

Does nutritional status constrain adoption of more costly and less risky foraging behaviour in an Amazonian shelter-building spider?

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ABSTRACT

Individual nutritional status may increase marginal foraging costs and potentially drive animal foraging strategies. Here, we investigated how it might affect foraging strategies of the shelter-building spider *Hingstepeira folisecens* (Hingston 1932) (Araneidae). This spider can catch prey using two strategies with different relative costs: 'pulling' (higher energy expenditure) and 'pursuing' (lower energy expenditure). We conducted experiments by offering prey at a fixed distance from the shelter entrance to investigate if spiders with lower nutritional status would exhibit riskier but less costly foraging behaviours more frequently than spiders with better status. The nutritional status did not affect the foraging behaviours adopted by *H. folisecens*. Additionally, the frequency of both foraging behaviours was similar. Therefore, our results did not provide any evidence that individual nutritional status is a factor driving the selection of foraging behaviours in *H. folisecens*. We suggest that the malnourished spiders should adopt additional strategies to compensate for the costs of pulling behaviour, especially when prey is far from the shelter. Furthermore, it is possible that other factors, like relative prey size in relation to web size, can help us to understand the threshold that determines when such individuals must adopt one of two possible behaviours.

ARTICLE HISTORY

Received 10 November 2015
Accepted 28 June 2016

KEYWORDS

Animal behaviour; optimal foraging theory; predation risk; spider nutrition

Introduction

The optimal foraging theory (OFT) predicts that natural selection should favour behaviours that maximize the relationship between energetic costs and benefits of prey capture by predators (MacArthur and Pianka 1966; Pyke 1984; Brechbühl et al. 2011). Therefore, predatory species must balance the energetic costs of prey capture with the nutritional pay-offs in the prey. Traditionally, OFT studies have focused mainly on the energetic cost to perform any foraging behaviour and the benefits resulting from catching prey when using it (MacArthur and Pianka 1966; Pyke 1984; Perry and Pianka 1997). However, such an approach is very simplistic because it ignores the influence of

extrinsic factors in foraging activity that can deeply affect individual foraging strategies, such as predation risk and nutritional status (Scharf et al. 2011). Therefore, empirical studies may offer important contributions in the evaluation of other factors associated with foraging strategies.

Predation risk is one example of a relevant, marginal foraging cost that needs to be considered in the OFT traditional approach (Scharf et al. 2011; Houston and McNamara 2014). Animals exhibit a large set of foraging strategies that vary widely in their intrinsic predation risk (see Lima and Dill 1990; Scharf et al. 2011; references therein), and neglecting such risks as a potential driver of foraging behaviour may deeply constrain our comprehension about the forces driving plasticity and evolution of animal foraging strategies. This link between predation risk and adoption of distinct foraging behaviour seems to be especially relevant to animals that build nests or shelters (e.g. Kinlaw 1999; Danks 2002). For these animals, foraging strategies that require a long time outside their nests or shelter would be a high-risk strategy because they increase their exposure to predators (Kotler 1984; Lima et al. 1985; Dill and Fraser 1997; Manicom et al. 2008). In these cases, it is expected that behaviours that increase animal exposure during foraging activities have high marginal costs and little effect or marginal benefit for individuals (McNamara et al. 2005; Scharf et al. 2011). Therefore, in habitats in which predation risk is low or highly variable in time and space, marginal costs related to predation risk decrease. Consequently, foraging behaviour that increases animal exposure might be positively selected as it can improve individual net energy intake (Lima and Dill 1990). Otherwise, under high predation risk, marginal costs of predation risk should constrain the adoption of such riskier behaviours even if it leads to a reduction in animal energy intake (Scharf et al. 2011).

Confronted with predation risk, animals that build shelters can reduce or change their foraging time (Strobbe et al. 2011), attract prey in shelters or nests (Tietjen et al. 1987), or even reduce the frequency of prey attack (Kotler et al. 1994). Although safer, each one of these predator-avoidance tactics has its own intrinsic energetic costs. In some cases, safer behaviours can be more energetically costly, constraining their use by individuals with different energy content (e.g. Gillette et al. 2000). Therefore, individual nutritional status would be a second force driving the foraging strategies of animals under the same predation pressure. When hungry, the risk of starvation becomes greater than the marginal risk of predation (Brown 1988; Uetz 1992; references therein). It may increase animal foraging investment regardless of the risk. Therefore, in the case of animals in which safer foraging behaviours are also the more expensive ones, it is possible that malnourished individuals living in shelters may adopt more frequently less costly but riskier foraging behaviours than better nourished individuals, despite exposure risk (Scharf et al. 2011; Houston and McNamara 2014).

Hingstepeira folisecens (Hingston 1932) (Araneae: Araneidae) is a sit-and-wait meso-predator spider that exhibits a complex set of foraging behaviours that differ in level of exposure as well as energetic costs. These spiders use a curled leaf as a retreat, attached to the upper half of a vertically oriented orb web (Levi 1995, Figure 1). During foraging, *H. folisecens* exhibits two possible behaviours of prey retrieval. When a prey falls on the web, spiders may pull the web below the shelter, bringing the prey near the shelter entrance, wrapping up the prey with silk (described as pulling behaviour hereafter). Additionally, spiders can also leave the shelter to approach

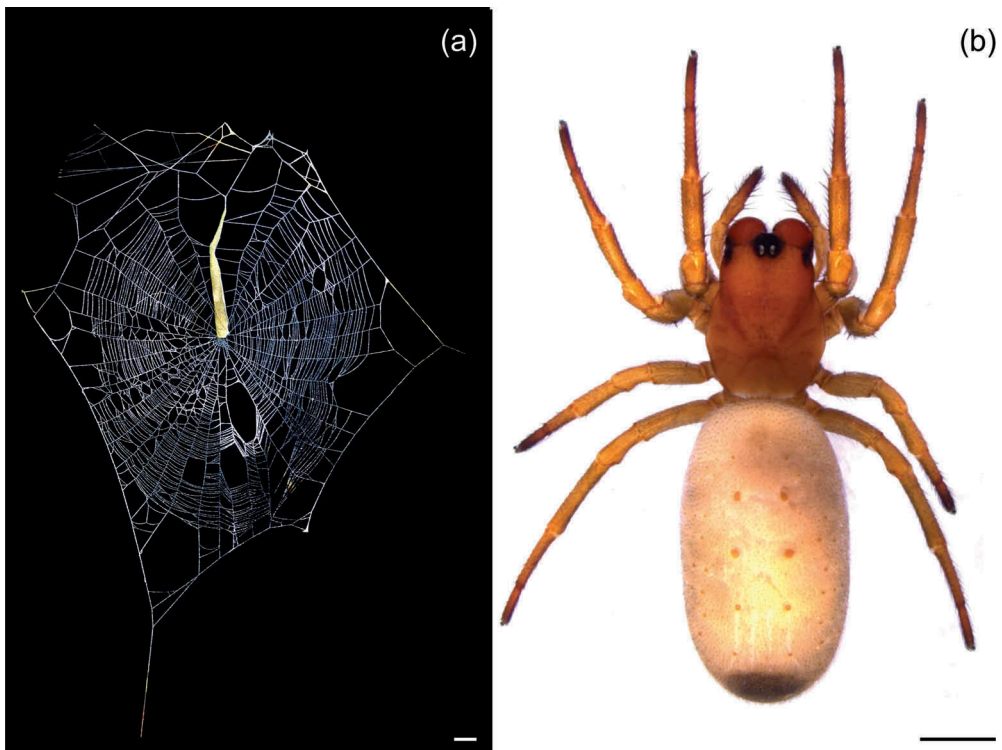


Figure 1. *Hingstepeira folisecens* (Hingston 1932) (Araneae: Araneidae) of Central Amazonia, Brazil. (a) Orb web of *H. folisecens* with the shelter formed by dry curled leaf (scale: 1 cm). (b) A sub-adult female of *H. folisecens* (scale: 1 mm).

the prey on the web, wrap it up with silk, moving or not the prey to the shelter (described as pursuing behaviour hereafter) (Rito et al. 2016). Pulling behaviour can be a more effective predator-avoiding behaviour because spiders do not leave the shelter during prey capture (Rito et al. 2016). However, it would be more costly because, in doing so, spiders destroy most of the web, which needs to be rebuilt after each foraging event (e.g. Peakall and Witt 1976; Tanaka 1989; Wilder 2011) and, as a consequence, they reduce the number of prey capture events throughout the day. Furthermore, spiders exhibiting such behaviour also face a higher probability of prey coming loose from the web. On the other hand, pursuing behaviour is less energetically costly but can be riskier because spiders need to spend more time outside the shelter. Although riskier, pursuing behaviour would be more effective in prey capture because spiders directly attack the prey after it falls on the web. Additionally, this behaviour allows for more capture events per web built because it usually does not harm the web structure (Rito et al. 2016).

Here, we propose that nutritional status should constrain adoption of more costly but less risky foraging behaviour in a shelter-building spider, *H. folisecens*. We hypothesize that the spiders with lower nutritional status would exhibit more frequently riskier but less costly foraging behaviours than spiders with better status. As the costs of pulling behaviour are higher the farther the prey is from the shelter entrance, we offered prey at

a fixed distance from the shelter in the lower web region and correlated the frequency of each catching-prey behaviour and nutritional status of individuals in each web.

Material and methods

General information

We conducted this study in the Km 41 reserve managed by the Biological Dynamics of Forest Fragments Project (a collaborative initiative between INPA and SRTI), located c. 80 km from the north of Manaus, Brazil, central Amazonia (02°24' S, 59°43' W). Rainfall ranges from 1900 to 3500 mm annually and the vegetation of the area is classified as upland tropical rainforest (for more specific information about the area, see Laurance et al. 2002, 2010).

Our model species was the spider *H. folisecens* (Hingston 1932) (Araneidae) (Figure 1). It is an orb-weaving spider endemic to Amazonia that uses a dry curled leaf attached to an upper web radius as shelter (Levi 1995), a common strategy against predation used by some spider species (Manicom et al. 2008). Spiders build the larger portion of the web below the shelter, with the entrance turned down (Figure 1).

In general, orb-weaving spiders are predated by predatory and parasitoid wasps, birds, damselflies and other spiders (e.g. Blackledge 1998; Gauld and Dubois 2006; Manicom et al. 2008). However, there is no published information about the predators of *H. folisecens*. Despite this, during the field work, we observed two predation events by Salticidae and Tetragnathidae spiders. These attacks occurred when *H. folisecens* individuals left the shelter to approach the prey on the web. Both attacks lasted less than one second. This observation suggests that a few seconds outside the shelter using pursuing behaviour is enough to enhance predation risk for spiders. Furthermore, we observed higher frequency of prey capture events during the daytime, suggesting that *H. folisecens* is a mainly diurnal predator.

Data collection

We selected the first 22 webs of *H. folisecens* found in the access trail to the camp, the camp surroundings and the main dirt road crossing the ARIE of Km 41 in July 2013. In each web, we offered a termite soldier (Isoptera: Termitidae) as a prey model certifying that termites were never bigger than spider body size. We placed the prey in the last 10% of the linear distance between shelter entrance and the web base. We adopted this distance to induce prey capture events for *H. folisecens* with higher energetic costs in the use of pulling behaviour (due to greater damage inflicted to the web during prey capture) and higher predation risk during pursuing behaviour (due to a greater time required to capture a prey outside the shelter).

After positioning the prey, we observed the web for 10 min or until the spider exhibited one of two possible behaviours. We discarded webs in which prey was not caught by the spiders after 10 min. We considered that the spider pulled the prey (pulling behaviour) when it pulled the web with the prey to the shelter entrance and wrapped the prey in silk threads. On the other hand, we considered that the spider

approached the prey (pursuing behaviour) when we observed the spider coming out of the shelter to catch prey in the place where it fell.

After the experiment, we collected 19 of 22 spiders used in each trial. Two spiders were not located inside the shelter and another was captured by a Salticidae spider. Therefore, we discarded these webs from our database. Only one from the 19 collected spiders was male, and all of them were in subadult stage. After collection, we measured the linear dimensions of the spiders (carapace length and width; abdomen length, height and width) using the Image J program (National Institutes of Health, Bethesda, MD). From these measurements, we estimated the carapace area using an ellipse area formula and the abdomen volume using an ellipsoid volume formula. Finally, we calculated the body condition index (BCI) as the standardized residuals from a regression of abdomen volume on carapace area (adapted from Jakob et al. 1996). We replaced body mass in the traditional BCI (Jakob et al. 1996) with abdomen volume and used it as a proxy of nutritional status. To evaluate if spiders exhibiting pulling behaviour would have higher BCI than spiders adopting pursuing behaviour, we used a logistic regression using the adoption of pulling behaviour and BCI as response and explanatory variables, respectively. We used R software version 3.2.1 (R Development Core Team 2015) for data analysis and graphics.

Results

The average distance between the shelter entrance and the web base was 12.45 ± 0.62 cm (mean \pm SE) and the mean time of spider response after prey offer was 3.78 ± 0.85 min. In 47.37% of capture events, spiders used pursuing to catch prey, whereas pulling was used in 52.63% of events. However, spiders' nutritional status did not determine the foraging strategy performed by *H. folisecens* ($\chi^2 = 1.20$, $df = 1$, $p = 0.27$; Figure 2). Average carapace area, average abdomen volume and mean BCI were 1.73 ± 0.15 mm², 9.02 ± 1.38 mm³ and 1.51 ± 0.23 , respectively.

Discussion

In this study, we empirically evaluated the effect of individual nutritional status on the foraging strategies of *H. folisecens*. Neither pulling nor pursuing behaviour was preferentially adopted by the spiders. In addition, such foraging strategies were not related to individuals' BCI. Therefore, our results did not provide any evidence to support our hypothesis that nutritional status of *H. folisecens* would constrain the adoption of more costly foraging behaviour.

The fact that spiders with different nutritional conditions are able to perform the same set of foraging behaviours does not imply that they are not performing complementary strategies to compensate for the costs of pulling behaviour. Web repair behaviour of *H. folisecens* has two main associated costs: (i) the energy spent in silk production and in movements during web repairing and (ii) the marginal risk of predation while the spider is exposed outside the shelter. Regarding the former cost, after catching prey using pulling behaviour, spiders will produce new silk threads in a better energetic condition than their condition before prey consumption. Furthermore, after damage to the web, they can ingest the silk and obtain a large part of the proteins required to build new orbs (Wilder 2011 and

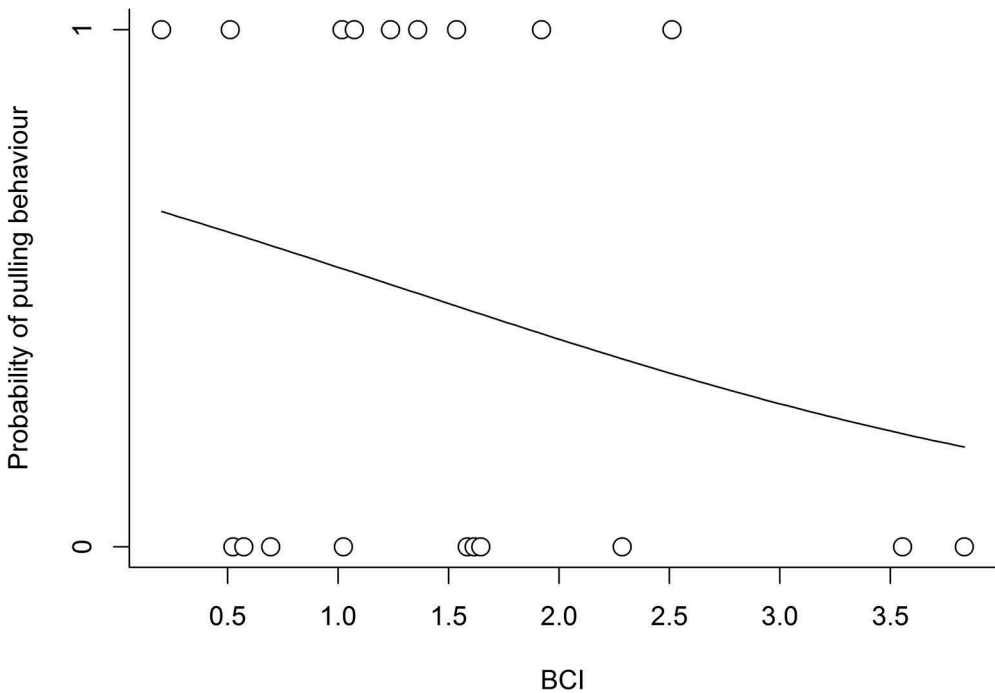


Figure 2. Relationship between predicted probability of spider *Hingstepeira folisecens* (Hingston 1932) (Araneidae) exhibiting a pulling foraging behaviour to catch prey and body condition index (BCI – standardized residuals from a regression of abdomen volume on carapace area) in one region of Central Amazonia, Brazil. ‘1’ represents occurrence of pulling behaviour and ‘0’ represents absence of spider response or use of pursuing behaviour ($n = 19$).

references therein). During web repair, spiders in worse energetic condition would still reduce the amount of silk deposited in each web, minimizing the cost of web building and still maintaining its potential to catch new prey (Venner et al. 2003). Regarding the marginal costs of predation, a malnourished spider would adjust its web repair behaviour accordingly with the photoperiod. In tropical environments, for example, orb-weaving spiders face higher predation pressure during the daytime than at night (Rypstra 1984), mainly because most spider predators (e.g. predatory and parasitoid wasps, birds, damselflies and other spiders) are visually oriented animals (Gauld and Dubois 2006; Manicom et al. 2008). Although we have not systematically observed spider web-repairing behaviour in our experiments, we followed some spiders ($n = 4$) for a few days before the beginning of our experiments, during pilot experiments. Indeed, we observed spiders repairing the webs (destroyed due to the use of pulling behaviour) only at night, which suggests that *H. folisecens* individuals may adjust web repair behaviour accordingly with the photoperiod.

Another point that needs to be considered here is that, although we found no evidence of individual nutritional status affecting spiders’ foraging behaviour choice, individuals still exhibited both foraging behaviours in similar proportion. Therefore, what is determining such behaviour choice? Rito et al. (2016) observed that *H. folisecens* is more prone to use pulling behaviour when prey are closer to the shelter entrance and pursuing behaviour when prey are far from the shelter. Here, we have offered prey in a fixed position from the

web entrance, but the variation in foraging behaviours persisted. Therefore, other factors not related to prey location on web or spider nutritional status are determining spider foraging behaviour. We believe that one potential factor influencing such choice is the relative size of prey items. It is reasonable to expect that catching large prey through pulling behaviour may cause greater web damage than small prey. However, such damage must be directly proportional to the relative size of the prey in relation to the web size. Here, we offered prey of similar size to the spiders but we did not consider the size of each focal web. Because of that, we are not able to directly evaluate our proposition. However, if our proposition is true, we expect that the probability of *H. folisecens* adopting pursuing behaviour should be higher as the proportion of the prey size in relation to the web size increases.

Finally, we did not find any evidence that individual nutritional status can be a factor driving the selection of foraging behaviours by *H. folisecens*. We suggest that the malnourished spiders would adopt additional strategies to compensate for the costs of pulling behaviour, especially when prey is far from the shelter. Furthermore, it is possible that the relationship between prey and web size is another potential factor influencing foraging behaviour choice by spiders. Including this factor in future studies investigating foraging behaviour of *H. folisecens* may help us to understand the threshold that determines when such individuals must adopt one of two possible behaviours.

Acknowledgments

We thank Dr Marcelo de Oliveira Gonzaga for his important suggestions in the manuscript. We also thank Dr Paulo E.D. Bobrowiec and Dr Paulo E.C. Peixoto for their help in the idea formulation. Finally, we are grateful to the two anonymous reviewers for their valuable suggestions. We highlight that this study complies with the current laws of Brazil.

Disclosure statement

The authors declare that they have no competing interests.

Funding

This study was carried out during the 2013 edition of '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, Graduate Program in Ecology and CAPES – PAEP. This is article No. 697 of the Technical Series of Biological Dynamics of Forest Fragments Project (PDBFF - INPA/STRI). Also R.R.M. receives financial support from Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais of Universidade Federal de Uberlândia (UFU) and T.G.K. from Fundação de Amparo à Pesquisa e Inovação do Espírito Santo [grant number 71277560/2015] and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) [grant number 300295/2016-2]. L.C.L. would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES – Brazil) for the post-doctoral scholarship.

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