ZOOLOGIA 33(3): e20150147
ISSN 1984-4689 (online)

SHORT COMMUNICATION

Optimal foraging or predator avoidance: why does the Amazon spider *Hingstepeira folisecens* (Araneae: Araneidae) adopt alternative foraging behaviors?

Kátia F. Rito[1], Fabio T.T. Hanashiro[2], Paulo E.C. Peixoto[3] & Marcelo O. Gonzaga[4]

[1]Departamento de Botânica, Universidade Federal de Pernambuco. Avenida Professor Moraes Rego, Cidade Universitária, 50670-901 Recife, PE, Brazil.
[2]Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Charles Deberiotstraat 32, B-3000, Leuven, Belgium. Corresponding author. E-mail: fabiotoshiro@gmail.com
[3]Laboratório de Entomologia, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana. Avenida Transnordestina, Novo Horizonte, 44036-900 Feira de Santana, BA, Brazil.
[4]Instituto de Biologia, Universidade Federal de Uberlândia. Avenida Pará 1720, Campus Umuarama, 38405-320 Uberlândia, MG, Brazil.

ABSTRACT. Strategies that increase foraging efficiency may also increase predation risk. We investigated how individuals of *Hingstepeira folisecens* Hingston, 1932, which build shelters at the orb hub, modulate their foraging behaviors in response to the trade-off between capturing prey and becoming exposed by leaving their shelters. We evaluated whether the position of the prey on the web alters the frequency at which spiders leave their shelters. *Hingstepeira folisecens* spiders were more likely to capture prey positioned below than above the entrance of the shelter. Moreover, when the prey was near the entrance of the shelter, the spider pulled the threads with the entangled prey without leaving the shelter. Conversely, when the prey was distant from the entrance of the shelter, an "attack" behavior (leaving the shelter) was favored. We argue that the "pulling behavior" may be an adaptation to reduce exposure to predators.

KEY WORDS. Orb-web spiders, prey selection, silk investment.

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, Verdolin 2006). Thus, organisms may adjust their behaviors in response to a trade-off between maximizing energy intake and minimizing predation risk (Hassell & Southwood 1978, Sih 1980).

The two-dimensional structure of orb webs allows exploitation of a large variety of prey types (e.g., Richardson & Hanks 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

Figures 1-2. *Hingstepeira folisecens* orb web in an area of the Amazon forest, Brazil: (1) vertical orb web with the rolled dry leaf used as a shelter by the spider attached to the hub; (2) shelter's detail showing the entrance oriented just downwards and the spider leaving it. Scale bars: 1 = 10 mm, 2 = 5 mm.

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. folicesens* 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 web region than at the upper region 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.

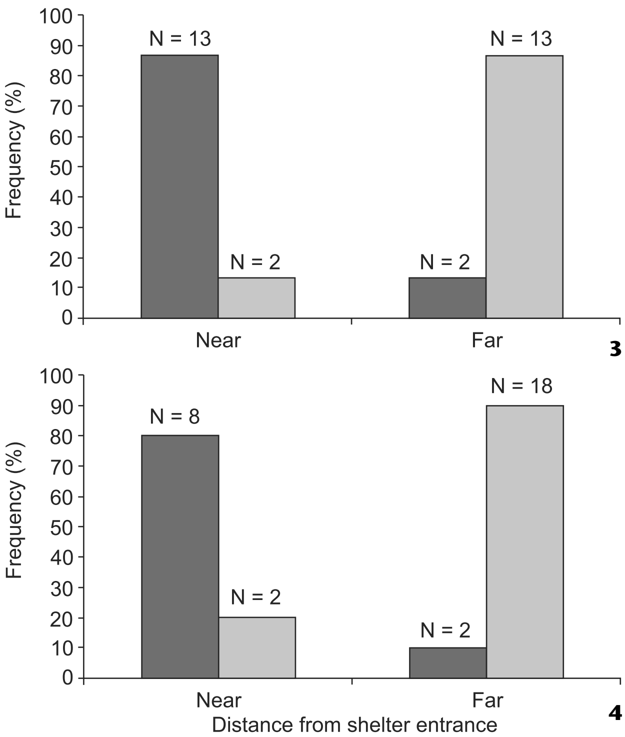
We conducted this research in August 2009, 2010 and 2012 at an area of the Amazon forest, located approximately 80 km north of Manaus, Brazil (2°24'S, 59°44'W). It belongs to the Area of Relevant Ecological Interest named Biological Dynamics of Forest Fragments Project. This site is characterized by a continuous "terra firme" tropical forest with 30-37 m high trees (more information in Lovejoy & Bierregaard 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).



Figures 3-4. Frequency of attack *versus* pulling behaviors in *Hingstepeira folisecens* according to prey distance from the entrance of the shelter: (3) considering the first behavioral response; (4) considering the behavioral response adopted by the spiders for some prey intercepted far from the shelter entrance after the initial spider manipulation. The black bars represent the pulling behavior and the grey bars represent the attack behavior.

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 araneophagic 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 were 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 at the lower web region (Nakata & Zschokke 2010). This is not only due to gravity, but also to the fact that, in order to run to the upper portion of the web, the spider has to first turn around, which may result in delays and increased chances of making mistakes while trying to capture the prey (Zschokke & Nakata 2010). Since the entrance of the shelter of *H. folisecens* is also oriented downwards, the constraints faced by this species may 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, Schemske 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 (Krebs & Davies 1993), it is clear that some pressures may favor sub-optimal behaviors in terms of energy intake (Dukas 2002, Sih et al. 2004, Lind & Cresswell 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.

ACKNOWLEDGMENTS

This research was conducted during the "Ecologia da Floresta Amazônica (EFA)" field course, supported by the Biological Dynamics of Forest Fragments Project (BDFFP) – Instituto Nacional de Pesquisas da Amazônia (INPA), the Smithsonian Institution, INPA Graduate Program in Ecology and CAPES – PAEP. We are grateful to Thiago Geckel Kloss for helping with the fieldwork and Marcos C. Vieira for helpful suggestions to the text. We also thank Fundação de Amparo à Pesquisa do Estado de Minas Gerais (Proc. APQ-02104-14, CRA-30058/12), Fundação de Amparo à Pesquisa do Estado de São Paulo (2008/02467-5) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (Proc. 306157/2014-4, 403733/2012-0, 445832/2014-2, 305561/2014-6, 245968/2012-1). This is the study #686 of the PDBFF – INPA/STRI.

LITERATURE CITED

Blackledge TA, Coddington JA, Gillespie RG (2003) Are three-dimensional spider webs defensive adaptations? **Ecology Letters 6**: 13-18. doi: 10.1046/j.1461-0248.2003.00384.x

Blackledge TA, Kuntner M, Agnarsson I (2011) The form and function of spider orb webs: evolution from silk to ecosystems. **Advances in Insect Physiology 41**: 175. doi: 10.1016/B978-0-12-415919-8.00004-5

Dukas R (2002) Behavioural and ecological consequences of limited attention. **Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357**: 1539-1547. doi: 10.1098/rstb.2002.1063

Gonzaga MO, Vasconcellos-Neto J (2005) Orb-web spiders (Araneae: Araneomorphae; Orbiculariae) captured by hunting-wasps (Hymenoptera: Sphecidae) in an area of Atlantic Forest in southeastern Brazil. **Journal of Natural History 39**: 2913-2933. doi: 10.1080/00222930500183520

Gonzaga MO, Sobczak JF (2011) Behavioral manipulation of the orb-weaver spider *Argiope argentata* (Araneae: Araneidae) by *Acrotaphus chedelae* (Hymenoptera: Ichneumonidae). **Entomological Science 14**: 220-223. doi: 10.1111/j.1479-8298.2010.00436.x

Gonzaga MO, Sobczak JF, Penteado-Dias AM, Eberhard WG (2010) Modification of *Nephila clavipes* (Araneae Nephilidae) webs induced by the parasitoids *Hymenoepimecis bicolor* and *H. robertsae* (Hymenoptera Ichneumonidae). **Ethology Ecology & Evolution 22**: 151-165. doi: 10.1080/03949371003707836

Hassell MP, Southwood T (1978) Foraging strategies of insects. **Annual Review of Ecology and Systematics 9**: 75-98. doi: 10.1146/annurev.es.09.110178.000451

Heiling AM, Herberstein ME (1998) The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. **Journal of Arachnology 26**: 91-96.

Krebs J, Davies N (1993) **An introduction to behavioural ecology.** Oxford, Blackwell Scientific.
Levi H (1995) Orb-weaving spiders *Actinosoma*, *Spilasma*, *Micrepeira*, *Pronous*, and four new genera (Araneae: Araneidae). **Bulletin of the Museum of Comparative Zoology 154**: 153-213.
Levinton JS (2001) **Marine biology: function, biodiversity, ecology.** New York, Oxford University Press.
Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. **Bioscience 48**: 25-34. doi: 10.2307/1313225
Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. **Behavioral Ecology 16**: 945-956. doi: 10.1093/beheco/ari075
Lovejoy TE, Bierregaard R (1990) Central Amazonian forests and the minimum critical size of ecosystems project, p. 60-71. In: Gentry AH (Org.). **Four neotropical rainforests.** New Haven, Yale University Press.
MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. **American Naturalist 100**: 603-609.
Manicom C, Schwarzkopf L, Alford RA, Schoener TW (2008) Self-made shelters protect spiders from predation. **Proceedings of the National Academy of Sciences 105**: 14903-14907. doi: 10.1073/pnas.0807107105
Nakata K, Zschokke S (2010) Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. **Proceedings of the Royal Society of London B: Biological Sciences 277**: 3019-3025. doi: 10.1098/rspb.2010.0729
Richardson ML, Hanks LM (2009) Partitioning of niches among four species of orb-weaving spiders in a grassland habitat. **Environmental Entomology 38**: 651-656. doi: 10.1603/022.038.0316
Rypstra AL (1984) A Relative Measure of Predation on Web-Spiders in Temperate and Tropical Forests. **Oikos 43**: 129-132. doi: 10.2307/3544758
Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? **Annual Review of Ecology, Evolution and Systematics 40**: 245-269. doi: 10.1146/annurev.ecolsys.39.110707.173430
Sih A (1980) Optimal behavior: can foragers balance two conflicting demands? **Science 210**: 1041-1043. doi: 10.1126/science.210.4473.1041
Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview. **The Quarterly Review of Biology 79**: 241-277. doi: 10.1086/422893
Venner S, Casas J (2005) Spider webs designed for rare but life-saving catches. **Proceedings of the Royal Society B: Biological Sciences 272**: 1587-1592. doi: 10.1098/rspb.2005.3114
Verdolin J (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. **Behavioral Ecology and Sociobiology 60**: 457-464. doi: 10.1007/s00265-006-0172-6
Zschokke S, Nakata K (2010) Spider orientation and hub position in orb webs. **Naturwissenschaften 97**: 43-52. doi: 10.1007/s00114-009-0609-7

Submitted: 22 September 2015
Received in revised form: 2 January 2016
Accepted: 16 March 2016
Editorial responsibility: Mauricio O. Moura

Author Contributions. KFR, FTTH, PECP and MOG formulated the hypotheses and predictions of the paper; KFR, FTTH, PECP and MOG designed the experiments; KFR and FTTH conducted the experiments and analysed the data; KFR, FTTH, PECP and MOG wrote the paper.
Competing Interests. The authors have declared that no competing interests exist.