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Predatory Behaviour is Plastic According to Prey Difficulty in Naïve Spiderlings

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Abstract Predatory behaviour is plastic towards different prey. However, prey differ in their defenses and predators should adjust in order to successfully subdue it. The variation in predatory behaviour could be either innate or developed from experiences. A feasible way to tease these factors apart is by studying inexperienced individuals. Here, I tested if the behaviour of inexperienced predators is different towards two prey types and if it correlates with the behaviour of the prey. I fed naïve spiderlings of the sheet weaver cellar spider *Physocyclus globosus* (Pholcidae) with either fruit flies or ants as prey (potential extremes in difficulty). I found that, regardless of prey type, individuals that exhibited active defensive behaviour (longer time twisting, moving legs and body segments) elicited a more intense predatory behaviour by the spiderlings (longer time touching and wrapping the prey, and giving more bites). Ants were often more difficult prey than flies, even damaging the spiderling's leg in five trials. A successful attack to difficult prey was associated with increased handling time of additional silk needed to immobilize it. The differences in the predatory behaviour showed by *P. globosus* spiderlings suggest plasticity since their first attack. This plasticity would be adaptive for naïve predators of any taxa that encounter a wide diversity of prey.

Keywords Araneae · *Drosophila melanogaster* · *Paratrechina longicornis* · prey–wrapping · *Physocyclus globosus* · Pholcidae

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Introduction

Predators aim to successfully subdue and consume their prey with less effort and few risks to themselves. Phenotypic features of the predator affect this outcome, such as its ontogenetic and sexual status, as well as its past experiences (Heiling and Herberstein 1999; Morse 2000; Shettleworth 2010). On the other hand, the potential prey aims to escape the encounter, and their morphological, chemical and behavioural defenses could favor its escape and survival (Jeschke and Tollrian 2000; Broom and Ruxton 2005; Nonacs and Blumstein 2010). Therefore, variation in the defenses of potential prey might affect the outcome of the interaction (Edmunds 1974; Caro 2005; Líznarová and Pekár 2013). Predators can adjust to that variation with plasticity in their attack tactics to facilitate capture (Théry and Casas 2002; Nelson and Jackson 2011). Consequently, the outcome is mediated by the interaction between the behaviour of both actors, which creates a feedback that affect their decisions; as shown recently in adult individuals of sea stars preying on snails (Pruitt et al. 2012), black widow spiders preying on crickets (DiRienzo et al. 2013), assassin bugs preying on web-building spiders (Soley and Taylor 2013), and spitting spiders preying on weaver spiders (Escalante et al. 2015).

Adaptive plasticity in predatory behaviour will favor performance that results in a successful attack (West-Eberhard 2003). Although widely studied in adults, is has been scarcely studied in inexperienced individuals. Nonetheless, predatory success is crucial right after hatching, that is, in the first encounter of a predator with potential prey. A successful attack is critical for inexperienced individuals to acquire food resources quickly to secure survival and development (Morse 2000). Hence, plasticity in predatory behaviour towards different types of prey will be beneficial for generalist animals.

Avid predators, like spiders, attack a wide variety of potential prey (Robinson and Olizarri 1971; Clements and Li 2005; Martins-García and Japyassú 2005). Adult spiders can adjust to the morphological and behavioural variation of the prey with plasticity in predatory tactics to facilitate prey capture (Jakob et al. 2011; Nelson and Jackson 2011). Additionally, the predatory behaviour and its effectiveness vary with ontogeny. For example, older spiderlings of *Nephila clavipes* capture *Drosophila melanogaster* fruit flies faster and they capture larger prey more often in the field than younger ones (Brown and Christenson 1983). Throughout experiences, spiderlings of *N. clavipes* changed their attack tactic to one used by adults: from throwing silk to doing a long bite (Higgins 2007). Behavioural variation with prey type in inexperienced spiderlings were found in the orientation of the attack and the distance jumped in *Phidippus regius* jumping spiders (Edwards and Jackson 1994) and in the capture success *Holocnemus pluchei* cellar spiders (Jakob 1991). However, there is no available information on whether the predatory behaviour of naïve individuals is plastic in response to the variation in defensive behaviour of different prey types.

Here, I studied the predatory behaviour of spiderlings of a cellar spider: *Physocyclus globosus* Taczanowski 1874 (Pholcidae), which weaves a loosely meshed irregular domed sheet web with a tangle above and is commonly found in human made structures (Eberhard 1992; Peretti et al. 2006; Escalante 2013). After hatching, pholcid spiders live in high density groups of siblings, and contests over prey occur (Jakob 1991, 1994; pers. obs.). So, if the prey that a spiderling is attacking escapes, it may strike another spiderling's web. Therefore, a quick successful attack on their prey by *P. globosus* spiderlings is expected. Also, during the first instar *P. globosus* spiderlings feed on many arthropod taxa, including conspecifics (pers. obs). Therefore, behavioural plasticity could favor predatory success right after hatching in response to different types of prey. Additionally, ontogenetic differences have been found in the web structure of this species (Escalante 2013), suggesting plasticity in early instars.

I tested for post–hatching plasticity in the predatory behaviour of *P. globosus*. I did this by recording the predator–prey interactions between spiderlings and two prey types that may represent opposite extremes in a range of difficulty once they are caught in the web: ants and fruit flies. Previous studies showed ants to be more difficult prey to wrap, bite, and handle by adults and older juvenile spiders, while flies were easier prey to subdue (Robinson and Olizarri 1971; Viera 1995; Martins-García and Japyassú 2005; Barrantes and Weng 2006; Pekár 2009; Kosiba et al. 2012; Líznarová and Pekár 2013). Therefore, I asked (1) does the predatory behaviour of spiderlings differ according to prey types? If the attack is plastic since their first experience I expected that spiderlings attacking difficult prey (ants) would take longer to wrap and handle difficult prey than spiderlings attacking easy prey (fruit flies). A null hypothesis will state that non-plastic predatory behaviour is performed in the same manner regardless of prey's features like difficulty. The lack of plasticity in naïve predators might result in unsuccessful attacks towards difficult prey. Additionally, (2) are the defensive behaviours different between the two prey types? Because ants have a long body, antennae, appendages and strong mandibles, I expected them to struggle more once caught compared to fruit flies. Finally, (3) does the behaviour of prey correlate with the behaviour of the predator? I expected difficult prey to elicit a stronger or longer predatory behaviour in the spiderlings.

Methods

Trials Methods I collected adult spiders in buildings on the campus of the Universidad de Costa, in San José, Costa Rica (1 160 m in elevation) on ceilings and furniture. I reared them in the lab (mean of 20 °C and 80 % relative humidity). After hatching from the egg, I placed each spiderling individually in a 50 ml plastic cup (4 cm height, 3 cm diameter). The cup was covered on the inside with white paper to allow spiderlings to attach threads. The opening was covered with a clear plastic sheet with a 0.5 cm longitudinal opening to introduce prey. The conditions in which the hatchlings were kept were the same prior to and during trials. I conducted trials 10 days after hatching (~ 20 % of spiderlings died after hatching, but none of the ones I used for the trails did), when the spiderlings had molted, built a web, and were hanging upside down in the center of the sheet, willing to attack. Thus, I studied the first attack of their life. Spiderlings measured ~2.0 mm long (from mouth to abdomen tip).

Naïve spiderlings were randomly divided in two treatments and offered only one of two prey types: (1) a worker ant of *Paratrechina longicornis* (Formicidae) (sample size: 30), which measured ~2.5 mm long (hereafter “ants”) which do not produce chemical defensive displays; or (2) a wild type fruit fly *D. melanogaster* (Drosophilidae) (sample size: 45), ~ 2.4 mm long (hereafter “flies”). Although I did not observe these species as prey items in *P. globosus* webs, other species of ants and flies of similar size are common prey for *P. globosus* in the collecting site and for other pholcids (Nentwig 1983; Kirchner and Opderbeck 1990; Eberhard 1992; pers. obs.). Using forceps, I placed the prey onto the wall of the cup to induce them to walk. I recorded the attack of the spiderlings with a SONY HandiCAM DCR-VX 1000 video camera, using three macro lens (+ 4 X each) and recording on mini-DV tapes at 30 frames per second. I digitized the videos using Microsoft Movie Maker.

Video Analyses I analyzed the videos using the software Etholog 2.2 (Ottoni 2000) and measured the frequency and duration of the behaviours I was able to clearly see during the attack by the spiderlings and the defensive behaviours of the prey. The attack was measured from the moment the prey touched the silk threads until the spiderling began feeding on it (therefore, a “successful” attack). The spiderling attacked prey by wrapping it with alternating leg IV movements until the prey was immobilized and then performed several bites (Japyassú and Macagnan 2004; Barrantes and Eberhard 2007). Since spiderlings performed the same behaviours while attacking both prey, I compared the attacks quantitatively. Originally, 23 variables derived from the video analyses, but after eliminating the statistically correlated variables ($r > 0.45$, and/or a correlation at the $P > 0.05$ level), I analyzed 12. Eight of them were durations of behavioural units (Table 1). I also measured the time delay between detecting the prey and the first touches to it, the time delay between the start of wrapping and the first bite given to the prey, and the number of short bites and the duration of all the bites given to each prey, as additional indicators of the predatory behaviour. Two qualitative variables arose from the analyses (occurrence of pull–prey, and if the prey escaped during the attack [see Table 1 for extensive definitions]). Because the prey escaped the web in some trials (See Results) I excluded from the analysis the information of the behaviour that occurred before the escape. Instead, I analyzed the attack in the attempt that finalized with the spiderling feeding.

For the defensive behaviour of both prey types I measured nine behaviours, but only analyzed and compared the five performed by both (Table 2). I opted for this approach, instead of a species-specific analysis of the prey’s behaviour, in order to have comparable information reflecting the challenges both prey types imposed to spiderlings. The behaviours were defensive because they were not performed until the prey touched the web (which occurred in a continuous manner) or the spiderling started the attack.

Statistical Analyses I tested whether the predatory behaviour of the spiderlings differed towards ants and flies with a discriminate function analysis (DFA), using the 12

Table 1 Definitions of the predatory behaviour of *Physocyclus globosus* (Araneae: Pholcidae) spiderlings while attacking two prey types (*Drosophila melanogaster* wild type fruit files and *Paratrechina longicornis* worker ants)

Module	Unit	Description
Detecting	Detect	The time elapsed between when the prey fell into the sheet or touched the threads on the walls and when the spiderling changed its body orientation and began moving. This delay is an estimate of the time between sensing the prey and responding.
	Approach	The spiderling walked towards the prey in the sheet or the threads of the web.
	Touch	The time spent by the spiderling making the initial taps on the prey before wrapping. Spiderlings touched the prey 3–5 times with their legs I or II.
	Prey pull[a]	The spiderling turned approximately 180° to face away from the prey after touching. Then it pulled threads or the legs of the prey with a strong flexing movement of one or both legs IV for ~0.23 s. This pulled the prey from the wall toward the center of the sheet, and moved it 0.5–1.0 cm closer to the spider. An entire pull prey sequence lasted 0.30–0.37 s. After 4–8 s, the spider continued wrapping or cutting threads near the prey. Sometimes the prey was not pulled, but the spiderling started the attack in the substrate, where in most cases the prey was tangled in the threads. Then the spiderling cut the threads around the prey and moved it (see below) upwards, away from the wall, toward the center of the sheet. On <15 % of the trials the spiderling also moved abruptly to the center of the sheet after the prey pull, and 4–8 s later resumed the attack. In one uncommon variant, the spiderling did not turn in front of the prey before pulling, and was thus still facing the prey when it pulled the prey toward itself flexing its legs I instead of legs IV. Four spiderlings reel in threads as described by Japyassú and Macagnan (2004) in association with gumfoot lines (see Escalante and Masís-Calvo 2014). The spiderling held a thread attached to the prey with the legs III or IV, and after the spider bent its legs, the prey moved upwards. Spiderlings performed more prey pulls when the prey escaped the web, when its movements released it partially or completely from the web; or in succession to get the prey towards the center of the web.
Wrapping	Wrap	The spider rapidly moved both legs IV alternately while pulling silk from the spinnerets and laying it onto the prey. The spiderling often held the prey with legs II and/or III while wrapping. Spiderlings moved their abdomens from side to side, but did not swing or incline it as do adults of the same species. The wrapping happened in several bouts during the attack, and it was alternated with other behaviours (short bites, cut threads etc).
Biting	Bite	The spider touched the prey with its chelicerae for less than 1 min several times during the attack, and short bites sometimes were performed when the prey was still moving.
	Feed[a]	Spiderling did a final bite and its chelicerae were more separated than during short bites; small dorso-ventral rhythmic pumping movements of the chelicerae were sometimes noticeable. This was the last behaviour performed. Feeding lasted 30–300 min.
Handling	Cut threads	The spider cut threads or silk away from the prey. It lowered its cephalothorax and brought its mouth close to threads, which then broke. About one third of the time the spiderling grabbed and pulled them near its mouth with its leg II or III to cut them. The spiderling cut 4–6 threads in each burst of thread cutting. The spiderling often moved away from the prey to cut threads.
	Touch threads	The spiderling touched the prey by tapping it with legs I or II after the wrapping had started. The taps seemed slower than the initial ones (above).
	Add threads	The spiderling added new threads to the prey package after the prey was already immobilized. The spiderling brought the tip of its abdomen into contact with the prey and attached a thread without using its legs (this movement thus differed from wrapping).

Table 1 (continued)

Module	Unit	Description
	Move prey	The spiderling moved the prey from one place to another, usually closer to the center of the web. The spiderling carried the already wrapped prey package or the prey itself by holding it with one or both legs IV.

The behavioural units are presented chronologically as they occurred in the attack

[a] Behaviours not included in the statistical analyses (see Methods). Note: the units are grouped in modules, which account for chronological and operational motivations of the behaviours (see Barrantes and Eberhard 2012). Most behaviours were previously described for another Pholcid species (*Pholcus phalangioides*; Japyassú and Macagnan 2004)

quantitative behaviours. I also tested if ants and flies differed in their defensive behaviour by performing a DFA with the five quantitative behaviours. I tested if the frequency of trials with a pull–prey behaviour or at least one escape by the prey differed

Table 2 Definitions of the defensive behaviours performed by two prey (*Drosophila melanogaster* wild type fruit files and *Paratrechina longicornis* worker ants) while being attacked by *Physocyclus globosus* (Araneae: Pholcidae) spiderlings

Unit	Description
Walk	After touching a substrate thread the prey walked and pulled it and sometimes a movement in the web was noted. This induced the spiderlings to follow them and begin (or restart) the attack.
Twist	Once in the sheet and after the spiderling started wrapping, the prey spun in circles or in an irregular trajectory due to the active movement of its body.
Move legs	The prey struck out the threads in the web with one or more legs in different directions.
Escape web[a]	During the first 60 s of the attack the prey struggled and often freed itself at least partly from the web, and continued walking on the wall of the cup. In many cases the prey still had a thread attached to its body, so the spiderling followed it. If not, the prey eventually touched another thread, and the spiderling then reached it and resumed the attack.
Squirm	After the wrapping progressed (~70 % of the total wrapping time) the prey moved its already wrapped appendages. This seldom resulted in the released of an appendage. It was noticeable when the spiderling paused during wrapping.
Move body segments	Throughout the attack the prey often moved its body segments laterally or dorso–ventrally. This happened mostly once the appendages were wrapped and immobile.
Move antennae[a]	The prey moved one or both antennae at the same time.
Move wings [a]	Only performed by flies. The fly moved both wings (if one was not already wrapped) with high frequency, which stroke the threads of the web.
Move mouth parts[a]	Only performed by ants. The ant opened its mandibles wide and closed them with variable speeds. This behaviour was apparently more common after the prey had its legs and antennae wrapped.

The behavioural units are presented chronologically as they occurred in the attack

[a] Behaviours not included in the statistical analyses (see Methods)

between the attack to flies and to ants with two proportion chi square tests. Additionally, to test for a relationship between the predatory behaviour of the spiderlings and the defensive behaviour of both prey types, I performed a canonical correspondence analysis (CCA). The CCA allowed me to produce correlations with multivariate scores derived from the variability of the 12 behaviours of the predator and the five behaviours of the prey. The CCA showed which behaviours contributed to the variance and consequently to the outcome of the interaction: feeding. I performed all the analyses in STATISTICA 8.0 (StatSoft, Inc. Tulsa, Oklahoma, USA, 2007). I used an alpha of 0.05 as the significance level. However, I did not correct my alpha values with the sequential Bonferroni correction (Rice 1989) because that method reduces the probability of finding general patterns of significance in a dataset with so many response and predictor variables. Additionally, even though my comparisons came from the same dataset, every test compared biologically and statistically different behaviours, in independent subjects. Also, there are important mathematical and practical objections to the Bonferroni correction that have raised concerns on its necessity (Moran 2003; Nakagawa 2004).

To test if potential genetic differences between the nine spiderling broods affected their behaviour I used generalized linear models (GLM), by using the scores of the first canonical variable of the CCA as response variable and the brood identity as random factor. Additionally, I tested if the prey defensive behaviour differed between broods with another pair of GLMs. However, due to logistic limitations, the number of individuals tested per brood varied. Nonetheless, there were no differences between three broods that attacked both prey types on how they attack each prey type (Brood $F_{2,41} = 0.06$, $p = 0.94$; brood*prey type interaction $F_{2,41} = 2.12$, $p = 0.13$); or in the defensive behaviour of the two prey types they attacked (Brood $F_{2,41} = 0.17$, $p = 0.86$, brood*prey type $F_{2,41} = 2.77$, $p = 0.08$). Five broods that only attacked flies did not differ on how they attacked them ($F_{7,37} = 1.70$, $p = 0.14$); and those flies did not show differences in their defensive behaviour between broods ($F_{7,37} = 1.99$, $p = 0.09$). Hence, this dataset showed no effect of brood.

Results

Predatory Behaviour The behaviour of the spiderlings while attacking each prey type differed quantitatively (Fig. 1, Appendix 1, Online Resource 1). The DFA cross–validation correctly classified 67 % of the attacks to ants and 87 % of the attack to flies based on the 12 predatory behaviour variables (Wilks' lambda = 0.58, $F_{12,62} = 3.67$, $p = 0.003$) (79 % of the total attacks were accurately classified). I found that spiderlings performed initial touches for longer on ants ($F_{1,62} = 17.26$, $p = 0.001$), wrapped the ants for longer time than the flies ($F_{1,62} = 10.71$, $p = 0.001$), and added threads to flies for longer than to ants ($F_{1,62} = 6.92$, $p = 0.01$) (Table 3, Fig.1). Other behaviours did not differ between attacks to ants or flies (Table 3). The percentage of spiderlings that pulled ants (79 %) or flies (64 %) did not differ (proportion Chi-square test: $X^2_1 = 2.03$, $p = 0.15$). Additionally, both prey commonly escaped at least once

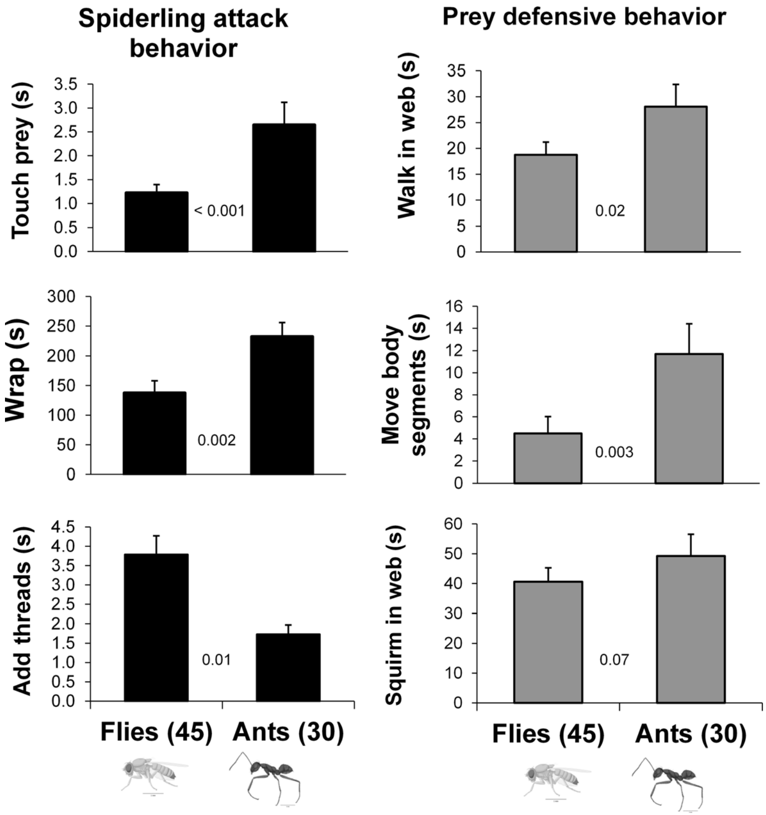

Fig. 1 Mean (+ standard error) of predatory behaviour by two groups of *Physocyclus globosus* (Araneae: Pholcidae) newly hatched spiderlings that attacked two prey types (left), and the defensive behaviours of the prey (right). Fruit flies were *Drosophila melanogaster* wild type and *Paratrechina longicornis* worker ants. These variables were the ones that significantly accounted for the classification of the predatory behaviour (left) and the defensive behaviour (right), respectively, in each discriminate function analysis (DFA) (see Results and Table 3 for more statistical details); squirm had marginal significance. Sample size is shown in parenthesis. Other comparisons of behaviours are shown in Appendix 1. Prey illustrations courtesy of JF Vargas

from the web in the same proportions (64 % of flies and 71 % of ants) (proportion Chi-square test: $X^2_1 = 0.16$, $p = 0.69$).

Defensive Behaviour The defensive behaviour of both prey types was different. The DFA cross-validation correctly classified 50 % of the ants and 91 % of the flies based on the duration of five defensive behaviours (Wilks' lambda = 0.78, $F_{5,69} = 3.86$, $p = 0.003$) (75 % of the total prey were accurately classified). Compared to flies, ants lasted longer walking ($F_{1,68} = 5.81$, $p = 0.02$), moving body segments ($F_{1,68} = 9.18$, $p = 0.003$), and showed a tendency of squirming in the web for a longer time, although this difference was not statistically significant ($F_{1,68} = 3.42$, $p = 0.06$) (Table 3, Fig. 1).

Qualitative observations also suggest that ants were a more difficult prey to attack. Five spiderlings terminated their attack on ants 3–4 min after they started wrapping it and moved away. Those spiderlings did not resume their attack; therefore they were not

Table 3 Contribution of the behavioural variables to the multivariate analyses of the interaction of newly hatched spiderlings of *Physocyclus globosus* (Araneae: Pholcidae) while attacking two types of prey (*Drosophila melanogaster* wild type and *Paratrechina longicornis* worker ants)

Behavioural variables	Discriminate Function Analyses			Canonical correspondence analysis	
	Wilks' lambda	*F*1,69	*P*	Canonical variables	
Spiderling predatory behaviour				1	2
Detect	0.60	1.55	0.22	−0.21	0.36
Detect - touch delay	0.58	0.01	0.90	−0.02	−0.01
Approach	0.61	2.42	0.12	0.02	*0.51*
Touch	0.75	17.26	*< 0.001*	−0.13	*0.40*
Wrap	0.69	10.71	*0.002*	*0.98*	0.11
Wrap - bite delay	0.61	3.16	0.08	0.38	*0.69*
Bites length	0.60	1.44	0.23	−0.14	−0.24
Short bites	0.59	0.55	0.46	*0.41*	−0.25
Add threads	0.65	6.92	*0.01*	0.02	−0.12
Touching prey	0.59	0.23	0.63	0.32	0.05
Cut threads	0.59	0.20	0.66	0.29	−0.09
Move prey	0.58	0.00	0.96	−0.08	0.09
Prey defensive behaviour					
Twist	0.78	0.20	0.65	*0.53*	0.57
Walk	0.85	5.81	*0.02*	0.00	*0.90*
Move body segments	0.89	9.18	*0.003*	*0.51*	−0.08
Squirm	0.82	3.42	*0.07*	0.35	*−0.29*
Move legs	0.78	0.00	0.99	*0.87*	0.04

Variables that contributed the most to both analyses are italicized

Left Contribution of each variable of spiderlings' or prey behaviour to each discriminate function analysis (one for spiderling predatory behaviour and one for prey defensive behaviour; see Results). *Right* Factor structure of each variable and its contribution to each of the two significant canonical variables (one CCA was performed to elucidate the predator–prey interaction based on their behaviour; see Methods)

included in the analyses. Two of those spiderlings had a fourth leg broken in the tarsus after the interaction. Also, ants performed two additional defensive behaviours (move mouth parts and move antennae, Table 2).

Predator–Prey Behavioural Correlation The predatory behaviour of the spiderlings strongly correlated with the defensive behaviour of the prey. The canonical correspondence analysis explained 100 % of the variance of the prey defensive behaviour and 49 % of the spiderling predatory behaviour by extracting five canonical variables, two of them with significant positive correlations (Table 4, Fig. 2). Regardless of type, the prey that twisted in the web, moved its legs and moved its body segments for longer time while being attacked were associated with the spiderlings wrapping them for longer time and giving them more bites (Fig. 2, Table 3). Those behaviours accounted for the variation in the first canonical variable (and *post hoc* simple linear correlations

Table 4 General results for the canonical correspondence analysis (CCA) of the interaction of the predatory behaviour by spiderlings of *Physocyclus globosus* (Araneae: Pholcidae) and the defensive behaviour of two types of prey (*Drosophila melanogaster* wild type and *Paratrechina longicornis* worker ants)

Canonical variables	1	2	3	4	5
Eigenvalues	0.85	0.51	0.31	0.20	0.03
Canonical R	0.92	0.71	0.55	0.45	0.17
Chi square	208.48	86.23	40.11	16.41	1.86
Df	60	44	30	18	8
P	*<0.001*	*<0.001*	0.10	0.56	0.98
Cummulative variance (%)					
Spiderling predatory behaviour	13	10	10	6	5
Prey defense behaviour	28	25	14	17	16

Significant correlations are italicized

showed the same pattern; Appendix 2). In the second significant canonical variable, the walking and squirming time of the prey was associated with the time the spiderling spent approaching, touching, and the length of the wrap–bite delay (Table 3). The ants showed more intense defense behaviour than flies, and predatory behaviour by the spiderlings lasted longer with ants than with flies (which was more clustered at the base of the correlation; Fig. 2). However, three flies were very active in their defense behaviour, therefore generating a more active predatory behaviour (Fig. 2). The

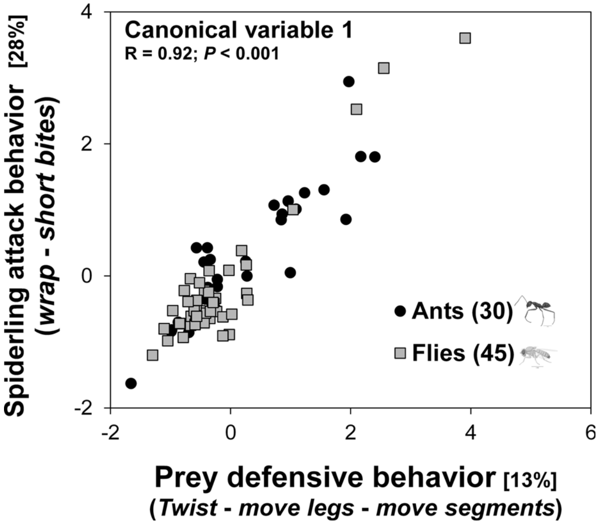

Fig. 2 Simple linear correlation between the scores for the predatory behaviour by spiderlings of *Physocyclus globosus* (Araneae: Pholcidae) and the defensive behaviour of two prey types (*Drosophila melanogaster* wild type fruit flies and *Paratrechina longicornis* worker ants), both from the first significantly correlated canonical variable of the canonical correspondence analysis. The percentage of total variance in model explained by each set of variables is shown in brackets in each axes. Also, the behaviours that accounted for the first canonical variables are shown in parenthesis (see Results and Table 3). Sample size is shown in parenthesis in the legend. Prey illustrations courtesy of JF Vargas

scattered pattern of ants in the correlation and the fact that less than half of the ants were accurately classified by the DFA (see above), indicates that this prey type greatly varied in their defensive behaviour, and consequently the behaviour that they generated in the predators.

Discussion

I found that naïve spiderlings varied their predatory behaviour, both quantitative and qualitatively, according to the difficulty of the prey. These findings are novel for our understanding of how predatory behaviour is performed in naïve spiderlings. Also, the defensive behaviours of the prey varied quantitatively between and within prey types (ants and flies). The behaviour of both the predator and the prey showed a strong predator–prey behavioural correlation, and it seemed to mediate the time required by the spiderling to subdue and begin feeding on the prey. This suggests that spiderlings adjusted to the difficulty of the prey based on the feedback received from their defensive behaviour. Consequently, this prey–predator behavioural feedback (Soley and Taylor 2013) mediated the progress of the attack. These results suggest that plasticity is important since early stage in predators.

Plasticity, however, does not exclude the possibility that the expression of the predatory behaviour can change throughout experiences, as shown in other spiders (Brown and Christenson 1983; Edwards and Jackson 1994; Morse 2000). In fact, in *P. globosus* first and second instar spiderlings some of the behaviours reported here changed (namely decreased in wrapping time and number of bites) throughout four consecutive experiences with either ants or flies (and even alternating the prey type sequence) (Escalante et al. *in prep.*). Therefore, plasticity in predatory behaviour can allow for learning in naïve predators.

The prey varied in their defensive behaviour both between and within prey types. My general finding was that ants were a more difficult prey to attack and subdue than flies. However, some flies behaved like ants and were attacked as such, and vice versa. This is supported by the fact that spiderlings took longer to wrap, bite, and handle difficult prey (which moved its appendages and body segments for longer time) and subsequently to successfully subdue and feed on it, regardless of whether the prey was an ant or a fly. Additionally, body size variation in the prey can affect this behavioural variation. Although this information is not available, since ants and flies came from a wild colony or lab culture, respectively, I expect size variation to be small. Consequently, the variation in the duration of the predatory behaviour of naïve and small spiderlings was promoted by the morphology of the prey, but more importantly here, the difficulty of their behaviour. These findings denote the potential importance of responding to the prey's behaviour with marked plasticity in the first experience of a predator's life. Ants sometimes caused damage to the spiderlings, they even broke their legs. This damage can have important implications for autotomy (Johnson and Jakob 1999), and even survival. Spiderlings seemed more cautious while attacking ants than flies, and spiderlings could handle flies better than ants. In summary, this evidence suggests that ants are more dangerous prey to spiderlings than fruit flies. Although two studies have found differences in the predatory behaviour of naïve spiderlings towards different prey (Edwards and Jackson 1994; Jakob 1991), my results are novel because they show that this variation seems to be driven by the variation in the defensive behaviour within and between prey types.

The situations tested in this project clearly reflect the potential extremes in the challenges that spiderlings in general may face. Although pholcid do eat ants (Kirchner and Opderbeck 1990; Eberhard 1992), the proportion of this prey in their diet or their environmental abundance is unknown. Based on their danger and extensive defensive behaviours, spiderling may feed on, and even attempt to attack, ants in lower proportions than for other easier prey. In general for spiderlings, detailed information on their diet composition is lacking as is information on the decisions made while facing two types of prey in their web. The initial prediction will be that dangerous prey would be less preferred than more abundant and easier prey (nonetheless, bold individuals may be more willing to attack a difficult prey; DiRienzo et al. 2013). My results can motivate future field and laboratory experimental research on the decision capabilities of naïve predators of any taxa.

My findings indicate that attacking difficult prey is costly for naïve spiderlings, as suggested by Forbes (1989) under the dangerous prey hypothesis. A successful attack on more active prey required more time, especially in the wrapping behaviour, which potentially results in a greater expenditure in protein spent in producing silk, and metabolizing ATP (Jakob 1991; Venner et al. 2000). Also, a longer and more active attack might expose the spiderling to predators and parasites. For pholcid spiderlings subduing a prey quickly is crucial given the high density of siblings in early instars, and infrequent prey capture in the field (Jakob 1991; Eberhard 1992; pers. obs.). In this project spiderlings recovered prey because both were in an enclosure, but in natural conditions if the prey escapes the web the spiderling will seldom recover it. If starved *P. globosus* spiderlings will perish 28–34 days after hatching (pers. obs.). In summary, behavioural plasticity could be adaptive in naïve predators that live in high density and encounter many prey with different morphological, chemical, and behavioural defenses. This plasticity will favor invertebrate predators in several taxa in which behavioural differences have been found in adults (Pruitt et al. 2012; Soley and Taylor 2013).

Further studies can focus on how the vibrational stimuli of the prey contacting the silk threads might contribute to the predator–prey behavioural interaction. The intensity of a given prey's vibrations in the web could indicate its difficulty and can be a cue for spiderlings while approaching it. Orb-weaver spiders have shown to be sensitive to longitudinal vibrations in the web, and have frequency-specific reactions (Klärner and Barth 1982). Changes in the vibration "echo" are then used as a cue to locate the prey (Klärner and Barth 1982). Landolfa and Barth (1996) found that different types of insect peak at different vibration frequencies in orb webs, which can also vary with the structural design and the size of a web, affecting how prey-specific vibrations are transmitted in the web and perceived by the spider (Landolfa and Barth 1996). Also, prey type varying in kinetic energy can affect the consequent expression of types of silk and web architecture in an orb-weaver (Blamires et al. 2010, 2011), suggesting that spiders can discriminate between fine-scale vibratory stimuli. Hence, if spiders can recognize the prey type by its vibratory features, they can also use the intensity of different sources of variation to evaluate the difficulty of a prey. Consequently, spiders can decide how to behave based on the vibratory information received, as suggested for a web spider when a spitting spider invades its webs (Escalante et al. 2015). Additionally, the initial touches to the prey observed in this project perhaps allowed spiderlings to identify the prey and its behaviour, as suggested for the cob web spider *Achaearanea tesselata* (Barrantes and Weng 2006).

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Appendix 1

Table 5 Summary values for predatory behaviour variables of newly hatched *Physocyclus globosus* (Araneae: Pholcidae) spiderling on two prey types (*Paratrechina longicornis* worker ants and *Drosophila melanogaster* wild fruit flies), and for two defensive behaviours of the prey

Behavioural variables	Fruit flies (*Drosophila melanogaster*)			Ants (*Paratrechina longicornis*)		
	X + SD (s)	Range (s)	*N*	*X* + SD (s)	Range (s)	*N*
Spiderling predatory behaviour						
Detect prey +	2.1 ± 2.9	0.54–16.5	45	2.5 ± 3.1	0.4–21.5	63
Approach prey +	2.8 ± 2.23	0.31–9.43	44	2.9 ± 2.8	0.3–14	58
Detect - touch delay	5.4 ± 7.3	1.27–39.1	44	3.2 ± 2.3	0.5–11.4	60
Wrap - first bite delay	140.8 ± 139.7	9.72–646.4	42	121.8 ± 98.5	16–470.9	60
Short bites (number) +	7.6 ± 3.9	1–18	42	8.9 ± 5.6	0–29	61
Biting time	81.9 ± 51.3	4.12–201	41	88.2 ± 60.8	17.4–283.2	28
Touching total time +	10.3 ± 11.4	0–60.3	43	12.0 ± 10.9	0–38.5	30
Cut threads total time +	24.5 ± 19.5	1.02–94.9	43	26.2 ± 28.2	4.5–128.6	30
Move prey total time +	12.9 ± 9.4	0–38.62	43	10.0 ± 22.1	0–121.6	30
Prey defensive behaviour						
Moving legs	86 ± 113.7	0–628.6	44	112.1 ± 84.7	13.3–291.1	30
Squirm once wrapped	40.6 ± 29.5	0–93.5	36	49.2 ± 38.6	0–154.3	28

Units are seconds, unless otherwise noted. Numbers represent mean (*X*) ± one standard deviation, minimum and maximum range, and *N* = sample size. Other comparisons are shown in Fig. 1

$^{+}$ Behavioural unit of the attack (definitions in Table 1)

Appendix 2

Table 6 Simple linear correlations for the *Physocyclus globosus* (Pholcidae) spiderling predatory behaviours (columns) and the defensive behaviours (rows) of two prey type (*Paratrechina longicornis* worker ants and *Drosophila melanogaster* wild fruit flies) (descriptions on Tables 1 and 2)

Prey/spiderling behaviours		Detect prey	Approach prey	Touch prey	Detect - touch prey delay	Wrapping	Wrap - first bite delay	Short bites	Biting time	Add threads	Touching prey	Cut threads	Move prey
Walk	r	0.34	0.45	0.42	0.02	0.20	0.51	0.01	0.04	−0.04	0.14	0.01	0.13
	N	74	74	74	74	73	69	70	68	70	72	72	72
	P	*0.002*	*<0.001*	*<0.001*	0.86	0.10	*<0.001*	0.97	0.78	0.72	0.26	0.90	0.26
Twist in the web	r	−0.13	0.01	−0.09	−0.10	0.43	0.81	−0.06	−0.24	−0.14	0.08	0.07	−0.11
	N	41	41	41	41	41	39	40	39	39	40	40	40
	P	0.26	0.95	0.57	0.54	*0.01*	*<0.001*	0.72	0.14	0.39	0.64	0.69	0.48
Move legs	r	−0.08	0.07	−0.05	−0.09	0.79	0.23	0.28	−0.15	−0.08	0.27	0.27	−0.09
	N	74	74	74	74	73	69	70	68	70	72	72	72
	P	0.53	0.53	0.69	0.45	*<0.001*	*0.05*	*0.02*	0.22	0.52	*0.03*	*0.02*	0.47
Move body segments	r	−0.07	0.14	−0.06	0.01	0.80	0.06	0.08	−0.11	−0.15	0.01	0.11	−0.12
	N	74	74	74	74	73	69	70	68	70	72	72	72
	P	0.56	0.44	0.75	0.96	*<0.001*	0.61	0.65	0.54	0.41	0.96	0.55	0.53
Squirm once wrapped	r	−0.14	−0.01	0.04	0.18	0.31	−0.07	0.28	0.09	0.01	0.13	−0.10	−0.17
	N	64	64	64	64	64	62	63	61	62	64	64	64
	P	0.23	0.94	0.77	0.16+	*0.02*	0.58	*0.03*	0.50+	0.98	0.31	0.44	0.17

Correlation coefficient (*r*), sample size (*N*), and significance at the 0.05 level (*P*) are shown. Significant correlations are italicized

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