



Article

Web Architecture Affects the Functional Response of the Space Web-Builder *Kochiura aulica* against *Trioza erytreae* in the Laboratory

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Abstract: The “citrus greening disease” or huanglongbing (HLB) is caused by the Gram-negative bacteria *Candidatus Liberibacter* spp. One vector of HLB, the African citrus psyllid *Trioza erytreae* (del Guercio, 1918), was recorded for the first time in 2014, in mainland Spain, and since then, it has spread throughout the Iberian Peninsula. Spiders could be natural enemies of *T. erytreae*. In this work, we assessed the potential of a model spider species, selected according to the most abundant guild in the field, as a natural enemy of *T. erytreae*. Theridiidae was the most successful family, capturing adults of *T. erytreae* in the field. *Kochiura aulica* (Theridiidae) was selected as a model for functional response assays in the laboratory. The effect of web-building plasticity on the functional response of *K. aulica* was investigated using two types of arena. The spiders developed tubular-like or branch-like webs according to the spatial constraints. The web architecture significantly shifted the trapping efficiency of *K. aulica*. Functional responses for tubular and branch webs were both Type-II, but more psyllid prey were captured and killed in the tubular webs than in branch webs. In addition, significantly more psyllids survived in branch-like webs. Our results suggest that web architecture is a key factor driving the number of captured adults of the psyllid. Space web builders could be successful natural enemies of *T. erytreae*, although further research is needed to clarify the influence of web-building plasticity on the functional response and trapping efficiency of spiders.

Keywords: predation; huanglongbing; spiders; biological control; web-building plasticity



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1. Introduction

The African citrus psyllid, *Trioza erytreae* (Del Guercio, 1918), is a vector of *Candidatus Liberibacter* spp., phloem-limited Gram-negative bacteria, putative causal agents of huanglongbing (HLB) or “citrus greening disease” [1]. During the last decades, the psyllid was introduced in Europe, firstly in Madeira (1994) and the Canary Islands (2002) [2,3], and in 2014, it was found in the continental territory of the Iberian Peninsula [4].

Once *T. erytreae* reached the continental territory, it was able to spread constantly throughout the northern regions of Spain and to the southern regions of Portugal [5]. The extent of the spread currently encompasses economically relevant areas of production, such as the Algarve (southernmost region of Portugal) and threatens other important citrus commercial regions in the Iberian Peninsula, such as Huelva and Valencia (Spain) [6].

HLB vector management is mandatory to prevent the disease [7]. A series of strategies are available in this regard, for example, quarantine measures (aiming to prevent the introduction or spread of the psyllid to vector-free areas), chemical control (focused on maintaining the population at low abundance levels), cultural control (such as cultural measures that hinder the psyllid development and spread), and biological control (using native or introduced predators, parasitoids, or entomopathogens to limit the psyllid population) [8]. Among these management options, the biological control approach em-

braces the environmentally friendly practices for organic cropping toward the sustainable agriculture paradigm.

Spiders are extremely diverse, naturally occurring ubiquitous predators in most ecosystems [9,10]. Due to their high diversity, spiders encompass a large number of guilds or functional groups (i.e., groups of species using the same class of resources in a similar way) according to their hunting strategies (see Uetz et al., 1999 [10] and Cardoso et al., 2011 [11]). These characteristics led to considering spiders as potentially successful natural enemies. However, the extent to which they are actually efficient for pest limitation depends on a series of traits, such as prey preference [12], prey switching behavior [13], the habitat structure and environmental conditions [14], and the attack rate and prey handling time [15]. The last two parameters are widely studied through functional response experiments to describe the predator feeding rates at increasing prey densities. Functional response assays usually offer different prey densities to a series of individuals of a selected predator and record the number of prey killed after a planned time for a pool of trials (i.e., repetitions). Finally, the parameters (attack rate and prey handling time) are estimated by modelling the data using different methods (see Bolker, 2008 [16] and Coblenz and DeLong, 2021 [17]). This type of assay allows the study of the functional response parameters for a fixed set of conditions. However, intraspecific variation, as well as the predator and prey traits may influence the functional response [17–19].

Different sources of variation in arachnids' foraging behavior, such as hunger level [20], age [21], and energy demand due to reproduction [22], raised interest and were studied using functional response experiments. Spiders can generally be divided into active hunters and web hunters, regarding the hunting strategy. The latter group uses the web to trap the prey instead of a pursuing or stalking strategy. The web is a key characteristic of spiders that has been extensively studied from different points of view, such as its evolution, diversity, and plasticity [23]. There is a high diversity of spider web architectures [24] and the effect of specific prey species, the nutritional quality of prey, and spatial constraints on web-building plasticity (i.e., ability of a spider to adapt its web-building behavior to different stimuli) has been addressed for orb-web-building spiders (see Blamires, 2010 [25] and Hesselberg, 2014 [26]). Nevertheless, the effect of the web-building plasticity of spiders on their functional response has been largely neglected.

In this work, we integrate two scopes, the potential of spiders as natural enemies of *T. erytrae*, and the effect of their web-plasticity on the functional response when preying on psyllids. The specific objectives were (1) to assess the potential of different spider webs to trap adults of *T. erytrae* in the field, (2) to select a model spider species, aiming to conduct subsequent functional response trials in the laboratory, and (3) to investigate in the laboratory the effect of web-building plasticity on the functional response of the spiders fed with the psyllid.

2. Materials and Methods

2.1. Study Area and Sampling of Canopy Spiders

A *Citrus limon* L. orchard (cv. "Lunario") was selected in Caracoi, Porto (North-western Portugal, 41°18'46" N 8°38'09" W) encompassed in the area colonized by *T. erytrae* (see DGAV, 2021 [5]). The orchard is a commercial grove of 1.35 ha surrounded by eucalyptus trees (*Eucalyptus globulus* Labill.) with flat topography and an average altitude of 160 m.a.s.l. The lemon trees are more than 20 years old, with a plantation distance of 6 m between rows and 2 m between trees. During the sampling period, the soil was not ploughed, not irrigated, and no phytosanitary treatments were applied. Canopy spiders were collected using the beating technique [27] and preserved in 70% ethanol in situ. A total of 10 sampling points (i.e., 10 trees) were selected along two rows of five points each throughout the orchard and spaced 36 m away from each other. Rows were spaced 14 m away. Each sample consisted of two beats at each cardinal point per tree (i.e., 8 beats/tree). Sampling was conducted on 14 August 2020, and repeated after a week so that 20 samples were collected. Once preserved, the material was transported to the laboratory and identified at the family level

(since all the captured individuals were found to be immature) using specific keys [28]. Finally, the pool of families was assigned to a guild following Uetz et al. (1999) [10] and Cardoso et al. (2011) [11].

2.2. Characterization of Spider Webs in the Field

A total of 100 webs, 50 above and 50 below 1.5 m, were visually inspected within the orchard on 21 August 2020. Webs were randomly chosen along the rows of the plantation throughout the orchard. The family of the spider and the number of adults of *T. erytreae* captured by each selected web were registered. The trapped individuals of *T. erytreae* were identified in situ using a hand 20× magnification lens. The registered families of spiders were subsequently assigned to a guild as in Section 2.1.

2.3. Selection of Model Species and Functional Response Trials

A species belonging to the dominant functional group found in the orchard (e.g., the highest number of webs and highest number of *T. erytreae* adults found trapped in them) was selected as model for the laboratory functional response assay. According to the field results, the spider species selected for subsequent laboratory assays was the web-builder *Kochiura aulica* (C.L. Koch, 1838). *Kochiura aulica* is a European widespread 3D-web-builder common on bushes and Mediterranean plants [28]. The species is present in the study area (Porto region) and widespread throughout the Iberian Peninsula [29]. In order to establish a healthy colony in the laboratory for the functional response assays, the spiders were captured by hand in the field throughout a Mediterranean shrubland (41°52'42" N 6°39'55" W) near Bragança (Portugal) due to their high density in this region during the development of this work. *Cistus ladanifer* L. dominated the area, and adult female spiders were collected by inspecting these plants. Once a web was detected, the spider was captured by hand using a Falcon tube (15 mL). The spiders were transported individually to the laboratory and then transferred to plastic cups (8 cm in diameter, 5 cm in height). All the individuals were fed *ad libitum* with *Drosophila melanogaster* Meigen twice a week, for two weeks, to homogenize the hunger level. Then, the spiders were starved for seven days before the functional response assay.

2.4. Functional Response Assays

Two types of arena were designed aiming to simulate two web-building scenarios: (1) the space between leaves and (2) the plant branches. The arenas consisted of a transparent cylinder (21 cm in height, 8 cm in diameter) made of transparent acetate enclosed with the top of a glass petri dish (8 cm in diameter) on the upper side and the base of a plastic cup (8 cm in diameter) on the bottom side (Figure 1).

The areas designed to simulate the space between leaves were used without any further modification, whereas a structure made of woody sticks was placed inside the arenas intended to simulate a branch. The wood structure consisted of a vertical stick (14 cm in height, 2 mm in diameter) and two small pieces (3 cm in length) of the same material attached to it at the height of 6 and 10 cm, respectively. The two small sticks were attached to the vertical one by the middle part and rotated 90 degrees one from another. After the starvation periods, each spider was transferred to the arenas and placed either on the top (in the case of the space-like arenas) or on the woody structure (in the case of the branch-like arenas) (Figure 2). A total of 35 spiders were used for each type of arena. All the spiders built their webs in one day so that the next day all the individuals were fed with increasing densities of *T. erytreae*. The densities of prey corresponded to 2, 5, 10, 15, 25, 50, and 100 adult individuals. Five samples (repetitions) per density were used (i.e., five spiders were tested for each initial prey density). The individuals of *T. erytreae* were obtained from the same lemon orchard where the spiders were captured using a mouth aspirator. The captured individuals were transferred in situ to a series of Falcon plastic tubes (50 mL) according to the different required prey densities. The time of the functional response experiments is usually set for 24 h; however, although the trials were conducted

the same day the psyllids were captured, due to their high mortality rate in the absence of food, the number of psyllids captured or killed by the spiders and the number of survivors were counted at the end of 6 h. Since every psyllid not captured by the spiders was alive after the time lapse, no further trials were conducted to assess the mortality of *T. erytreae* in the absence of spiders. Adult males and females of *T. erytreae* were indistinctly used as prey. The trials were conducted at 24.5 ± 1 °C, $50 \pm 10\%$ HR, and under direct warm light (1000 lux).



Figure 1. Example of the arena structure designed for the functional response experiments.

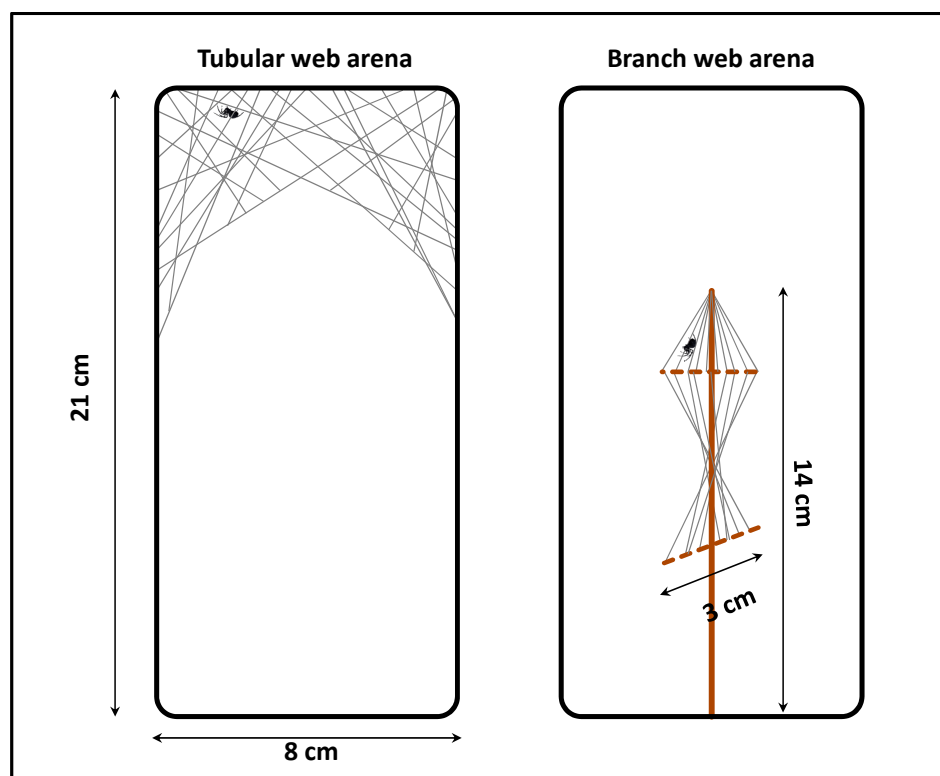


Figure 2. Schematic view of the two types of arena designed for the functional response experiments.

2.5. Data Analysis

All the analyses were conducted in R [30]. The number of canopy spiders belonging to each functional group captured by beating was compared using a generalized linear model with Poisson distribution followed by a post hoc Dunn test ($\alpha = 0.05$). The functional response parameters were estimated using the functions provided in the package “frair” [31]. For each dataset, i.e., tubular-like webs (aerial space webs) and branch webs (aerial sheet-like webs), the type of functional response was selected and modeled for the number of prey killed and captured as follows: (1) the number of prey killed and captured was initially fitted to a type-I functional response model as:

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

where N_e represents the number of prey killed or captured, N_0 represents the initial prey density, a represents the attack rate, and T is the time of the experiment. (2) Since the data did not fit the type-I response, the “frair_test” function was used to select the final shape of the functional response by fitting two models by logistic regression:

$$\text{Killed/not-killed} \sim \alpha + \beta \times \text{Density} \quad (2)$$

$$\text{Killed/not-killed} \sim \alpha + \beta_1 \times \text{Density} + \beta_2 \times \text{Density}^2 \quad (3)$$

where Density is the initial prey density, Killed is the number of prey killed or captured, and not-killed is the difference between them. The output provides the sign and p -values of 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 functional response (i.e., the number of prey killed hyperbolically approaches to an asymptote) whereas a positive linear coefficient (β_1) and a negative quadratic coefficient (β_2) means the data fit a type-III functional response (i.e., the attack rate (a) is a hyperbolic function of prey density) (see Juliano, 2001 [32]). (3) Since all the datasets fitted the type-II functional response and due to the lack of prey replacement during the experiments, the Rogers’ type-II decreasing prey function was used to model the data as:

$$N_e \sim N_0 \{1 - \exp [a(N_e \times T_h - T)]\} \quad (4)$$

where N_e is the number of prey killed or captured, N_0 is the initial prey density, a is the attack rate (searching efficiency per time), T_h is the handling time, and T is the time of the experiment (see Bolker, 2008 [16]). (4) Finally, the attack rate (a) and handling time (T_h) were bootstrapped using the “frair_boot” function by resampling the previously fitted models and the 95% confidence intervals for each parameter were estimated. The whole empirical 95% confidence interval for each curve was generated using the “drawpoly” function.

For each assay, the number of prey that survived was modelled using third-grade polynomials, then the 95% confidence interval was estimated for each curve for comparison between cases (tubular web vs. branch web).

3. Results

3.1. Sampling of Spiders and Webs in the Field

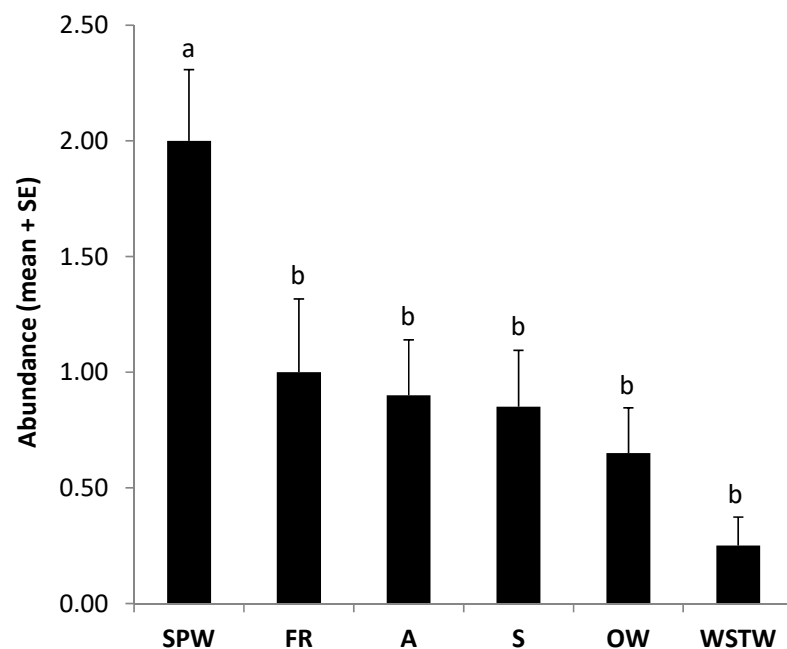
A total of 122 spiders, encompassing ten families and six guilds, were captured in the lemon orchard, using the beating technique, with Dictynidae and Oxyopidae as the most and least abundant families, respectively (Table 1).

In terms of guilds, the abundance of space web builders in the canopy was significantly higher than any other functional group ($\chi^2 = 34.65$; $df = 5$; $p < 0.001$) (Figure 3).

The highest number of spider webs found above 1.5 m corresponded to the family Theridiidae, whereas below 1.5 m, the most abundant webs corresponded to Linyphiidae (Table 2). In both cases, the two families corresponded to the highest number of captured adults of *T. erytrae* (Table 2). Among the remaining families, Araneidae and Salticidae were the only families that presented at least one individual of *T. erytrae* in the web (Table 2).

Table 1. Abundance of each guild of canopy spiders collected by beating branches in lemon trees in North-western Portugal.

Guild	Family	N
Space web builders	Dictynidae	26
	Theridiidae	14
Foliage runners	Anyphaenidae	12
	Cheiracanthiidae	8
Ambushers	Philodromidae	10
	Thomisidae	8
Stalkers	Salticidae	15
	Oxyopidae	2
Orb-weavers	Araneidae	13
Wandering sheet/tangle weavers	Linyphiidae	5
Immatures not identified	-	9
Total		122

**Figure 3.** Canopy spiders' abundance of each guild collected by beating branches in lemon trees in North-western Portugal. SPW: space web-builders; FR: foliage runners; A: ambushers; S: stalkers; OW: orb-weavers; WSTW: wandering sheet/tangle weavers. Different letters above bars indicate significant differences ($p < 0.05$).**Table 2.** Functional group, family, number of webs inspected, and total number of adults of *T. erytreae* captured per family of spiders in a citrus orchard in North-western Portugal at two vertical strata (above and below 1.5 m). SPW: space web-builders; FR: foliage runners; A: ambushers; S: stalkers; OW: orb-weavers; WSTW: wandering sheet/tangle weavers.

Functional Group	Family	Height > 1.5 m		Height < 1.5 m	
		Webs (N)	Adults of <i>T. erytreae</i> (N)	Webs (N)	Adults of <i>T. erytreae</i> (N)
A	Thomisidae	1	0	0	0
FR	Anyphaenidae	1	0	0	0
OW	Araneidae	11	4	16	2
SPW	Theridiidae	32	68	0	0
S	Salticidae	5	3	0	0
WSTW	Linyphiidae	0	0	34	28
Total		50	75	50	30

3.2. Functional Response Experiments in the Laboratory

The four cases considered among the two functional response experiments yielded a type-II functional response (Table 3). In both cases, considering captured and killed individuals, the curves significantly differed between web architectures (Figure 4).

Table 3. Summary statistics for the selection of functional response type for each web architecture and response variable.

Response	Type of Web	Linear Coefficient	SE	Z-Value	<i>p</i>	FR Type
Prey captured	Tubular	−0.009	0.002	−3.581	<0.001	Type-II
	Branch	−0.026	0.002	−11.542	<0.001	Type-II
Prey killed	Tubular	−0.018	0.002	−8.370	<0.001	Type-II
	Branch	−0.014	0.002	−6.332	<0.001	Type-II

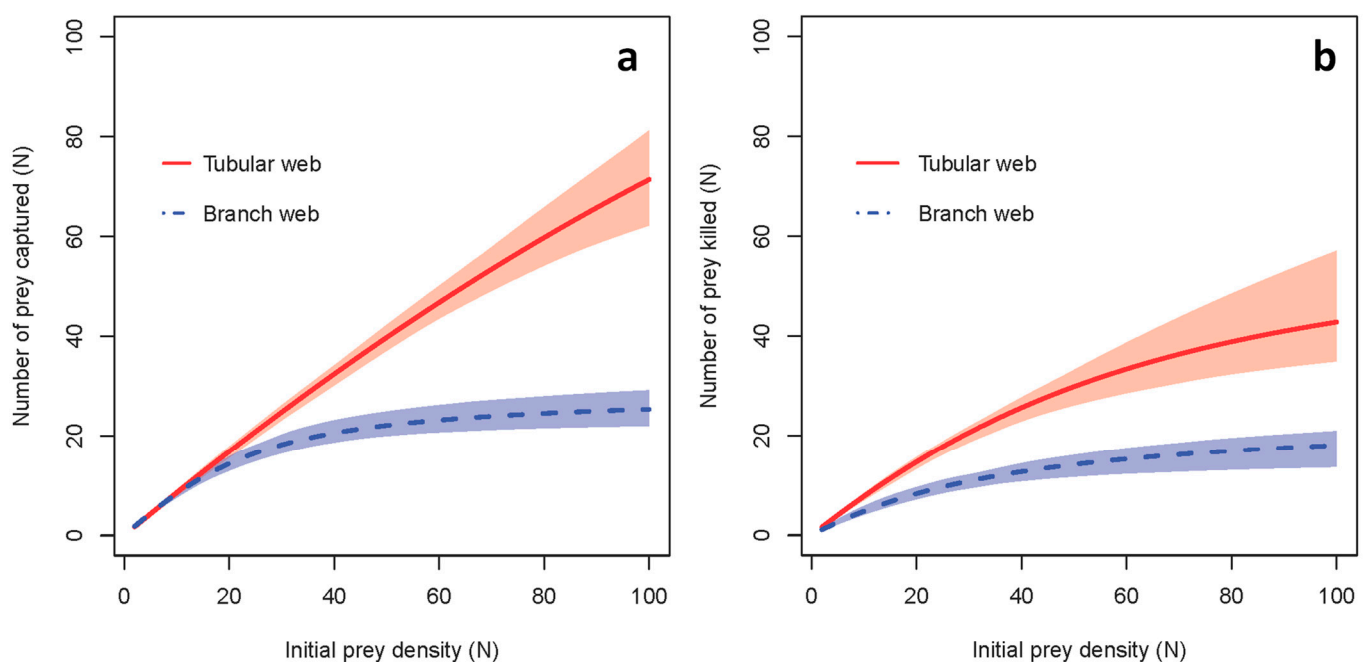


Figure 4. Functional responses of *Kochiura aulica* adult females fed, for 6 h, on differing densities of *Trioza erytreae* adults using two web architectures. (a): Curves for captured individuals. (b): Curves for killed individuals. Thick lines represent the fitted values of empirical data, and the polygons represent the limits of the confidence interval of the curves.

During the experiments, the highest and lowest attack rates were found for the branch architecture, although only the attack rate considering the number of prey killed as response significantly differed from the remaining (Table 4). In the case of the handling time, the estimate was significantly higher for the branch webs, regardless of the type of response considered (Table 4).

The abundance of individuals of *T. erytreae* found alive after the 6 h of the functional response experiments increased with the initial prey density in a sigmoid-like way for the two web architectures (tubular-like web: $F = 35.245$, $df = 3$, $p < 0.001$; branch web: $F = 563.12$, $df = 3$, $p < 0.001$). However, the number of survivors was significantly higher in the case of the branch web (Figure 5).

Table 4. Summary of statistics for the attack rate (a) and handling time (T_h) of the functional response of *Kochiura aulica* fed on *Trioza erytreae* using the prey captured or killed as response and two web architectures. Significant differences for the estimate are indicated by lower case and capital letters for the attack rate and handling time, respectively.

Response	Type of Web	Parameter	Estimate	SE	Z-Value	p	95% CI
Prey captured	Tubular	a	0.334 a	0.031	10.905	<0.001	[0.256, 0.419]
		T_h	0.031 A	0.007	4.275	<0.001	[0, 0.052]
	Branch	a	0.423 a	0.055	7.622	<0.001	[0.297, 0.633]
		T_h	0.209 B	0.017	12.423	<0.001	[0.161, 0.251]
Prey killed	Tubular	a	0.285 a	0.028	10.079	<0.001	[0.222, 0.381]
		T_h	0.095 C	0.010	9.225	<0.001	[0.052, 0.155]
	Branch	a	0.137 b	0.023	5.939	<0.001	[0.090, 0.202]
		T_h	0.253 B	0.040	6.303	<0.001	[0.172, 0.375]

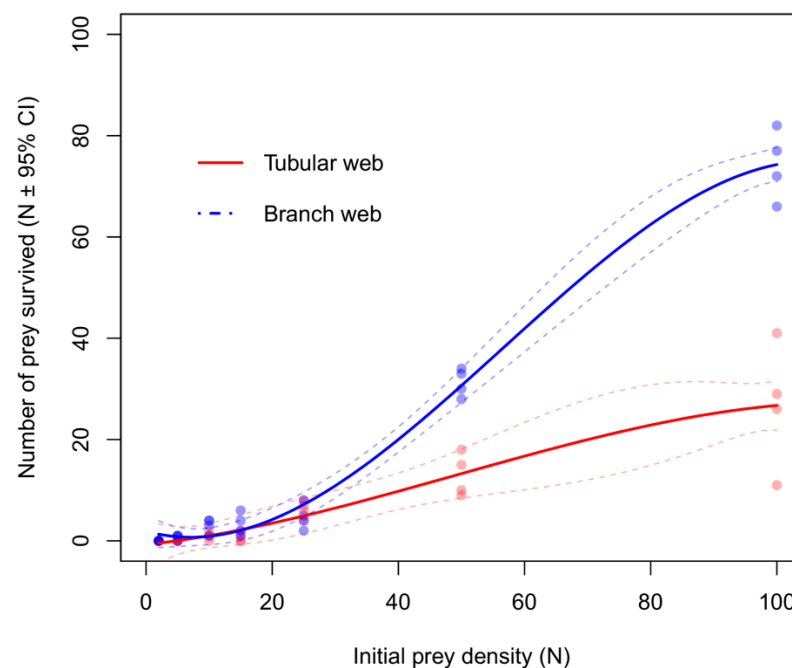


Figure 5. Sketched curves for the number of survived individuals of *Trioza erytreae* after 6 h of functional response experiment for two web architectures of *Kochiura aulica*. Dots represent the observed data, thick lines represent the fitted values, and dashed lines represent the 95% confidence interval for each curve.

4. Discussion

In this work, we conducted a survey of spiders and their webs in the canopy of a lemon orchard in North-western Portugal. The resulting assemblage of spiders allowed selecting a model species, the spatial web builder *K. aulica*, for subsequent functional response assays in the laboratory. The laboratory assays were conducted, aiming to investigate the potential of common spiders inhabiting the orchard as natural enemies of the African citrus psyllid, *T. erytreae*, the current potential vector of HLB in Europe. Moreover, the effect of the ability of the selected web-builder to adapt its web to different spatial constraints was assessed.

We found that spatial web builders were the most abundant among the registered guilds in the canopy. In addition, the highest numbers of captured adults of *T. erytreae* were found in their webs. Our results agree with the observed families of spiders found by Van den Berg et al. (1987) [33], in the Transvaal region (South Africa). Among the reported families, Araneidae, Dictynidae, Salticidae, Theridiidae, and Thomisidae were also found in our survey. On the other hand, although spiders have been recorded in Madeira (Portugal)

and the Canary Islands (Spain), no predatory activity on the psyllid has been reported (see Cocuzza et al., 2017 [8]). Notwithstanding, a positive correlation between the abundance of *T. erytreae* and web-building spiders was found by Van den Berg et al. (1992) [33], in a citrus orchard in Lowveld (South Africa).

The family Dictynidae was the most abundant, according to the results of our survey of canopy spiders, although the theridiid *K. aulica* was selected as a model spider for the laboratory functional response trials, according to the number of detected webs. The higher number of theridiid webs found by visual inspection is most likely subject to detectability bias, since the bigger spatial webs of theridiids are easier to see than the smaller foliar webs of dictynids. However, the abundance of psyllids found trapped in the webs and the reported diversity of theridiids as a species that preyed on *T. erytreae* by Van den Berg et al. (1992) [34] supported our choice. Nevertheless, although the dictynids' webs are small compared with those of orb-weavers and other aerial web-builders, future studies should consider the potential efficiency of dictynids in limiting the population of *T. erytreae* due to their abundance.

We found a type-II functional response, when feeding females of *K. aulica* with adults of *T. erytreae*. To the best of our knowledge, no other studies have been carried out in the laboratory involving spiders and the African citrus psyllid. In this work, the spiders were able to adapt their webs to the spatial constraints of two types of arena. When a central, simulated branch structure was provided, the web design was sheet-like and surrounded the woody structure. In contrast, the webs followed a tubular (almost funneled) design when no other structures but the arena cylinder were provided. In general, Theridiids build loose and tangled, but somehow organized, webs during the night with trapping threads regularly studded with glue drops (see Foelix, 2011 [35]). Interestingly, the less efficient web design exhibited by *K. aulica* in this study (i.e., branch webs) better fitted the design observed in nature on the branches of *C. ladanifer* plants (J. Benhadi-Marin pers. obs.). Further studies should assess the spatial web architecture exhibited by *K. aulica* in lemon plants, aiming to test if the spiders more often produce such a design if leaves allow them to do so. A certain degree of web-building plasticity has been observed in orb-weavers that could be a response to the sensory input and a behavioral response to different situations [34]. In this work, we provide strong evidence for the adaptive hunting capacity of *K. aulica* to different scenarios of spatial limitation.

The difference in the spatial architecture of the web significantly affected the predatory behavior and efficiency of the spiders preying upon *T. erytreae*. Thus, the branch sheet-like webs were significantly less efficient in trapping the psyllids compared to the tubular-like webs and, consequently, a significantly higher number of psyllids were able to survive at the end of the experiments. The same pattern was found despite the response considered for modelling (i.e., captured or killed individuals of *T. erytreae*).

Although the estimated attack rate did not significantly vary among trials, except for the sheet-like webs considering the killed prey, the handling time was consistently significantly lower in the tubular-like webs. The handling time encompasses the required time to pursue, subdue, feed, and restart hunting [36], which suggests that the architecture design of tubular webs facilitated the hunt. These could be related to a more intricate structure of threads or a higher density of glue drops. In any case, the funneled structure of the web certainly reduced the chances of escape for the psyllids. Since no constraint for the psyllids, in terms of spatial limitations (i.e., the cylinder), is expected to occur in the field, we recommend further specific trials, such as functional response mesocosm experiments, instead of extrapolating these results. In addition, a systematic classification of web types throughout the crop would be useful to assess whether captures are consistent with the laboratory results.

Among the web-building spiders reported by Van den Berg et al. (1992) [34] in a lemon orchard, the family Araneae (orb-web builders) encompassed four genera as for theridiids; however, it has been shown that cobweb weaver spiders (Theridiidae) could be more efficient in trapping insects due to stiffer and tougher glue droplets compared to

orb-weavers [37]. In the absence of further data, it is not currently possible to establish a degree of the efficiency of space web builders compared to other guilds, thus, more assays involving other guilds of spiders are crucial to shed light on this.

In this work, we used a model spider species as the predator selected among spatial web builders. Future experiments, aiming to investigate the role of spiders as natural enemies of *T. erytrae*, should consider an abundant species present in the orchard in the field, and take into account the behavior plasticity of web builders, according to the physical conditions imposed by the arena design in the laboratory.

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