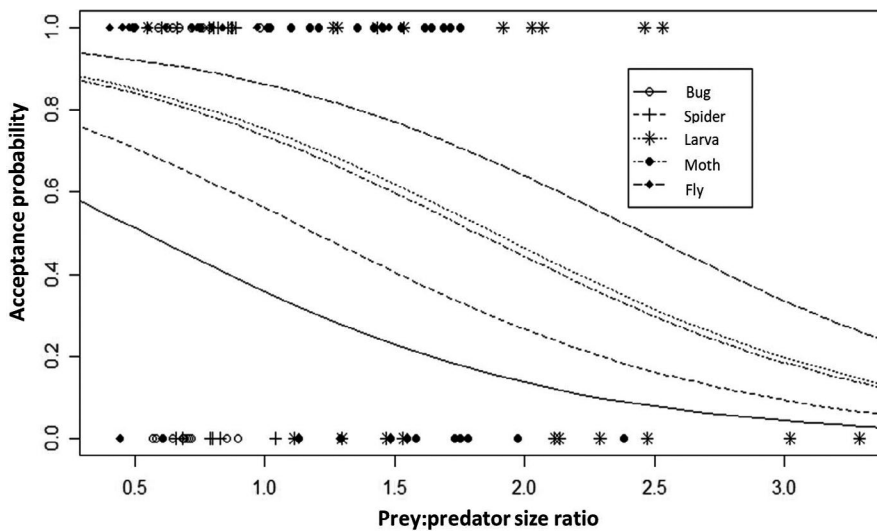


FIGURE 2 Acceptance probabilities of *Lycosa thorelli* on bugs (*Piezodorus guildinii*), spiders (*Lycosa inornata*), moths (*Spodoptera frugiperda*), caterpillars (*Spodoptera frugiperda*) and flies (cf. *Oxysarcodexia* sp.). Regression lines were estimated using binomial GLMs

and size ratio might also have a hump-shaped relationship (See Okuyama, 2007), quadratic term for prey:predator size ratio was also included as an explanatory variable. Possible interactions between prey and the prey: predator size ratio and its quadratic term were explored as well. We performed a different number of observations for each prey type, depending on their availability in the field (see Table 1).

Using the data for accepted prey, we also estimated the immobilization time. This was considered as the time lapse that occurred since the first spider bite until the prey was incapacitated and stopped moving. Immobilization time was compared between prey types using a Gamma generalized linear model (GLM-g) based on data distribution (Pekár & Brabec, 2016). The immobilization time was used as the response variable, and prey: predator size ratio and the prey type were used as explanatory fixed variables. When necessary, post hoc analyses were done using a Tukey test.

For analysing the predatory sequence, an ethogram of prey capturing was first built for all prey types following Rovner (1980) and Lacava (2014), with some modifications according to our own prior

experiments. Behavioural sequences were obtained using the software Jwatcher and analysed using a first-order Markov chain with the TraMineR package (Gabadinho, Ritschard, Mueller, & Studer, 2011). To evaluate whether behavioural sequences followed a random pattern, a matrix for expected frequencies was created, and compared with an observed-frequencies matrix using a chi-square test, Yates correction was applied when necessary (Lehner, 1998).

We also analysed the effect of both prey types and prey: predator size ratio on the behavioural sequence length. Data were analysed using a GLM with a Gamma distribution based on the model fit.

3 | RESULTS

3.1 | Prey attack and acceptance

We did not detect significant differences regarding the attack rate of offered prey (GLM-b: $\chi^2_5 = 9.06$, $p = .10$; Figure 1). Similarly, we did not find significant effect of prey size on attack probability (GLM-b:

FIGURE 3 Immobilization times of *Lycosa thorelli* against bugs (*Piezodorus guildinii*), spiders (*Lycosa inornata*), moths (*Spodoptera frugiperda*), caterpillars (*Spodoptera frugiperda*) and flies (cf. *Oxysarcodexia* sp.). Points represent means, lines are 95% confidence intervals, both estimated using a linear model. Different successive letters indicate significant differences

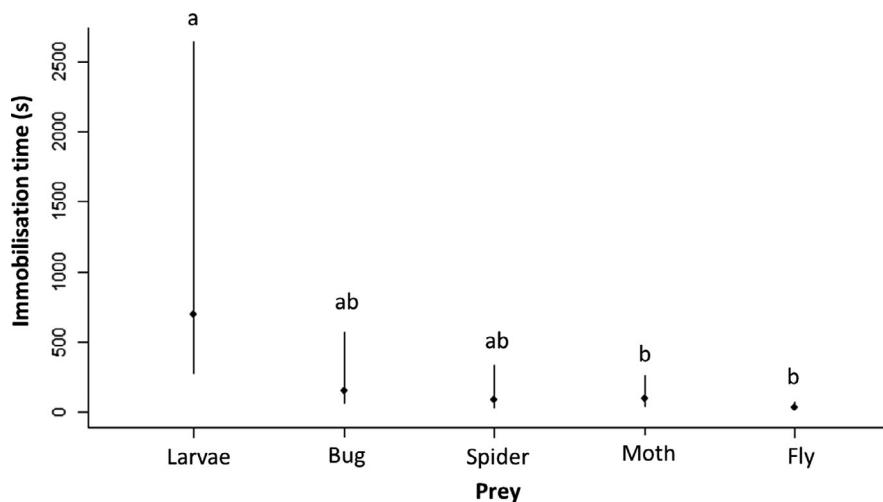


TABLE 2 Behavioural acts observed during prey capture in *Lycosa thorelli*

Behavioural act	Description
Aggressive display	Spider rises the two first pair of legs while chelicerae remain open
Approach	Spider walks towards prey
Bite	Spiders pierces body prey with its chelicerae
Feeding	Spiders crushes and manipulates immobilized prey using chelicerae and pedipalps
Grasp	Spider grasps the prey with its two first pair of legs
Grooming	Spider passes its legs and pedipalps repeatedly by its chelicerae
Immobility	Spider remains motionless
Leg tapping	Spider touches prey repeatedly with the first pair of legs and pedipalps
Lunge	Spider jumps towards prey
Move away	Spider moves in the opposite direction of prey
Orientation	Spider turns in direction to prey
Release	Spider releases prey after biting
Substrate rubbing	Spider rubs its body and chelicerae against substrate

$\chi^2_1 = 1.22, p = .26$). As for consumption, there was a significant difference between prey types (GLM-b: $\chi^2_4 = 12.44, p = .01$). Carabids were never consumed, and post hoc comparisons revealed significant differences only between bugs and flies (Figure 2). We found a significant and negative relationship between size and consumption (GLM-b: $\chi^2_1 = 4.50, p = .03$); however, there was no significant interaction between prey type and size ratio (GLM-b: $\chi^2_4 = 4.53, p = .33$). We did not find a significant effect of the quadratic term for size on the acceptance (GLM-b: $\chi^2_2 = 4.69, p = .09$), neither a significant interaction between prey type and the quadratic term for size (GLM-b: $\chi^2_8 = 6.19, p = .62$).

3.2 | Immobilization time

We found significant differences in immobilization time among prey types (GLM-g model, $F_{(4, 57)} = 76.43, p < .01$; Figure 3). The main differences were observed for the larvae of *S. frugiperda*, which needed a longer time to be paralysed when compared to flies and moths.

No significant differences were observed for flies, moths, spiders and bugs regarding to immobilization time. We did not find a significant effect of size on the immobilization time (GLM-g, $F_{(1,57)} = 1.43, p = .50$).

3.3 | Predatory sequence

The behaviours involved in the predatory sequence of *L. thorelli* for different prey are described in Table 2. We found that the predatory sequence for all prey, including bugs ($\chi^2_{42} = 575.15, p < .01$), flies ($\chi^2_{42} = 442.08, p < .01$), larvae ($\chi^2_{80} = 1,411.40, p < .001$), moths ($\chi^2_{80} = 805.06, p < .01$) and spiders ($\chi^2_{80} = 223.04, p < .01$), followed a non-random pattern. Overall, we found a significant positive correlation between the effect of prey: predator size ratio on the number of sequences (GLM-g, $F_{(1,57)} = 8.20, p < .01$), which also varied between the different prey offered (GLM-g, $F_{(4,58)} = 36.06, p < .01$), where bugs had significantly longer sequences than spiders, flies and moths (contrasts method, $p < .05$; Figure 4). No significant differences were

observed between the other prey types. Although sequences for larvae were not significantly different from the remaining prey, these were slightly longer. The predatory sequences were qualitatively more complex for *L. thorelli* against pest arthropods (Figure 5), when compared to non-pest arthropods (Figure 6).

4 | DISCUSSION

Overall, we found that the spider *L. thorelli* attacked all offered prey, and accepted and consumed most of them by employing alternative prey capture strategies. This confirms the previously supposed euryphagous and generalist habits of this species, and fits to several similar studies on other wolf spider species (Edgar, 1969; Holmberg & Turnbull, 1982; Kuusk & Ekbohm, 2010; Radermacher et al., 2020). When comparing the acceptance rates, we found that *L. thorelli* had a marked acceptance over flies, followed by larvae, moth, spiders and bugs, while it actively rejected carabid beetles. We attribute the rejection of carabids to the defensive secretions they produce, which prevents attack and consumption by spiders, as well as to their powerful jaws that may deter potential predators (Lečić et al., 2014). Overall, we found that acceptance decreased with prey size as it has been shown for other generalist spiders (García, Viera, & Pekár, 2018). Nevertheless, *L. thorelli* consumed larger flies followed by moth adults and larvae, spiders and bugs.

The high consumption and low immobilization times against flies can be explained by their poor defensive mechanisms (Viera, 1995) compared to, for example spiders, bugs or caterpillars. In addition, the lack of defences might have allowed the spiders to consume larger dipterans when compared to other prey, using a relatively simple strategy composed by few behavioural units as reported in other spiders (Viera, 2005). The consumption of decomposers such as dipterans and other groups like collembolans by spiders is a common phenomenon, considered very important for keeping the spider presence in crops. Many decomposers indeed act as an alternative food resource for spiders when pests are not or little present (Agustí et al., 2003). Although there are not local records for the abundance

of dipterans such as Sarcophagids in crops from Uruguay, the marked consumption of this prey by *L. thorelli* suggests it might be a common and alternative food source for *L. thorelli* as reported for other wolf spider species in other crops (Ishijima et al., 2006; Kuusk & Ekbohm, 2010). A similar trend can also be expected for other dipterans with similarly low defence mechanisms.

Intraguild predation is a common trait among spiders, since it can represent an input of nutritionally high-quality food (Mayntz, Raubenheimer, Salomon, Toft, & Simpson, 2005), which is also the case for wolf spiders. However, it was an unexpected result that generalist spiders like *L. thorelli* would consume other similarly sized spiders (see: García et al., 2018; Michálek, Petráková, & Pekár, 2017), here *L. thorelli* feeding upon *L. inornata*. We hypothesize that the consumption of large wolf spiders might be a consequence of territorialistic behaviour, as *L. thorelli* exhibited some behaviours related to menacing, such as aggressive displays that were not observed against other prey. Attack and consumption of similarly sized spiders has been reported in other species of *Lycosa* while defending their territory, where agonistic displays may end in consumption (Moya-Laraño, Orta-Ocaña, Barrientos, Bach, & Wise, 2002). Therefore, a similar trend might occur between *L. thorelli* and *L. inornata* where an agonistic display might end in consumption. It is important to note that the use of small-sized cages might have biased this result, and the potential prey having few places to hide might alter a more natural predator-prey interaction (Kreuzinger-Janik, Brüchner-Hüttemann, & Traunspurger, 2019). In addition, predatory sequences were less complex than when capturing other less dangerous prey such as bugs or larvae, and immobilization times were similar to the aforementioned prey. These simple prey capture sequence and short immobilization times might be due to the fact that other spiders, which are dangerous prey, should be paralysed in short times and with simple sequences so that the probability of retaliation would be reduced (Mukherjee & Heithaus, 2013). A similar trend has been observed in some other spiders such as the generalist *Harpactea* when consuming wolf spiders (García et al., 2018). Intraguild predation is a common phenomenon in spiders, and whether this behaviour interferes with the potential biological control of other predators remains

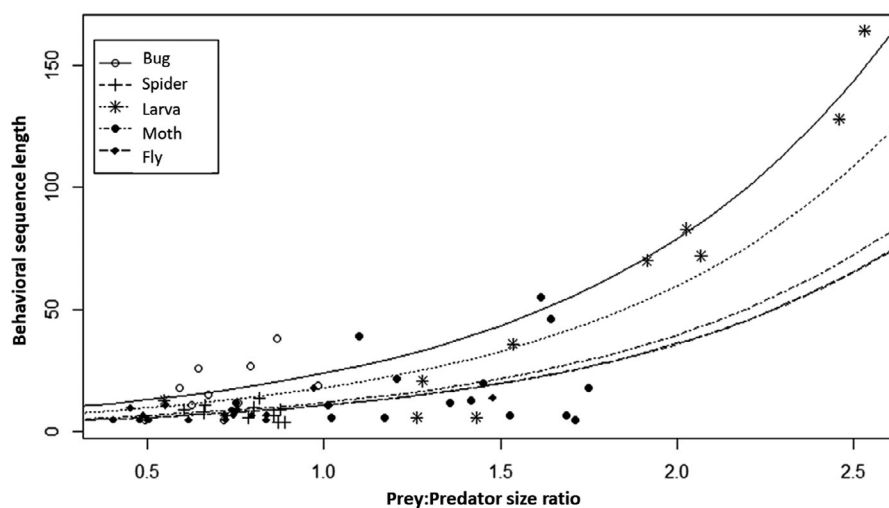


FIGURE 4 Relationships between prey: predator size ratio and behavioural sequence length of *Lycosa thorelli* when attacking bug (*Piezodorus guildinii*), spider (*Lycosa inornata*), moth (*Spodoptera frugiperda*), caterpillar (*Spodoptera frugiperda*) and fly (cf. *Oxysarcodexia* sp.). Regression lines were estimated using a Gamma-GLM

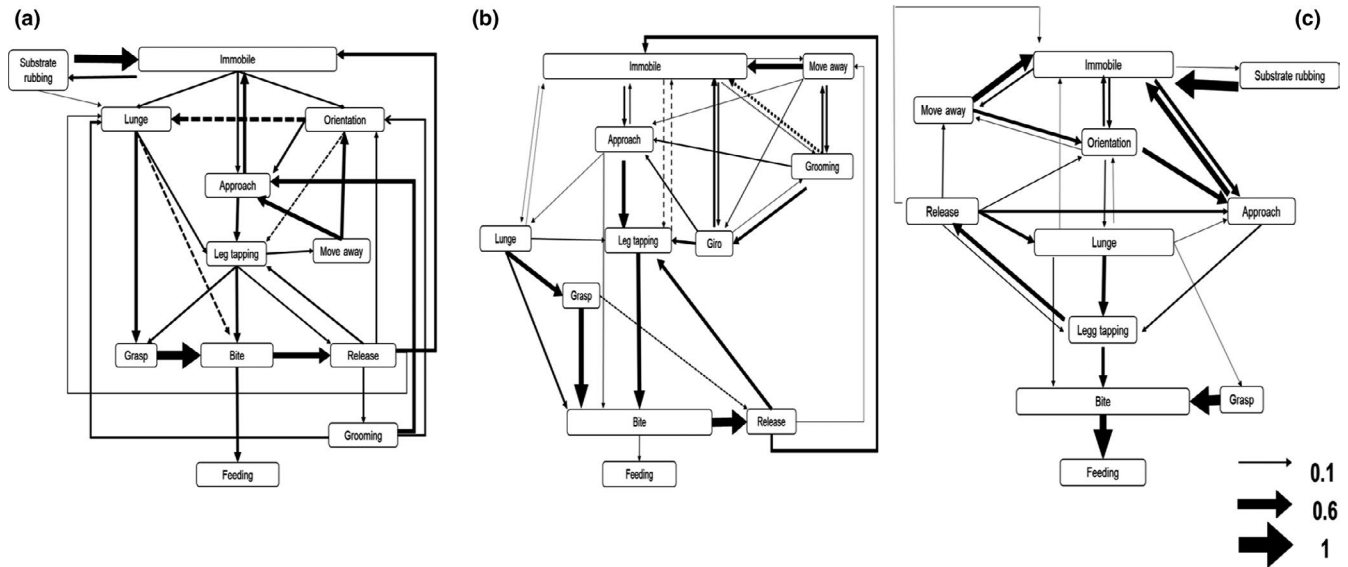
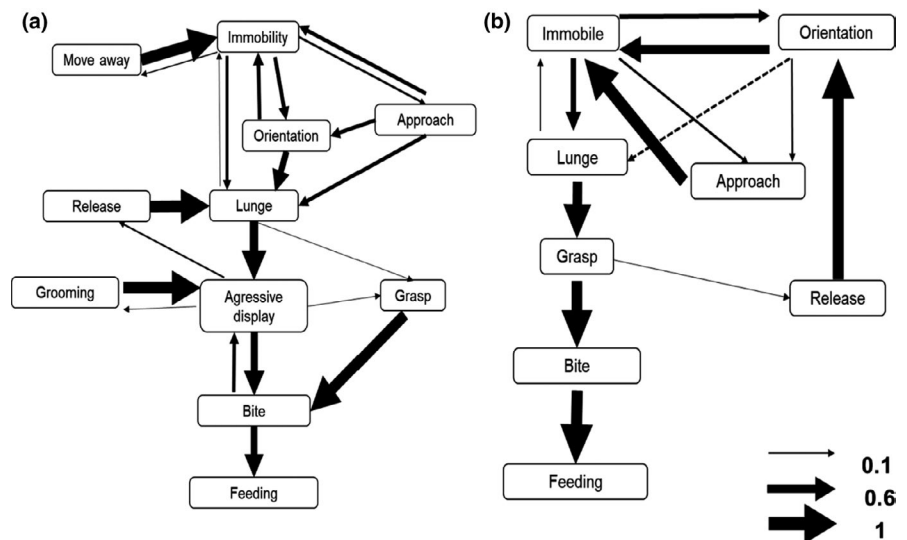


FIGURE 5 Predatory sequence of *Lycosa thorelli* against (a) bugs (*Piezodorus guildinii*), (b) caterpillars (*Spodoptera frugiperda*) and (c) moths (*Spodoptera frugiperda*). Dashed lines were used to facilitate sequence visualization. Transition probabilities are given below the figure

FIGURE 6 Predatory sequence of *Lycosa thorelli* against (a) wolf spiders (*Lycosa inornata*) and (b) flies (cf. *Oxysarcodexia* sp.). Dashed lines were used to facilitate sequence visualization. Transition probabilities are given below the figure



unclear (Michalko, Pekár, Dul'a, et al., 2019). However, intraguild predation is affected by factors such as habitat structure and prey availability (Chacón & Heimpel, 2010; Janssen, Sabelis, Magalhães, Montserrat, & Van der Hammen, 2007); therefore, the potential interferences of *L. thorelli* with other predators should be evaluated under natural, field, conditions.

Although moth adults and larvae were consumed in similar proportions, important differences were found regarding the immobilization times and predatory sequences, which were higher and longer, respectively, for larvae when compared to moths (adult form). Wolf spiders are known to efficiently paralyse and consume caterpillars (Rendon, Whitehouse, & Taylor, 2016); however, the differences observed against *S. frugiperda* might be explained as these larvae regurgitate to defend themselves, and are able to bite potential predators. This defensive behaviour turns caterpillars into a less suitable prey when compared to other less aggressive larvae, and

explains the long times and sequences employed by *L. thorelli* when attacking this prey type, since regurgitation has been shown to provide some protection to caterpillar when attacked by wolf spiders (Smedley, Ehrhardt, & Eisner, 1993). In addition, the fact that spiders have consumed a lower proportion of larger larvae suggests that *L. thorelli* might be more efficient in attacking smaller stages of *S. frugiperda*. However, further evidence is needed to support this hypothesis. We also found that a high efficiency against adults could turn *L. thorelli* into a potentially useful predator against adults. Therefore, the predation rates of *L. thorelli* should be further analysed during its reproductive season and the first developmental stages of *S. frugiperda*, especially in some crops where both species coexist, such as soybean and rice fields.

Bugs were consumed in a lower proportion than other prey, likely because of their defensive secretions (Pareja, Borges, Laumann, & Moraes, 2007). Nevertheless, the fact that this prey type has been

consumed was quite unexpected, since it produces a highly repellent secretion for several predators including other spider species (Cheli, Armendano, & González, 2006). Interestingly, we observed a particular feeding strategy by *L. thorelli* based on rubbing its chelicerae against substrate after an attack, which allowed it to overcome bugs, confirming the potential use of this wolf spider species against this prey type. Consumption on *P. guildinii* was previously reported in few other spider families, such as Oxyopidae and Thomisidae (González et al., 2009; Tillman, Greenstone, & Hu, 2015). Nevertheless, to our knowledge, there were no records of a similar grooming-like behaviour in other predators when attacking *P. guildinii*. Such a behaviour can be seen as a way to remove noxious chemical, because it is similar to the grooming behaviour displayed by other wolf spiders when exposed to toxic substances (Tahir et al., 2019). The chemical defence of bugs may also explain the long behavioural sequences displayed against this prey, since it has been shown that spiders may use a higher number of behavioural sequences against well-defended prey (García et al., 2016; Viera, 2005). These results suggest that *L. thorelli* has the potential to be a natural biological control agent predator of *P. guildinii* in crops where both species coexist (e.g. soybeans). However, some additional aspects related to its actual predatory efficiency, such as the functional response or feeding rate under field conditions on bugs, remain to be tested under natural conditions.

A varied prey capture strategy influenced by prey type and size often reflects a wide fundamental trophic niche, which can be an important trait for generalist spider species present in crops if they are considered as biological control agents (Michalko & Pekár, 2016). Feeding plasticity allows generalist predators to consume a wide variety of prey, including several pest species (Alderweireldt, 1994). This is the case of *L. thorelli* because its predatory versatility led this spider to feed upon pests with constrating morphologies such as bugs and lepidopterans, both larvae and adults. As a consequence, we can hypothesize that *L. thorelli* might feed on these prey in crops depending on their local abundance, just like it has been shown in other generalist predators (Líznarová et al., 2013), which may temporarily specialize on the most abundant local prey (Dall, 2010). Also, its feeding versatility might allow them to display some behaviours like prey switching and fed even on alien pests (Jaworski, Bompard, Genies, Amiens-Desneux, & Desneux, 2013). In addition, a marked predatory versatility has shown to be an important trait for spiders found in highly disturbed locations, like some linyphiid spiders found in crops (Alderweireldt, 1994), and this also might be the case of wolf spiders, given their high local abundance in several crops (Djoudi et al., 2018).

In conclusion, our results cannot determine whether *L. thorelli* is an effective biological control agent, but our experimental design clearly indicates the potential use of this species. We also showed that the predatory versatility of this species may allow it to consume potential pests with very different traits and defensive mechanisms (e.g. caterpillars, bugs), and also to feed on alternative prey (e.g. dipterans, other spiders). Further studies should explore additional aspects related to feeding behaviour, such as the functional

response of wolf spiders against evaluated prey as well as their consumption rates under different natural, field conditions.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

Luis Fernando García conceptualized the study; Erika Núñez, Mariángeles Lacava, Luis Fernando García and Horacio Silva contributed to methodology; Erika Núñez, Mariángeles Lacava, Luis Fernando García and Julien Pétilion involved in formal analysis and investigation; Luis Fernando García, Julien Petillon and Mariángeles Lacava involved in writing—original draft preparation; Luis Fernando García, Julien Pétilion and Sebastian Martínez involved in writing—review and editing; Sebastián Martínez and Luis Fernando García provided funding acquisition; Luis Fernando García supervised the study.

DATA AVAILABILITY STATEMENT

Original data can be requested to corresponding author.

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