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SHORT COMMUNICATION

Seasonal patterns of microhabitat selection by a sub-tropical whip spider, *Phrynus longipes*, in the Luquillo Experimental Forest, Puerto Rico

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Abstract. *Phrynus longipes* (Pocock 1894) is a top predator among arboreal invertebrates in the Luquillo Mountains of Puerto Rico, but many aspects of its ecology remain poorly understood. We sampled four of the most abundant tree species in the Luquillo Mountains during the dry and wet seasons of 2008 to evaluate microhabitat preferences of this species. In the dry season, *P. longipes* occurred significantly less frequently on a palm, *Prestoea acuminata* var. *montana* (Arecaceae), than the other tree species. Carapace length and the diameter of the tree on which an individual was found were positively correlated, suggesting competition for substrates. Microhabitat selection shifted in the wet season. Individuals occurred as frequently on *P. acuminata* as on any other species. The seasonal shift in substrate use could result from altered distribution or abundance of prey, an ontogenetic shift in substrate preference or greater competition arising from an increased abundance of *P. longipes*.

Keywords: Amblypygi, resource availability, competition, fitness, arboreal predators

Habitat selection contributes to individual fitness by affecting the ability to acquire resources, survive and reproduce (Rosenzweig 1981; Huey 1991). Furthermore, intra- and interspecific competition influence the ability of individuals to occupy optimal habitats (Whitham 1980; Stamps 1991). Habitat selection is likely to be affected by temporal changes in food availability, reproductive activity and the emergence of young, all of which occur seasonally (Wolda 1978). Therefore, a comprehensive understanding of habitat selection requires comparisons among seasons.

Whip spiders (Amblypygi) are nocturnal ambush predators that use vertical substrates, such as trees or rocks, for hunting and nearby crevices as mating or retreat sites. Adults of many species defend a small home range near the structure they employ for hunting (Weygoldt 2000). Patterns of habitat use are poorly known for most amblypygid species, but some factors associated with amblypygids that inhabit tropical forests have been identified. In the central Amazon Basin, *Heterophrynus longicornis* (Butler 1873) occurs most often on large trees with buttressed roots (Dias & Machado 2007). In contrast, Porto & Peixoto (2013) found that individuals were more likely to maintain their territory on a tree if a burrow was present at its base, regardless of tree size. The presence of termite nests at a tree base is another indicator of higher *H. longicornis* abundance (Carvalho et al. 2012). In Costa Rica *Phrynus parvulus* Pocock 1902 selects habitats based on tree surface area, the presence of buttresses and moss cover (Hebets 2002). Large trees with buttresses might be preferable if they provide high prey density in the deep leaf litter between roots (Heyer & Berven 1973), or areas for mating or retreat sites.

Phrynus longipes (Pocock 1894) inhabits caves and forests on Hispaniola, Puerto Rico and the Virgin Islands (Quintero 1981), but relatively little is known about its ecology or behavior. A previous study of *P. longipes* in the Luquillo Mountains of northeastern Puerto Rico found individuals most often on the sierra palm, *Prestoea acuminata* var. *montana* (Arecaceae) (Bloch & Weiss 2002). This is unusual compared to the habits of other whip spiders, as *P. acuminata* has a relatively small diameter compared to other trees in this forest and lacks buttresses. Two explanations could account for this unexpected pattern of habitat use. First, neither the sampling methodology nor the statistical analyses of Bloch & Weiss (2002)

explicitly accounted for tree species abundance, so *P. longipes* may have appeared to prefer *P. acuminata* simply because it was the most abundant substrate within the sampling plots. Second, the extensive anthropogenic and natural disturbance history of northeastern Puerto Rico might contribute to unique habitat characteristics and population dynamics. Until the 1930s, much of the land below 600m was used for farming, logging and coffee cultivation (Thompson et al. 2002). In addition, hurricanes of moderate to high intensity hit the forest every 50–60 years on average, and storms of lesser intensity occur more frequently (Scatena & Larson 1991). This disturbance regime would have necessitated adaptation by organisms to a heterogeneous, frequently changing environment, and could have affected patterns of habitat use.

This study evaluated whether *P. longipes* in the Luquillo Mountains actually selects substrates differently from other species of forest-dwelling whip spider, or if the unusual pattern of habitat use observed by Bloch & Weiss (2002) emerged simply because of a sampling bias. We compared use of *P. acuminata* to use of three other abundant trees in the Luquillo Mountains to determine whether *P. acuminata* was occupied more than expected by chance or was simply used in proportion to abundance. We also compared substrate use between dry and wet seasons to assess the effects of seasonality.

The Luquillo Experimental Forest (LEF) is an 11,300-ha reserve in the Luquillo Mountains of northeastern Puerto Rico, and is a site in the National Science Foundation's Long-Term Ecological Research Network (Hobbie et al. 2003). This study was conducted near the El Verde Field Station (18°19'16.83"N, 65°49'10.13"W), in the north-western region of the LEF, where elevation ranges from approximately 300 to 400 m. Total annual precipitation at the El Verde Field Station averages 335 cm year⁻¹ (Heartsill-Scalley et al. 2007). Precipitation is mildly seasonal, with a relatively dry period from January to April (McDowell & Estrada Pinto 1988). For 1975–1989, average monthly precipitation for the dry (January–April) and wet (May–December) seasons was approximately 22 cm and 35 cm, respectively.

To determine the most dominant tree species in the area we sampled based on basal area (Thompson et al. 2002). From these common species, we selected four of the most abundant within our sampling area, each of which has a distinct root system. *Prestoea*

Table 1.—Data for each of the two sampling periods are presented. The number (n) of each tree species (Cs, *C. schreberiana*; Mb, *M. bidentata*; Pa, *Prestoea acuminata*; Sb, *Sloanea berteriana*) sampled, DBH for each of the four species and two seasons are included, as well as values combined for both sampling periods. The number of adult and juvenile *P. longipes* recorded on each species is also listed by tree species and season.

		n	Average DBH (cm)	Maximum DBH (cm)	<i>Phrynus longipes</i>	
					Adults	Juveniles
Dry Season	Cs	25	18.9	36	1	2
	Mb	55	19.5	59.6	3	1
	Pa	121	10.1	19.1	2	0
	Sb	84	7.2	44.6	8	5
	Total	285			14	8
Wet Season	Cs	56	20.3	41.3	5	7
	Mb	80	18.2	77	3	4
	Pa	214	13.6	46	25	36
	Sb	115	9.2	38.4	4	18
	Total	465			37	65
Combined	Cs	81	19.9		6	9
	Mb	135	18.7		6	5
	Pa	335	12.3		27	36
	Sb	199	8.4		12	23
	Total	750			51	73

acuminata has a tightly packed system of prop roots, *Cecropia schreberiana* (Urticaceae) has widely spaced branching roots that angle off from the main stem, *Sloanea berteriana* (Elaeocarpaceae) develops buttresses as it grows, and *Manilkara bidentata* (Sapotaceae) has a straight trunk devoid of buttresses (Thompson et al. 2002).

Surveys were conducted in March 2008 (dry season) and from June to August 2008 (wet season). Sampling was conducted by two researchers and occurred between 20:00 and 02:00. As many trees as possible of each target species were found, and each was visually inspected up to a height of 2m, including all visible crevices, buttresses, and exposed roots. Total body length (TBL, the length of the abdomen and carapace) of each whip spider was measured using dial calipers (Table 1). Diameter at breast height (DBH) was measured using a diameter tape for all trees, regardless of presence or absence of whip spiders (Table 1).

Currently, there is no documentation of the size at which *P. longipes* becomes sexually mature. A congener, *Phrynus marginemaculatus* Koch 1840, is sexually mature when it has reached approximately half of its average adult size (Weygoldt 2000). Typical adult size of *P. longipes* is roughly 35 mm (Weygoldt 2000), so individuals were considered adults if TBL ≥ 18 mm. All remaining individuals were considered juveniles. Although 18 mm is an arbitrary threshold, changing this value by a few mm did not substantively alter the results.

Chi-square contingency table analyses were used to test the null hypothesis that *P. longipes* occupied tree species randomly (i.e., in proportion to abundance). If there was a significant result, standardized residuals were examined to determine which species contributed most to the overall significant result. If a standardized residual exceeded two standard deviations (i.e., $-2.0 > z > 2.0$), the associated count was considered to be significantly different from the expected.

Pearson's Product-moment Correlation Coefficient was used to test for an association between TBL of *P. longipes* and the DBH of trees on which individuals were found. For each season, analyses were conducted for all individuals, as well as for adults and juveniles separately. Further analyses assessed the relationship between TBL and DBH separately for each tree species.

Microhabitat selection by *P. longipes* was non-random in the dry season ($\chi^2 = 14.24$, $df = 3$, $P = 0.003$; Fig. 1a). Standardized residuals indicated that whip spiders were observed more frequently

than expected on *S. berteriana* ($z = 2.61$) and less frequently than expected on *P. acuminata* ($z = -2.38$). TBL of *P. longipes* was significantly and positively correlated with the DBH of trees on which it was found ($r = 0.68$, $P = 0.001$, $n = 22$) when all individuals were included in the analysis and for adults only ($r = 0.59$, $P = 0.026$, $n = 14$). Furthermore, the significant positive correlation between TBL of individuals and the DBH of *S. berteriana* on which they were found ($r = 0.72$, $P = 0.005$, $n = 13$) suggests that, as occurs in other amblypygid species, larger individuals were selecting and defending territories on larger trees. However, for the remaining tree species, or when only juveniles on all trees were considered, TBL was not significantly correlated with DBH, suggesting that some individuals were unable to acquire or defend territory on the preferred trees. This may also correspond to the relatively small size range observed for the other tree species, especially *P. acuminata*, which rarely exceeded 20 cm DBH.

In the wet season, substrate use was non-random among the four tree species ($\chi^2 = 11.01$, $df = 3$, $P = 0.012$; Fig. 1b). Whip spiders were observed less frequently than expected on *M. bidentata*, the species with the simplest above-ground component of the root system and the least surface area ($z = -2.21$). This was also true if the analysis was restricted to juvenile whip spiders ($z = -2.14$). Other species did not differ significantly in frequency of occupancy. TBL was not significantly correlated with DBH when all individuals and all trees were tested together ($r = -0.05$, $P = 0.642$, $n = 102$) or for adults ($r = 0.03$, $P = 0.857$, $n = 37$) and juveniles ($r = -0.17$, $P = 0.179$, $n = 65$) analyzed separately. However, individuals that occupied *S. berteriana* displayed a positive correlation between TBL and DBH ($r = 0.59$, $P = 0.004$, $n = 22$), while TBL was negatively correlated to DBH for individuals on *C. schreberiana* ($r = -0.63$, $P = 0.029$, $n = 12$). For individuals found on *M. bidentata*, a negative correlation approached significance ($r = -0.69$, $P = 0.085$, $n = 7$), but TBL of individuals found on *P. acuminata* was not significantly correlated to the DBH of the tree on which they were found ($r = 0.03$, $P = 0.828$, $n = 61$).

In the LEF, *S. berteriana* has similar characteristics (i.e., buttressed roots and large DBH) to those of trees that are selected by *H. longicornis* in northern Brazil (Dias and Machado 2007) and *P. parvulus* in Costa Rica (Hebets 2002) and may therefore provide the same putative benefits. Nevertheless, Bloch & Weiss (2002) report that a palm, *P. acuminata*, was the tree most often occupied by

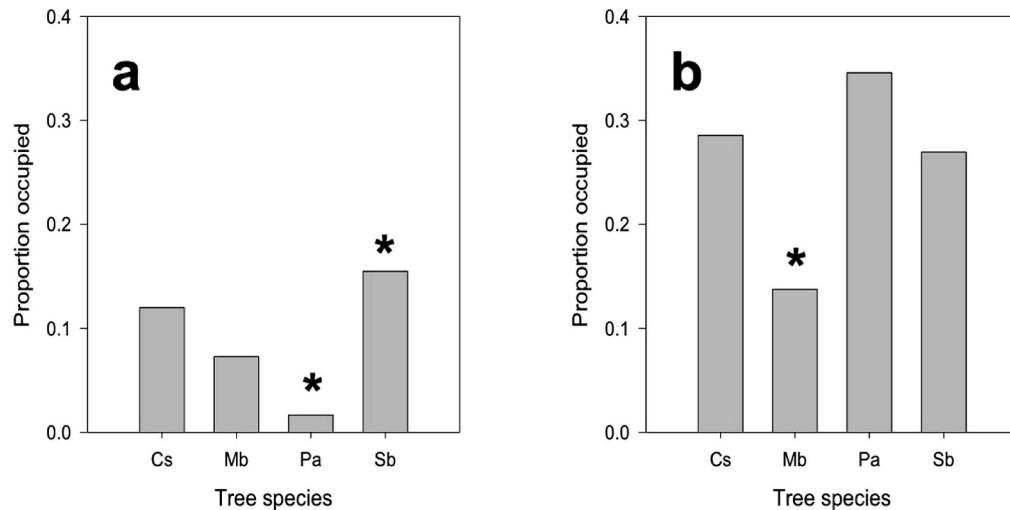


Figure 1.—Patterns of substrate use by *Phrynus longipes* in the Luquillo Experimental Forest. The proportion of individuals of each tree species (Cs, *C. schreberiana*; Mb, *M. bidentata*; Pa, *Prestoea acuminata*; Sb, *Sloanea berteriana*) occupied by *P. longipes*. a. Dry season; b. Wet season. Asterisks above bars indicate significant departures from expected occupancy based on standardized residuals of chi-square contingency tables.

amblypygids in the LEF. We reconcile the observations of Bloch & Weiss (2002) with other studies by demonstrating changes in microhabitat use between sampling periods.

Two lines of evidence are consistent with the hypothesis that large, buttressed *S. berteriana* are preferred substrates for *P. longipes* in the LEF. First, *S. berteriana* was among the most frequently occupied tree species, regardless of season, especially if only relatively large trees are considered. In the dry season, *P. longipes* occupied 86% of *S. berteriana* that measured ≥ 20 cm and 53% that measured ≥ 10 cm, compared to only 7.2% that measured < 10 cm. This pattern was repeated in the wet season, as *P. longipes* occupied 75% of *S. berteriana* ≥ 20 cm, 58% ≥ 10 cm, but only 11% that were < 10 cm. Second, the positive correlation between TBL of *P. longipes* and DBH of *S. berteriana* suggests that larger individuals were best able to defend a territory on large, buttressed trees.

There was a considerable shift in microhabitat use between seasons, however, with individuals avoiding *P. acuminata* in the dry season but using it as frequently as *C. schreberiana* and *S. berteriana* in the wet season. Several reasonable hypotheses may explain this pattern. Abundance or quality of prey may change seasonally, making *P. acuminata* trunks better hunting sites in the wet season than in the dry season. For example, foraging activity of *P. longipes* (Pfeiffer 1996) and insect abundance (Garrison & Willig 1996) are greater during rainy than dry periods, suggesting that higher prey capture rates are possible during such times, even on trees that represent less suitable habitat during dry periods.

Alternatively, decreased use of *P. acuminata* in the dry season may reflect that it is unsuitable for mating, or that an ontogenetic shift in substrate selection occurred. The courtship display of many species of whip spider requires a sheltered, level area (Weygoldt 2000), such as the root surface or the caverns that form under the roots of the most frequently selected trees. The roots of *P. acuminata* generally lack such spaces. The small crevices found between *P. acuminata* roots are, however, useful as retreat sites, especially for small individuals, and may therefore provide higher quality habitat in the non-breeding season and for juveniles.

The population density of *P. longipes* was greater during the wet season than the dry season, as indicated by much higher proportional occupancy of all four tree species (Figs. 1a,b). The increase in density is probably driven by the emergence of juveniles that hatched late in

the dry season or early in the wet season. As a result, competition for optimal substrates was considerably lower in the dry season than in the wet season. In the wet season, two adults were observed occupying the same tree once (on *S. berteriana*), and an adult was observed on the same tree as a juvenile in two cases (once each on *P. acuminata* and *S. berteriana*), and multiple juveniles were observed on a single tree for all species except *M. bidentata*. This suggests that food was abundant enough throughout the wet season that it did not influence habitat selection.

To maximize fitness, individuals must respond to geographic and temporal changes in resource availability either by selecting a territory that provides them with high-quality habitat in all seasons or by moving to a different, higher-quality site when resources decline. Here, we provide evidence of a shift in substrate occupation from the wet season to the dry season in a sub-tropical whip spider, *P. longipes*. Given the limitations of this study, further research is needed to determine whether our observations are consistent with a long-term pattern or if the years we sampled represent an anomaly. Nevertheless, our findings are partially consistent with other research on habitat selection by amblypygids, particularly regarding tree selection in the dry season. However, the wet-season shift to occupying what we assume are lower-quality trees indicates that although habitat characteristics such as tree size are likely to determine whether or not a tree is suitable habitat, biotic interactions such as those that occur among *P. longipes* in the wet season are likely to further influence the small-scale distribution of a species.

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