

Plant architectural traits influence residence time of a specialist jumping spider

Paula M. de Omena¹  · Tiago N. Bernabé^{1,3} · Mônica F. Kersch-Becker¹ ·
Fátima C. Recalde^{1,2} · Pablo A. P. Antiqueira^{1,2} · Camila Vieira⁴ ·
Gustavo H. Migliorini^{1,3} · Sandra Benavides-Gordillo^{1,2} · Gustavo Q. Romero¹

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Abstract The patch residence time of spiders has long been attributed to prey availability. We provide empirical evidence that plant architecture determines the residence time of a bromeliad-living spider. The residence time of spiders was longer on rosette-shaped plants. Males left their host plant faster than females, likely due to their mate-searching activity. We demonstrate that plant architectural traits mediate the patch-leaving tendency of specialist spiders.

Keywords Salticidae · Mutualism · Plant selection · Spider–plant interaction · Bromeliad

Introduction

Habitat selection and patch residence time of spiders have been consistently attributed to food availability or predation risk (Morse 2007). Several spider species, however,

live exclusively associated with plants, using them not only as foraging sites, but also for breeding, as nurseries, and shelter (Dias and Brescovit 2004; Romero and Vasconcellos-Neto 2004, 2005). Spiders that live closely associated with plants may strongly rely on plant traits to select microhabitat and foraging sites, and not only prey-availability cues (Morse 2007; de Omena and Romero 2010; Tedore and Johnsen 2015, 2016). The role of host plant traits in the residence time of specialist spiders, however, still remains unclear.

While several species of jumping spiders (Salticidae) live associated with many bromeliad species, the spider *Psecas chapoda* lives almost exclusively on a single rosette-shaped host plant species, *Bromelia balansae* Mez. (Romero 2006). *P. chapoda*–host plant specialization is linked to microhabitat structure and not to plant species per se (de Omena and Romero 2008). The selective forces that shaped *P. chapoda* specialization have yet to be determined, but it is likely that the large availability of plants with a specific architecture played a critical role in its host plant specialization (Romero 2006).

This spider–plant association is widely distributed over a large area of savanna-like vegetation and margins of semi-deciduous forests (Romero 2006). *P. chapoda* inhabits sun-exposed areas within patches of a mix of shrubs, grasses, and bromeliads (especially *B. balansae*). When spiders disperse from one bromeliad to another, they unavoidably move across plants with distinct architectures. Therefore, a fast and accurate microhabitat selection is particularly important to increase the reproductive success and survival rate of *P. chapoda*, especially because spiders are more vulnerable to predators and harsh climatic conditions when not on their host plants (Romero and Vasconcellos-Neto 2005; Romero 2006). Age and sex of spiders are known to influence substrate selection (Persons

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✉ Paula M. de Omena
paulaomena@gmail.com

¹ Laboratório de Interações Multitróficas e Biodiversidade, Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, SP, Brazil

² Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas, Campinas, SP, Brazil

³ Programa de Pós-Graduação em Biologia Animal, Universidade Estadual Paulista “Júlio de Mesquita Filho”, São José Do Rio Preto, SP, Brazil

⁴ Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais, Departamento de Ecologia, Universidade Federal de Uberlândia, Uberlândia, Brazil

1999). Adult male are often more active due to mate-searching activity, which may influence both site selection and host plant residence time (HPRT) (Cady 1984; Framenau 2005). Here we evaluate *P. chapoda* HPRT of males and females when placed on plants with distinct architectural traits. We predict that HPRT of both adult males and females will be longer on rosette-shaped plants (like *B. balansae*). We also expect that males of *P. chapoda* will leave the host plants faster due to their mating behavior.

Materials and methods

We collected 54 adult males and 54 females of *P. chapoda* spiders on *B. balansae* in a cerrado fragment (20°48S, 49°19W) in São José do Rio Preto, São Paulo, Brazil. In the laboratory, we stored individual spiders in dram vials for 2 days (12 h light at 24–34 °C) with unlimited prey resources (*Drosophila melanogaster*) and a piece of moist cotton.

To evaluate whether *P. chapoda* adult male and female spiders can distinguish among preferred and non-preferred host plant architectural traits we performed a no-choice experiment. We placed one spider on each plant. We then compared the HPRT of *P. chapoda* among plants with distinct architectural traits. We used six plant species arranged in a circle per block; four rosette-shaped plants (*B. balansae*, *Aechmea distichantha*, *Aechmea blanchetiana*, and *Aechmea fasciata*—all Bromeliaceae) and two eudicotyledons [*Croton floribundus* (Euphorbiaceae) and *Delonix regia* (Fabaceae)]. *B. balansae* and *A. distichantha* have long and narrow leaves with margins covered by spines. *A. blanchetiana* and *A. fasciata* present broad leaves; however, *A. blanchetiana* has medium leaf length, and *A. fasciata* has short leaves. Regarding the non-rosette-shaped plants, *C. floribundus* shows long and wide leaves, while *D. regia* has large compound leaves with minute leaflets. For more details on the plants' architecture, see supporting information (S1).

One day before beginning the experiment, we transplanted all the plants ($n = 108$) previously maintained in a greenhouse to an old field at the experimental station of the Universidade Estadual Paulista Júlio de Mesquita Filho. We started the experiment on 25 November 2007. We placed all the plants in open areas with free prey colonization. However, it is important to highlight that none of the experimental plants had structures to attract insects such as flowers and extrafloral nectaries, so we assumed that prey availability was the same among plants. We arranged all plants within a block in a circle; all plants were 1 m apart from the nearest neighbor and blocks were at least 3 m from each other. We set up nine blocks for each spider sex (18 blocks total). We randomly assigned each

block to receive either male or female spiders, and each plant received only one spider. To quantify the HPRT of spiders we checked the experimental blocks daily between 7:30 a.m. to 8:00 p.m. At the beginning of the experiment, we checked the experimental blocks continuously for 4 h, then checked them every 30 min until the end of the experiment. Since Salticidae spiders are most active during the day (Foelix 2011), we did not perform nocturnal observations. At the beginning of each observational day (7:30 a.m.), we inspected all plants to record whether spiders were on them. If a plant did not have a spider on it, we considered the end of HPRT as 8 p.m. of the previous day. This was a conservative approach to account for the spiders that left the plants between 8 p.m. and 7:30 a.m. We removed all spiders that left their plants from the experimental area.

To compare the HPRT of the different treatments, we used survival-reliability analyses. We tested the effects of host plants, spider sex and host plant-by-spider sex interaction using Cox's proportional hazard model. This model has been consistently used to examine patch-leaving tendency (Haccou and Meelis 1994). The cumulative hazard rate, which is the probability per unit of time that an individual leaves the host plant, is calculated by the combination of the baseline residence time (no effect of any factors) and the effects of explanatory variables (host plant, sex, and host plant-by-sex interaction) (Haccou and Meelis 1994). We performed all analyses in JMP Pro version 11 (SAS 2015).

Results

HPRT was influenced by the host plant-by-spider sex interaction ($\chi^2 = 16.27$, $df = 5$, $P = 0.006$; Fig. 1). HPRT of females was longer on *B. balansae* and *A. distichantha*, whereas males showed longer HPRT only on *B. balansae*. HPRT of females on *B. balansae* and *A. distichantha* did not differ (*B. balansae* vs. *A. distichantha* $\chi^2 = 0.04$, $df = 1$, $P = 0.842$), but they remained on *B. balansae* and *A. distichantha* longer than on other plants ($\chi^2 = 71.37$, $df = 5$, $P < 0.001$; Fig. 1a). HPRT of males on *A. distichantha* was similar to that on *A. blanchetiana* (*A. distichantha* vs. *A. blanchetiana* $\chi^2 = 1.1$, $df = 1$, $P = 0.295$; Fig. 1), but higher than that on *A. fasciata* ($\chi^2 = 9.17$, $df = 5$, $P = 0.003$; Fig. 1b). When placed on non-rosette-shaped plants, both males and females promptly left the plants; they remained less than 3.5 min (mean) on *C. floribundus* and on *D. regia*. HPRT was strongly influenced by host plant species ($\chi^2 = 141.39$, $df = 5$, $P < 0.001$; Fig. 1). Mean (\pm SE) HPRT of females (141 ± 37 h) was 23 times longer than that of males (6 ± 2 h; $\chi^2 = 31.19$, $df = 1$, $P < 0.001$; Fig. 1).

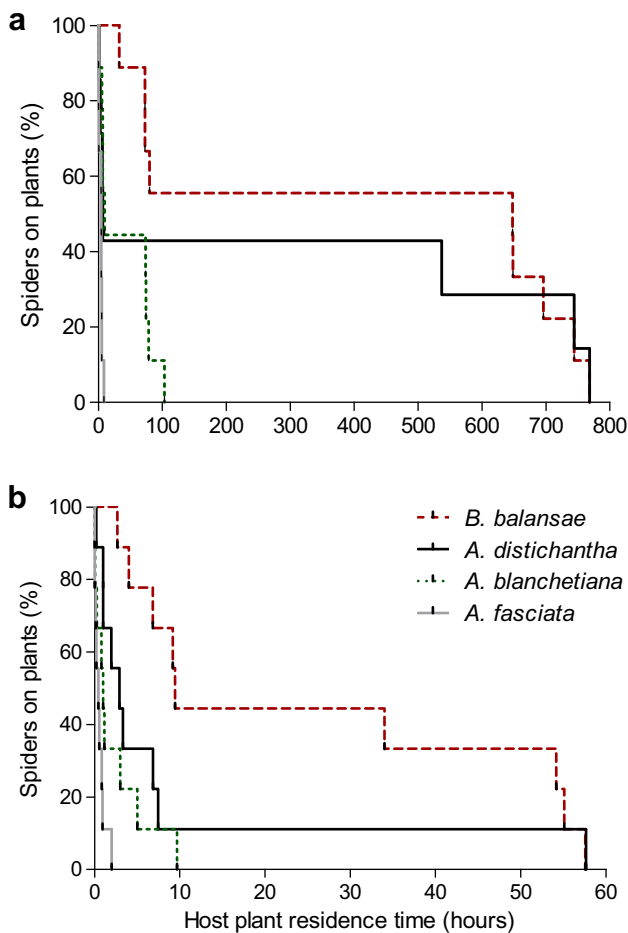


Fig. 1 Host plant residence time of *Psecas chapoda* **a** females and **b** males in response to different host plant species (*Bromelia balansae*, *Aechmea distichantha*, *Aechmea blanchetiana*, and *Aechmea fasciata*). Because of lower host plant residence time (less than 3.5 min), data for *Croton floribundus* and *Delonix regia* are not shown

Discussion

P. chapoda lives almost exclusively on *B. balansae* in a mutualism (Romero et al. 2006), but it can also inhabit other plant species with similar architectural traits (de Omena and Romero 2008). Once on a plant, *Psecas* is able to distinguish rosette-shaped from non-rosette-shaped plants; as a result, the residence time of *P. chapoda* on rosette-shaped bromeliads was longer. A previous study of this system showed that *P. chapoda*, guided by visual stimuli, have a strong preference for rosette-shaped plants bearing long and narrow leaves (i.e., *B. balansae* and *A. distichantha*) (de Omena and Romero 2010). Our findings complement these results showing that the residence time of spiders on bromeliads with narrow and long leaves is longer than that on bromeliads with different leaf traits and non-rosette-shaped plants.

Most theoretical and empirical studies on patch residence time of arthropods have considered prey availability as a primary influence on the patch-leaving tendency (Cassini et al. 1990; Persons and Uetz 1996; Miyashita 2005; Morse 2007). The residence time of two *Nephila* species (*Nephila maculata* and *Nephila clavata*) on different habitats varies according to life history traits (Miyashita 2005). *N. maculata* has a larger body size and shorter residence time than *N. clavata*. However, under food supplementation, *N. maculata* dramatically increased its residence time, suggesting that patch residence time is linked to food availability (Miyashita 2005). Additionally, the wolf spider *Schizocosa ocreata* remained longer in patches with both visual and vibratory cues from prey (Persons and Uetz 1996). Here we showed that habitat traits could also influence the patch residence time of spiders. It is likely that the residence time of spiders that live closely associated with plants is strongly influenced by host plant traits and not only food availability.

We also found that *P. chapoda* females remained longer on their host bromeliads than males. This result may be related to the reproductive behavior of *P. chapoda*. Adult females display maternal care; they construct their egg sacs on the concave side of the leaves under a plain silk cover and remain there to ensure clutch survival (de Rossa-Feres et al. 2000; Vieira and Romero 2008). This behavior could explain the longer residence time on rosette-shaped plants with long and narrow leaves; traits that enhance nest building. The leaves of *B. balansae* are also used during courtship; females remain on the base of the rosette, while males occupy the upper side of the leaves and display courtship behavior there (de Rossa-Feres et al. 2000). In this study we observed that males left the plants they were placed on and move towards rosette-shaped bromeliads harboring females (i.e., *B. balansae* and *A. distichantha*). Indeed, male spiders become more active after the last molt and tend to leave their habitats to search for females (Foelix 2011). Males of *Phidippus clarus* (Salticidae) walk more than females and show lower site fidelity than them (Hoefler and Jakob 2006). Because we only used adult males of *Psecas*, the lower site fidelity and higher dispersal rates help explain our findings in which males left the plants faster than females.

We conclude that *P. chapoda* spiders can distinguish between preferred host and non-host plants once on plants. Sex strongly influenced residence time; female spiders remained longer (almost 1 month) on rosette-shaped bromeliads than males. It is likely that males readily dispersed to search for females. Although prey availability has been considered the main driver of the residence time of spiders, our findings demonstrated that plant architectural traits play an important role in patch residence time of bromeliad specialist spiders.

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Compliance with ethical standards

Human and animal rights statement All the applicable international, national, and institutional guidelines for the care and use of animals were followed.

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