



Predation strategy of the brown widow spider *Latrodectus geometricus* Koch, 1841 against prey with different defensive mechanisms

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Abstract

Predators, such as spiders, may modulate their predatory behavior according to the defensive mechanisms of their prey. This study analyzed the prey capture behavior of *Latrodectus geometricus* spiders, specifically through the parameter's acceptance of the prey, immobilization time, and bitten areas. A total of 80 adult female spiders were used, and they were fed cockroach nymphs and fasted for seven days. After this period, spiders were divided into four groups where prey with different defensive mechanisms were offered: cricket nymphs, ants, juvenile scorpions, and cockroach nymphs. Spiders were successful in catching prey in 86.25% of the observations, with crickets and scorpions being the prey having the highest and lowest acceptance rates, respectively. Our results showed that crickets and cockroaches were the prey most rapidly immobilized, and scorpions were the prey that required more time to be immobilized. These results indicate that *L. geometricus* individuals prefer prey with more fragile defenses. We also observed that spiders prefer to bite areas away from the defensive mechanisms of dangerous prey. Thus, our findings suggest that the spider *L. geometricus* possesses the ability to modulate its predatory behavior according to the defensive mechanism of its prey.

Keywords Theriididae · Predatory versatility · Behavioral plasticity

Introduction

Predator–prey interactions are one of the most important dynamics between interspecific ecological relationships, determining the success of predators in obtaining food resources (e.g., Curtsdotter et al. 2018; Portalier et al. 2018; Pomeranz et al. 2018). Throughout species evolutive processes, prey develop defensive and escape mechanisms, while predators develop morphological and physiological adaptations to present better predation strategies (DiRienzo

et al. 2013; García et al. 2016). Previous studies established that predators exhibit behavioral plasticity depending on prey behavior (Wignall and Taylor 2009; Nelson and Jackson 2011), and that such plasticity seems to be positively related to predation success rates (Hayes and Lockley 1990; Nelson and Jackson 2011; Escalante 2015; García et al. 2016). Through studies of predation mechanisms, improvements in the understanding of complex predator–prey relationships may be promoted, consequently aiding in unraveling food chain dynamics (Taucare-Ríos and Canals 2015).

Spiders are a well-studied group of venomous arthropods, with extensive data encompassing their predatory versatility (e.g., Jackson and Hallas 1986; Foelix et al. 1984; Hódar and Sánchez-Piñero 2002; Jarman and Jackson 1986). These arachnids are an excellent model for analyzing the trophic behavioral specialization of predators, which may be a basis for contextualizing the evolutionary and ecological aspects of morphological, metabolic, and venom adaptations (Pekár and Toft 2014). For example, the spider *Taieria erebus* (Koch 1873) uses kleptoparasitism, invading other spider webs for stealing their prey. In addition, *T. erebus* individuals perform vibratory behaviors to attract the resident spider and attack them, and they commonly prey on segestriid

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spiders (Jarman and Jackson 1986). Furthermore, the spider *Pholcus phalangioides* (Fuesslin, 1775) has a similar tactic to that observed on *T. erebus*, using adhesive shoes on the ends of the threads of their web-sheet to capture forager organisms (Japyassú and Macagnan 2004). Due to the wide range of predatory behaviors, it is important to clarify whether prey species may affect spider predatory dynamics. This facilitates the exploration of predator–prey interactions, thereby predicting how predators may modify their behavior with the various environments with different prey species availability.

The wide variability of prey in which *Latrodectus geometricus* Koch, 1841 feed (Guimarães et al. 2012) indicates that this spider species may present behavioral plasticity to successfully obtain food, which could manifest as different predatory strategies. However, behavioral studies with *L. geometricus* have largely focused on reproduction (Guimarães et al. 2012; Segoli et al. 2008), with the records of its predatory strategies limited to opportunistic observations of prey capture (e.g., Lira and Costa 2014; Noriega 2016; Rocha et al. 2017; Luna et al. 2020). This study aimed to assess the predatory behavior of *L. geometricus* spiders facing prey with different defensive mechanisms. More specifically, we analyzed the acceptance rate, the time to immobilize, and the bite areas on the prey. We tested the following hypotheses: (i) prey defensive abilities will affect spiders' acceptance rate and time interval to immobilize them, and (ii) the prey defensive mechanisms will affect the areas biting by the spiders. Considering that prey with a high defensive ability will have difficult predatory behavior, we expect that prey with less defensive abilities will be more predated and more quickly immobilized than those with more defensive abilities. We also expect that spiders will preferably bite areas far from the defensive structures of the prey.

Materials and methods

Specimen collection and maintenance

We collected 80 *L. geometricus* adult females (carapace length size 2.8 ± 0.2 mm) from the Recife municipality ($8^{\circ}04'S$, $34^{\circ}55'W$), Pernambuco state, Brazil. The specimens were collected during the dry season (September–2018). The individuals were obtained in urban zones in the corners of walls, posts, and furniture (e.g., tables, chairs, cabinets). Once collected, spiders were placed individually in transparent plastic terraria (14 cm \times 10 cm \times 8 cm) containing a small piece of wet cotton. Before the experiment, the animals were kept in the laboratory for 15 days at 24 ± 2 °C temperature, $70 \pm 5\%$ relative humidity, and 12 h:12 h light/dark photoperiod to allow the spider to build their web. To standardize the hunger level of spiders, 7 days prior to the

experiment, spiders were fed on *Nauphoeta cinerea* (Olivier, 1789) cockroach nymphs.

Prey selection

To assess the predatory behavior of *L. geometricus* spiders, we used prey of similar body sizes (4.8 mm–5.0 mm). The following prey items were used based on their defensive mechanisms: nymphs of crickets *Achaeta domestica* (Linnaeus, 1758) which have hind legs capable of kicking, ant workers *Atta* sp. which have powerful fangs that may be used to defend themselves, juvenile scorpions *Tityus stigmurus* (Thorell, 1876) which have venomous stings and pincer-like defensive appendages, and nymphs of cockroach *N. cinerea* which apparently have fewer morphological defense mechanisms than the other prey species. Crickets and ants were collected in areas where *L. geometricus* naturally lives, and scorpions and cockroaches were reared at a laboratory at the Universidade Federal de Pernambuco.

Experiment of predatory behavior

Spiders were divided into four groups ($N=20$) according to the prey offered. Considering that *L. geometricus* individuals are active at night (Muller 1993; Eberhard et al. 2010), behavioral trials were conducted between 17:00 and 19:00 in a darkroom under red light, which did not affect the animals' activities (Machan 1968). Prior to the trials, spiders were transported with their individual terraria to a bench and acclimated for 15 min. As *L. geometricus* individuals built their webs on the superior corner of their terrarium, after acclimation, the prey was gently placed inside the terrarium, positioned on the ground opposite to the spider. Both spiders and prey were used once a time, and all observations were performed by two researchers (LEAG and AFAL). We evaluated the following behaviors: prey acceptance was recorded if the spider moved toward the prey at a maximum period of 20 min after we introduced the prey in the terrarium; wrap times was estimated as the amount of wrap events and wrap duration; wrapping duration represented time spent wrapping the prey; latency to start feeding was the time interval encompassing the beginning of the experiment and the moment at which spiders started feeding the prey. Both wrap duration and latency to start feeding were recorded in seconds, although we presented 'latency to start feeding' in minutes due to the long duration of this behavior (Figs. 1 and 2). During prey immobilization, the number of bites was also quantified, while the prey was immobile. Bites were counted when the spiders touched the prey body with their chelicerae. Biting areas were estimated as the areas where different prey were bitten. To estimate biting areas, we divided the prey body into legs, cephalic, thoracic, and abdominal zones.

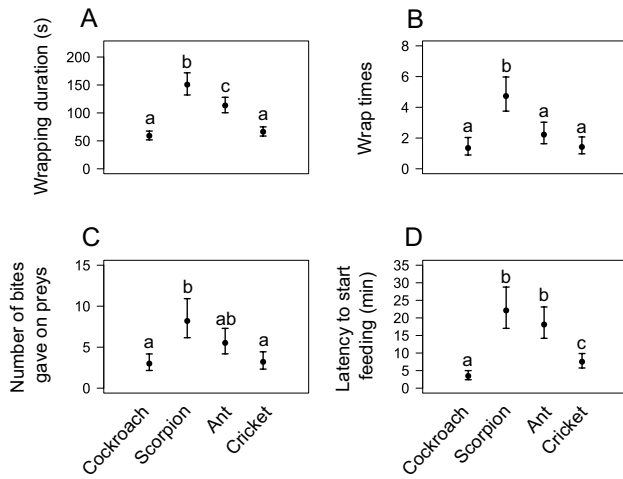


Fig. 1 Effect of different prey types (cockroach, scorpion, ant, and cricket) on spider wrap duration (A), wrap time (B), number of bites gave on prey (C), and latency to start feeding (D). Different letters indicate significant differences

Data analysis

Generalized linear models (GLM) were used to analyze the effects of prey type (i.e., ant, scorpion, cockroach, and cricket) on predatory behavior by spiders. The spider behaviors included prey acceptance, wrapping duration, wrap times, number of bites that spiders preyed on, and latency to start feeding. To analyze the wrap times, a GLM with a Poisson error distribution was used. Due to the overdispersion (residual deviance/residual *d.f.* > 2), the wrapping duration, number of bites provided on prey, and latency to start feeding were analyzed using GLM with a negative binomial distribution. To analyze prey acceptance, a GLM with binomial distribution and logit function was used. Prey type was used as a predictor variable, and behaviors related to predation were used as response variables. We also tested whether the interaction between prey type and the number of bites affected the spider latency to start feeding. The normality of residuals was evaluated with normal Q–Q plots, and the presence of outliers was evaluated, but none was found (Cook’s distance > 1). The analysis was performed

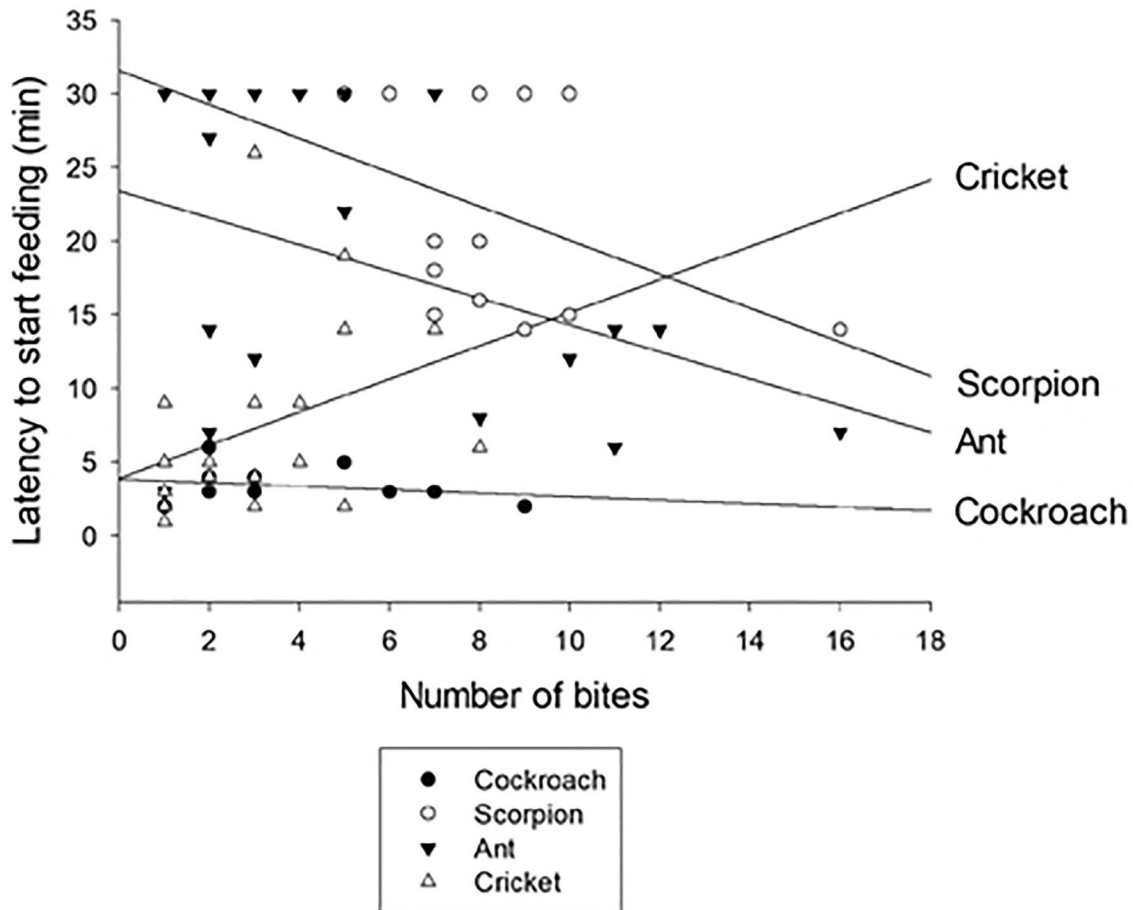


Fig. 2 Effect of the interaction between number of bites gave by spiders and prey type on the spider latency to start feeding

using MASS package in software R version 3.2.0 (R Core Team 2015; Ripley et al. 2018).

To compare differences among the body parts (i.e., head, legs, thorax, and abdomen) where spiders bit their different prey types, permutational multivariate analysis of variance (PERMANOVA) was used. The PERMANOVA model was run with 9999 permutations. Permutational multivariate analysis of dispersion (PERMDISP) was used to assess heterogeneity of 999 permutations (Anderson 2006). Tukey's post hoc test was performed to conduct pairwise comparisons among the prey types. The analysis was performed using vegan (for PERMANOVA), permute, and lattice packages in R software version 3.2.0 (R Core Development Team 2015; Oksanen et al. 2019; Simpson et al. 2019; Sarkar 2020).

Results

Spiders successfully captured the prey in 69 out of 80 of the experimental arenas. Despite, *L. geometricus* captured more crickets ($n = 19$), ants ($n = 18$) and cockroaches ($n = 17$) than scorpions ($n = 15$), prey type did not affect prey acceptance by spiders ($X^2_{3,76} = 60.346$; $P = 0.293$). Wrap duration was statistically higher when spiders were facing scorpions than the other prey types, while crickets and cockroaches were wrapped more rapidly ($X^2_{3,65} = 67.226$; $P < 0.001$, Fig. 1A). The wrap times depended on prey type, and scorpions were statistically wrapped more times than the other arthropod species ($X^2_{3,65} = 26.887$; $P < 0.001$, Fig. 1B). In addition,

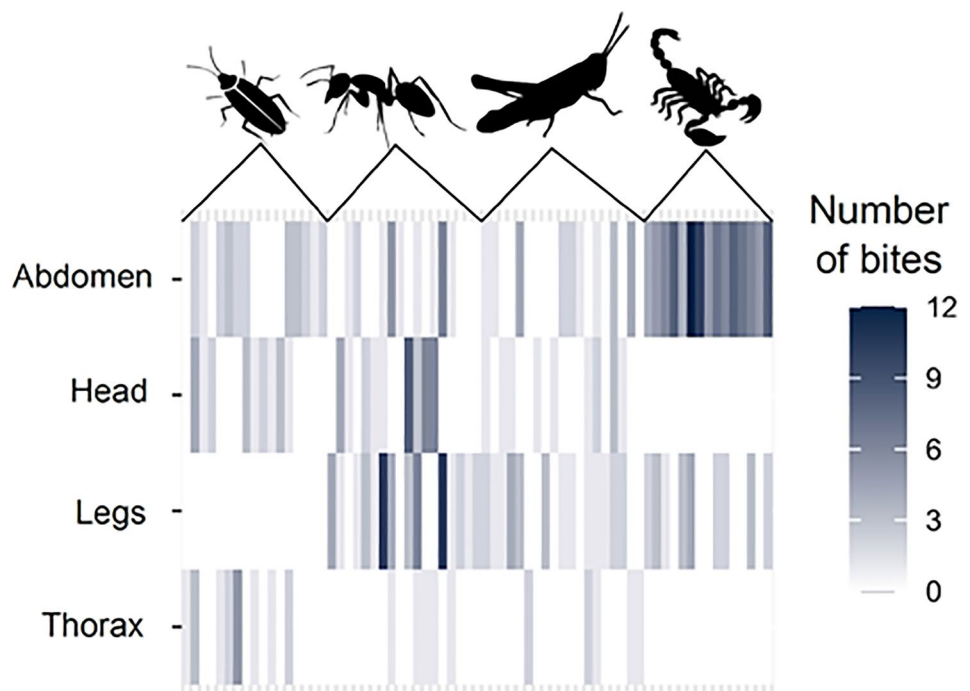
spiders bit scorpions more than cockroaches and crickets, and spiders bit ants significantly more than cockroaches ($X^2_{3,68} = 77.853$; $P < 0.001$, Fig. 1C). Spiders took longer to start feeding on scorpions and ants than on cockroaches and crickets ($X^2_{3,63} = 77.514$; $P < 0.001$, Fig. 1D). In addition, the interaction between prey type and number of bites significantly affected the spider latency to start feeding ($X^2_{3,59} = 64.916$; $P = 0.016$). Latency to start feeding was negatively related to the number of bites when spiders were facing scorpions and ants; however, latency to start feeding was positively related to the number of bites when spiders were facing crickets (Fig. 2).

Body parts of prey that were bit by spiders were significantly different among the different prey types (PERMANOVA, $F_3 = 9.127$; $P = 0.001$). Spiders did not bite the legs and cephalothorax of cockroaches and scorpions, respectively (Fig. 3). Ants and crickets were bit on almost the entire body, except on the thorax (Fig. 3). There was a statistical difference in the dispersion of variances for each prey type (PERMDISP, $F_3 = 18.005$; $P < 0.001$). Dispersion of the variances differed statistically between the data from scorpion and the other prey types (Fig. 4).

Discussion

This study described the prey acceptance behavior of the brown widow spider *L. geometricus* against prey with similar body size but different defensive mechanisms. Our results indicate that this spider species exhibits behavioral plasticity

Fig. 3 Heat map of spider bites distribution among different body parts in four prey types (cockroaches, ants, crickets, and scorpions)



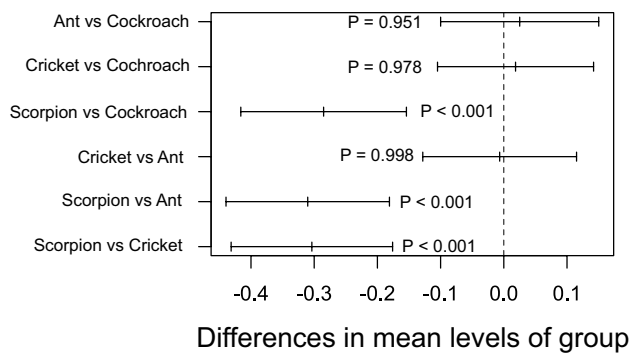


Fig. 4 Paired post-hoc Tukey test values of PERMDISP analysis to data that comprises body parts bitten by spiders in multivariate dispersion among the prey types tested in this experiment

in prey capture strategies, being able to react according to the prey's defensive mechanisms. This plasticity is in accordance with those described for other generalist predators, such as planarians, beetles, and scorpions (e.g., Prasniski and Leal-Zanchet 2009; Rewicz and Jaskula 2018; Simone et al. 2018). The behavioral predatory responses in *L. geometricus* can be modulated according to factors such as prey acceptance, wrap time, number of bites, and preference of bite location.

The differential time spent to subdue prey (e.g., wrap time and number of bites) by *L. geometricus* individuals varied according to the defensive mechanisms of their prey. According to the dangerous prey hypothesis, predators may need more time to handle defended prey individuals than undefended ones (Forbes 1989). We found that spiders invested more bites and longer time wrapping dangerous prey (scorpions and ants) compared to less dangerous prey (crickets and cockroaches). Both ants and scorpions may damage *L. geometricus*, as recorded in some observations ($n = 5$) where scorpions held one of the legs of the spider with its pedipalps. Thus, the longer wrap time observed for scorpions and ants is probably due to their dangerous defensive mechanisms, which results in a more careful predator behavior of *L. geometricus* spiders. Previous studies have shown that spiders can modulate their decisions during hunting process (e.g., Eisner and Dean 1976; Olive 1980; Jackson et al. 2002). For example, the cribellate-web spider *Titanoeca quadriguttata* (Hahn 1833) bit their dangerous prey and immediately retreat, whereas for non-dangerous prey, spiders bit and held it in the chelicerae (Tsai and Pekar 2019). Nonetheless, other factors, such as cuticle thickness, may influence the immobilization time (Segovia et al. 2015; Diluzio et al. 2017). Long immobilization periods have been reported in other spider species when facing potentially dangerous prey, such as spiders of the genus *Paratropis* Simon, 1889 when attacking carabid beetles (García et al. 2021), or

spiders of the genus *Scytodes* Latreille, 1804 when attacking large-bodied prey (Li et al. 1999). According to these data, we suggest that predator energetic expenditures are modulated according to prey defensive traits, and prey species with more defensive mechanisms demand higher energy expenditure than less defensive ones. However, it is important to consider that this study was conducted under laboratory conditions, which may affect prey–predator dynamics when compared to natural conditions. The exploratory behavior of animals allows them to gather information about their surroundings, and when a species is placed in a new environment, in this case a plastic terrarium, it is common for the individual to adopt a cautious, even fearful behavior (Wood-Gush and Vestergaard 1989).

Depending on the prey type, the spiders distributed bites in different body regions. Scorpions were the most attacked prey, and their metasoma was the most intensely bitten area. Based on previous studies (Wigger et al. 2002; Casewell et al. 2013), we believe that bites on scorpion metasoma allow spiders to paralyze the scorpion sting and avoid a dangerous pedipalp counterattack. Furthermore, ants were the second prey that received the second largest number of bites, with their head and legs being the most frequent targets. Similar to scorpion prey, spiders often bite the head of the ants as a strategy to limit ant counterattacks, accelerating the paralysis of such prey (Pekar 2004; Tsai and Pekar 2019; Pekar and Toft 2015). Therefore, our results suggest that *L. geometricus* spiders may disable the main defensive mechanisms of their prey.

Our findings indicate that *L. geometricus* can use alternative predatory strategies for different prey species. This spider species is a generalist species (Pekár and Toft 2015) that consumes a wide variety of prey types, as observed in other predator species (e.g., other spiders and scorpions, see García et al. 2016; Simone et al. 2018). Their generalist feeding strategy may explain the synanthropic habits of *L. geometricus* (Taucare-Ríos and Canals 2015), because its ability to consume a wide variety of prey probably helps to colonize new environments. This study points to *L. geometricus* as a species capable of modulating its behavior according to the intrinsic characteristics of its prey, especially its defensive mechanisms.

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Author contributions All authors contribute to the manuscript. AL and GM designed the study. LG and AL collected the spiders and conducted experiments. LG drafted manuscript. RS analysed data and performed the figures. All authors read and revised the submitted manuscript.

Conflict of interest Experiments using invertebrate animals conducted in Brazil do not require approval by the Ethics Committees, as established by the Brazilian Council for the Control of Animal Experimentation (CONCEA) (Law 11.794/08, § 3).

Declarations

Conflict of interest The authors report no declarations of interest.

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