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Plant structure specialization in *Paraphidippus basalis* (Araneae: Salticidae), a jumping spider of the Madrean Sky Islands

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Abstract. *Paraphidippus basalis* (Banks, 1904) is a large jumping spider that occurs in the sky islands of the southwestern United States and northern Mexico. To date, *P. basalis* has only been incidentally reported on rosette-forming plants in the family Asparagaceae (yucca, agave, and sotol), even though the sky islands support a rich and diverse vegetation community. This apparent specialization is unusual because jumping spiders do not typically have strong associations with the plants on which they live. However, given that the ecology of *P. basalis* has yet to be studied, the microhabitat preferences of *P. basalis* remain unclear. We investigated microhabitat choice in *P. basalis* in the Patagonia Mountains of southeastern Arizona, to determine whether these spiders were specifically associated with rosette-forming plants. We surveyed 160 plots for jumping spiders, 80 with rosette-forming plants and 80 without. *P. basalis* was found only in rosette-forming plants, whereas other species of jumping spiders showed no preference for rosette or control plots. Larger rosette plants were more likely to contain *P. basalis*. This study provides an unusual example of host plant structural specificity in a jumping spider.

Keywords: Agave, Arizona, microhabitat, sotol, yucca

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Habitat structure has long been recognized as an important driver of spider distribution and abundance (Lowrie 1948; Uetz 1991; Wise 1993). For spiders that live in vegetation, plants are complex structures that provide refuge against predators and the elements and offer attractive sites for prey (Wise 1993). Site abandonment for web-building spiders comes at a high energetic cost, since sedentary spiders must build a new web (Tanaka 1989) and avoid predation during and after relocation (Lubin et al. 1993). In contrast, since microhabitat relocations are part of the foraging strategy of spiders that actively hunt (Ford 1978; Wise 1993), cursorial spiders such as jumping spiders are not as dependent as web-building spiders on specific habitat structures. Reports of host-plant specificity in jumping spiders are rare (Vasconcellos-Neto et al. 2017), and only a few studies have reported them living on specific plant species (Taylor & Jackson 1999; Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2005; Meehan et al. 2009). Thus, our understanding of the associations of jumping spiders with particular plant species remains limited.

Paraphidippus basalis (Banks, 1904) is a large jumping spider that occurs in Arizona and New Mexico in the United States, and in Sonora, Mexico (Richman et al. 2011). Despite its large size rivaling that of salticids in the genus *Phidippus* CL Koch, 1846, and its conspicuous abdominal pattern that enables relatively easy identification in the field, the ecology and natural history of *P. basalis* have not been studied. Incidental reports of *P. basalis* indicate that this species is associated with the woodland habitats of mountain ranges known as the Madrean Sky Islands (Cowles 2018; GBIF.org 2019a), which are mountain ranges that stand above the desert lowlands and form isolated woodlands between the Rocky Mountains and the Mexican Sierra Madres (Warshall 1995). The majority of anecdotal observations of *P. basalis* have reported this species on agave, yucca, and sotol (Cowles 2018; GBIF.org 2019a; Richman et al. 2019) and the common name used in iNaturalist (2020) for *P. basalis* is the "agave jumping spider." Other anecdotal observations have rarely reported *P. basalis* on the ground (GBIF.org 2019a).

Agaves, yuccas, and sotols are rosette-forming plants in the family Asparagaceae that occur in subtropical, semi-arid, and arid regions. These plants are similar in appearance in that they have relatively rigid, long, and fibrous to succulent leaves that radiate from a central stem, and form radially symmetric rosettes. The relatively large rosette structure of agaves, yuccas, and sotols is unique compared to the structure of other plants in the Madrean Sky Islands. Floral diversity in the Madrean Sky Islands is very high, because these islands straddle two major floristic realms (Neotropic and Holarctic), occur at the convergence of three major climatic zones (tropical, subtropical, and temperate), and have a diverse geological composition (Warshall 1995). Given the preponderance of anecdotal observations of *P. basalis* on agave, yucca, and sotol, in an area known for its rich floral diversity, we tested the hypothesis that *P. basalis* specializes on rosette-forming plants. In addition, to better understand habitat use by *P. basalis*, we investigated whether the presence of *P. basalis* was related to rosette size.

METHODS

Study Sites.—We conducted this study in July through October, 2019 and March through April 2020 at four locations in the Patagonia Mountains, Santa Cruz County, Arizona (Fig. 1). These sites contained rosette-forming plants within different plant communities, which provided the opportunity to investigate a diversity of plant species as potential habitat choices for *P. basalis*. Site A (31.4969°N, 110.7592°W, elevation 1450 m) was an east-facing hillside dominated by broad-leaf hopbush (*Dodonea viscosa*) and bunchgrasses (Poaceae), with scattered oaks (*Quercus* spp.), ocotillo (*Fouquieria splendens*), and beargrass (*Nolina microcarpa*). Site B (31.4906°N, 110.7513°W, elevation 1500 m) was a

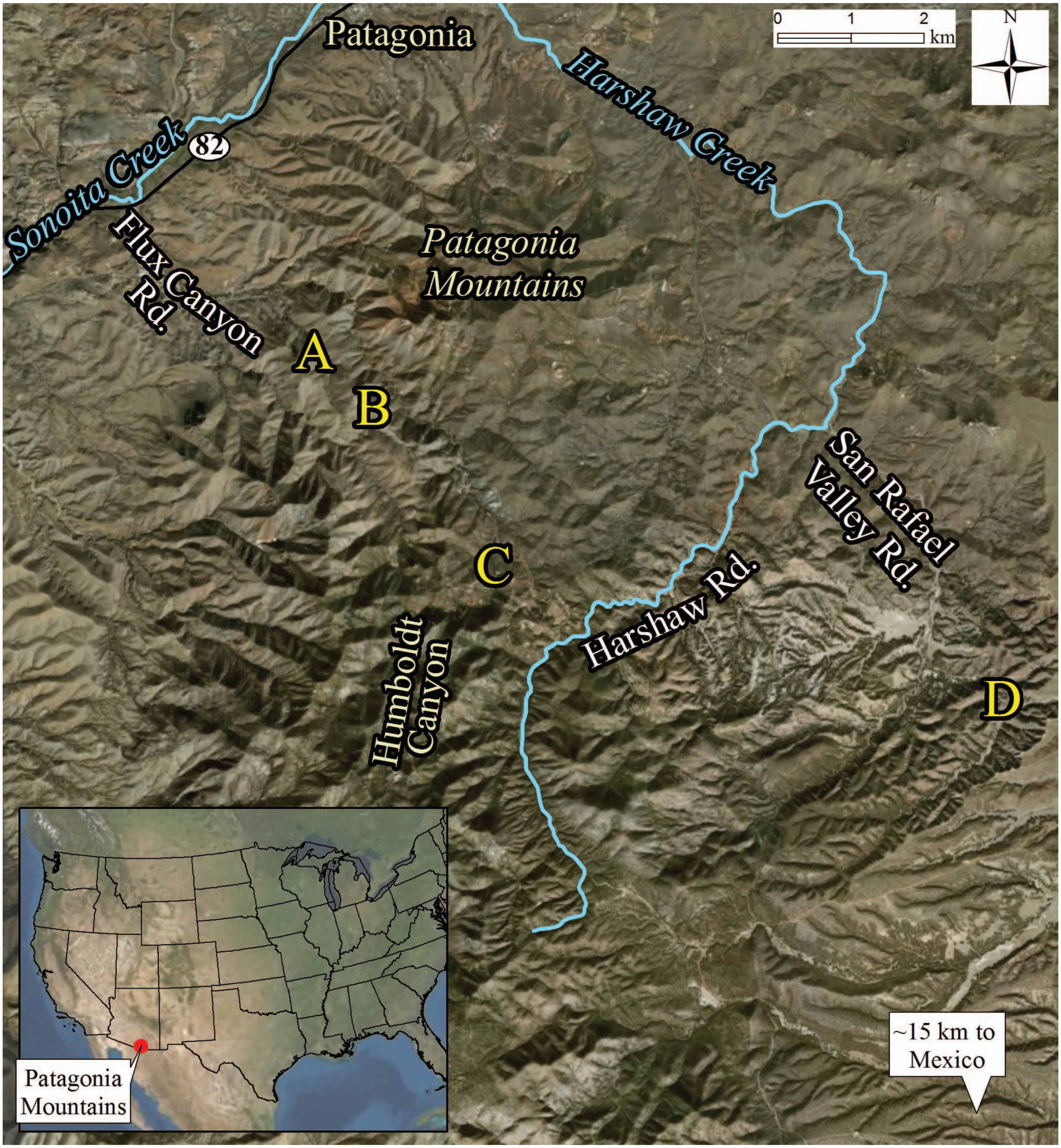

Figure 1.—Map of our four study sites (A-D) in the Patagonia Mountains of Arizona, USA.

south-facing hillside dominated by bunchgrasses with occasional Emory oak (*Quercus emoryi*), alligator juniper (*Juniperus deppeana*), and cacti. Site C (31.4729°N, 110.7333°W, elevation 1470 m) was a west-facing hillside at the mouth of Humboldt Canyon, dominated by oaks, alligator juniper, pines, and bunchgrasses, with a variety of forbs in the understory. Site D (31.4547°N, 110.6603°W, elevation 1500 m), was a southwest-facing hillside dominated by bunchgrasses and scattered oaks. Three species of large rosette-forming plants were common at our sites: Palmer's agave (*Agave palmeri*), mountain yucca (*Yucca madrensis*), and common sotol (*Dasylirion wheeleri*) (Fig. 2).

Figure 2.—a. Adult female *Paraphidippus basalis*. b. Mountain yucca (*Yucca madrensis*). c. Common sotol (*Dasylirion wheeleri*). d. Palmer's agave (*Agave palmeri*).

Field observations.—At each site, we established 20 pairs of 2 m × 2 m plots, with each pair consisting of a plot containing at least one individual rosette-forming plant (rosette plot), and of a plot without any rosette-forming plant (control plot). Plots in each pair were 4 m apart, and the direction of the control plot relative to the rosette plot was chosen in a statistically random way. If the location of the control plot generated by this method failed to avoid a rosette or vegetation disturbed by the observers when approaching the plots, a new random location was generated relative to the rosette plot. Upon completing our search of a control plot for jumping spiders, we established the next rosette plot to be sampled by identifying the nearest rosette that we could observe from the control plot we had just completed. If the nearest rosette plot overlapped with a previously sampled plot, then the next nearest rosette was used to establish the rosette plot instead. The distance between control plots and the next nearest rosette to be sampled ranged between approximately 5 m and 30 m. For each plot, we recorded the abundance of *P. basalis*, as well as the substrate on which they were found. We also recorded that information for other jumping spiders present in our plots, to compare their habitat use with that of *P. basalis*. In rosette plots, we measured the height and maximum width of each rosette plant to estimate rosette volume, following the formula for the volume of an ellipsoid.

All vegetation within the sample plots, including non-rosette vegetation in the rosette plots, was visually inspected up to 2 m height. The vegetation we inspected included entire grasses, forbs, shrubs, and trees, as well as plant parts (branches, trunks, leaves) that occurred within the plots, and desiccated or dead plants and their parts. The ground was also inspected, and the underside of rocks examined when possible. Our plot inspections included searches for silk shelters, which we carefully opened to check for the presence of jumping spiders. The location of these shelters was noted when they contained a jumping spider. Adult and immature *P. basalis* were readily identifiable in the field by their abdominal pattern of white spots on a solid black background, and a basal band on the abdomen that is white to orange depending on age. Jumping spiders other than *P. basalis* were identified to genus or species, when possible, and photographed. Individuals that that could not be reliably identified to genus, or that belonged

Table 1.—Total number of jumping spiders in plots with rosette-forming plants and control plots without rosettes, and the substrates on which the spiders were found.

Species	With Rosette	Control	Substrate
Paraphidippus basalis Banks, 1904	59	0	Palmer's agave* (*Agave palmeri*), mountain yucca* (*Yucca madrensis*), common sotol* (*Dasylirion wheeleri*)
Phidippus cf. *carneus* Peckham & Peckham, 1896	24	14	Alligator juniper (*Juniperus deppeana*), Palmer's agave*, mountain yucca, common sotol, pricklypear (*Opuntia* sp.), Emory oak (*Quercus emoryi*), Arizona baccharis* (*Baccharis thesioides*), hopbush (*Dodonea viscosa*), velvetpod mimosa (*Mimosa dysocarpa*), pointleaf manzanita (*Arctostaphylos pungens*), grass (Poaceae), ground
Metacyrba taeniola similis Banks, 1904	9	10	Under rocks*, ground with oak leaf litter
Sassacus papenhoei Peckham & Peckham, 1895	7	8	Hopbush*, Emory oak*
Phidippus carneus Peckham & Peckham, 1896	2	0	Mountain yucca, ground
Habronattus pugillis Griswold, 1987	1	1	Common sotol, ground
Phidippus octopunctatus (Peckham & Peckham, 1883)	0	1	Yerba de pasmo* (*Baccharis pteronioides*)
Paramaevia poultoni (Peckham & Peckham, 1901)	1	0	Common sotol
Colonus hesperus (Richman & Vetter, 2004)	1	0	Arizona white oak (*Quercus arizonica*)
Unidentified	12	7	Common sotol*, hopbush*, mountain yucca, Arizona white oak debris, grass, ground, rocks

* Some individuals were found within their shelters on this substrate type

to species that were rare ($n < 10$) in our plots, were excluded from the analysis.

Statistical analyses.—We compared the presence and absence of *P. basalis* on rosette plots and control plots using McNemar's test for paired binary responses, to test the null hypothesis that the presence of *P. basalis* did not differ between rosette plots and control plots. A test for paired data was chosen because the rosette and control plots were sampled as pairs, and because the environmental conditions within plots in each pair were similar due to their relative proximity. The same test was applied to the other most abundant jumping spiders in our plots. The effect of rosette volume on the presence of *P. basalis* within rosettes was examined using logistic regression to test the null hypothesis that the presence of *P. basalis* in rosettes was not linked to rosette volume. The regression modeled the relationship between rosette volume and *P. basalis* presence and absence in rosettes, by using a logistic function to estimate probabilities of presence and absence. Given that agaves, yuccas, and sotols differ in leaf density and leaf dimensions, which are characteristics that affect the total surface area available to spiders, the relationship between the volumes of these plants and *P. basalis* occupancy was analyzed separately. All statistical analyses were conducted in R 3.6.1 (R Development Core Team 2019).

RESULTS

***Paraphidippus basalis* observations.**—We observed a total of 59 individual *P. basalis* on 41 of the plot pairs. This species only occurred within rosette plots (McNemar's $X^2 = 39.02$, $P < 0.001$). In these plots, *P. basalis* was observed on Palmer's agave, mountain yucca, and common sotol. It was not found on any other plant species within the rosette plots and did not occur in any of our control plots. We observed adults of both sexes and immatures of different instars of *P. basalis* within the three species of rosette-forming plants. Rosettes occupied by this species contained between one and five *P. basalis*, consisting of one or two adults, one or more immatures, or a combination of adults and immatures. Their shelters were typically present in rosette plants that contained *P. basalis*. On several occasions, they were found inside their shelter; all other *P. basalis* detections consisted of individuals on rosette leaves; either in a sit-and-wait hunting position or actively moving on the leaves.

Observations of other jumping spiders.—We observed a total of 96 jumping spiders in our plots other than *P. basalis*. These jumping spiders were mainly represented by unidentified immature *Phidippus* with a red dorsum, *Metacyrba taeniola similis* Banks, 1904, and *Sassacus papenhoei* Peckham & Peckham, 1895. The observation of several adult *Phidippus carneus* Peckham & Peckham, 1896, within and near our plots suggests that at least a portion of the immature *Phidippus* belonged to this species. Given that immature *Phidippus* with a red dorsum cannot be reliably assigned to species, all individuals with a red dorsum are hereafter referred to as "*Phidippus* cf. *carneus*." *Paramaevia poultoni* (Peckham & Peckham, 1901), *Habronattus pugillis* Griswold, 1987, *Colonus hesperus* (Richman & Vetter, 2004), and *Phidippus octopunctatus* (Peckham & Peckham, 1883) were represented by no more than two individuals across all plots.

The presence of *P.* cf. *carneus* was not significantly different on rosette and control plots, (McNemar's $X^2 = 0.96$, $P = 0.32$) and individuals were observed on diverse substrates, including trees, shrubs, rosette-forming plants, grasses, and the ground (Table 1). On several occasions, we found *P.* cf. *carneus* in rosette plants occupied by *P. basalis*. *Sassacus papenhoei* occurred on both rosette and control plots (McNemar's $X^2 = 0$, $P = 1$), but was not observed on rosette plants. *S. papenhoei* was found mainly on hopbush (*Dodonaea viscosa*), and occasionally on Emory oak (*Quercus emoryi*). *Metacyrba taeniola* also occurred on both rosette and control plots (McNemar's $X^2 = 0$, $P = 1$), and was only observed under rocks, or on the ground.

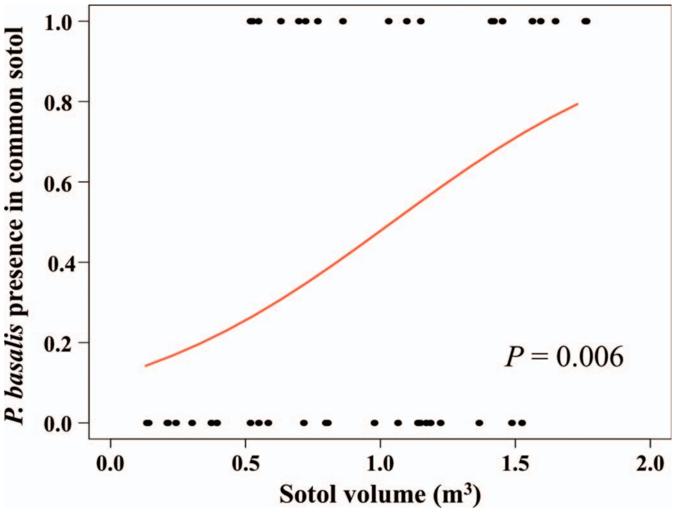

Figure 3.—Relationship between estimated plant volume and probability of *Paraphidippus basalis* presence for common sotol (*Dasylirion wheeleri*), as modeled by logistic regression. *P. basalis* were scored as present (1) or absent (0) in each plant.

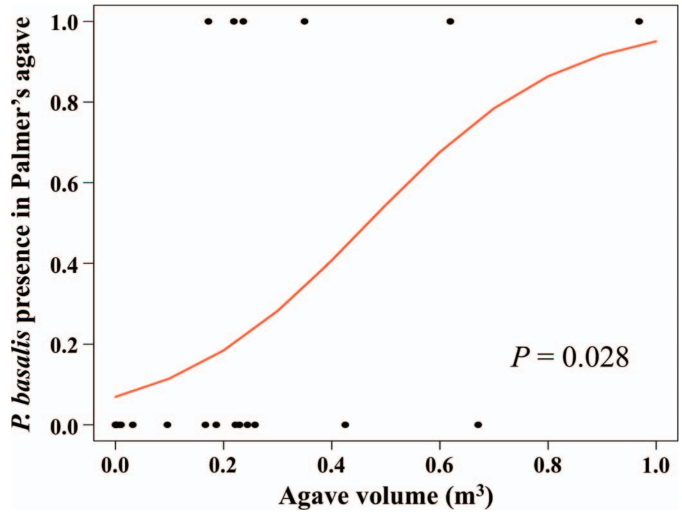

Figure 4.—Relationship between estimated plant volume and probability of *Paraphidippus basalis* presence for Palmer's agave (*Agave palmeri*), as modeled by logistic regression. *P. basalis* were scored as present (1) or absent (0) in each plant.

Effect of rosette size on *P. basalis* detections.—We documented the presence or absence of *P. basalis* on 46 common sotols, 28 Palmer's agaves, and 42 mountain yuccas throughout our rosette plots. The logistic regression showed that the probability of detecting *P. basalis* within sotols and agaves significantly increased as plant size increased (common sotol: coef. = 1.966 ± 0.724 *s.e.*, $z = 2.713$, $P = 0.006$; Palmer's agave: coef. = 5.555 ± 2.530 *s.e.*, $z = 2.195$, $P = 0.028$; Figs. 3 and 4). Similarly, we detected *P. basalis* more frequently in larger mountain yuccas, although the relationship between *P. basalis* presence and yucca volume was not significant (coef. = 0.973 ± 0.569 *s.e.*, $z =$ -1.71, $P = 0.087$; Fig. 5).

DISCUSSION

Habitat structure has a major influence on the local distribution of species because it affects important abiotic and biotic habitat variables, including temperature, vapor pressure deficit, wind speed, and light intensity (Geiger 1950), refuge availability, prey availability, and the intensity of competition and predation (Sunderland & Samu 2000). Vegetation provides a diversity of structural microhabitats to which spiders are sensitive, and the role of plants in shaping spider communities has been documented at different spatial scales, from specific plant parts to patches of vegetation (Wise 1993; De Souza & Martins 2005; Vasconcellos-Neto et al. 2017). The responses of spiders to vegetation structure may differ depending on their mobility levels when foraging. Jumping spiders are active hunters that pursue their prey (Ford 1978; Wise 1993), whereas web-building spiders are restricted to specific sites and adopt a sit and wait foraging strategy. The mobility of cursorial spiders provides them with greater flexibility to leave areas with low prey availability or unfavorable microclimate (Samu et al. 1999), compared to web-building spiders. As a result, jumping spiders may use not only their immediate surroundings, but also suitable habitats several meters away (Ehmann & MacMahon 1996; Sunderland & Samu 2000; Cobbold & MacMahon 2012).

We found *P. basalis* only on rosette-forming plants in the family Asparagaceae, despite the diversity of plant species and plant structures available to *P. basalis* in our plots. Several observations that we made in the vicinity of our study sites indicate that *P. basalis* not only prefers rosette-forming plants but also completes its life cycle on these plants. Specifically, we observed egg masses guarded by adult females, nests with spiderlings, and courtship and copulation events on these rosette-forming plants. In addition, *P. basalis* shelters were present in rosette-forming plants that contained *P. basalis,* and a shelter in one of the rosettes in our plots contained a *P. basalis* molt.

The preference of *P. basalis* for rosettes was not simply due to those structures providing generally good jumping spider

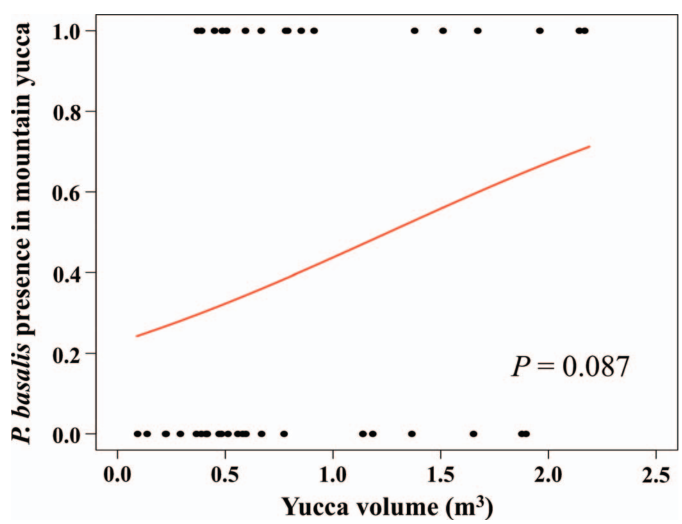

Figure 5.—Relationship between estimated plant volume and probability of *Paraphidippus basalis* presence for mountain yucca (*Yucca madrensis*), as modeled by logistic regression. *P. basalis* were scored as present (1) or absent (0) in each plant.

habitat, as other sympatric jumping spiders did not exhibit this preference. In contrast with *P. basalis*, there was no significant difference in the abundance of *P.* cf. *carneus* on the control and rosette plots. We found several instances of *P.* cf. *carneus* on Palmer's agave and common sotol, indicating some degree of habitat overlap with *P. basalis*. However, unlike *P. basalis*, *P.* cf. *carneus* was a generalist at our sites, in that it also occurred on several plant species that differed greatly in structure, such as grasses, prickly pear cactus, and alligator juniper. Our findings regarding *P.* cf. *carneus* habitat choice concur with Edwards (2004), who mentions that *P. carneus* is known to frequent agaves and prickly pear cacti, but that this species also occurs on other substrates. It is also possible that our "*P.* cf. *carneus*" included other *Phidippu*s species, thereby potentially increasing the number of substrate choices that we observed. For instance, *Phidippus* species with a red dorsum that may occur in and near the Patagonia Mountains include *P. ardens* Peckham & Peckham, 1901, *P. tyrrelli* Peckham & Peckham, 1901, *P. phoenix* Edwards, 2004, *P. californicus* Peckham & Peckham, 1901, and *P. apacheanus* Chamberlin & Gertsch, 1929 (Edwards 2004). There was no significant difference in the abundance of *Sassacus papenhoei* and *Metacyrba taeniola* on control and rosette plots, but we didn't find these species on rosette-forming plants. *Sassacus papenhoei* is known from desert shrubs, lupine, alfalfa, and cotton (Richman 2008), and is not specialized on any particular plant type. Members of the genus *Metacyrba* occur on foliage, bark, and stones (Barnes 1958), as indicated by our findings of *M. taeniola* on the ground and under rocks only.

Few examples of close associations between jumping spiders and specific plant species have been previously reported (Vasconcellos-Neto et al. 2017). Meehan et al. (2009) document the almost exclusive association of *Bagheera kiplingi* Peckham & Peckham, 1896 with the plant *Vachellia* sp., on which *B. kiplingi* nests, breeds, and feeds on specialized leaf tips (Beltian bodies). *Trite planiceps* Simon, 1899, a common New Zealand jumping spider, inhabits primarily the rolled-up leaves of New Zealand flax bushes (*Phormium tenax*) and similar plants (Forster & Forster 1973; Taylor & Jackson 1999), on which it hunts for prey and interacts with conspecifics, and it builds its nests within the desiccating rolled-up leaves of the plant. Romero & Vasconcellos-Neto (2004) report strict associations between *Eustiromastix nativo* Santos & Romero, 2004, *Pachomius* sp. Peckham & Peckham, 1896 (originally reported as *Uspachus* sp., Galiano, 1995), and *Psecas sumptuosus* (Perty, 1833) with terrestrial bromeliads in Brazil. *Psecas chapoda* (Peckham & Peckham, 1894) inhabits and breeds on only one specific bromeliad species, *Bromelia balansae*; this strict association occurs over a large geographic range (Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2005).

The strict associations between jumping spiders and bromeliads described by Rossa-Feres et al. (2000), and Romero & Vasconcellos-Neto (2004, 2005), are particularly relevant to our findings, because the terrestrial bromeliads described in those studies are rosette-forming plants with a three-dimensional architecture that is very similar to that of the plants on which we observed *P. basalis* (Palmer's agave, mountain yucca, and common sotol). We found that *P. basalis* was more likely to be present in larger rosette-forming plants, a result that is also similar to that reported by Romero & Vasconcellos-Neto (2005), who found that the jumping spider *Psecas chapoda* was more abundant on bromeliads with a larger surface area. It is possible that the lack of significant relationship between the volume of mountain yuccas and spider occupancy in our study originates from the existence of a trunk in some of the yuccas in our plots, which reduced the similarity of the shape of the plant to that of an ellipsoid, especially when the trunk was relatively long. The logistic regression models predicted probabilities of occupancy based on the range of volumes that were available in our plots. For instance, the agaves in our plots were generally smaller compared to the sotols and yuccas, such that the largest agaves were approximately half the volume of the largest sotols and yuccas. As a result, the volume at which the logistic regression predicted an equal likelihood of presence or absence of *P. basalis* was likely to be smaller for agave compared to sotol and yucca. Our results do not indicate specific volume thresholds for occupancy, but rather a general positive relationship between occupancy and rosette volume.

Rosette-forming plants such as Palmer's agave, mountain yucca, and common sotol likely provide beneficial microhabitat features for *P. basalis,* such as shelter from predators and from the elements, and larger plants provide more opportunities to use these beneficial features. The Madrean Sky Islands experience intense sun exposure and periodically receive heavy monsoon rains. Rosette-forming plants have long leaves with different angles and that face in all directions, which enables the spider to choose from multiple locations for the best shelter at any given time. For instance, we observed *P. basalis* resting on the side of the rosette plants that were in the shade during the hottest part of the day, and we have noticed *P. basalis* remaining active during light rains. Also, when approached, *P. basalis* typically retreated to the bottom or backside of the rosette leaves, or moved around the plant to avoid the observer. The spines and teeth of agave, yucca, and sotol, and the location of *P. basalis* shelters at the base of the leaves, are likely efficient defenses against vertebrate predators, and these defenses might be especially important for such a visually conspicuous spider. The layers of elongate leaves facing different directions in rosette-forming plants also provide *P. basalis* with a relatively large surface area from which the spider can locate prey from a distance. Larger plants may offer more prey, provide greater opportunities to locate and capture prey, and support more individual *P. basalis*.

Our observations of *P. basalis* of various ages, of their shelters and molts, and of behaviors such as predation, copulation, and nesting on rosette-forming plants, combined with the absence of *P. basalis* on non-rosette plants, demonstrate that this species is specifically associated with rosette-forming plants such as agave, yucca, and sotol. We have made incidental observations of *P. basalis* and their shelters on one additional species of rosette plant in the Patagonia Mountains, banana yucca (*Yucca baccata*), further supporting the specialization of *P. basalis* on rosette structures. While we did not observe any individuals on substrates other than rosette plants in this study, there is evidence that *P. basalis* disperses on the ground, as suggested from anecdotal observations (GBIF.org 2019a). The strong association of *P. basalis* with rosette-forming plants likely has strong implications for the ecology and evolutionary trajectory of this species. Currently, no other species of *Paraphidippus* FO Pickard-Cambridge, 1901 are known to specialize on specific plant structures. However, the microhabitat and substrate preferences of the other fifteen species of *Paraphidippus* remain poorly documented, and several of the Mexican species are represented by specimens of unclear origins (Richman et al. 2011; Hill & Edwards 2013). *Paraphidippus aurantius* (Lucas, 1833), which is the only species in the genus that is widely distributed in North America (Hill & Edwards 2013), has been reported on trees and shrubs in riparian areas (Richman et al. 2019), silverleaf oak (*Quercus hypoleucoides*; GBIF.org 2019b), and ponderosa pine (*Pinus ponderosa*; Mooney & Haloin 2006), suggesting a lack of specialization for specific plant structures. *Paraphidippus fartilis* (Peckham & Peckham, 1888), which occurs in the United States and Mexico (Richman et al. 2011), has been documented on tree leaves (Banks 1909) and on white mangrove (*Laguncularia racemosa*; Navarro-Rodríguez et al. 2016). Within the closely related genus *Phidippus*, Edwards (2004) mentions several species that appear to be closely associated with a particular plant, such as *Phidippus aureus* Edwards, 2004 on creosote (*Larrea tridentata*), *Phidippus vexans* Edwards, 2004 on sotol, and *Phidippus pruinosus* Peckham & Peckham, 1909, which is described as only having been found on juniper (*Juniperus* sp.) in central Texas. However, these associations have not been systematically tested. More systematic field observations are needed to determine if close associations exist between other members of *Paraphidippus* or closely related species such as *Phidippus*, and particular plant structures.

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