





Does the superfluous killing exhibited by spiders mask the functional response parameters? A case study from the perspective of biological control

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Abstract

The meadow spittlebug *Philaenus spumarius* L. (Hemiptera: Aphrophoridae) is a xylem-sap feeder and the most abundant and widespread vector of *Xylella fastidiosa* (Xanthomonadales: Xanthomonadaceae) throughout Europe. Control strategies for the disease are based on containment and eradication measures regulated by the European Union. Within the context of biological control, the use of natural enemies aims at limiting the insect vector population in agroecosystems. Spiders are generalist predators with potential as biological control agents occupying all the habitats within crops. Crab spiders (Thomisidae) could be potential natural enemies against *P. spumarius*. The functional response (FR) of a predator represents the intake rate as a function of food availability and allows estimating feeding behaviour parameters such as the prey handling time and attack rate. However, spiders often kill more prey than they consume, unveiling their capacity as natural enemies. We assessed and compared the FR of *Xysticus acerbus* (Thomisidae) fed on *P. spumarius* in the laboratory considering (1) the total number of dead individuals and (2) only the consumed ones. We found that although both FRs were of type-II, they significantly differed. The values of attack rate and handling time for consumed were 0.1 and 3.6, respectively, while for dead, the attack rate was 0.3 and 1.1, being both significantly different. Moreover, the number of overkilled individuals reached a plateau at the highest prey densities. *Xysticus acerbus* could be a potential natural enemy of *P. spumarius*. Nevertheless, we suggest that the effect of including the killed but not consumed prey individuals in FR studies using wasteful killing predators should be considered and further studied.

KEYWORDS

attack rate, handling time, spittlebugs, Thomisidae, *Xylella fastidiosa*

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1 | INTRODUCTION

The meadow spittlebug *Philaenus spumarius* L. (Hemiptera: Aphrophoridae) is a xylem-sap feeder entailed as the most abundant and widespread vector of *Xylella fastidiosa* (Wells et al., 1987) (Xanthomonadales: Xanthomonadaceae) throughout Europe (European Food Safety Authority (EFSA), 2020). *Xylella fastidiosa* is widely spread in the Americas, but has become a new agricultural threat in Europe since the first detection in Apulia (Italy) in 2013 (EFSA, 2020; Saponari et al., 2013). It is able to infect more than 600 plant species among ornamentals, crops and wild plants (European Food Safety Authority (EFSA) et al., 2021; Thompson et al., 2023).

In Europe, spittlebugs emerge as nymphs in early spring in the herbaceous cover vegetation forming spittle for protection during five nymphal stages (López-Mercadal et al., 2021). In late April, the adults emerge and inhabit the cover vegetation until it dries in summer and then they migrate to tree canopies (López-Mercadal et al., 2021). Once the cover vegetation regrows, the adults return to it mating and finishing the life cycle. During the time spent by the adults feeding in the tree canopies, *X. fastidiosa* transmission is susceptible to occur. Since the genus *Philaenus* have transmission rates higher than other vectors (López-Mercadal et al., 2021), control measures against the vector are necessary to limit the spread of the disease (Cavaliere et al., 2019). Control strategies for the disease are based on containment and eradication measures regulated by the European Union (Cornara et al., 2018; EFSA, 2020) such as limiting the insect vector either with biological, chemical or cultural strategies (Janse & Obradovic, 2010; Morelli et al., 2021).

Regarding biological control of *P. spumarius*, some parasitoids have been described, such as the egg parasitoid *Ooctonus vulgatus* Haliday, 1833 (Mymaridae) (Manzano et al., 2021) or the adult parasitoid *Verrallia aucta* (Fallen 1817) (Pipunculidae) (Molinatto et al., 2020; Whittaker, 1973). Also, potential predators for *P. spumarius* have been cited in the literature, like *Zelus renardii* Kolenati, 1857 (Hemiptera: Reduviidae) (Liccardo et al., 2020) (Mesmin et al., 2022; Whittaker, 1973).

In the context of biological control and due to the life cycle of *P. spumarius*, the pest control exerted by natural enemies can occur throughout the different strata of the agroecosystem (e.g. canopy, cover vegetation or shrubs) (Liccardo et al., 2020). In this regard, spiders (Arachnida: Araneae) encompass the pool of potential natural enemies of *P. spumarius* (Benhadi-Marín et al., 2020; Samu et al., 2013). Spiders are ubiquitous generalist predators exhibiting a great number of hunting strategies with a key role in pest limitation in agroecosystems (Rodrigues et al., 2022; Turnbull, 1973). However, ecological traits such as habitat requirements, feeding preferences and attack rate may drive the extent to which spiders are efficient in limiting the populations of *P. spumarius*. The capacity to limit a pest will partially depend on the natural enemy's functional response (hereafter FR) (Uetz et al., 1999). FR would be a useful approach to assessing key ecological traits (Pekár, 2005; Solomon, 1949).

The analysis of the parameters derived from the FR analysis of a predator, such as the prey handling time and the attack rate, helps

to characterize the predatory profile of a potential biological control agent (Liccardo et al., 2020). The handling time represents the time necessary to pursue, subdue, feed and restart hunting, whereas the attack rate is the searching efficiency per time (Holling, 1959a, 1966; Maupin, 1997).

The FR of a potential natural enemy is an important feature emerging from predator-prey dynamics since it is an expression of the relationship between predator consumption rate and prey density (Bolker, 2008). For instance, there are three main types of FR described in the literature by Holling (1966). The three response types differ in the way that consumption rate increases with food abundance (Maupin, 1997). In type I, the number of prey killed increases constantly as prey density increases (rectilinear relation). This FR type is exemplified by a predator exhibiting a random search pattern and maintaining a consistent search rate even as prey density increases (Holling, 1959a; Maupin, 1997). Type II is considered the most common response, in which prey killed is characterized by a curvilinear increase. Finally, in type III there is a sigmoidal increase until the curves reach an asymptote, also known as an S-shaped functional response (Holling, 1959a). The initial lag is due to learning how to handle the prey that followed by an exponential increase in capture rates (Maupin, 1997; Riechert, 1974). Among the predators that exhibit type III FR, spiders display a relatively high plateau due to a tendency to accept a large portion of the available prey, sometimes in excess of the amount actually eaten (Riechert, 1974).

Invertebrate predators often exhibit special feeding behaviours, which may increase their efficacy on pest limitation (Holling, 1959b). These include the capture of multiple prey items the simultaneous feeding on them and the partial consumption of prey (Lucas, 1985; Samu & Biro, 1993). Spiders exhibit a predatory behaviour called overkilling (Michalko et al., 2019). This behaviour is a component of hunger-motivated behaviour (i.e. temperament motivated) consisting of capturing and killing preys that are not finally eaten or are partially consumed (Cloarec, 1991; Johnson et al., 1975; Lucas, 1985; Samu & Biro, 1993). Overkilling is usually observed in generalist spiders, and it is positively correlated with prey density (Korenko et al., 2019; Mansour & Heimbach, 1993). Pest regulation by overkilling would constrain the ability of insect pest populations, aligning them with the equilibrium observed in natural ecosystems. In these environments, spider communities manage insect numbers to levels sufficiently low, averting the risk of population explosions (Maupin, 1997). For example, overkilling was reported in up to 65% in lycosids (*Pardosa* sp C. L. Koch, 1847), up to 75% in linyphiids (*Erigone atra* Blackwall, 1833 and *Tenuiphantes tenuis* (Blackwall, 1852)), and nearly 100% in *Zodarion* Walckenaer, 1826 spiders (Korenko et al., 2019; Mansour & Heimbach, 1993; Solomon, 1949). However, studies on the role of the overkilling phenomenon in the FR of spiders are still scarce.

The crab spider *Xysticus acerbus* Thorell, 1972 (Araneae: Thomisidae) proved to prey upon spittlebugs in the field and the prey DNA can be detected in the gut at least up to 70h post-feeding (Turnbull, 1973). This study aimed to assess the FR of *X. acerbus* on *P. spumarius* in the laboratory from a biological control perspective with an emphasis on how the phenomenon of overkilling affects the

FR. We aimed to target potential natural enemies for *P.spumarius* following the protocol proposed by Benhadi-Marín et al. (2020). The protocol developed is based on using classical functional response tests to target potential natural enemies. In that case, it was possible to determine the potential predatory efficiency of two spiders, commonly found in Portuguese fields, of *P.spumarius* (Benhadi-Marín et al., 2020).

2 | MATERIALS AND METHODS

2.1 | Prey and predator species origin and rearing

Adults of *P.spumarius* were captured by using an entomological sweep net (38cm diameter) from the spontaneous vegetation cover of an urban green area in Bragança (northeastern Portugal) (41°48'09" N; 6°44'46" W) in October 2021. The insects were immediately transported to the laboratory and the colony was maintained in an aerated acrylic cage (40cm in height, 30cm in length and 43cm in width) with plants and fed ad libitum on plants (*Chlorophytum comosum* (Thunb.) Jacques, 1862) in a climatic chamber at 18±1°C, 65±10% RH and 16:8hL:D photoperiod.

Females of *X.acerbus* were collected using the same sweep net in Rabal (41°51'30" N, 6°44'53.4" W) near Bragança (northeastern Portugal), in October 2021. Once captured, the spiders were in situ placed individually (to avoid cannibalism) in perforated plastic tubes and immediately transported to the laboratory. Each individual was then transferred to a plastic pot (4.2cm in height, 3cm in diameter) and fed ad libitum with *Drosophila melanogaster* Meigen, 1830 for 1 week. Water was provided to each spider by placing a drop of sodium acrylate gel on the pot base. The colony was reared in a climatic chamber at 25±1°C, 65±10% RH and 16:8hL:D photoperiod. All the individuals were starved for 5 days before the FR assay for a standardized hunger level.

2.2 | Experimental design

Once the spiders reached the adult stage, each individual was transferred to a glass Petri dish (1.8cm in height, 7cm in diameter) (Figure 1). The assay consisted of supplying the spiders with a series of increasing densities of *P.spumarius* (1, 3, 5, 8, 16 and 20 specimens). Eight spiders (i.e. repetitions) were used for each prey density, so a total of 48 spiders were used for the whole FR assay. The number of spittlebugs found dead in each Petri dish was recorded after 24h. Among the dead individuals, the number of (1) consumed (i.e. those dead and internal body parts emptied by spider digestion) and (2) only killed spittlebugs (i.e. those maintaining the inner body parts not digested) were separately registered. Discrimination between both types of dead prey was visually assessed using light in negative contrast. The experiment was conducted in a climatic chamber under direct fluorescent cold white light at 18°C, 65% RH and 2625 lux.

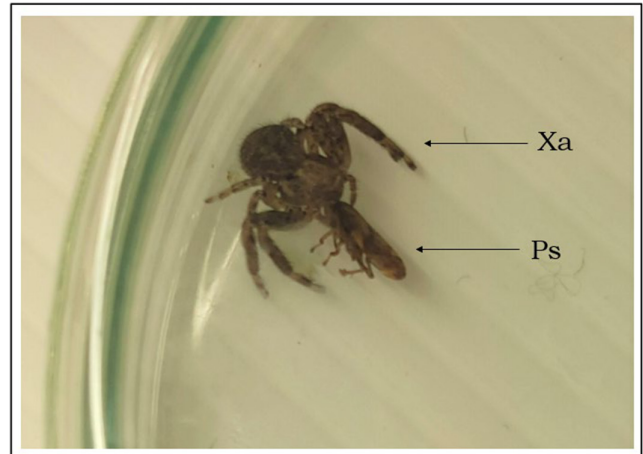


FIGURE 1 Adult female of *Xysticus acerbus* (Xa) preying upon *Philaenus spumarius* (Ps) during the functional response assay. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.13233)]

2.3 | Data analysis

The FR was estimated for the prey consumed (i.e. prey killed and consumed) and dead (i.e. the sum of prey consumed and killed) using the package 'frair' (Pritchard et al., 2017) in R (Holling, 1959a). The data were firstly modelled using linear regression to assess the fitting to a type-I FR (i.e. a generic linear response assuming the response is independent of handling time) as:

$$N_e = a \times N_0 \times T \quad (1)$$

where N_e is the number of consumed or killed prey, N_0 is the initial prey density, a is the attack rate and T is the exposure time (24h).

Then, logistic regression was used to select between type-II FR (i.e. assuming a decelerating intake rate of prey) or type-III FR (i.e. the functional response becomes progressively sigmoid). The proportion of prey consumed or killed was modelled as a function of the number of prey offered using the *frair_test* function.

$$\text{Killed / notkilled} \sim \alpha + \beta \times \text{Density} \quad (2)$$

$$\text{Killed / notkilled} \sim \alpha + \beta_1 \times \text{Density} + \beta_2 \times \text{Density}^2 \quad (3)$$

where density represents the initial prey densities, killed is the number of prey killed and not-killed is the difference between them. The function's output provides the sign and p -values of the coefficients (β_1 and β_2) used to select between type-II or type-III response.

A negative linear coefficient (β_1) means a better adjustment to type-II, whereas a positive linear coefficient (β_1) and a negative quadratic coefficient (β_2) imply that the data fit a type-III FR (R Core Team, 2019; Trexler et al., 1988). Since prey was not replaced during the trials, the Rogers' random predator equation was used to fit a type-II FR as:

$$N_e = N_0 \times (1 - \exp(a \times (N_0 \times h - T))) \quad (4)$$

where N_e is the number of killed prey, N_0 is the initial prey density, a is the attack rate, h is the handling time and T is the exposure time (24h).

The Lambert's transcendental equation was used to solve the equation (Juliano, 2001).

Finally, the type-III FR was tested using the Hassell's type-III response without replacement which follows the same Roger's Type-II model (Equation 2), assuming that the attack rate (a) changes with prey density with the hyperbolic relationship:

$$a = \frac{(b \times N_0)}{(1 + c \times N_0)} \quad (5)$$

where b and c are coefficients to be estimated and N_0 is the initial prey density.

The confidence limits (95%) for each curve were estimated by bootstrapping (999 replicates) using the *frair_boot* function. The maximum attack rate (T/h) and its 95% confidence limits were estimated using the function *Max_attackRates* from the 'simar' package (Bolker, 2008).

Due to the sigmoid nature of the data, the model of the type-III FR Hassell equation (Equation 5) was used to fit the number of overkilled spittlebugs (i.e. prey killed and not consumed).

3 | RESULTS

Evidence for a type-II FR was found for both the number of consumed spittlebugs ($\beta_1 = -0.125$, SE=0.018, $Z = -7.050$, $p < 0.001$) and the total dead individuals ($\beta_1 = -0.281$, SE: 0.072, $Z = 4.051$, $p < 0.001$) (Figure 2a). On the other hand, the number of overkilled spittlebugs followed a sigmoid pattern ($\beta_1 = 0.446$, SE=0.110, $Z = 4.051$, $p < 0.0001$; $\beta_2 = -0.15$, SE=0.004, $Z = -3.473$, $p < 0.001$) with $b = 0.004$ (SE=0.001, $Z = 3.308$, $p < 0.001$), $c = 0.064$ (SE=0.039, $Z = 1.657$, $p = 0.097$) and $h = 0.002$ (SE=0.003, $Z = 0.677$, $p = 0.498$) (Figure 2b).

Considering the total number of dead individuals, the FR was significantly higher than that of consumed individuals (Figure 2a). The attack rate in dead individuals was twice higher than in consumed ones, while handling time was three times higher in consumed than in dead individuals (Table 1). The maximum attack rate showed the highest maximum number of prey attacks for dead specimens (Table 1).

4 | DISCUSSION

In this work, we selected a species of spider to assess its FR on *P. spumarius* and target potential natural enemies for this vector of *X. fastidiosa* following the protocol proposed by Benhadi-Marín et al., 2018. In the laboratory, *X. acerbus* fed on *P. spumarius* adults showing a type-II FR (consumed and dead insects). In the type-II response, the number of preys approaches the asymptote hyperbolically as prey density increases (inverse density dependence) (Benhadi-Marín et al., 2018), meaning that the consumed and dead *P. spumarius* by *X. acerbus* will not increase with higher densities and may depend on the satiation and digestion of the spider. On the other hand, the number of overkilled individuals of *P. spumarius* approached the asymptote as a sigmoid function due to a dependency on the prey density until the inflection point where prey killed will start to decrease (Benhadi-Marín et al., 2018).

According to the results of the FR assays, the number of dead individuals was significantly higher than the consumed ones, indicating a potential overkilling behaviour in *X. acerbus* when fed with *P. spumarius*. Overkilling, or killing without feeding or discarding partially consumed prey, may result from an imbalance between the time required for digestion and handling (Cloarec, 1991; Jeschke et al., 2002). This behaviour could be associated with the prey size (Riechert & Maupin, 1998). Nevertheless, despite potential

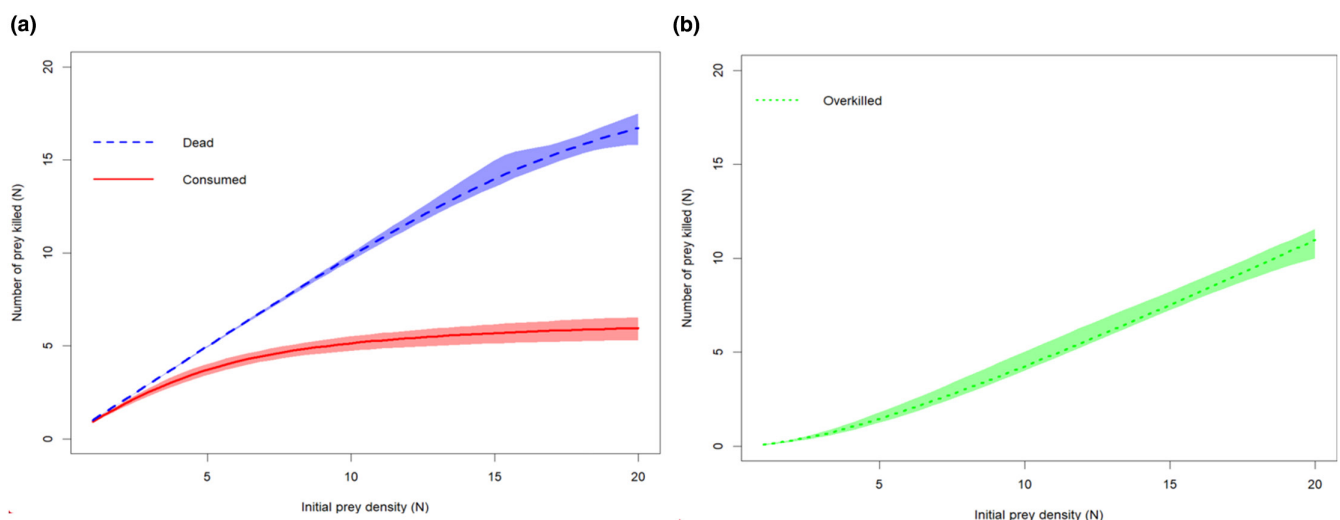


FIGURE 2 (a) Fitted functional response models obtained for *Xysticus acerbus* fed on different densities (1, 3, 5, 8, 16 and 20 individuals) of *Philaenus spumarius* adults during 24 h (FR type II). 'Consumed' stands for the prey killed and digested and 'Dead' stands for the total number of attacked prey. (b) Fitted model for the number of individuals of *P. spumarius* killed but not consumed by *X. acerbus* (FR type III). Thick lines represent the fitted values of empirical data and the shaded areas represent the 95% confidence limit. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Estimated parameters for the number of prey consumed and dead against prey density for the species of spider studied in the functional response assay.

	Estimate	SE	CI	Z-value	Pr(> Z)
Consumed					
<i>a</i>	0.127	0.032		3.914	<0.001
<i>h</i>	3.561	0.416		8.560	<0.001
<i>T/h</i>	6.74		6.71, 7.00		
Dead					
<i>a</i>	0.298	0.066		4.484	<0.001
<i>h</i>	1.074	0.113		9.531	<0.001
<i>T/h</i>	22.35		21.93, 2.73		

drawbacks, overkilling has the potential to increase the overall count of deceased prey, offering potential advantages in the context of biological control (Riechert & Maupin, 1998).

Although under laboratory conditions, it was suggested that type-III is the only FR type that can stabilize the prey-predator system and, therefore, keep the pest under control (Aljetlawi et al., 2004; Sinclair et al., 1998), in field conditions, generalist spiders commonly switch between FR types depending on the prey community composition (Sinclair et al., 1998). Other studies of the FR of spiders using *P. spumarius* as prey showed that the orb weaver *Araniella cucurbitina* (Clerck, 1757) (Araneidae) responded with a type-II FR, whereas the ambusher *Synema globosum* (Fabricius, 1775) (Thomisidae) with a type-I FR (Samu et al., 2013).

The maximum attack rate helps to assess the capacity of a predator to attack a number of prey individuals for a given time (Benhadi-Marín et al., 2018). Benhadi-Marín et al. (Samu et al., 2013) found a maximum attack rate of 50.52 individuals in 24 h for *A. cucurbitina* preying upon *P. spumarius*. In this work, we estimated a maximum attack rate of *X. acerbus* of 22.3 individuals in 24 h. These findings imply that *A. cucurbitina* could potentially function as a more efficient predator. Nevertheless, an analysis of their natural habitats reveals a greater alignment between the favoured environments of *X. acerbus* (predominantly located in meadows) and *P. spumarius*. This alignment is more prominent when compared with *A. cucurbitina*, which primarily inhabits trees and bushes at heights exceeding 1.5 meters (Samu et al., 2013). Accordingly, direct comparisons between the potential efficiency of predators based only on the FR parameters estimated in the laboratory must be carefully derived.

5 | CONCLUSION

This research offers valuable perspectives on the feeding behaviour of *X. acerbus* concerning *P. apumarius*. The findings suggest that *X. acerbus* can potentially serve as a natural enemy of *P. spumarius*. However, further studies are needed to assess its behaviour in the field. Finally, although *X. acerbus* is well spread over Europe, studies

on other species sharing the same predatory traits (e.g. related crab spiders locally abundant) would be useful to develop successful biological control programs.

AUTHOR CONTRIBUTIONS

Júlia López-Mercadal: Conceptualization; methodology; investigation; funding acquisition; writing – review and editing; data curation; writing – original draft; formal analysis. **Jacinto Benhadi-Marín:** Conceptualization; writing – original draft; writing – review and editing; methodology; validation; formal analysis; data curation; supervision; investigation; funding acquisition. **Isabel Rodrigues:** Writing – review and editing; methodology; data curation. **Miguel Ángel Miranda:** Funding acquisition; writing – review and editing; supervision; writing – original draft. **José Alberto Pereira:** Conceptualization; investigation; funding acquisition; methodology; validation; writing – original draft; writing – review and editing; supervision; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting the information shown in the results have been uploaded to Zenodo (<https://zenodo.org/>) (López-Mercadal et al., 2023).

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