According to the optimal foraging theory, natural selection favors organisms that adopt behaviors that maximize the difference between energy gained and energy expended in foraging (MacArthur & Pianka 1966, Krebs & Davies 1993, Levinton 2001). However, individual foraging behaviors may be constrained by predator avoidance (Lima 1998, Verdolven 2006). Thus, organisms may adjust their behaviors in response to a trade-off between maximizing energy intake and minimizing predation risk (Hassell & Southwood 1978, Shi 1980).

The two-dimensional structure of orb webs allows exploitation of a large variety of prey types (e.g., Richardson & Hans 2009) and sizes (Blackledge et al. 2011, Venner & Casas 2005). However, while two-dimensional webs are an efficient strategy to capture prey, they also increase the exposure of spiders to predators (Blackledge et al. 2003, Gonzaga & Vasconcellos-Neto 2005) and parasitoids (Gonzaga et al. 2010, Gonzaga & Sobczak 2011). To avoid such exposure, some spider species build shelters that help to protect and conceal the individual when it is on the web. These shelters are often composed of silk, leaves and debris (Manicom et al. 2008).

The endemic Amazonian forest spider *Hingstepeira folisecens* (Hingston, 1932) builds shelters of dry rolled leaves (open only at the bottom; Figs. 1-2) at the hub of its vertical orb web (Levi 1995). Their web is asymmetrical, with a larger extent of the capture area located below the entrance of the shelter. *Hingstepeira folisecens* display two different foraging behaviors: 1) individuals leave the shelter to attack intercepted prey; or 2) they capture the prey by pulling the threads, without leaving the shelter (hereafter “pulling behavior”, pers. obs.). During the pulling behavior, the web is temporarily deformed (and occasionally it may be damaged), returning to its original configuration after the prey is wrapped in silk. Since the entrance of the shelter faces the ground, the pulling behavior is possible only when the prey is intercepted below it. We believe that the shelter and the pulling behavior are strategies to avoid predators and parasitoids, since the spider does not become exposed during it. However, since the pulling behavior promotes deformations, and sometimes damages, to the orb structure, the spider may need to repair the web after a capture event. This means that...
when prey is intercepted far from the entrance of the shelter, the pulling behavior may result in energetic costs and exposure to predators during web repairs. In addition, if prey is intercepted at the upper web region, the spider will have to leave the shelter, turn around and move from the center upwards. Since this sequence of movements may demand more time outside the shelter, the spiders should be less prone to capture prey intercepted at the upper web region when compared to prey intercepted at the lower web region.

In this study, we aimed to understand the trade-offs involved in the choice to adopt the pulling or the attacking behavior to capture prey. We investigated whether the behavior adopted by *H. folisecens* during prey capture depends on the position and distance of the intercepted prey from the entrance of the shelter. Our hypothesis is that these spiders adopt behaviors that minimize costs (silk and time used to repair damaged webs), but also reduce the time individual's spend outside the shelter. The predictions of this hypothesis are: (1) *H. folisecens* captures more prey at the lower region of the web and (2) individuals will leave the shelter to attack prey that is intercepted far below the entrance of the shelter, but will employ the pulling behavior when prey is positioned near the entrance.

We conducted this research in August 2009, 2010 and 2012 at an area of the Amazon forest, located approximately 80 km north of Manaus, Brazil (2°24'S, 59°44'W). It belongs to the Area of Relevant Ecological Interest named Biological Dynamics of Forest Fragments Project. This site is characterized by a continuous "terra firme" tropical forest with 30-37 m high trees (more information in Lovejoy & Bieregaard 1990). We found *H. folisecens* webs attached to vegetation about 0.5 to 1.5 m high in both interior and edges of the forest. All spiders used in the experiments were adult or subadult females with body length (distance between cephalothorax and abdomen) of about 4.8 ± 1.05 mm (mean ± SD).

To evaluate if *H. folisecens* individuals are more efficient in capturing prey in the lower region of the web, we placed two termite workers (Isoptera: Termitidae) of similar size (we only used termites that were visually smaller than the spider in each trial) in each of 22 webs, to simulate intercepted prey. We placed one termite at the upper region of the web (5 cm above the shelter) and another at the lower region (5 cm below the entrance of the shelter) with one hour interval between placements, and randomly assigned the web region on which we placed the first termite. After provisioning each prey, we observed the spider's...
response for a maximum of four minutes. We adopted this time interval based on previous observations that, after four minutes, there is a high probability that the prey will drop to another region of the web. We categorized the spider’s response as: (1) positive – when the spider captured the prey (either after leaving the shelter or using the pulling behavior) or (2) negative – when the spider did not capture the prey, even if it had left the shelter. We considered that the spider captured the prey when the prey was wrapped. If the spider’s response was positive, we removed the prey before the spider began to carry it into the shelter. We did this to prevent the spider from satiating its hunger before the end of the experiment. We compared the frequencies of spiders’ responses to prey at different web regions using a chi-square test.

To evaluate if the behavior adopted to capture prey was dependent on the distance from the prey to the entrance of the shelter, we used 30 webs of *H. folisecens* (not used in the previous experiment) to perform two treatments that consisted of offering prey at the lower web region at two different distances from the entrance. We also used subadult and adult spiders with body length similar to the individuals in the previous experiment. In the “near” treatment we placed the prey at about 1.5 cm below the entrance of the shelter, and in the “far” treatment we placed the prey at about 1.5 cm above the outermost lower web spiral (we assigned only one treatment to each web). After placing the termite on the web, we continuously observed the spider’s behavior until it captured the prey. We classified the capture behavior as: (1) “pulling” – when the spider did not leave the shelter, but pulled the silk threads to carry the prey to the entrance of the shelter; and (2) “attack” – when the spider left the shelter and moved toward the prey without pulling the silk threads, and then wrapped the prey in silk. Often, the spider rapidly returned to the shelter after wrapping the prey and only later it returned to transport it to the shelter. The pulling behavior always seemed to happen at a slower pace than the attack behavior, although spiders were usually successful in their capture attempts. Although the mean distance between the entrance of the shelter and the most external spiral varied between webs (12 ± 3.5 cm, n = 22), it is important to note that we were interested in evaluating spider behavior in two extreme situations (one that, according to our hypothesis, would favor the pulling and the other that would favor the attack behavior). In this sense, because web size is often related to spider size (e.g., Heiling & Herberstein 1998), the placement of the termite at the same distance from the most external lower spiral standardized the situation that should favor the attack behavior according to the spider size. We used a chi-square test to compare the frequency of pulling and attack behaviors in relation to the different prey distances to the entrance.

Regardless of prey position at the lower or upper web region, spiders typically exhibited a behavior of plucking some web threads after prey were intercepted by the web. When the prey was positioned below the entrance of the shelter it was captured more often by the spiders (75% of the time) than when interception was at the upper region ($\chi^2 = 5.012$, df = 1, $p = 0.025$) (40% of the time).

The capture behavior of *H. folisecens* varied according to how distant the prey was with respect to the entrance of the shelter ($\chi^2 = 16.13$, df = 29, $p < 0.001$). When we placed the prey near the entrance, spiders adopted the pulling behavior in 13 out of 15 (86.7%) times. In contrast, they adopted this behavior only two times (13.3%) when we positioned the prey far from the entrance (Fig. 3). In 5 out of 15 occasions, in which we assigned the treatment “near”, spiders initially adopted a pulling behavior, then dropped the prey away from the entrance while they were still manipulating it. When this occurred, these spiders stopped pulling and changed to attack behavior. However, even if we consider that these five cases of attack occurred when the prey was far from the entrance of the shelter (20 samples in contrast to 10 samples in which the prey remained near the entrance), the frequency of “pulling” and “attack” behaviors remained dependent on prey distance from the entrance ($\chi^2 = 9.9$, df = 1, $p = 0.002$). Using this new assignment, 80% of the spiders adopted the pulling behavior when we placed a prey near the entrance, while 10% adopted this behavior when a prey was far from the entrance (Fig. 4).

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Our findings show that *H. folisecens* is more likely to capture prey that falls at the lower region of the web and will preferentially adopt the pulling behavior when prey are near the entrance of the shelter. This indicates that when a prey is intercepted near the entrance, the pulling behavior might be effective in reducing the time outside the shelter and minimizing damages to the web structure. Although we have no data on predation of this spider by natural enemies, observation of interactions with araneophageic spiders were recorded two times in another study and, in both situations, the spider was outside the shelter (T. Kloss, pers. comm.).

It is not clear why *H. folisecens* individuals less likely to capture prey intercepted at the upper portion of the web. It may take the spider longer to detect and to reach the prey when it is up. However, we have no data supporting this hypothesis. In species of *Cyclosa*, Menge, 1866, the downward orientation of individuals on the web facilitates a faster run to capture prey intercepted near the entrance, the pulling behavior might be similar to those described for *Cyclosa*. *Hingstepeira folisecens* adopt different behaviors to capture prey according to the distance of the prey from the entrance of the shelter. Since spiders adopted the pulling behavior more often when the prey was near the shelter, but attacked it when the prey was distant from the entrance (close to the web edge), there could be different costs associated with each foraging behavior. In fact, when the prey is intercepted near the entrance of the shelter, the spider may cause less damage to the web by remaining inside the shelter and adopting the pulling behavior. However, when the prey is far from the entrance, the deformation caused by performing the pulling behavior may be stronger and affect future capture efficiency. In addition, since predation pressure on spiders seems to be more important in tropical than in other regions of the world (Rypstra 1984, Schenske et al. 2009), and since predation seems to occur when the spider is outside the shelter, the pulling behavior may be used whenever it does not compromise web structure.

Although it may seem that individuals that maximize their foraging efficiency will be favored by natural selection (Kiers & Davies 1993), it is clear that some pressures may favor sub-optimal behaviors in terms of energy intake (Dukas 2002, Shi et al. 2004, Lind & Creswell 2005, Verdolin 2006). Therefore, individuals that are capable of altering their feeding behavior in order to maximize their energy intake under different circumstances should be favored. The foraging behavior of *H. folisecens* seems to be a clear example of this. Since these spiders are less likely to capture prey above the entrance of the shelter, they may miss some foraging opportunities. On the other hand, the alternation between pulling and attack behaviors may be an adaptation to capture prey and at the same time reduces exposure outside the shelter.

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