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Morphological and behavioral traits associated with myrmecomorphy in *Sarinda marcosi* Piza, 1937 (Araneae: Salticidae: Sarindini)

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Abstract. *Sarinda marcosi* Piza, 1937 is an ant-like jumping spider that shares its microhabitat with the carpenter ant *Camponotus mus* Roger, 1863 (Hymenoptera: Formicidae). The objectives of this study were to record *S. marcosi* from Uruguay, to describe the type of mimicry present in this species, and to determine the ant model it mimics and how closely it resembles it. We recorded measurements of the prosoma, opisthosoma and sternum of *S. marcosi* and *Aphirape flexa* Galiano, 1981 (Salticidae), a sympatric non-mimetic jumping spider, to calculate mimicry indices as indicators of mimicry. We created three experimental groups in which we exposed: (1) *S. marcosi* vs. *C. mus*, to test Peckhamian mimicry; (2) *S. marcosi* vs. *A. flexa*, to test the response of *S. marcosi* in front of a potential predator; and (3) *A. flexa* vs. one juvenile of *Phiale roburifoliata* Holmberg, 1875 (Salticidae), to test the response of *A. flexa* in front of a non-mimetic jumping spider ($n = 15$, for each experimental group). We observed similarities between *S. marcosi* and *C. mus*, both in coloration and morphology. All mimicry indices obtained were indicators of mimicry for *S. marcosi*. There were no attacks by *S. marcosi* towards *C. mus* and no successful attacks of *A. flexa* on *S. marcosi*, but *A. flexa* successfully attacked *P. roburifoliata*. According to these results, *S. marcosi* is a Batesian mimic and *C. mus* serves as its model. This study indicates that mimicry provides protection against predators to *S. marcosi*. Additionally, we provided new data about the taxonomy of the spider.

Keywords: Arachnida, Amycoida, ecology, antipredator adaptation, South America.

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The jumping spider family Salticidae is the most species rich in the order Araneae, with 646 genera and 6,222 species (World Spider Catalog 2020). This group includes spiders of small and medium sizes, distributed throughout the world. All known species are diurnal, they hunt by stalking and jumping on their prey and have highly developed vision (Jocqué & Dippenaar 2006). Myrmecomorphy is a type of mimicry in which organisms imitate certain species of ants, both in their morphology and behavior (Reiskind 1972). For example, some morphological adaptations to mimicry can include constrictions to the prosoma and/or opisthosoma, thin legs, and the presence of setae with colors similar to model ant species, among other characteristics (Oliveira 1988; Cushing 2012). Some salticid species present myrmecomorphy as a mechanism of protection against predators, or to feed on the ant species they imitate, or both (Cushing 2012). Ants have different defense mechanisms such as formic acid secretions, the presence of spines, stings associated with venom glands, hard integuments, strong jaws and group defense (Reiskind 1977; Oliveira 1988; Hölldobler & Wilson 1990; Cushing 2012). This tends to make ants unappetizing for generalist arthropod predators, including spiders, although a few species feed exclusively on them (Nelson et al. 2004). In spiders, there are two types of mimicry linked to myrmecomorphy (Cushing 2012). One is known as aggressive or Peckhamian mimicry, in which the spider imitates the species of ant on which it feeds. For example, *Aphantochilus rogersi* O. Pickard-Cambridge, 1871 (Thomisidae) morphologically imitates *Cephalotes pusillus* Klug, 1824 (Formicidae), and attacks the ants when they are approaching (Castanho & Oliveira 1997). The other type of mimicry is Batesian or defense mimicry, in which the spider imitates a species of ant which is unappetizing to predators. This is the case of *Myrmecotypus iguazu* Rubio & Arbino, 2009 (Corinnidae), which imitates *Camponotus sericeiventris* Guérin-Méneville, 1838 (Formicidae) both in its morphology and behavior, thus reducing predation (Rubio et al. 2013). Because ants are found in almost all terrestrial environments and have few specialized predators, they present a stable model of Batesian mimicry (Oliveira 1986).

Sarinda Peckham & Peckham, 1892 is a genus of jumping spiders represented by 17 species distributed mainly in Central and South America (World Spider Catalog 2020), all of which are myrmecomorphs (Franganillo 1930; Galiano 1965, 1967, 1969, 1981, 1996). However, the type of mimicry *Sarinda* species present has not yet been determined. The objectives of this study are to determine the type of mimicry present in *S. marcosi* Piza, 1937, to determine the ant model it mimics and how closely it resembles it. Additionally, we report the genus and species from Uruguay for the first time, provide a diagnosis for the species and provide new data on its natural history and distribution. In doing so, we hypothesize that *S. marcosi* is a Batesian mimic of the carpenter ant *Camponotus mus* Roger, 1863 (Hymenoptera: Formicidae: Camponotini).

METHODS

Taxonomy and distribution.—We examined specimens deposited in the arachnological collection of the Facultad de Ciencias (FCE-Ar), Universidad de la República (UdelaR), Montevideo, Uruguay. We determined the identification of individuals of *S. marcosi* based on the descriptions and diagnostic characters indicated by Piza (1937) and Galiano (1965). We took photographs of diagnostic somatic and genitalic characters using a Nikon YS100 stereomicroscope and a JEOL 5900 Scanning Electron Microscope from Servicio de Microscopía Electrónica de Barrido, Facultad de Ciencias, Universidad de la República. The photographs of the individuals in their natural environment were taken with an Olympus Stylus Tough Tg-4 digital camera.

We constructed a distribution map of *S. marcosi* in Uruguay using SimpleMappr (Shorthouse 2010).

Mimicry indices and measurements.—We calculated mimicry indices to test if they were appropriate mimicry indicators in *S. marcosi*. To calculate the different morphological mimicry indices, we followed Reiskind (1970). We measured the prosoma, opisthosoma and sternum width and length of ten males and ten adult females of *S. marcosi* and *Aphirape flexa* Galiano, 1981, the latter a non-mimetic and sympatric jumping spider. We calculated the indices as follows: prosoma index = prosoma width / prosoma length $\times$ 100; sternum index = sternum width / sternum length $\times$ 100; and opisthosoma index = opisthosoma width / opisthosoma length $\times$ 100. Any elongation of structures (prosoma, sternum or opisthosoma) will result in low index values. Ant-like spiders should have low indices, since thinness of the body usually enhances the mimetic resemblance. We also measured the total length of the body and the length of each leg, and for 10 worker ants of the species *Camponotus mus*, we measured the length of the body, antenna and three pairs of legs. We took all the measurements under a microscope (Nikon SMZ-10) using an ocular micrometer.

Myrmecomorphy description and experimental trials.—We collected 15 individuals of *S. marcosi*, 15 individuals of *A. flexa*, 15 juvenile individuals of *Phiale roburifoliata* Holmberg, 1875 (*A. flexa* and *P. roburifoliata* represent non-mimetic jumping spider species) and 45 worker ants of *C. mus* in shrubs and cacti from Facultad de Ciencias, Montevideo, Uruguay (34°52′56″S, 56°07′04″ W). The individuals were collected manually during sunny days between the months of October and December 2018. As we collected the individuals of each species, we performed field observations and recorded descriptive data about the natural history of *S. marcosi*, noting especially how it interacted with ants, with potential predators and with prey. We housed the captured spiders in plastic petri dishes with moistened cotton in water and fed them three times a week with *Drosophila melanogaster* Meigen, 1830 *ad libitum*. The subadults were raised to adulthood under laboratory conditions. The ants were captured on the days when the experiments were carried out, in the same place where the individuals of *S. marcosi* had been collected.

To study the type of mimicry represented by *S. marcosi*, we designed three experimental groups ($n = 15$ for each group). In Group 1, one specimen of *S. marcosi* was exposed to three worker ants of *C. mus* to check for aggressive mimicry. The three ants were placed on the test arena for between one and two minutes to allow for acclimation, before introducing the spider. In Group 2, one individual of *S. marcosi* was exposed to an individual of the sympatric jumping spider species *A. flexa*, under similar conditions to those of Group 1. According to field observations, *A. flexa* has a larger body size, is found in greater abundance in the same microhabitat as *S. marcosi*, and includes in its diet other jumping spider species, meaning *A. flexa* is a potential predator of *S. marcosi*. In Group 3, an individual of *A. flexa* was exposed with a juvenile of *P. roburifoliata*, a non-mimetic jumping spider of smaller size collected in the same microhabitat of *A. flexa* and *S. marcosi*. This group acted as a control to verify that *A. flexa* feeds on other sympatric jumping spiders. We used adult individuals of *S. marcosi* and *A. flexa* of both sexes indistinctly and randomly. Each experimental group consisted of 15 trials, which were carried out in glass petri dishes (100 mm in diameter $\times$ 15 mm in height) with white filter paper under the base of the container to improve contrast during the recording of behaviors and videotaping. The order of the trials was alternated between the three groups to reduce the effect of the method.

The trials were carried out between November 1 and December 11, 2018. The temperature of the room averaged 24.5 ± 1.1°C (21–28°C) and humidity was 58.7 ± 9.6% (47–80%). The observations were made in a room with natural lighting conditions in the period between 14:30 and 18:30 hours, a time-period in which the spiders had been seen to be active under natural conditions. Each spider was starved for three days prior to observations, as a way to standardize their hunger levels. After each observation, we offered each individual of *S. marcosi* and *A. flexa* a regular prey such as the fruit fly *Drosophila melanogaster* and recorded if the attack occurred. This was done to check the degree of starvation of the spiders and rule out the possibility that the absence of attacks was due to reasons such as the health status of the animal or satiety. All observations corresponding to the experimental groups were recorded with a video camera (SONY-SR87) for 20 minutes following the introduction of the ants or spiders.

We analyzed the videos with the behavior analysis package JWatcher (Blumstein et al. 2000), generating descriptions for each behavior and recording their durations. We also recorded the frequencies of attacks in each group; those attacks in which *A. flexa* managed to capture and feed on its prey (carried out to completion) were considered to be successful attacks. We analyzed the interactions between species and constructed flow diagrams of the behaviors with frequencies between 0.2501 and 1. We performed Markov analysis to evaluate if there were statistical associations between behavioral transitions (Blumstein & Daniel 2007) (see figures in Supplementary File 2, online at https://doi.org/10.1636/JoA-S-19-069.s2, and File 4, online at https://doi.org/10.1636/JoA-S-19-069.s4). The individuals of *S. marcosi* and *A. flexa* used in the experimental groups were deposited in the arachnological collection of the Facultad de Ciencias, Universidad de la República (UdelaR).

Statistical analyses.—We analyzed the existence, latency and number of attacks of *S. marcosi* on *C. mus* (Group 1), of *A. flexa* on *S. marcosi* (Group 2), and of *A. flexa* on *P. roburifoliata* (Group 3). We used Fisher's test to compare differences in attack frequencies within the experimental groups. We also investigated normality (Shapiro-Wilk test) and homogeneity of variances (Levene test) of the data. Because variances were not homogeneous, we used the non-parametric Wilcoxon paired test to compare the number of frequencies between the experimental groups. To verify if the corporal index affected the frequency of attacks, we performed a simple linear regression between those variables. We applied

Past (Hammer et al. 2001) and STATISTICA 8 (Weiβ 2007) statistical packages.

RESULTS

TAXONOMY

Family Salticidae Blackwall, 1841
Subfamily Salticinae Blackwall, 1841
Clade Amycoida Maddison & Hedin, 2003
Tribe Sarindini Simon, 1901
Genus *Sarinda* Peckham & Peckham, 1892
Sarinda marcosi Piza, 1937
(Figs. 1–5)

Sarinda marcosi Piza, 1937: 309, pl. 1, figs. 1, 2. Galiano, 1965: 292, pl. II, figs. 1–7, pl. III, fig. 4, pl. IV, fig. 3, pl. V, fig. 6, pl. VI, fig. 3, pl. VIII, figs. 1, 4. Jackowska & Prószyński, 1975: 42, fig. 4h.

Sarinda australis Mello-Leitão, 1944: 387, fig. 85 (synonymized by Galiano, 1965: 292).

Diagnosis.—Males of *Sarinda marcosi* can be distinguished from all other species in the genus, except *S. capibarae* Galiano, 1967, by the presence of a ventral tibial apophysis (Figs. 1E, F); and can be further distinguished from *S. capibarae* by the more elongated ventral apophysis (see Galiano 1967, figs. 20, 21). Females resemble *S. ruficeps* (Simon, 1901), *S. cayennensis* (Taczanowski, 1871) and *S. capibarae*, in the shape of the genitalic structures (Figs. 1I, J). It can be distinguished from *S. cayennensis* by the lack of a projection on the posterior margin of the atrium ("horseshoe" shape) (see Galiano 1965, pl. III, fig. 8), from *S. ruficeps* by the wider atrium (see Galiano 1965, pl. III, fig. 7), and from *S. capibarae* by the larger size of the posterior spermathecae (see Galiano 1967, fig. 23).

Taxonomic note.—The types of *S. marcosi* deposited in Escola Superior de Agricultura da Universidade de São Paulo, Brazil were not examined. The type material of *S. australis* Mello-Leitão, 1944 deposited in the Museo de La Plata is damaged (lacking legs and pedipalps) (Pereira et al. 1999), and a paratype deposited in the Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ) was destroyed by fire in 2018 (World Spider Catalog 2020).

Material examined.—URUGUAY: *Canelones*: 1 ♂, Estación Atlántida, 34°44′56″S, 55°46′06″W, 25 November 2018, P. Martínez (FCE-Ar 9773); 1 ♂, Neptunia, 34°47′23″S, 55°52′34″W, 25 November 2018, D. Hagopián (FCE-Ar 9672); 1 ♀, same data (FCE-Ar 9914); 1 ♂, same data (FCE-Ar 9769); 1 ♂, San Ramón, 34°17′26″S, 55°57′22″W, 05 November 2018, R. Lauría (FCE-Ar 9669); 1 ♀, Toledo, 34°44′28″S, 56°05′24″W, 29 November 2018, R. Lauría (FCE-Ar 9772). *Cerro Largo*: 1 ♀, 1 ♂, Sierra de Ríos, 32°11′11.50″S, 53°51′34.22″W, 20 April 2019, D. Hagopián (FCE-Ar 10575); 4 ♂, Arévalo, 32°29′36″S, 55°06′32″W, 31 October 2019, D. Hagopián (FCE-Ar 10511). *Maldonado*: 1 ♂, Campus of Centro Universitario Regional Este (CURE), 34°54′54″S, 54°56′32″W, 09 December 2016, D. Hagopián (FCE-Ar 7401); 1 ♀, Playa Grande, 34°51′13″S, 55°17′50″W, 03 November 2018, D. Hagopián (FCE-Ar 9770); 1 ♂, Punta Negra, 34°52′57.6″S, 55°13′14.1″W, 02 December 2018, R. Roibal (FCE-Ar 9014); 1 ♂, same data except 16 September 2017 (FCE-Ar 9013). *Montevideo*: 1 ♀, Carrasco, 34°52′42″S, 56°03′11.7″W, 01 October 2017, A. Mailhos (FCE-Ar 9006); 1 ♂, same data except 13 November 2016, D. Hagopián (FCE-Ar 7908); 1 ♀, same data (FCE-Ar 7910); 1 ♂, José Dodera Street 747, 34°54′37″S, 54°57′35″W, 05 October 2017, C. Costa (FCE Ar-9005); 1 ♂, Malvín Norte, Campus of Facultad de Ciencias, 34°52′56″S, 56°07′04″W, 06 November 2018, D. Hagopián (FCE-Ar 9666); 1 ♂, same data except 15 November 2018, (FCE-Ar 9667); 1 ♂, same data except 22 March 2017, (FCE-Ar 9015); 1 ♂, same data (FCE-Ar 9011); 1 ♂, same data except 16 October 2018, (FCE-Ar 9668); 1 ♂, same data except 22 March 2018 (FCE-Ar 9012); 1 ♀, same data, (FCE-Ar 9007); 1 ♂, same data (FCE-Ar 9670); 1 ♂, same data except 01 October 2016 (FCE-Ar 7398); 1 ♂, same data (FCE-Ar 7397); 1 ♂, same data (FCE-Ar 7396); 1 ♀, same data except 22 November 2016 (FCE-Ar 7912); 1 ♀, same data (FCE-Ar 7911); 1 ♀, same data (FCE-Ar 7913); 1 ♂, same data (FCE-Ar 7402);1 ♂, same data except 25 September 2018 (FCE-Ar 9671); 1 ♂, same data except 01 October 2016 (FCE-Ar 7397); 1 ♂, same data except 05 October 2018 (FCE-Ar 9767); 1 ♀, same data except 15 November 2018 (FCE-Ar 9768); 1 ♀, same data except 01 December 2018 (FCE-Ar 9771); 1 ♀, same data except 22 November 2018 (FCE-Ar 7914); 1 ♂, same data except 08 November 2018 (FCE-Ar 9774); 1 ♂, same data (FCE-Ar 9775); 1 ♂, same data except 05 October 2018 (FCE-Ar 9767); 1 ♂, Parque Lecocq, 34°47′32″S, 56°20′02″W, 23 October 2018, M. Simó (FCE-Ar 9624); 1 ♂, Prado, Castillo Soneira, 34°51′31″S, 56°11′51″W, 08 October 2015, D. Hagopián (FCE-Ar 7400); 1 ♂, same data (FCE-Ar 7399); 1 ♂, same data (FCE-Ar 7909). *Rocha*: 1 ♀, Santa Teresa, 33°58′43″S, 53°32′05″W, 18 November 2017, Curso Artrópodos 2017 (FCE-Ar 9008). *Tacuarembó*: 1 ♀, INIA, 31°44′19″S, 55°58′43″W, Á. Laborda (FCE-Ar 9402); 1 ♀, same data (FCE-Ar 9403).

Distribution.—This species has previously been recorded from Brazil (São Paulo) (see Piza 1937) and Argentina (Santa Fe, Chaco, Salta, Tucumán and Buenos Aires) (see Galiano 1965). We report the first record of the species from Uruguay (Canelones, Cerro Largo, Maldonado, Montevideo, Rocha and Tacuarembó) (Fig. 2).

Natural history.—*Sarinda marcosi* was found on sunny days during warmer months on grasses, shrubs, cacti (*Opuntia monacantha* Haw.) (Cactaceae) (Fig. 3A) and vines (*Ipomoea* sp.) (Convolvulaceae), associated with foraging sites of the ant *Camponotus mus*, in natural habitats as well as urban zones (gardens and exterior walls of houses). These observations agree with those mentioned by Galiano (1965), who reported this species walking on the grasses of marshes and lagoons, together with ants of the genus *Camponotus*. The behaviors observed in the field agree with those observed in the laboratory. It was difficult to distinguish the spiders from the ants while they moved or stayed still (Figs. 3B,C). *Sarinda marcosi* moves with quick and random movements, raising the first pair of legs and touching the ground with just the ends of the tarsi, simulating the antennae of the ants. Individuals can curve the opisthosoma against the substrate, touching it with the spinnerets, similarly to what these ants do with their abdomen during locomotion. When disturbed, these jumping

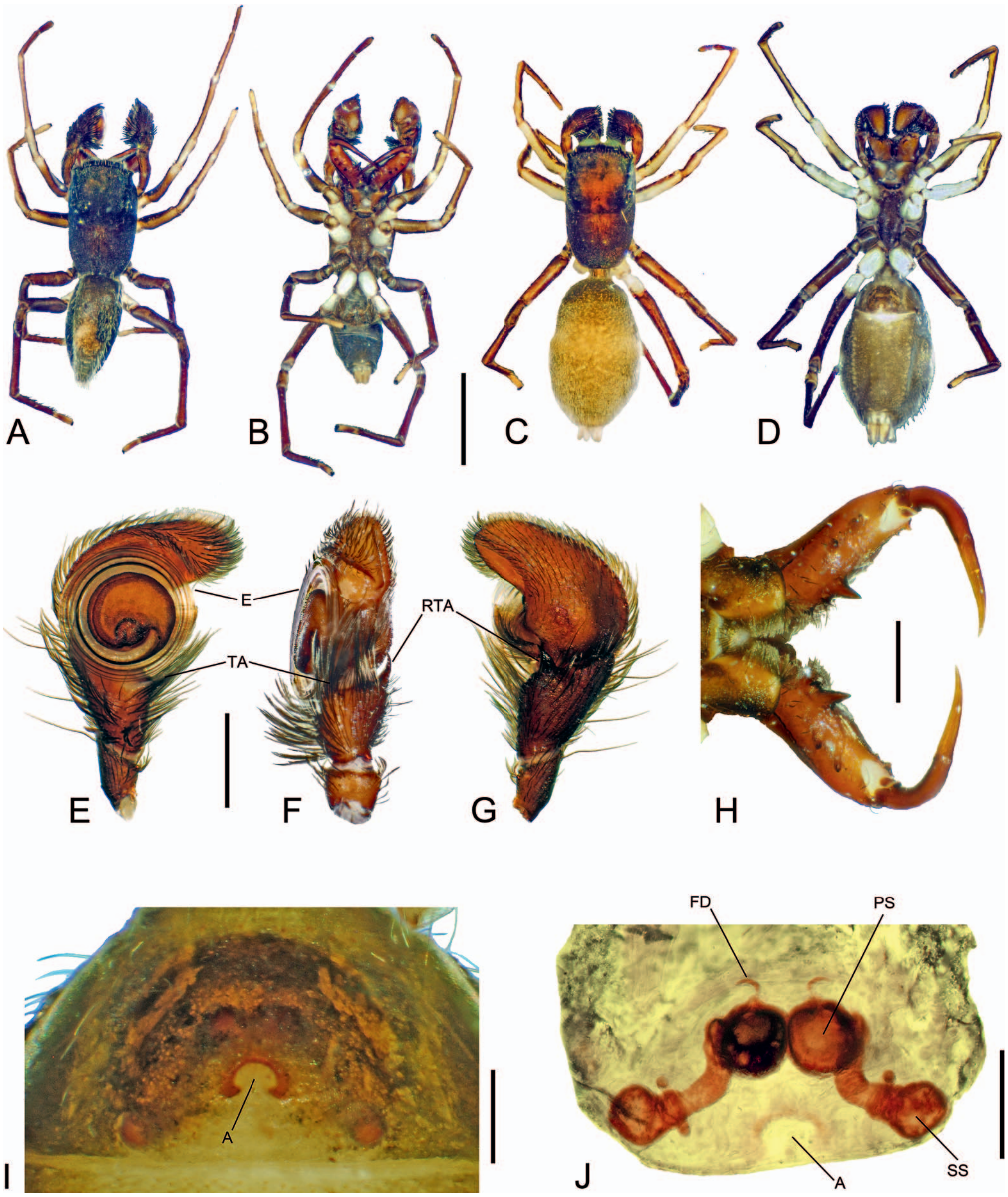

Figure 1.—*Sarinda marcosi*. A. Male dorsal habitus. B. Male ventral habitus. C. Female dorsal habitus. D. Female ventral habitus. E. Pedipalp ventral view. F. Pedipalp retrolateral view. G. Pedipalp dorsal view. H. Male chelicerae. I. Epigynum ventral view. J. Epigynum dorsal view. Abbreviations: A = atrium; E = embolus; FD = fertilization duct; PS = primary spermatheca; RTA = retrolateral tibial apophysis; SS = secondary spermatheca; TA = tibial apophysis. Scale bars: 2 mm (A–D); 0.5 (E–H); 0.2 mm (I, J).

spiders can choose different escape strategies. As a first strategy, individuals stay still, raise the legs I and direct pedipalps towards the direction of the attack (Fig. 3D). If the threat persists, they can maintain that position and walk backwards while still facing the attacker, moving the legs I up and down while joining and separating the pedipalps, in a similar fashion to the movement of ant jaws. After this, they turn and run fast. As a second strategy, the individual can drop from where it is located, either from the stem of one cactus to another, or to the ground. They can also fix a silk thread and keep suspended in the air. As a third defense strategy the spiders can move from one side to another of a leaf or stem very quickly. These strategies are also performed by *C. mus*. When finding a potential prey item, individuals approached them rapidly, moving legs I up and down, and in turn separating and joining the pedipalps. When they got close enough to the prey, they stopped while maintaining the movements of legs and pedipalps and jumped to attack. We observed them capturing small Diptera (including Chironomidae) (Fig. 3E), but never ants of any species. At sunset, *S. marcosi* individuals take refuge in small silk retreats they construct in dry leaf folds (as other jumping spiders do), sometimes with up to three retreats of different individuals per leaf.

Morphological traits associated with myrmecomorphy.—The *C. mus* worker ants present an opaque black coloration on their body with scattered golden hairs, with the exception of 2/3 of their abdomen on which these hairs are evenly distributed,

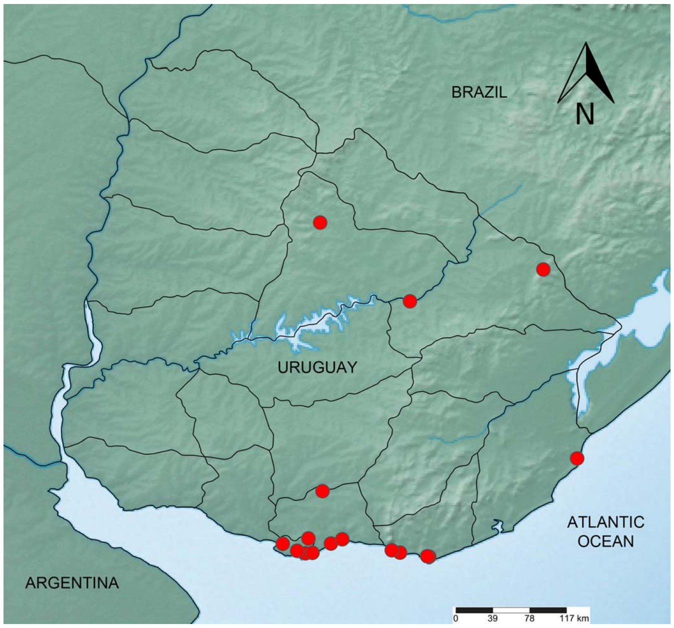

Figure 2.—Records of *S. marcosi* in Uruguay.

the same pattern of coloration as observed in both sexes in *S. marcosi* (Figs. 4A–C). The pedipalps of *S. marcosi* present a broadened and rounded cymbium in adult males (Fig. 4A) and have a slightly more oval shape in females (Fig. 4C) and juveniles (Fig. 4D), resembling the head of an ant. In males, females or juveniles, the pedipalps present abundant long black setae on the prolateral face of the patella, tibia and cymbium where the pedipalps touch, giving the impression of being fused. The position of leg I is like that of the antennae of *C. mus*; the patella and tibia resemble the scape of the antenna, and the metatarsus and tarsus look similar to the flagellum (Figs. 5A,B). The morphological similarities of *S. marcosi* to *C. mus* are also evidenced by the narrow prosoma of the spider, which tapers towards the pedicel. *Sarinda marcosi* presents a constriction between the cephalic and thoracic regions of the prosoma, which resembles the division between the mesonotum and pronotum of the thorax of *C. mus* (Figs. 5C,D). The rest of the legs present at an angle of 90° between the femur, patella and tibia, generating a posture like the legs of the ants. The opisthosoma is oval in both males and females and has no sclerites or constrictions. The morphological similarity with *C. mus* is reinforced by the general coloration of the body. The pedipalps and prosoma present an opaque black coloration, with golden setae scattered on the posterior part of the constriction of the prosoma. The legs are dark brown, showing a more translucent coloration at the tips, except in the first pair where the tip is darker than the rest of the leg; the coxae and trochanters of legs I, II and IV are translucent yellow. This translucent coloration in the distal parts generates an appearance of thinner legs. They show golden setae similar to those of *C. mus* but these are shorter in the opisthosoma (Figs. 5E,F), and denser posteriorly. We observed small projections on the setae of the abdomen of *S. marcosi* and *C. mus* (Figs. 5G,H), which generates a golden color that reaches a certain brightness according to the incidence of light. The morphological indices used as mimicry

Table 1.—Results of the three indices used as mimicry indicators. Prosoma index = prosoma width / prosoma length × 100; sternum index = sternum width / sternum length × 100; and opisthosoma index = opisthosoma width / opisthosoma length × 100.

	Sarinda marcosi (mimetic)		*Aphirape flexa* (non-mimetic)	
Index	Male	Female	Male	Female
Prosoma	47-65	44-65	74-80	77-109
Sternum	40-50	40-50	60-70	63-84
Opisthosoma	46-62	50-68	52-80	64-87

indicators for *S. marcosi* are detailed in Table 1. Low indices indicate the occurrence of mimicry adaptations.

The measurement ranges were as follows: (a) workers of *C. mus* body length (4.0–7.4 mm; $n = 10$) and leg lengths, III (5.0–7.2 mm; $n = 10$), I (3.8–5.3 mm; $n = 10$), II (3.6–4.7 mm; $n = 10$), from the longest to the shortest; (b) females of *S. marcosi* (4.5–6.0 mm; $n = 5$); and (c) males (3.6–4.5 mm; $n = 10$); leg lengths, IV (4.9–5.5 mm; $n = 15$), I (3.5–4.5 mm; $n = 15$), III (3.0–4.2 mm; $n = 15$), II (2.5–4.0 mm; $n = 15$), from the longest to the shortest in both sexes.

Behavioral trials.—We summarize the descriptions and durations of attack and defensive behaviors in Table 2. Results of the experimental trials for each group are shown in Table 3. There were no attacks by *S. marcosi* towards *C. mus* in Group 1. Individuals of *Sarinda marcosi* moved legs I up and down as they walked, just touching the ground with the end of the tarsi. At certain moments, individuals stopped locomotion and turned towards *C. mus*. In five trials, *S. marcosi* lifted legs I and remained facing the ants (see Video 1 in Supplementary File 1, online at https://doi.org/10.1636/JoA-S-19-069.s1). The contact of both species occurred randomly while they were moving. When this happened, *S. marcosi* individuals moved quickly in the opposite direction to the ants, which could flee in the opposite direction to the spider or remain still with jaws open and raised antennae (see Flow chart 1 in Supplementary File 2, online at https://doi.org/10.1636/JoA-S-19-069.s2). Only in one of the 15 trials did we observe an attack of *C. mus* on *S. marcosi*. The ant attacked the spider with jaws and formic acid, curving the abdomen and orienting it towards the spider. After the attack, *S. marcosi* remained motionless on its back, exhibited sudden shakes or spasms, and after a few seconds, it began to move again. In Group 2, attacks of *A. flexa* towards *S. marcosi* were recorded in 5 of the 15 trials, but in none of the cases were they successful (see Video 2 in Supplementary File 3, online at https://doi.org/10.1636/JoA-S-19-069.s3). During the trials, no attacks of *S. marcosi* towards *A. flexa* occurred. *Sarinda marcosi* moved in a similar way as in Group 1, raising and lowering the first pair of legs, barely touching the surface with the tips of the tarsi. In all the trials, after stopping and orienting their prosoma towards *A. flexa*, *S. marcosi* individuals raised their legs I and joined the pedipalps while facing the other spider (unlike what happened when they were exposed to ants) (Fig. 6). If *A. flexa* did not approach, *S. marcosi* walked typically again. But if *A. flexa* oriented the prosoma towards it, *S. marcosi* fled, first walking backwards in the same position with the legs I raised always facing *A. flexa*

Figure 3.—*Sarinda marcosi* in its natural environment. A. *Opuntia monacantha*. B. *C. mus*. C. *S. marcosi*. D. Female of *S. marcosi* in defensive posture. E. Male of *S. marcosi* feeding on a chironomid.

Table 2.—Descriptions and durations (in seconds) of the behaviors related to the interactions in Group 1 and 2. Behaviors performed by: *S. marcosi* (S) and *A. flexa* (A).

Experimental group	Behavior	Description	Duration (mean ± SD)
Sarinda marcosi vs. Camponotus mus (Group 1)	Lifts legs I	*S. marcosi* lifts legs I synchronously.	0.2 ± 0.6
	Visually orientates$_{(S)}$	*S. marcosi* orientates to *C. mus* direction.	1.2 ± 1.1
	Open the mandibles	At least one ant stays still with the mandibles opened.	0.1 ± 0.6
Sarinda marcosi vs. Aphirape flexa (Group 2)	Lifts legs I	*S. marcosi* lifts legs I synchronously.	1.1 ± 1.5
	Flees	*S. marcosi* walks backwards with the legs I lifted.	0.6 ± 0.7
	Escapes from the attack	*S. marcosi* escapes from the attack of *A. flexa*.	-
	Visually orientates$_{(S)}$	*S. marcosi* orientates to *A. flexa* direction.	0.4 ± 0.3
	Visually orientates$_{(A)}$	*A. flexa* orientates to *S. marcosi* direction.	2.3 ± 2.1
	Approximates	*A. flexa* stalks slowly moving towards *S. marcosi*.	0.8 ± 1.1
	Attacks with jump	*A. flexa* jumps to attack *S. marcosi*.	-

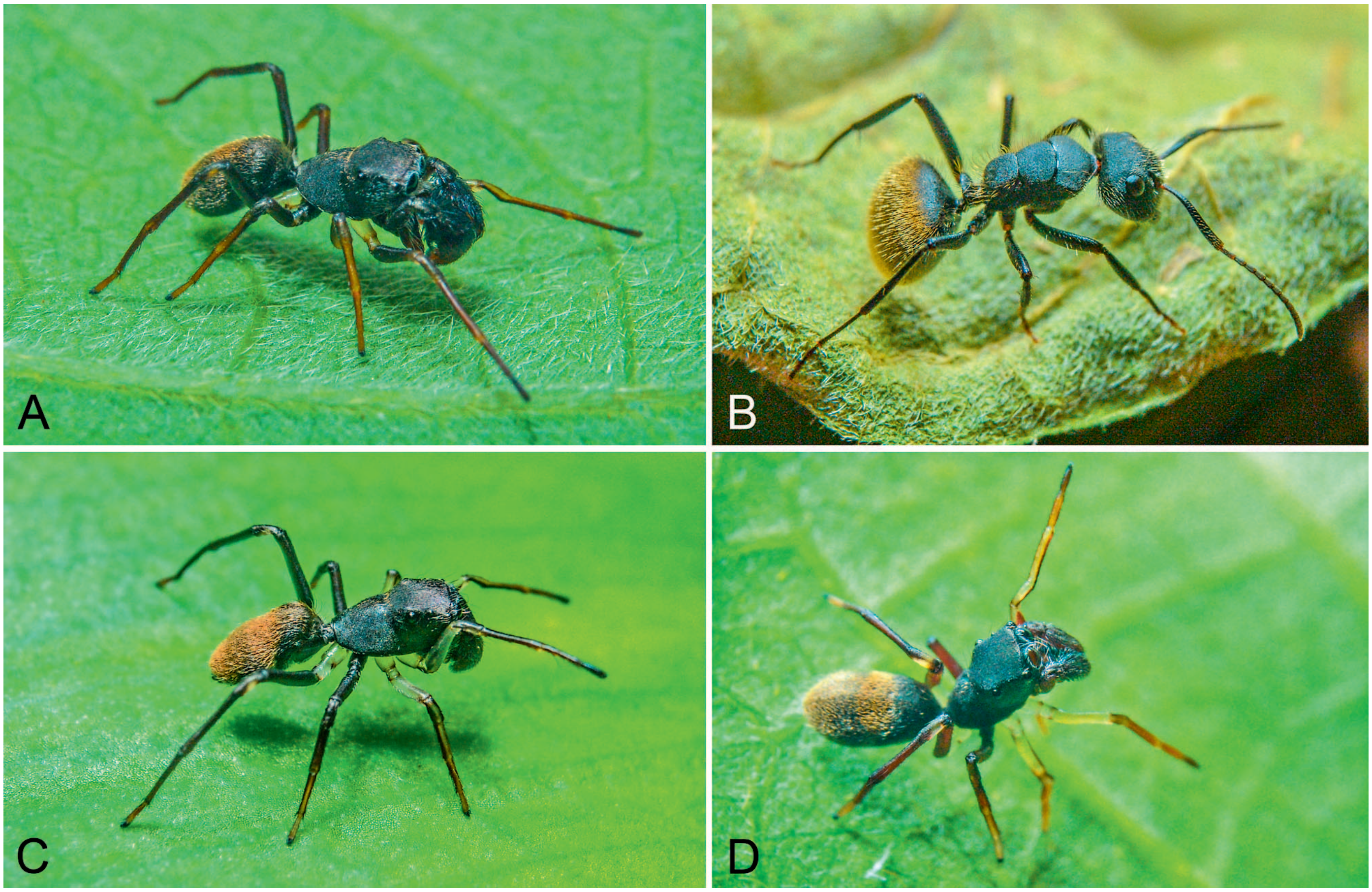

Figure 4.—Individuals of *Sarinda marcosi* (A, C, D) and *Camponotus mus* (B). A. Male. B. Worker ant. C. Female. D. Juvenile.

and then turning to walk quickly. In five trials, *A. flexa* quickly approached *S. marcosi* and jumped to attack it. Even though in those jumps *A. flexa* was able to hold *S. marcosi*, in none of the cases were they able to kill the spider, and released it after the initial capture (see Flow chart 2 in Supplementary File 4, online at https://doi.org/10.1636/JoA-S-19-069.s4).

Attacks.—During the trials, no attacks by *S. marcosi* on *C. mus* occurred, but in all the cases, *S. marcosi* attacked *D. melanogaster* when offered after the experiment (Fisher's test: $P = 0.00001$). The frequency of attack attempts from *A. flexa* to *S. marcosi* (Group 2) and *P. roburifoliata* (Group 3) was similar (Fisher's test: $P = 0.36$), but there were only successful attacks (carried out to completion) from *A. flexa* on *P. roburifoliata* in four of the 15 trials (Fisher's test: $P = 0.04$). Regarding the attack latency of *A. flexa*, no significant differences were recorded towards *S. marcosi* or *P. roburifoliata* (Wilcoxon Nonparametric Test: $W = 16$, $P = 0.32$). The body condition index does not seem to affect the frequency of attacks of *A. flexa* on *S. marcosi* ($R = 0.41$, $F = 2.91$, $P = 0.11$), but it positively affected the frequency of attacks on *P. roburifoliata* ($R = 0.79$, $F = 22.84$, $P = 0.0003$, $\beta = 0.787$). This result indicates that the higher the body condition index in individuals of *A. flexa*, the greater the possibility of attacks on *P. roburifoliata*.

DISCUSSION

This is the first study of mimicry in the species *Sarinda marcosi* and the first record of the genus and the species from Uruguay. The species of ants associated with the mimicry have been recorded for other species of *Sarinda*, but those studies are based only on field observations (Jackson & Drummond 1974).

Table 3.—Results of the trials in each experimental group. Attacks in Groups 2 and 3 were always carried out by *A. flexa* on the other species.

	Attack latency (mean ± SD, in secs.)	N° of trials with attack	N° of succesful attacks	N° of occurrences of "Lifts legs I" (mean ± SD)
S. marcosi vs. C. mus (Group 1)	-	0	0	7.00 ± 5.83
S. marcosi vs. A. flexa (Group 2)	336.00 ± 444.75	5	0	24.93 ± 15.39
A. flexa vs. P. roburifoliata (Group 3)	200.33 ± 148.87	6	4	-

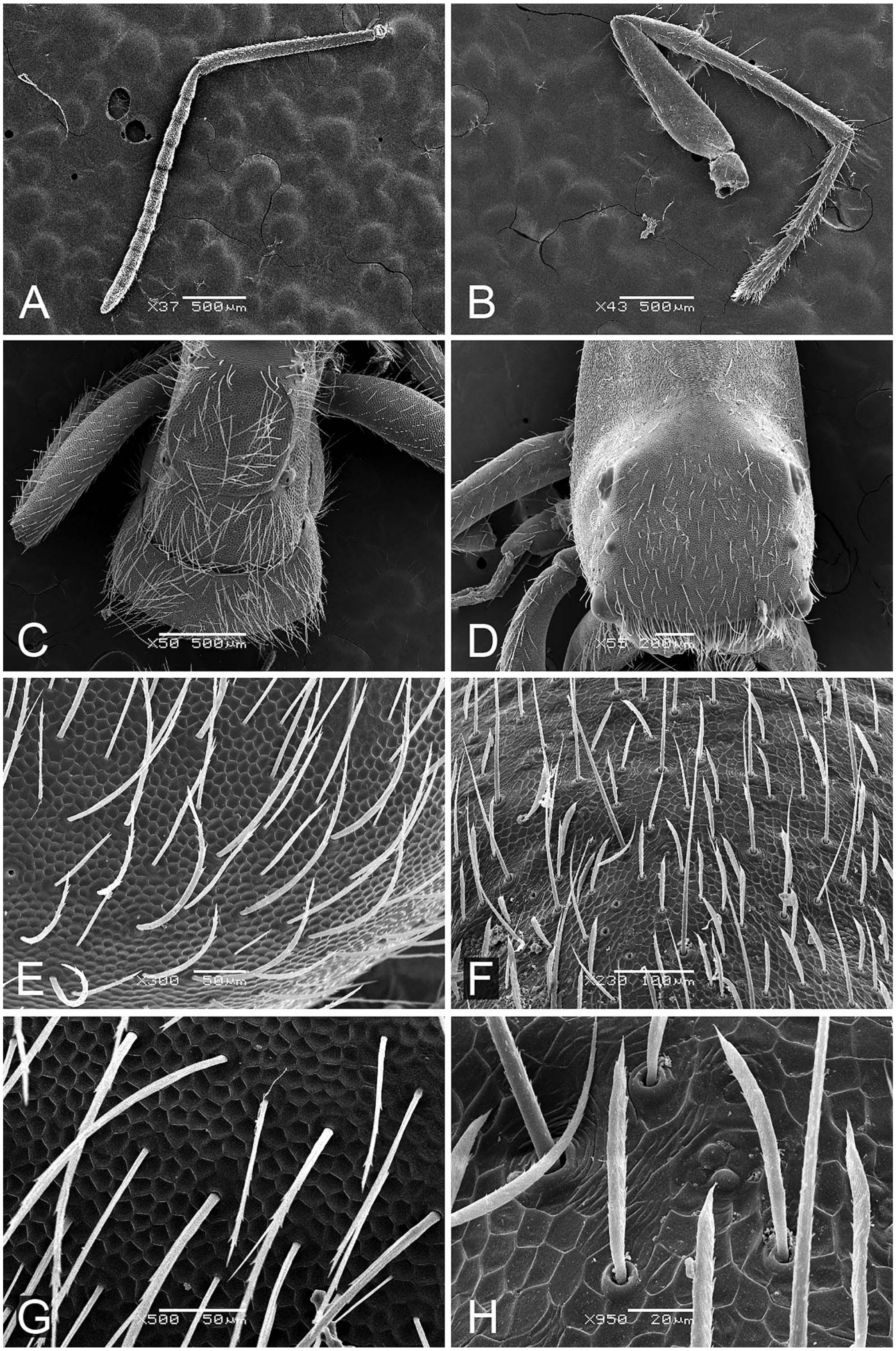

Figure 5.—Microphotographs of somatic structures. A. Antenna of *C. mus*. B. Leg I of *S. marcosi*. C. Thorax of *C. mus*. D. Prosoma of *S. marcosi*. E. Abdomen setae of *C. mus*. F. Opisthosoma setae of *S. marcosi*. G. Abdomen setae structure of *C. mus*. H. Opisthosoma setae structure of *S. marcosi*.

In this study we used the "direct" and "indirect" observations of Reskind (1977) to determine the kind of mimicry displayed by *S. marcosi*. As a direct test, we experimentally introduced the myrmecomorphic spider to enclosures with the model ants. Indirect indicators of mimicry included observations documenting: (1) sympatry between the spiders and the model ants; (2) similarity in overall morphology and behavior; and (3) species specificity, or the occurrence of structures seen

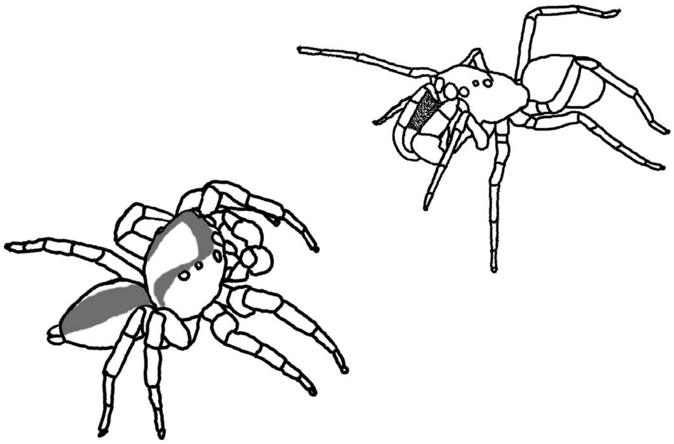

Figure 6.—Encounter of *S. marcosi* (right) with *A. flexa* (left). Note the posture of raised legs I and the joined pedipalps of *S. marcosi*.

in the mimic, analogous to the model that do not occur in other species of *Sarinda*.

All mimicry indices obtained were indicators of mimicry for *S. marcosi*. The ratios of the ant mimic prosoma and sternum were lower than those of *A. flexa*, but the opisthosoma index of *S. marcosi* was not as low due to the globose abdomen of *C. mus*, similar to that observed with *Myrmecotypus iguazu* and *Camponotus sericeiventris* by Rubio et al. (2013). *Sarinda marcosi* shows great similarities with *C. mus* both in morphology and coloration; one of the most conspicuous similarities is in the golden setae that both species present on the abdomen. Those golden setae are reflective to light because they have small microscopic projections, which generate structural colors according to the incidence of light, as seen in other types of setae in certain jumping spider species (Foelix et al. 2013; Pekár et al. 2017).

The majority of myrmecomorphic spider species described show Batesian mimicry (Reiskind 1977; Oliveira 1986; Cushing 2012), although there are species that feed on the model they imitate, presenting aggressive or Peckhamian mimicry, e.g. the African jumping spider *Mexcala elegans* Peckham & Peckham, 1903 (Salticidae) that mimics *Camponotus cinctellus* (Gerstäcker, 1859) (Formicidae) (Pekár & Haddad 2011). Generalist predators commonly avoid ants, which are considered aggressive prey (Hölldobler & Wilson 1990). *Camponotus mus* exhibits aggressive behavior when attacked and in turn releases large amounts of formic acid. Because of these defenses, *C. mus* is rarely targeted as prey, and the same is true for other species of the genus *Camponotus* (Debandi & Roig-Juñent 1999; Durkee et al. 2011; Rubio et al. 2013). Peckhamian mimicry can be ruled out for this species of myrmecomorphic spider because in none of the experiences *S. marcosi* attacked its model and escaped from it if they came into contact. Rather, this myrmecomorph appears to be a Batesian mimic and its behavior, both in the lab and in nature, supports this hypothesis.

We observed a greater frequency of the behavior "Lifts legs I" in the Group 2. This strategy of lifting the first leg pair seems reminiscent of defensive displays performed by ants with their antennae (Hölldobler 1983; Hölldobler & Wilson 1990). It could allow the spider to intimidate the predator, which could agree with the fact that this behavior presented a higher average duration in the experiences with *A. flexa*. This movement of legs I to simulate antennae is known as "antennal illusion", according to Reiskind (1977). All the transitions in Groups 1 and 2 were significant, suggesting that the observed behaviors are stereotyped and agree with observations in nature reporting very frequent interactions between the species used in the trials.

Although there were only successful attacks from *A. flexa* towards *P. roburifoliata*, the number of trials with attacks and the attack latency in Groups 2 and 3 were similar. This similarity in the results may be due to the methodology of the trials, performed in a small place such as the petri dishes, an artificial environment very different from nature, where potential prey can hide or flee, as indicated by Durkee et al. (2011), or be mistaken for the surrounding ants.

Predators identify prey in a multisensory manner, both in form, movement or by the chemical defenses that they emit (Bro-Jørgensen 2010; Pekár et al. 2017). Due to the observed behaviors of *S. marcosi* when it was attacked by *A. flexa*, an hypothesis is proposed: *S. marcosi* would have another type of additional defense against contact by predators, but another type of study is needed to test this hypothesis.

We propose that *Sarinda marcosi* presents defensive or Batesian mimicry in its myrmecomorphy, using *Camponotus mus* as a model. This defensive mimicry would protect *S. marcosi* from visual predators that avoid ants, including jumping spiders, birds (Palmgren et al. 1937), predatory wasps (Edmunds 1993) and mantids (Nelson et al. 2006). Future studies will focus on checking whether *S. marcosi* presents additional tactile or chemical defense, which would allow individuals of this species to escape from predators after contact. Similar and comparative studies will also be carried out with other species of the genus, to determine if they also present Batesian mimicry.

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SUPPLEMENTARY FILES

Supplementary File 1.—Video 1, Behavior of *Sarinda marcosi* in the presence of *Camponotus mus*. Online at https://doi.org/10.1636/JoA-S-19-069.s1

Supplementary File 2.—Flow chart 1, showing frequencies of behavioral units of *Sarinda marcosi* and *Camponotus mus*. Online at https://doi.org/10.1636/JoA-S-19-069.s2

Supplementary File 3.—Video 2, Behavior of *Sarinda marcosi* and *Aphirape flexa*. Online at https://doi.org/10.1636/JoA-S-19-069.s3

Supplementary File 4.—Flow chart 2, showing frequencies of behavioral units of *Sarinda marcosi* and *Aphirape flexa*. Online at https://doi.org/10.1636/JoA-S-19-069.s4

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