



Factors influencing predation on Odonata by *Argiope trifasciata* (Forsskål, 1775)

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Abstract. Despite a high number of incidental online records of spiders preying upon dragonflies/damselflies, studies on these interactions are scarce. Here, we describe the predatory behavior of *Argiope trifasciata* on the two most common odonate species in the study area, and whether various factors (web width, web length, spider body length, odonate body length, distance of the web from the edge of water body, and height of the web above ground) are related to the number of odonates captured. *Argiope trifasciata* employed stalking and frontal approaches as Odonata predation strategies. Our findings showed that larger Odonata are preyed upon by larger spiders. The greatest numbers of prey were caught in wider, higher webs, whereas narrow webs closer to the ground caught more small prey. Capturing success by *A. trifasciata* was similar in webs at different distances from the water for both species. Contrary to our hypothesis, there was no relationship between capturing success in either prey species and the distance of the web from the water. Habitat architecture may be more important to this interaction, as vegetation attracts both spiders (for anchoring webs) and odonates (as perch sites).

Key words. Arachnids, dragonflies, damselflies, Neotropics.

Research Article

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All relevant data are
within the paper and its
[Supporting Information files](#).

Introduction

Predation is a ubiquitous interaction that shapes the predator–prey behavior of species, influences population dynamics, transforms ecosystems, and drives model population dynamics (Lapiedra et al., 2018). Predator–prey interactions regulate food webs and affect community assemblies (Portalier et al., 2019; Start et al., 2020), rendering it crucial to evaluate the effects of predators on the population dynamics of their prey, including aspects such as prey selection, predation rates, and foraging behavior (Hayes & Lockley, 1990; Seibold, et al., 2018).

Spiders are among the most abundant and diverse groups within Arthropoda with more than 45,000 defined species in all terrestrial ecosystems and zoogeographical regions of the world (Coddington & Levi, 1991; Foelix, 2011; Platnick, 2014; Selden et al., 1991). The geographical distribution of spiders is closely linked to biotic and abiotic factors such as temperature, humidity, zones of habitat, vegetation, predators, and food availability (Foelix, 2011; Gonzaga et al., 2007). Although spiders' diets include some supplemental plant materials, other spiders, and non-arthropod prey (Foelix, 2011; Nyffeler et al., 2016), almost all spiders are carnivores and predominantly feed on insects (Birkhofer & Wolters, 2012; Pekár & Toft, 2015). Likewise, most spiders are polyphagous predators (i.e., feed on a high diversity of prey), consuming whatever they find or catch, which could benefit their growth and survival rates (Toft & Wise, 1999). Sensory systems in spiders are highly evolved due to their diverse range of lifestyles and foraging behaviors (Barth, 1997).

Spiders around the world are estimated to consume between 400 and 800 million tons of prey annually (Nyffeler & Birkhofer, 2017), mostly in the shape of insects of the orders Diptera, Hemiptera, Hymenoptera, Coleoptera, Lepidoptera, and Orthoptera in savannas, grasslands, and forests in the Tropics (Nyffeler & Birkhofer, 2017). They employ diverse strategies to capture prey, including building orb webs, which are highly efficient and specialized traps (Foelix, 2011; Herberstein & Tso, 2000; Zschokke et al., 2006). Orb-web spiders are sit-and-wait predators, selectively hunting insects that depend on vegetation for their activities (Shear, 1986). Ambushing is a predation strategy that reduces energy expenditure and mortality risks while optimizing energy gain (Sih, 1993).

Web-building spiders can be used as model organisms to study trophic interactions because predator–prey interactions are relatively easy to quantify (Arvidsson et al., 2020; Ludwig et al., 2018; Michalko et al., 2021). In the evolutionary history of orb-web spiders, there is strong evidence for evolution towards increased body sizes, larger and stronger webs, and high-performing silks (Hormiga et al., 2000; Sensenig et al., 2010). These characteristics may allow larger spiders to capture larger or more prey (Harmer et al., 2015).

Formal and incidental records show that *Argiope* spp. predate upon several dragonfly and damselfly species (see [Supplementary material](#)). *Argiope* species exhibit bodies with brightly-colored markings that function as attractive visual signals to increase capturing success (Craig & Ebert, 1994). Furthermore, inefficient Odonata maneuverability and perception of webs may increase the hunting success of the spiders (Rehfeldt, 1992). From all the above, studying spider predation on Odonata may help with understanding its impact on population dynamics, including adult population size and reproductive success, which depend on lifespan (Banks & Thompson, 1987; Fincke, 1988; Hilfert-Rüppell, 1999).

Although most spider species are generalist predators with diets that mainly include herbivores and detritivores (Birkhofer & Wolters, 2012; Nyffeler & Sunderland, 2003), other predators are also included (e.g., odonates and other spiders). Thus, it is interesting to study predation on odonates, and to find out whether web size, spider body length, prey length, distance of the web to the edge of a body of water, and height of the web above the ground influence the trapping success of these predators (i.e., Odonata) in a locality.

We assessed the predation of *Argiope trifasciata* (Forsskål, 1775) on two odonate species: *Mesamphiagrion laterale* (Selys, 1876) and *Rhionaeschna marchali* (Rambur, 1842). The main aims of the study were to i) describe the predatory behavior of *A. trifasciata* on these two odonate species, and ii) determine if web and predator characteristics are related to the mass, size, and number of dragonflies captured by *A. trifasciata*. Our hypothesis was that larger spiders in larger webs that are closer to the water would capture more and larger dragonflies.

Material and methods

Study area

Our study site, the Club Náutico El Muña, is a protected area situated in the Colombian municipality of Sesquilé (near Bogotá) at an elevation of 2,600 m at the freshwater reservoir Embalse del Tominé (4°50'9.80" N and 73°55'0.70" W). The vegetation here includes wild Andean Forest species and introduced plant species, such as *Acacia* sp., *Juncus* sp., *Commelina* sp., *Brachiaria* sp., *Polygonum punctatum*, *Bidens laevis*, *Carex* sp., *Alnus acuminata*, *Typha latifolia*, *Azolla filliculoides*, *Lemna gibba*, *Pennisetum clandestinum*, and *Eichhornia crassipes*. Flora and fauna in the area have been protected for more than 50 years, preventing deforestation and fragmentation. The area includes a stream named Agua Clara, which originates in the Paramo ecosystem. This area offers a variety of habitats, including preserved Andean forests, old abandoned plantations of *Acacia* sp. and eucalyptus, and grasslands, which have contact with the stream and dam. Furthermore, this protected area is important in that it is located in a zone with many disturbed ecosystems and harbors dragonfly species that have disappeared from surrounding areas.

Studied species

Argiope trifasciata, the Banded Garden Spider (Figs 1a–c), is a medium-sized spider (4–25 mm) of the family Araneidae with an oval abdomen and a silvery dorsal side with transverse black lines, which become more crowded posteriorly. This species is distributed in at least 50 countries across six continents (Abel et al., 2020).

Rhionaeschna marchali is an aeshnid species with large adults (body length 56–63.5 mm) with yellow mesepimeral and metepimeral stripes on the thorax and a pale reddish brown abdomen with light blue and yellow spots (von Ellenrieder, 2003). It is a territorial species found in crop fields and pastures and along streams and ponds with muddy bottoms surrounded by *Juncus* spp. (Juncaceae) and *Typha* spp. (Typhaceae) (Limongi, 1983).

Mesamphiagrion laterale is a medium-sized coenagrionid (body length 26–36 mm). Mature adults exhibit brown or black colors with light blue postocular spots, thoracic stripes, and the same color on the insides of the femurs and dorsally between the 7–9 (males) or 8 (females) abdominal segments, and they have hyaline wings (Bota-Sierra & Wolff, 2013). This species inhabits areas adjoining reservoirs, small lakes, marshes, impoundments, and swamps, using grasses and bushes for shelter (Álvarez-Covelli et al., 2015; Palacino-Rodríguez et al., 2020a, b). *Rhionaeschna marchali* and *M. laterale* were selected because they were the most abundant odonates in the study area and most common prey in *A. trifasciata* webs.

Data collection

Data were recorded during 480 h on 60 days between October 2020 and February 2021 in an area of 1,980 m² (66 × 30 m). In this area, the location of each spider and its orb web was marked using pennants. One square meter of grassland may host 1 to 20 webs. If a web is structurally damaged, the occupant spider may rearrange it or weave a new one within a few minutes. We observed hundreds of small spiders moving about in the webs of several adults while these were feeding.

We recorded the heights of the webs and their distances to open water. The size of each spider was recorded by measuring body length, both with and without leg length. Dragonfly prey were identified and body lengths were measured. The measurements were taken with a Vernier caliper and decameter (both US Tool™,

California, USA). Each measurement was taken three times and averaged for our analyses.

Data analyses

The association between number of dragonflies/damselflies captured and explanatory variables was estimated as per a Generalized Linear Model (GLM) in R software v. 4.3.1 (R Core Team, 2010), with $p < 0.05$ being considered statistically significant. The number of prey odonates was modeled with a Poisson distribution, and an iterative approach was used to choose the explanatory variables in the GLM (Kleinschmidt et al., 2001). The best GLM model was selected using the Akaike information criterion and its explanatory power with pseudo-R-squared measurements (Heinzl et al., 2005).

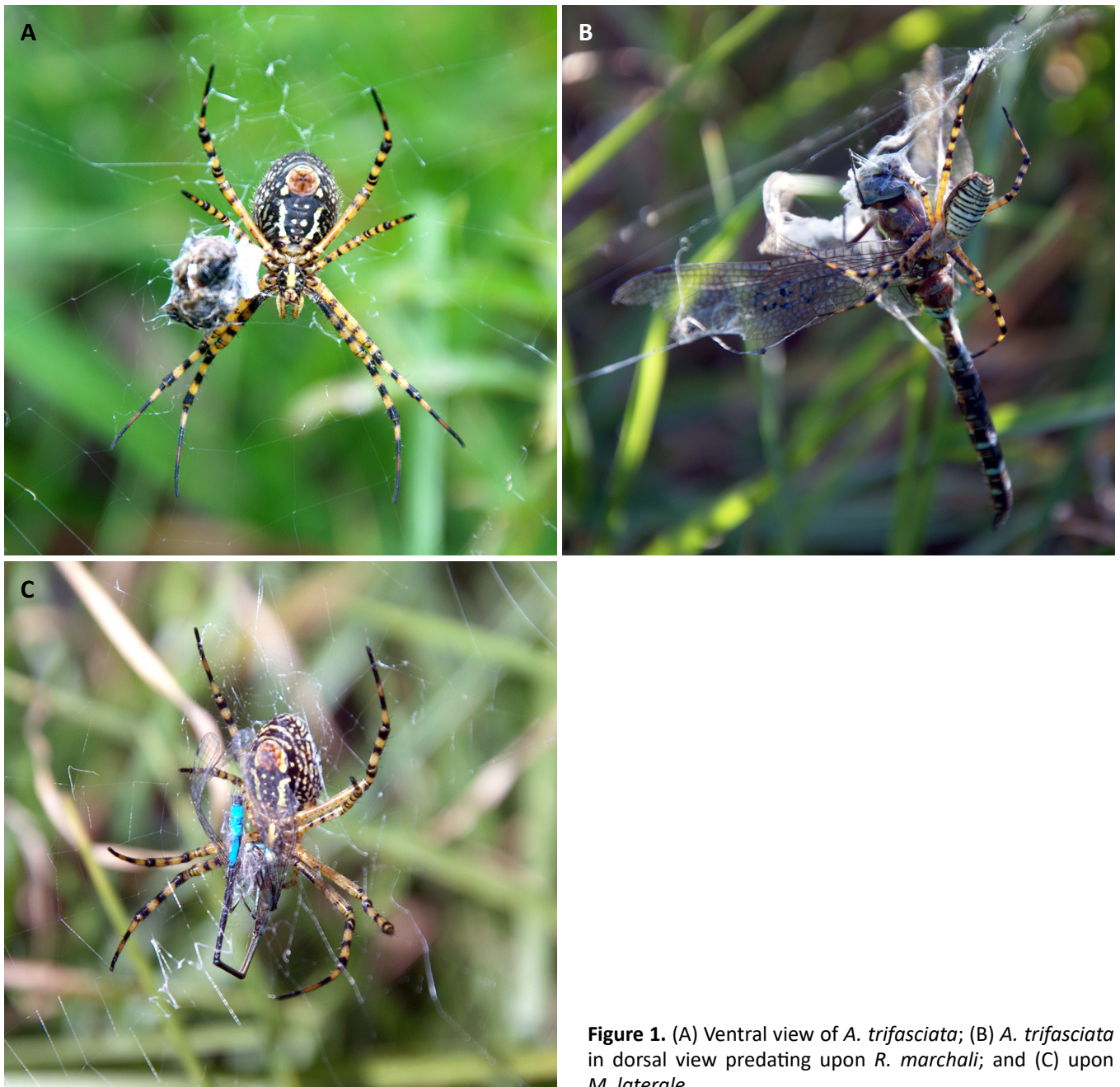


Figure 1. (A) Ventral view of *A. trifasciata*; (B) *A. trifasciata* in dorsal view predated upon *R. marchali*; and (C) upon *M. laterale*.

Table 1. Descriptive statistics about the measured variables for *R. marchali*. n, number of individuals; min, minimal value; max, maximum value; sd, standard deviation.

	n	min	max	mean	sd
Distance from water	364	3	33.8	18.49	8.95
Spider web height (in cm)	364	30	80	55.83	14.65
Spider web width (in cm)	364	20.1	50	35.65	9.09
Spider web length (in cm)	364	25	49	37.46	6.8
Body spider length (in mm)	364	12	18	14.84	1.72
Body spider length with legs (in mm)	364	20	44	36.43	3.93
Odonata body length (in mm)	364	60	65	62.41	1.43

Table 2. Descriptive statistics about the measured variables for *M. laterale*. n, number of individuals; min, minimal value; max, maximum value; sd, standard deviation.

	n	min	max	mean	sd
Distance from water	258	3	33.8	18.17	8.80
Spider web height (in cm)	258	30	80	52.93	14.65
Spider web width (in cm)	258	20	50	35.17	8.86
Spider web length (in cm)	258	25.2	48.8	37.30	6.74
Body spider length (in mm)	258	12	18	14.95	1.66
Body spider length with legs (in mm)	258	30	44	36.72	3.93
Odonata body length (in mm)	258	29	32	30.52	0.86

Table 3. General linear model results showing the relationships between numbers of prey items captured and explanatory variables. Std, standard error; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Covariates	Estimate	Std	z value	Pr(> z)
(Intercept)	-1.676207	0.4590425	-3.652	0.000261***
Distance to water	-0.000802	0.0041135	-0.195	0.845424
Spiderweb height	-0.000806	0.0024819	-0.325	0.745521
Spiderweb width	0.0008935	0.0040474	0.221	0.825276
Spiderweb length	0.0012731	0.0053602	0.238	0.812264
Body spider length	0.0120632	0.0214361	0.563	0.573603
Body spider length including legs	0.0017332	0.0011309	1.533	0.125378
Odonata body length	0.0283852	0.0017133	16.567	< 2e-16***

Subsequently, descriptive analyses of patterns in predator and prey size frequencies were visualized with bar graphs and box graphs (not shown here), respectively. To test for the existence of significant differences in the amount of prey according to their body size, a Mann-Whitney test was applied, since the distribution of the data was judged not normal. Likewise, a normal approximation test (z) was performed (Hajian-Tilaki, 2014). Then, the relationship between the amount of prey and the distance of the web from the edge of the nearest body of water was assessed with the non-parametric Spearman rank correlation test.

Results

Argiope trifasciata predatory behavior

Individuals of *A. trifasciata* may or may not have been visible in their webs. If not visible, they appeared rapidly on the scene in the presence of large prey such as *M. laterale* or *R. marchali*; however, this was not the case when smaller prey, such as mosquitoes or heteropteran bugs, became entangled in the web. The presence of an odonate in the web elicited two kinds of behaviors from *A. trifasciata*: stalking (with *R. marchali*) and a frontal approach (with *M. laterale*). In response to the struggles of an *R. marchali*, the spider would bite

the dragonfly and then move to the far side of the web. After 30 s to 1 min, while the dragonfly was still moving, the spider would approach it again and cocoon its thorax and often also its head and legs. In the presence of *M. laterale*, the spiders would directly attack and bite the dragonfly between the head and thorax, immediately cocooning the head, thorax, legs, and sometimes the abdomen of the prey.

Factors affecting predation on odonates

From the variables we measured (Tables 1–2), the GLM indicated that more *R. marchali* individuals were caught than *M. laterale* ($R^2 = 0.66$, $p < 0.001$, AIC = 1742.2) (Table 3). The total number of *R. marchali* captured, however, was positively associated with web width and web height above ground (Fig. 2a). In contrast, the total number of *M. laterale* captured was negatively correlated with web width and web height above ground (Fig. 2b), with more prey caught in smaller webs close to the ground. We found that the same spider could have one *R. marchali* individual per web, but two, three, or even four individuals could also be found in its web at the same time (Fig. 3). The amount of prey caught by *A. trifasciata* in webs located at different distances from the water was similar for both species.

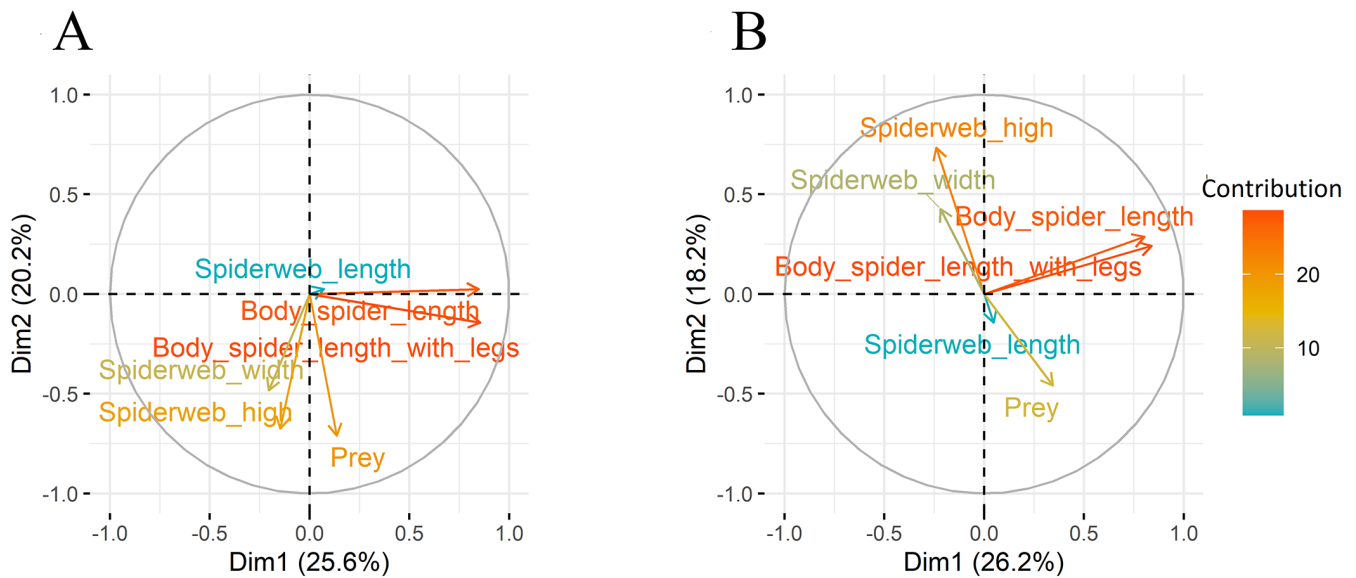


Figure 2. Factors affecting predation on odonates. (A) Web width, height above ground, and number of *R. marchali* captured by *A. trifasciata*. (B) Web width, height above the ground, and number of *M. laterale* captured by *A. trifasciata*.

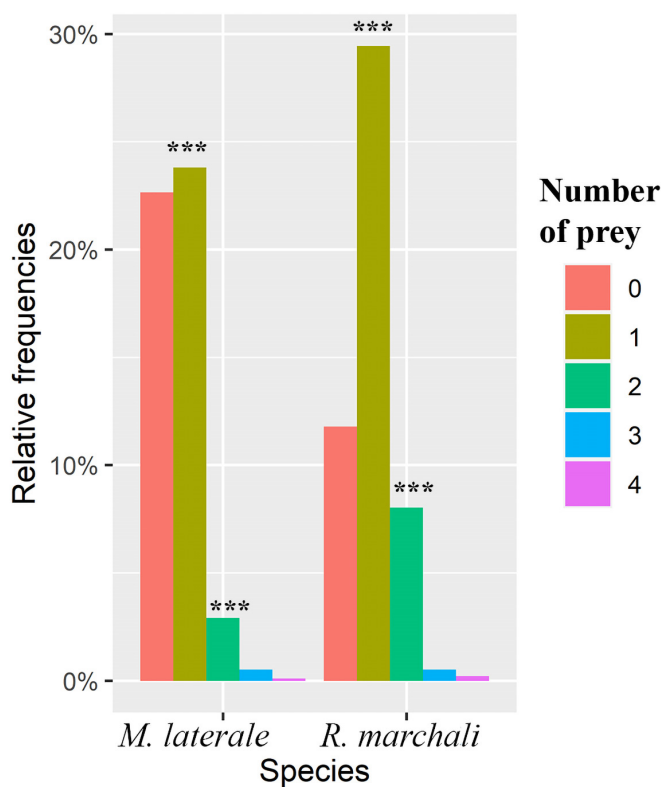


Figure 3. Number of individuals of *R. marchali* simultaneously trapped by *A. trifasciata*. In all cases, prey individuals had been captured on the same day.

Discussion

First, we must clarify the limitations of our study. Although the number of individuals sampled in our study was adequate, our data lack both replications of sites and seasons. Thus, it should be considered that with a

small sample size, it is difficult to generalize our findings, and our conclusions should be extrapolated only with circumspection. We hypothesized that the number of odonates captured by the orb-weaving spider *A. trifasciata* should increase with increased web size and proximity to water. Neither hypothesis was supported. The only significant determinant was prey body size, but this was largely due to the greater capture rate of the larger species (i.e., *R. marchali*). Prey composition of predatory spiders has been explained by predictors such as hunting guild, habitat type, environmental temperature, and body size (Birkhofer et al., 2022; Michalko et al., 2021). The hunting success of web-building spiders depends on the heterogeneous architecture of plants, a relatively low frequency of disturbance, and the availability of suitable attachment points for their webs in their habitats (Barriga et al., 2010; Diehl et al., 2013; Greenstone, 1984; Prieto-Benitez & Mendez, 2011).

In our study, *A. trifasciata* inhabited grassland microhabitats in a protected area with high plant heterogeneity of the native Andean Forest. This grassland consists of at least ten species of herbaceous plants, which provide a variety of places for attaching webs. Furthermore, this grassland is where the two Odonata species predated by *A. trifasciata* perch and rest. Thus, these dragonflies and damselflies regularly fly or perch in this area, and therefore they are constantly exposed to the risk of predation by spiders. In addition, *R. marchali* and *M. laterale* render themselves vulnerable to being captured due to their high mobility in appropriate zones of the habitat in which they are unlikely to detect or evade the webs, and have an adequate size for web size and strength (Turnbull, 2011).

The size and type of prey for spiders have been explained by functional traits of the spider species, such

as hunting guild and body size, and that larger spiders can capture larger prey if such is available (Birkhofer et al., 2022). Differences in web size are associated with sex, with larger individuals building larger webs. Thus, similar to other species in the *Argiope* genus, *A. trifasciata* females (body length ~15–25 mm) build larger webs than males (~4–5 mm) (Griffith & Gillett-Kaufman, 2019), enabling them to capture more size-varied prey.

Larger webs allow the capture of a greater number of prey or larger prey with higher energy content, which will supply energy to grow and build larger and resistant webs (Brown, 1981; Florez et al., 2004; Foelix, 1996). However, larger webs are also more likely to be destroyed by vertebrates, so that there is probably a trade-off (*A. Cordero-Rivera pers. comm.*). In addition, an increase in spider corporal size facilitates simultaneous improvements in other characteristics, including the production of more viscous silk and more diverse vertical structures qualified to intercept and hold larger prey animals with their higher kinetic energy output during impact and struggle (Harmer et al., 2011).

On the other hand, it is known that web-building spiders may alter their web properties to maximize the interception of the preferable or available prey (Tso et al., 2007). Like in other species of the *Argiope* genus, *A. trifasciata*'s web architecture plays a significant role in maximum web performance vis-à-vis prey with high kinetic energy (Harmer et al., 2015). Additional features of webs used to capture such larger prey may include larger sticky spiral spacing, a location closer to an approximately vertical substrate, greater amounts of adhesive on sticky lines, a tighter web, and more radii (Eberhard, 2013). Thus, longer radials could be more advantageous because they better absorb the the struggling prey animal's kinetic energy by dissipating it more widely (Harmer et al., 2015). However, future studies are required to measure and clarify these topics.

Differential capture of Odonata prey by *Argiope trifasciata* webs located at different heights above the ground is in agreement with the previously described perching behavior of *R. marchali* and *M. laterale* (Palacino-Rodríguez et al., 2020a). For instance, *M. laterale* perch directly on the ground or grass and other herbs, which is probably associated with capturing prey and thermoregulation (Palacino-Rodríguez et al., 2020a); therefore, *M. laterale* individuals are routinely located closer to the ground and can be captured in more lowly set webs. On the other hand, *R. marchali* individuals prefer higher perches close to running brooks (Limongi, 1983), leading to their more frequent capture in higher webs. Our observations in the field indicate that *R. marchali* preferably rest on taller grasses, where they are captured by spiders building more highly set webs. Apparently, this aspect is more relevant to the behavior of predation by *A. trifasciata* than the distance of a web to the nearest body of water because the entire area provides places for odonates to perch and, correspondingly, for the spiders to build their webs.

Our findings provide important insights about factors affecting spider predation on Odonata. Nonetheless, future studies are needed to understand the strategies of prey and predators to maximize their fitness, as well as the effects of fragmentation, pollution, and deforestation on seasonal and spatial patterns of population dynamics for both odonates and spiders as a result of their predator-prey interactions.

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Supplementary material

Supplementary Material 1. Odonata species predated by *Argiope* spiders.