

Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi)

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Abstract Animals that select and defend suitable habitats against conspecifics may be favored by maximizing prey encounter rate, gaining protection, or securing matings. However, the identification of habitat selection and territoriality may be hindered in observational studies in sedentary species with low-density populations, such as the whip spider *Heterophrynus longicornis*. To circumvent such difficulties, we adopted an experimental field approach to evaluate if *H. longicornis* selects and defends habitat in Central Amazon. To evaluate whether individuals perform habitat selection, we monitored the permanence of 29 experimentally released individuals in buttressed trees with a wide variation in diameter at breast height (DBH), with and without burrows at their bases. To evaluate whether individuals are territorial, we experimentally removed 21 individuals from their previously occupied trees and monitored the recolonization of these trees. If *H. longicornis* were territorial, we predicted that the recolonizers would be smaller than the removed individuals. We found 12 individuals in the trees where they were released on subsequent days, none of them in trees without burrows. The individual permanence was related to the presence of burrows, and not to DBH. There was recolonization by smaller males and females on ten trees

from which the amblypygids were removed. In combination, the permanence of individuals in trees with burrows, the rapid recolonization of experimentally vacated trees by smaller individuals, and the preponderance of one individual per tree, suggest that both male and female *H. longicornis* perform habitat selection and also that after selecting a site, they defend it against conspecifics.

Keywords Buttressed trees · Microhabitat use · Territorial defense · Territorial payoff · Agonistic interactions · Phrynidae

Introduction

According to habitat selection theory (Morin 1999) individuals that actively choose high quality habitats should be favored by natural selection (e.g. Switzer 2002; Robakiewicz and Daigle 2004). High quality sites are often represented by places with better shelter, low chances of encountering predators or high chances of finding prey and mates (Cody 1985; Martin 2001). The selection of such sites may be affected by the spatial and temporal distribution of resources and predators (e.g. Hammond et al. 2012), and also by individual condition related to age, hunger, and reproductive or social status (Rosenzweig 1981; Bergin 1992; Bonte and Maelfait 2004).

Because high quality habitats are generally scarce and patchily distributed (Adam 2009; Chouet et al. 2011), individuals that, in addition to selecting such places and establishing territories of exclusive use (i.e. actively expelling rivals that try to use the same patch) may be further favored since they may increase the benefit provided by the selected site (Whitham 1980). However, the possession of a territory also incurs costs for territorial

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individuals, since they often spend energy, and sometimes suffer physical damage, in disputes against conspecific intruders that try to gain access to the disputed resource (Meuche et al. 2012). During fights, it is common that the individual in best condition (often the one with greater size, mass or energy reserves) imposes more costs on rivals and often wins the contests over territory possession (Arnott and Elwood 2009). However, since fights generate costs for both rivals, the adoption of territorial defense may be affected by the relative availability of territorial sites. In particular, territorial defense should be adopted when there are few individuals per territory site since the frequency (and consequently the energetic costs) of territorial disputes should be low (e.g. Alcock and O'Neill 1986).

If individuals in a population adopt territorial behavior, it should be expected to find one organism per defended site. However, because individuals of some species may actively select specific habitats without defending them against conspecifics (e.g. Choult et al. 2011), the observation of one individual per site without detecting other cues associated with exclusive use of an area does not indicate the adoption of territorial behavior. This is particularly important in less active and sedentary animals, such as whip spiders (Amblypygi), that often occur widely apart from each other (e.g. Hebets 2002; Weygoldt 2008). In such species the rarity of interactions between rivals for the possession of territorial sites should hinder the detection of territorial behavior by simple observation without any manipulative approach.

The whip spider *Heterophrynus longicornis* (Butler 1873) is a large arachnid (ca. 4 cm total body length, excluding legs and pedipalps), often found in fallen logs, termite nests and living trees in the Amazon Forest and Cerrado (a savannah-like biome) in north, northeast and midwest regions of Brazil (Lourenço and Heurtault 1978; Weygoldt 2002; Carvalho et al. 2011). The adult prosoma width range from 9.2 to 14.9 mm for males ($\bar{x} = 12.4$; $SD = 1.2$) and from 9.2 to 12.6 mm for females ($\bar{x} = 10.7$; $SD = 1.3$ mm) (Dias and Machado 2007). There are at least three observational studies with contrasting results about habitat selection and territoriality in this species (Weygoldt 1977; Dias and Machado 2007; Carvalho et al. 2012). One study reported that, because larger individuals are frequently singly found in larger buttressed trees with burrows at their bases, they must be territorial (Dias and Machado 2007). The other two studies suggest that individuals of *H. longicornis* do not select specific sites and are also tolerant to conspecifics (Weygoldt 1977; Carvalho et al. 2012). Since these contradictory results cast doubt on the occurrence of habitat selection and territoriality in *H. longicornis*, a manipulative field study could help to disentangle these alternatives.

Buttressed trees may provide a larger area for foraging and courtship for *H. longicornis* in relation to other trees types. In particular, the burrows at the bases of these trees are used as diurnal shelters by these exclusively nocturnal arachnids (Weygoldt 2000; Dias and Machado 2007). Consequently, trees with these characteristics may represent high-quality resources to be defended. Therefore, in this study we experimentally investigated whether individuals of *H. longicornis* are able to select and defend exclusive territories in high quality sites. We hypothesized that (1) individuals prefer bigger trees with burrows, which offer higher protection, and increased foraging area; and that (2) due to their low density, *H. longicornis* are territorial. If hypothesis 1 is true, we expect that experimentally released individuals in trees with different diameters and burrow occurrence at their bases, will only remain in the large trees with burrows. According to hypothesis 2, we expect that after experimentally removing whip spiders from their trees, smaller colonizers will occupy these sites.

Materials and methods

Study area

We conducted the study in August 2009, in the Central Amazon Forest in a reserve known as ARIE Km-41 (2°24'S, 59°43'W), located approximately 80 km north of Manaus, Amazonas, Brazil. This area is a “terra firme” (unflooded) primary forest with mean annual temperature of 27 °C and rainfall varying from 1,900 to 2,500 mm annually. The vegetation is characterized by upland forest that has a mean canopy height of approximately 35 m (Pires and Prance 1985; Lovejoy and Bierregaard 1990). The reserve has an area of approximately 10,000 ha of continuous forest, with many trails spaced at 100 m in both the north–south and east–west directions, which we used for locating *H. longicornis* individuals.

Occupation experiment

To evaluate if individuals choose trees based on tree size and the presence of burrows, we performed an occupation experiment. To conduct this experiment, we collected 29 adult *H. longicornis* (14 males and 15 females) during the night, marked each one with a combination of white dots in the pro- and opisthosoma, and released them individually during the same night on 29 new buttressed trees, at least 100 m distant from the capture tree. Before releasing, we carefully checked the release tree for previous occupants (including the burrows) to make sure that they were unoccupied. Afterwards, we released the individuals by opening the box where they were kept near the tree trunk at

approximately 1 m from the ground. Before capturing individuals, we previously selected the release trees in order to provide a wide range in diameter at breast height (DBH) and also variation in the presence and absence of burrows at their bases. The release trees with burrows at their bases presented DBH varying from 16.1 to 90.1 cm ($n = 16$), while the release trees without burrows at their bases presented DBH varying from 8.3 to 67.2 cm ($n = 13$). We only used buttressed trees because they are the most frequently used habitat occupied by whip spiders in this region (Dias and Machado 2007).

We randomly allocated each captured whip spider to a release tree. After releasing the whip spiders, we monitored each tree for two consecutive days (between 8:00 h and 11:00 h) and nights (between 20:00 h and 01:00 h) for the presence of marked individuals. We considered that the whip spider did not abandon the tree when it was observed at least once in the released tree up until the last monitored night.

We used a multiple logistic regression to assess whether the presence (response variable) of individual *H. longicornis* was related to the DBH, the presence of burrows at the tree base and the interaction between burrow presence and DBH (predictor variables). We used the Akaike Information Criterion corrected for small samples (AICc) to evaluate the relative importance of different combinations of the explanatory variables in this relationship (Burnham and Anderson 2002).

Removal experiment

To investigate whether adults of *H. longicornis* defend their territories, we conducted another field experiment in the same period and area over four nights. During the first night, we collected, between 20:00 h and 1:00 h, 24 adults of *H. longicornis* (14 males and 10 females) in 22 trees distributed along three 700-m-long trails. After collecting each individual, we identified its sex and measured the largest width of the prosoma with a caliper (0.05 mm accuracy). Among the trees from which we removed the whip spiders, 13 presented burrows at their bases and 9 did not. The DBH varied between 13.22 and 123.25 cm.

We marked all trees from which we removed the resident whip spider and checked each one for three consecutive nights after the first removal for the presence of substitute individuals that may have taken it over. Whenever we found a substitute, we collected it, measured the largest width of prosoma and identified its sex. We used a paired *t*-test to compare the prosoma width of the removed individuals with that of the substitute individuals in each tree. We performed all analyses in R software, version 2.15.0 (R Development Core Team).

Results

Occupation experiment

Among the 29 individuals, 12 (seven males and five females) remained in the trees where they were released (Fig. 1). The pattern of permanence on the first night of monitoring remained virtually unchanged until the end of the experiment. No permanence was recorded for trees without burrows at their base ($n = 13$). All observations occurred during nocturnal searches. During diurnal searches, we observed the released whip spiders sheltered in the burrows of five trees. In the others, the burrows were too deep to allow an accurate search.

The DBH of the trees in which the individuals remained ranged from 16.1 to 90.1 cm ($\bar{x} = 47.09$; $SD = 23.32$), while the DBH of the trees that were abandoned ranged from 8.3 to 67.2 cm ($\bar{x} = 34.47$; $SD = 14.59$; (Fig. 1). The general model indicated a relationship between the permanence of individuals, DBH and presence of burrows at the tree base ($\chi^2 = 21.52$; $df = 3$; $p < 0.001$; Table 1). However, the most parsimonious candidate model included only the presence of burrows as the determinant of whip spider permanence. This model indicated that the permanence probability of *H. longicornis* individuals increased with the presence of burrows at the tree base ($\chi^2 = 21.34$; $df = 1$; $p < 0.001$).

In two trees (both with burrows and $DBH > 40$ cm) we observed interactions between males. These individuals remained at a distance of approximately 20 cm from each other, with pedipalps opened at an angle of 90° between the femur and the patella. Frequently the males touched the

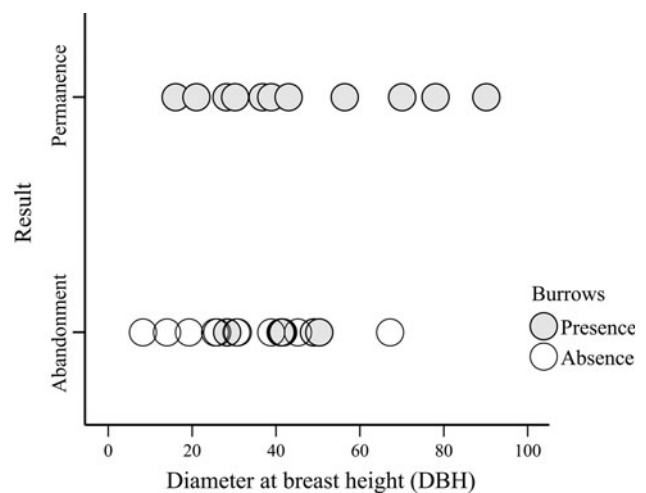


Fig. 1 Relationship between the permanence of *Heterophrynus longicornis* individuals after their experimental deposition on a tree, the tree DBH (diameter at breast height) and the presence of burrows at the tree base in Km-41 Reserve, Central Amazonia, Amazonas State, Brazil

Table 1 Summary of the logistic models describing the probability of an individual of *Heterophrynus longicornis* staying in a tree after its experimental deposition in relation to the tree diameter at breast height (DBH) and the presence of burrows at the tree's base

Model	AIC _c	df	ΔAIC _c	w _i
Burrows	22.5	2	0.0	0.482
DBH + burrows*DBH	24.8	3	2.3	0.151
Burrows + burrows*DBH	24.8	3	2.3	0.151
Burrows + DBH	24.8	3	2.3	0.151
Burrows + DBH + burrows*DBH	27.5	4	5.0	0.039
Burrows*DBH	28.3	2	5.9	0.026
DBH	40.6	2	18.2	<0.001
Null model	41.5	1	19.0	<0.001

Models are ranked in ascending order of AIC_c (AIC_c represents the value of Akaike information criterion corrected for small samples; Δ_i represents the difference between the model *i* and the most parsimonious model; w_i is the Akaike weight of model *i*)



Fig. 2 Interaction between males of *Heterophrynus longicornis* in a tree during a manipulative field experiment conducted in August 2009, in Km-41 Reserve, Central Amazonia, Amazonas State, Brazil (photo by TJ Porto)

other individual with his first pair of sensory legs (Fig. 2). These interactions did not involve evident physical damage and in both only the larger male remained in the monitored tree the night after the interaction.

Removal experiment

Substitute individuals occurred in 10 out of 22 trees that had the original *H. longicornis* removed. All occupations occurred only in trees that had just one individual during the removal. The sex of the resident individual was unrelated to the sex of the substitute. Females substituted males in two among the four trees originally occupied by males, while males substituted females in three trees originally occupied by females. The substitute individuals occupied

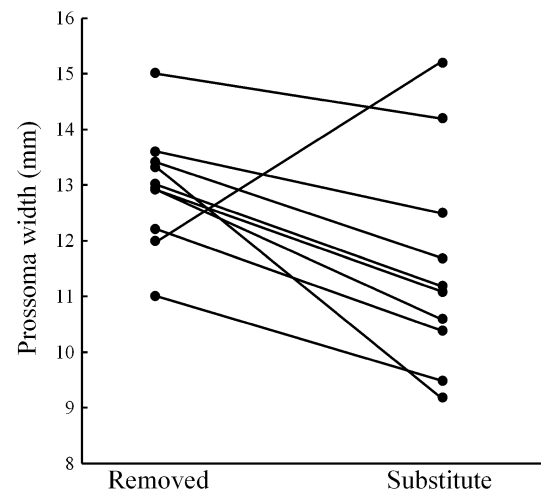


Fig. 3 Comparison of the prosoma width of *Heterophrynus longicornis* removed from the tree and the individual that subsequently occupied the same site (substitute individual) in Km-41 Reserve, Central Amazonia, Amazonas State, Brazil. Each line connects the prosoma width of the original and substitute individuals in the same tree

both buttressed ($n = 4$) and non-buttressed trees ($n = 6$). Eight colonized trees presented burrows at its base and two did not. The DBH of the colonized trees varied from 17.52 to 123.25 cm. The prosoma width of substitute individuals ($\bar{x} = 11.56$; SD = 1.93) was on average significantly smaller than that of removed individuals ($\bar{x} = 12.93$; SD = 1.07) ($t = 2.36$, $df = 9$, $p = 0.042$; Fig. 3).

Discussion

We showed that the whip spider *H. longicornis* preferentially stayed in trees with burrows, independent of tree size. This indicates that the presence of a burrow at the tree base increases the site quality for the whip spider and also that both males and females actively perform an evaluation before deciding on their permanence in a given site. The colonization pattern observed in the removal experiment reinforces the possibility of active habitat selection, since substitutes colonized 45 % of the trees from which we removed residents. For a nonvisual animal that often occurs in low density, this high frequency of movement suggests that they may actively select habitats. Because the substitute individuals were also smaller than their resident pairs, it is also possible that *H. longicornis* individuals defend a territory when established in a tree. Territorial behavior has been previously recorded for other amblypygid species (Weygoldt 2000), but some amicable (tolerant, nonaggressive) tactile interactions were also recorded in some species (Rayor and Taylor 2006).

Previous studies have suggested that larger buttressed trees with burrows at their base are the preferred habitat for

H. longicornis (Dias and Machado 2007). This preference contradicted the abundance pattern of individuals of *H. longicornis* at a larger spatial scale, since their abundance was similar between areas that differed in the availability of large trees (Carvalho et al. 2012; Laurance et al. 2000). However, by applying an experimental approach, we were able to show that the permanence of individuals in a tree is not directly linked to tree size. Therefore, the similarity in the abundance of *H. longicornis* between the interior and the edge of the forest fragments (Carvalho et al. 2012) may be explained by a similar number of trees with burrows at their base. These burrows may, in fact, represent important diurnal shelters to whip spiders, where they can avoid light stress and protect themselves from predators (Coddington and Colwell 2001), such as owls, bats and some invertebrates already reported as predators of whip spiders of similar size to *H. longicornis* (Hebets 2002). It is important to note that we found a marginally significant positive correlation between the tree size and the permanence of the released whip spider ($p = 0.074$) and also, that a previous study related a positive correlation between whip spider size and tree size (Dias and Machado 2007). However, it is possible that larger trees, because they are older, are more likely to present burrows at their base, creating a spurious correlation between tree size and whip spider distribution.

The occupation of trees by a smaller individual after the removal of the original one indicates that both males and females of *H. longicornis* may establish territories of exclusive use in trees. The low frequency of trees with more than one whip spider previously related by Dias and Machado (2007) also reinforces this possibility. In addition, the size difference between the original and substitute individuals indicate that size may determine the individual fighting capacity. Although fights in some species may be settled based on disputes without injuries or motivational differences (e.g. Santer and Hebets 2009), it is possible that larger individuals of *H. longicornis* may be able to expel smaller intruders from their territories due to a higher fighting capacity (Vieira and Peixoto 2013). In fact, if disputes were based solely on motivation asymmetries, physical or physiological differences between residents and substitutes or between winners and losers should not be found (Arnott and Elwood 2008). However, we cannot exclude the possibility that the individual motivational state interacts with fighting capacity to determine the winner of a territorial contest, since our experiment did not allow direct fights between rivals or control for differences in resource value between them (e.g. Peixoto and Benson 2011).

Adults, especially males, of many whip spider species are territorial and may fight for the possession of the defended sites (Weygoldt 2000). Consequently, the observed interactions between males may represent an

interaction for territory ownership. Nevertheless, since the sex of the original individual was unrelated to the sex of the substitute in the removal experiments, it is probable that males also fight against females for tree ownership, indicating that this type of territoriality is not directed to mate acquisition. Maybe they defend foraging sites or sheltered areas due to the burrow presence. However, since we found two original adult whip spiders in the same tree on two occasions during the removal experiment, it may be that there are situations in which they tolerate conspecifics (Weygoldt 1977; Carvalho et al. 2012). Since such trees were large and presented burrows at their bases, it is improbable that they were low quality sites that were not valuable enough to trigger territorial fights (Fowler-Finn and Hebets 2006; Rayor and Taylor 2006). Some amblypygid species may increase their aggregation behavior in the presence of simulated predators (Rayor and Taylor 2006). Perhaps the observed individuals sharing a tree were in a similar predatory situation. Alternatively, they may represent individuals that did not reach a contest decision about the territory possession. In some species, for example, the dispute between rivals may last for longer periods, with neither of them abandoning the defended site (Arnott and Elwood 2009).

Habitat selection and territoriality should be favored when the resources are scarce, patchily distributed and when population density is low to moderate (Emlen and Oring 1977; Morin 1999). Nonetheless, species with low population density and cryptic behavior may hinder the identification of habitat selection and especially territoriality in purely observational studies, due to difficulties in observing aggressive behaviors or disentangling the effects of low density and expulsion of rivals in determining why individuals occur singly in specific sites. Using an experimental approach, we were able to demonstrate that a species with low population density and cryptic behavior actively selects areas that presumably increase their protection and may defend these areas. Studies about territoriality are often focused on more active and conspicuous organisms that are typically concentrated in territories (Arnott and Elwood 2008, 2009). However, since many arthropods (mainly nocturnal arachnids) have population and behavioral patterns similar to *H. longicornis* (Marshall 1996; Birkhofer et al. 2006), it is likely that territoriality is more common than previously thought. Consequently, the identification of habitat selection and territoriality in species with low density and low activity can help us in clarifying how different selective pressures shape the evolution of such behaviors in animal species.

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