

Natural history of two spider species of the genus *Phonotimpus* (Araneae: Phrurolithidae) endemic to Chiapas, Mexico

Historia Natural de dos especies de arañas del género *Phonotimpus* (Araneae: Phrurolithidae) endémicas de Chiapas, México

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ABSTRACT. *Phonotimpus pennimani* and *P. talquian* (Phrurolithidae) are common spider species inhabiting leaf litter in tropical environments of Chiapas, Mexico. This study summarizes laboratory and field observations on their natural history. Both species were observed preying on Tomoceridae springtails in the field and exhibited a preference for springtails in laboratory conditions. Both species continued feeding well beyond maturity, and juveniles were capable of subduing large springtails. Females continued feeding even while guarding their egg sacs. Both species constructed disk-like egg sacs and guarded them until offspring emergence, demonstrating maternal care. Juveniles and penultimate instars typically constructed retreats for molting. Additionally, we documented the parasitism on *P. pennimani* eggs by a Scelionidae wasp.

Key words: egg sac; maternal care; molting retreat; parasitoids; springtails

RESUMEN. *Phonotimpus pennimani* y *P. talquian* (Phrurolithidae) son especies de arañas comunes que habitan la hojarasca en ambientes tropicales de Chiapas, México. El presente estudio resume las observaciones de campo y laboratorio sobre su historia natural. Se observó a ambas especies depredando colémbolos de la familia Tomoceridae en el campo, y mostrando una preferencia por colémbolos en condiciones de laboratorio. Ambas especies continuaron alimentándose incluso después de alcanzar la madurez, y los juveniles fueron capaces de someter colémbolos grandes. Las hembras continuaron alimentándose incluso durante el cuidado de sus ovisacos. Ambas especies construyeron ovisacos con forma discoidal, custodiándolos hasta la emergencia de las arañas, lo que evidencia un comportamiento de cuidado maternal. Los juveniles y los estadios penúltimos construyeron, de manera regular, refugios para la muda. Adicionalmente, se documentó el parasitismo en huevos de *P. pennimani* por una avispa de la familia Scelionidae.

Palabras clave: colémbolos; cuidado maternal; ovisaco; parasitoides; refugio de muda

INTRODUCTION

The family Phrurolithidae comprises 25 genera and 404 species globally (World Spider Catalog, 2024). Approximately half of all Phrurolithidae species have been described within the past five years, primarily from Asia and North America, this last is a region recognized as a major center of diversity despite being considerably neglected (Platnick, 2019; World Spider Catalog, 2024). As with many other spider groups, most information derives from original taxonomic descriptions, which generally lack natural history data. Consequently, knowledge of this family's natural history is sparse and scattered throughout the literature. These spiders are known to be very small, ground-dwelling species inhabiting microhabitats such as under stones, fallen wood, and leaf litter (Dondale & Redner, 1982; Kaston, 1948). Females construct a scale-like egg sac, which is attached to stones, some abandon their egg sacs after completion while others guard them until hatching (Dondale & Redner, 1982; Platnick, 2019). Laboratory observations indicate that phrurolithids have a prey preference for springtails (Angulo-Ordoñez *et al.*, 2019; Pekár & Jarab, 2011). Until recently, the mating behavior of Phrurolithidae remained virtually unknown, with Mu *et al.* (2022) providing the first brief description. The limited information available on phrurolithids is likely attributable to their small size and cryptic coloration.

Phonotimpus Gertsch & Davis, 1940, a Mexican genus of Phrurolithidae, comprises 32 species, each characterized by a restricted geographic distribution (Platnick *et al.*, 2022; World Spider Catalog, 2024). *Phonotimpus pennimani* Chamé-Vázquez, Ibarra-Núñez & Jiménez, 2018 and *P. talquian* Chamé-Vázquez, Ibarra-Núñez & Jiménez, 2018 are two small-sized spiders (1.9–2.7 and 2.3–3.3 mm total length, respectively), highly abundant components of soil spider assemblages (Chamé-Vázquez *et al.*, 2018). *Phonotimpus pennimani* inhabits leaf litter of shade coffee plantations at 920 m a.s.l., while *P. talquian* inhabits leaf litter of cloud forest at 2010 m a.s.l. on the slopes of Tacaná Volcano, Chiapas, Mexico (Chamé-Vázquez *et al.*, 2018). Despite the abundance of both species (Chamé-Vázquez, 2011, 2015), no basic natural history information is available for either, or for any *Phonotimpus* species. This study presents laboratory and field observations on the natural history of both *Phonotimpus* species, encompassing prey capture, egg sac morphology, fecundity, maternal care behaviors, and molting retreats. Additionally, we report

an interaction between a parasitoid wasp and *P. pennimani*. Furthermore, this study was part of a broader effort aimed at contributing to the taxonomy and phenology of both species.

MATERIALS AND METHODS

Most observations were conducted under laboratory conditions, with additional field observations made during sampling events. All spiders were collected from the type localities of *P. pennimani* (Alpujarras, 15.066878°N, 92.165833°W) and *P. talquian* (Talquián, 15.0875°N, 92.0989°W), both situated on the slopes of Tacaná Volcano in Chiapas, Mexico. Spiders were collected monthly by hand from March 2016 to October 2019 by dispersing leaf litter onto a white fabric sheet and capturing individuals using an aspirator. Voucher specimens are deposited at the Colección de Arácnidos del Sureste de México (ECOTAAR), El Colegio de la Frontera Sur, Tapachula, Chiapas, Mexico.

In the laboratory, each spider was housed individually in a 9 x 9 x 7 cm plastic container filled with a moistened plaster of Paris and activated charcoal substrate. While initially provided with dried leaves for shelter, these were replaced with translucent plastic straws due to a lack of observable behavior. Spiders were initially fed with Collembola, Psocoptera, and Formicidae. However, after observing a preference for springtails (Collembola), a diet of cultured springtails was provided twice per week. This diet consisted of *Proisotoma* sp. (Isotomidae), *Pseudosinella* sp., *Lepidocyrtus* sp. (Entomobryidae), and *Cyphoderus* sp. (Cyphoderidae). All spiders were maintained under laboratory conditions at $26 \pm 1.3^{\circ}\text{C}$, $57 \pm 4.3\%$ relative humidity, with a 12:12 light:dark photoperiod, which corresponds to most of the year in this region. Further details on laboratory rearing can be found in Angulo-Ordoñez *et al.* (2019).

We adopted the life cycle terminology of Alvarado-Castro and Jiménez (2016) with the following modifications. A "juvenile" was defined as a spider from the first instar to the antepenultimate stage. The "penultimate" instar referred to the stage immediately preceding the adult molt. Penultimate males were identified by swollen tarsi lacking sclerotized structures, while penultimate females exhibited a slightly sclerotized gonopore region but lacked a vulva. An "adult male" possessed modified pedipalps (sclerotized copulatory bulb with discernible sclerites, and palpal tibia with apophyses), and an "adult female" had a distinct epigynum and vulva. Developmental stage determination was based on external morphology.

The shape, number of eggs, number of egg sacs per female, and embryonic period of egg sacs were estimated for females captured in the field with egg sacs and for females that produced egg sacs in the laboratory. We recorded the presence or absence of retreats and the molting dates of juveniles and penultimate individuals reared in laboratory. A total of 34 males, 56 females (including four with egg sacs collected from the field), eight penultimate males, five penultimate females, and 50 juveniles (plus 30 juveniles hatched in the laboratory) of *P. pennimani* were reared (Fig. 1A–C). For *P. talquian* (Fig. 2A–C), 11 males, 22 females, 15 penultimate males, seven penultimate females, and 60 juveniles were reared.

RESULTS

Prey capture. In the field, we observed and captured a female of *P. pennimani* (21 February 2019) consuming an unidentified springtail of the family Tomoceridae (Collembola). Additionally, we collected a female of *P. talquian* (26 March 2019) ingesting a *Pogonognathellus* sp. (Tomoceridae) springtail. In the laboratory, juvenile, penultimate, and adult individuals of both species preyed on springtails that wandered nearby (Figs. 1J–K, 2E–F). Capture involved a short jump (less than one leg span) followed by subduing the prey with the forelegs and subsequently with the chelicerae.

Even while guarding their egg sacs, *P. pennimani* females consumed springtails. In one instance, a juvenile of *P. pennimani* with the ventral macrosetae of its forelegs raised for a moment attacked a springtail larger than itself (Fig. 1L). The springtail attempted to escape, jumped two times with the spider grasping it, but the escape mechanism was not effective, and the spider subdued its prey.



Figure 1. A–L. *Phonotimpus pennimani*. A. Female habitus. B. Male habitus. C. Penultimate male habitus. D–F. Female guarding egg sac. G. Exuvia and retreat. H–I. Molted juvenile with retreat and exuvia. J. Female consuming a springtail. K. Male consuming a springtail. L. Juvenile (first instar) consuming a springtail.



Figure 2. A–J. *Phonotimpus talquian*. A. Female habitus. B. Male habitus. C. Juvenile habitus. D. Female guarding egg sac. E. Female consuming a springtail. F. Male consuming a springtail. G. Juvenile molting. H. Exuvia and retreat. I–J. Molted juveniles with retreat and exuvia.

Retreat for molting in laboratory conditions. Juvenile and penultimate individuals of both species constructed a silk retreat for the molting process. These retreats were found at the top of the container, within the straws, or on the bare substratum. The retreats were variable (compare Figs. 1G–I, 2H–J) but typically consisted of two layers. The basal layer was generally more densely woven than the upper layer, with silk threads evident in both layers. During growth, some individuals constructed a retreat for one molting event but not for the subsequent ones. When juveniles did not build a retreat, they adhered to the top or walls of the container using their legs and molted (Fig. 2G). No silk was found upon subsequent inspection. Several juveniles died during or immediately after the molting process. In one instance, a juvenile was unable to release its legs and became trapped in the exuvia, resulting in death.

Eggs sac, clutch size, and embryonic period. In the field, we observed four *P. pennimani* females with egg sac laid in dried leaves. The egg sacs were disk-like, with a hue ranging from pinkish to

whitish. Under laboratory conditions, 21 *P. pennimani* females constructed their egg sacs on the bare substratum, within straw or in container corners, while one *P. talquian* female laid her egg sac on a dried leaf (Figs. 1D–F, 2D, 3A). All egg sacs constructed under laboratory conditions were also disk-like, resembling those observed in the field, and composed of two layers: the upper layer appeared more densely woven than the basal one, with eggs packed in the center (Fig. 3B–E). Neither species spun an extra layer of silk to protect themselves or the egg sacs. Twenty-one *P. pennimani* females built at least one egg sac, nine constructed a second, three built a third one, and one produced a fourth, whereas the single *P. talquian* female did not constructed other egg sac after the first one.

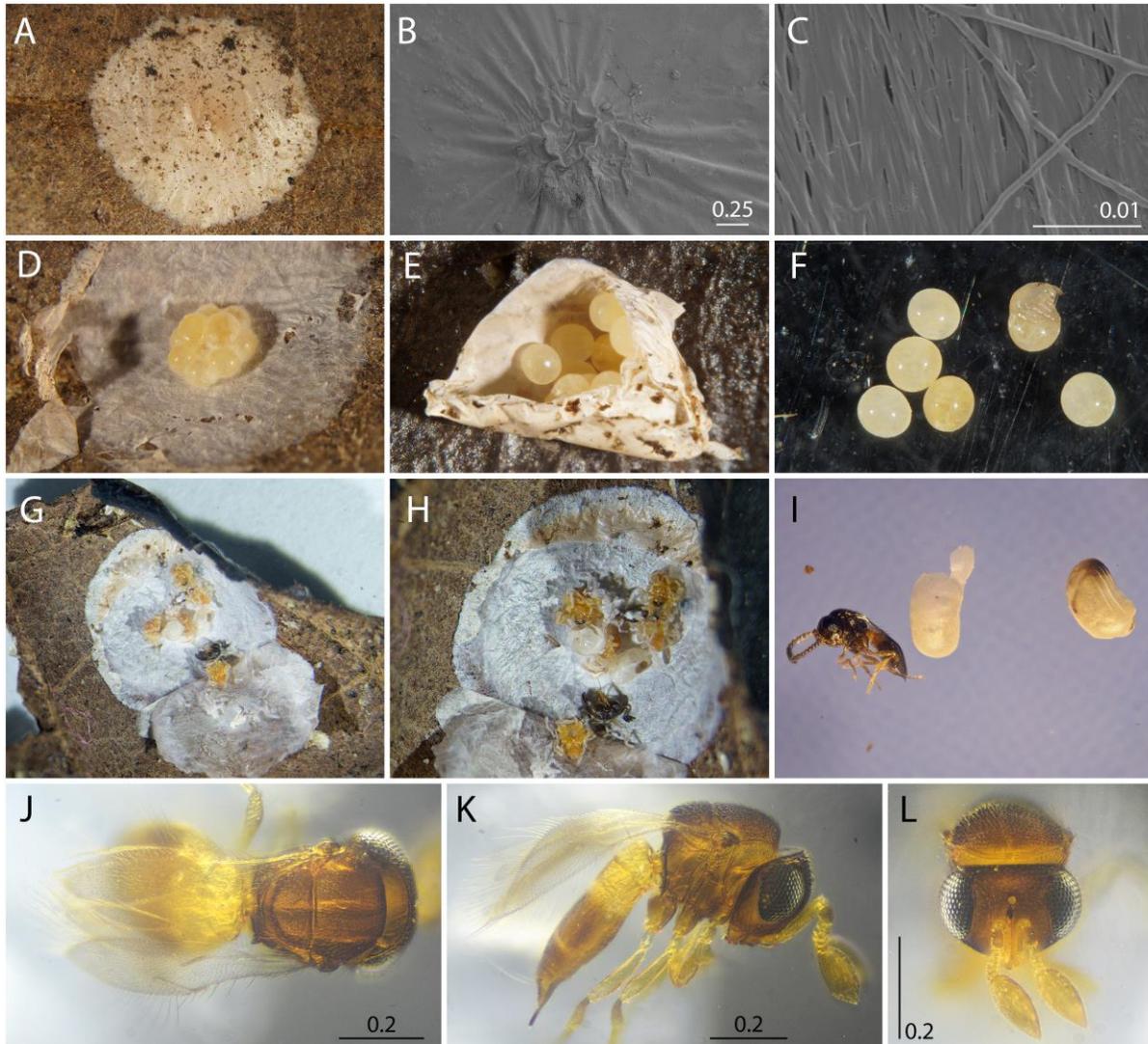


Figure 3. A, D–E. Egg sac of *P. pennimani*. B–C. Scanning electron micrograph (SEM) of egg sac upper layer detail. F. Eggs at different stages of embryonic development. G–H. Egg sac with parasitoid wasp *Idris* sp. I. Parasitoid wasp with puparium. J–L. Details of female parasitoid wasp of *Idris* sp.

For *P. pennimani*, the mean egg sac diameter was $5.62 \text{ mm} \pm 0.69 \text{ SD}$ ($n = 16$), the mean number of eggs per sac was $8.93 \text{ eggs} \pm 2.64 \text{ SD}$ ($n = 16$), with a range of six to 15 eggs, and the mean egg diameter was $0.49 \text{ mm} \pm 0.09 \text{ SD}$ ($n = 14$). The mean embryonic development time, from oviposition to spiderling emergence, was $22.66 \text{ days} \pm 4.72 \text{ SD}$ ($n = 3 \text{ egg sacs}$). Furthermore,

the female was not essential for offspring emergence; in two instances, offspring emerged from the egg sac after the females died. In a related case, a female built and guarded a second egg sac two days before the first clutch hatched and subsequently constructed a third egg sac two days before the second clutch emerged. We were unable to measure or count the eggs in the single *P. talquian* egg sac due to its loss before the offspring emergence.

Maternal care. In the field, we observed four *P. pennimani* females positioned themselves above their egg sacs. Under laboratory conditions, 21 *P. pennimani* females and one *P. talquian* female that constructed egg sacs exhibited maternal care by guarding their egg sacs. Females positioned themselves above their egg sacs, as observed in the field, or maintained contact using at least one leg (Figs. 1D–F, 2D). When disturbed during feeding, females rapidly sought refuge but subsequently returned to their egg sacs after several minutes, hours, or in some cases, not at all.

Endoparasitoids. Two female *P. pennimani* guarding their egg sacs were collected in the field (18 April 2018 and 14 January 2019). Each egg sac was attached to a dried leaf, and neither exhibited visible perforations or damage to the upper surface upon inspection. From both egg sacs emerged *Idris* sp. wasps (Scelionidae: Scelioninae; Fig. 3J–L). A male wasp emerged from the first egg sac, leaving a circular opening in the upper layer. Inside the egg sac, we found five dead juveniles, one dead female wasp, and two wasp puparia (Fig. 3G–H). The second egg sac contained an intact puparium, a male wasp (Fig. 3I), seven dead juveniles, and two unfertilized spider eggs.

DISCUSSION

Prey capture. Here, we provide the first anecdotal field observation of *P. pennimani* and *P. talquian* preying on Tomoceridae springtails. Recently, Angulo-Ordoñez *et al.* (2019) described the predatory behavior of *P. pennimani* and *P. talquian* against four prey types under laboratory conditions. Their results indicated a preference for Collembola (springtails) over Hemiptera or Psocoptera, with both species employing ambush or active searching strategies. Pekár and Jarab (2011) observed broad prey acceptance in laboratory conditions for two phrurolithids, *Liophrurillus flavitarsis* (Lucas, 1846) and *Phrurolithus festivus* (C. L. Koch, 1835). Both species were more successful at capturing *Sinella curviseta* Brook, 1882, an Entomobryidae springtail, than fruit flies or aphids, and preferred prey smaller than their body size (Pekár & Jarab, 2011).

In our observations, both juveniles *P. pennimani* and *P. talquian* were capable of subduing large springtails, and no evidence of silk use for prey capture was observed, neither in the field nor under laboratory conditions. The long, ventral, and movable macrosetae on the tibia and metatarsi of the forelegs of both species appear to be adaptations for prey capture. *Triaeris stenaspis* Simon, 1892, a goblin spider (Oonopidae), resembles both *P. pennimani* and *P. talquian* in size and in possessing leg macrosetae on the tibia. Similarly, it does not construct a web for prey capture but instead employs a grasp-and-hold tactic (Korenko *et al.*, 2014). *Triaeris stenaspis* has even been observed grasping springtail prey in a rodeo-riding manner (Korenko *et al.*, 2014), as we observed in a juvenile *P. pennimani* capturing a large springtail.

Adult individuals of both sexes of *P. pennimani* and *P. talquian* continued feeding long after reaching maturity, with females even preying while guarding their egg sacs. For males, this continued feeding likely provides additional energy for mate searching. For females, it may have contributed to nutrients and energy reserves for oviposition and parental care. Some Lycosidae species feed during maternal care, albeit at lower rate, as noted by Nyffeler (2000). This is because it is well known that egg laying is an energy-consuming process (Foelix, 2011).

Retreat for molting. To our knowledge, no reports of molting retreat construction exist for any Phrurolithidae species. We therefore report this behavior in laboratory conditions for the first time,

but this may also occur in natural conditions, although it is difficult to observe due to the small size of the specimens and their habit of living among leaf litter. This strategy is employed by both juvenile and penultimate individuals of *P. pennimani* and *P. talquian*, indicating that it is not restricted to early developmental stages. Individuals of both species appear to allocate resources to enhance their safety during the critical and vulnerable molting process. Not all spiders construct a retreat for molting; differences among families or even among species within the same genus have been documented (Austin, 1984a; Foelix, 2011; Nentwig & Heimer, 1987). Some Salticidae species, such as *Servaea incana* (Karsch, 1878) and *Phidippus johnsoni* (Peckham & Peckham, 1883), build a retreat for molting, although they also utilize it for courtship and as a refuge during breeding (McGinley *et al.*, 2015; Jackson, 1979). The plasticity of the retreat constructed by both *Phonotimpus* species may be due to multiple factors, including the overall condition of the individuals and the structures available at their environment. For example, well-fed females of *Tigrosa helluo* (Walckenaer, 1837) are more likely to construct burrows than individuals with higher levels of hunger, as burrow construction can be an energy-intensive task (Walker *et al.*, 1999).

Eggs sac, clutch size, and embryonic period. In spiders, the shape and conformation of an egg sac exhibit high variability, ranging from simple structures consisting of a few silk threads enveloping the eggs to elaborate egg sacs composed of multiple layers. In some cases, the egg sac is located within a retreat or nest (Foelix, 2011). Disk-shaped egg sacs appear to be common among phrurolithids, as evidenced by other genera such as *Phrurotimpus* sp. and an undescribed *Phonotimpus* species from central Mexico, which also construct similar egg sacs. *Phrurotimpus* sp. attaches its egg sacs to stones, while *Phonotimpus* secures them on dried leaves, with eggs clustered in the center (Kaston, 1948; unpublished data), resembling those of *P. pennimani* and *P. talquian*.

Although families related to phrurolithids produce egg sacs of diverse shapes, some exhibit similarities. For example, certain species within the genera *Clubiona* (Clubionidae), *Castianeira* Karsch, 1880 (Corinnidae), *Agroeca* Westring, 1861 (Liocranidae), *Trachelas* L. Koch, 1872 (Trachelidae), *Callilepis* Westring, 1874, *Cesonia* Simon, 1893, *Herpyllus* Hentz, 1832, *Zelotes* Gistel, 1848, and *Drassodes* Westring, 1851 (Gnaphosidae) also construct flattened oval or lenticular egg sacs (Kaston, 1948). Interestingly, all these related families inhabit microhabitats similar to those of phrurolithids.

The number of eggs laid, and the number of egg sacs constructed by a female spider vary among species, ranging from a single egg to thousands and from one to ten egg sacs (Kaston, 1948). Families related to Phrurolithidae, such as Clubionidae, Trachelidae, Corinnidae, and Gnaphosidae, produce between 8 and 60 eggs per egg sac (Kaston, 1948). The phrurolithids *L. flavitarsis* and *P. festivus* lay a mean of 4.7 and 4.1 eggs per clutch, respectively, and females of both species construct multiple egg sacs under laboratory conditions (Pekár & Jarab, 2011). In contrast, the Nearctic *Phrurotimpus alarius* produces 13 eggs per egg sac under laboratory conditions (Kaston, 1948; Montgomery, 1909). Available data indicate that phrurolithids, which are small-sized spiders, lay fewer eggs per egg sac but construct up to four egg sacs under laboratory conditions. Marshall and Gittleman (1994) reported a correlation between female spider body size and the number of eggs laid, with larger species producing more eggs. Finally, prior to this work, no data on the embryonic period for any phrurolithid species were known.

Maternal care. Parental care is any trait that enhances the fitness of a parent's offspring; for instance, by protecting them from predators, cannibalism, parasitoids, fungal infections, food shortages, and harsh environmental conditions (Santos *et al.*, 2017; Smiseth *et al.*, 2012; Tallamy, 1984). The most common forms of care in spiders involve egg sac construction, egg sac guarding,

and brood care by the female (Yip & Rayor, 2014). Some spiders carry the egg sac or their offspring post-hatching (Kaston, 1948; Yip & Rayor, 2014), while others provide food, such as prey, regurgitated fluids, or trophic eggs, or engage in matrophagy (Ibarra-Núñez, 1985; Kim & Roland, 2000). However, most spiders typically abandon their egg sacs upon completion (Foelix, 2011).

Prior to Platnick's (2019) work, it was commonly accepted that phrurolithids abandoned their egg sacs. Specifically, Dondale and Redner (1982) stated that females of *Phrurotimpus* abandon their scale-like egg sacs. Based on the label of a female specimen collected by William Shear, Platnick (2019) asserted that *Phrurotimpus borealis* (Emerton, 1911) guards its egg sac and suggested the adoption of the common name "guardstone spiders" for all Phrurolithidae. Here, based on observations made in the field and under laboratory conditions, we found that females guard their egg sacs, and even when disturbed, they typically return to mount guard for most of the embryonic period. Additionally, field observations of an undescribed *Phonotimpus* species indicate that egg sac guarding might be shared by most, if not all, *Phonotimpus*. Some species related to phrurolithids, such as clubionids, gnaphosids, and salticids, also exhibit egg sac guarding until the emergence of offspring (Austin, 1984a; Kaston, 1948; Jackson, 1979).

The sole presence of a mother can increase the survival of progeny by deterring predators and parasitoids (Vieira & Romero, 2008). However, in some cases, such protection does not prevent parasitism (Barrantes & Weng, 2007) or is ineffective against larger predators like mantispids (McGinley *et al.*, 2015; Vieira & Romero, 2008). Future studies should investigate the efficacy of guarding by females of *P. pennimani* and *P. talquian* in deterring natural enemies and reducing parasitism by *Idris* wasps or other natural enemies.

Endoparasitoids of *P. pennimani*. Here, we document the first record of an *Idris* sp. wasp (Scelionidae) parasitizing eggs of Phrurolithidae, with the wasp representing a putative new species of *Idris* (Margaría, 2019 *in litt.*). The wasp genera *Baeus* Haliday, *Ceratobaeus* Ashmead, *Idris* Förster, and *Odontacolus* Kieffer (Baeini, Scelioninae) specialize in exploiting spider eggs (Araneae) with a high degree of host specificity (Austin, 1984b; Austin *et al.*, 2005; Barrantes & Weng, 2007; Loíacono & Margaría, 2013). Prior to hatching, the larva of scelionid wasp consumes the contents of the host egg and pupates within it (Austin *et al.*, 2005). In the Neotropical region, *Idris* spp. wasps are known to attack spider eggs of *Ctenus* sp. (Ctenidae), *Pardosa* ca. *flavipalpis* F. O. Pickard-Cambridge, 1902 (Lycosidae), and *Sumampattus hudsoni* Galiano, 1996 (Salticidae), among other unidentified spiders (Jiménez, 1987; Loíacono & Margaría, 2013).

The use of only two *P. pennimani* eggs by the *Idris* sp. wasp on each egg sac, may represent a strategy to avoid resource depletion. As observed in other Baeini (Scelioninae) wasps, the mortality of eggs caused by *Ceratobaeus* spp. and *Baeus* sp. wasps is limited to approximately 30% of total egg clutch in spiders such as *Clubiona* sp. (Clubionidae) and *Theridion evexum* Keyserling, 1884 (Theridiidae), respectively (Austin, 1984b, Barrantes & Weng, 2007). Austin (1984b) suggested that Baeini wasps can recognize their host using cues from the silk of egg sacs or retreats. Furthermore, it is known that Baeini female wasps can enter egg sacs to access eggs or oviposit by piercing the chorion through the thin silk of the host egg sac (Austin *et al.*, 2005; Loíacono & Margaría, 2013). Future research should determine how the *Idris* sp. wasp locates Phrurolithidae egg sacs and whether *Idris* female wasps oviposit before or after *P. pennimani* seals her egg sac.

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