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Egg sac construction and camouflage behaviors of *Deinopis* cf. *cylindracea* (Araneae: Deinopidae)

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Abstract. Spiders exhibit various egg sac construction behaviors using camouflage to protect the eggs from predators and parasitoids and also perform parental care to increase offspring survival. In this study, we describe the egg sac construction behavior of *Deinopis* cf. *cylindracea*, and the camouflage characteristics of egg sac when left without the female's active protection. Our observations showed that *D. cf. cylindracea* builds a fairly compact egg sac, with an outermost layer composed of dense silk. This outermost layer is dark brown, perhaps to camouflage with the substrate on which the egg sac is deposited. Moreover, females tend to hide their egg sacs with dry leaves in the litter. In addition, the overall color, shape, and size of the egg sac resemble the dry seeds of *Plinia cauliflora*, the plant on which *D. cf. cylindracea* was found. Two female spiders were positioned on their egg sacs; however, whether this behavior reflects maternal care remains unknown. Therefore, the overall egg sac construction behavior of *D. cf. cylindracea* may be related to a strategy for increasing fitness. This is the first behavioral record for a South American deinopid species.

Keywords: Reproduction, maternal care, egg sac camouflage, concealment of egg sac, Serra do Japi.

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Spiders exhibit various egg sac construction behaviors, which have evolved to maintain the appropriate and essential microenvironmental conditions for embryonic development. Spiders also perform active parental care to protect eggs and embryos from predators and parasitoids (Austin 1985; Barrantes et al. 2014). Typically, the structure of the egg sac comprises an internal basal and an outer cover plate (Foelix 2011). The cover plate (outer layer) serves as a mechanical barrier and thermal insulation against fluctuating ambient temperature. Egg sacs are of several shapes and colors. Their outer layer is often the hardest one and has a very compact consistency. Occasionally it is concealed in debris, a behavior that has presumably evolved to reduce the visibility of egg sacs to natural enemies (Barrantes 2007; Barrantes et al. 2013).

The egg sac coloration varies widely among spider species; however, there is no information on the pigments responsible for different colors or their roles in camouflage (Barrantes et al. 2013). The effectiveness of camouflage depends on the color, shape, decoration, oviposition substrates, and specifically the contrast of the outer layer of egg sac against the visual background (Craig 2003; Bauer et al. 2019). In the Uloboridae, a sister family of Deinopidae, females of different species use different mechanisms to protect their egg sacs. *Miagrammopes animotus* Chickering, 1968, for example, place their egg sacs in the capture web in vertical lines. Subsequently, the female aligns vertically with egg sacs to have a twig-like shape. In addition, the color of both egg sac and female are similar, ranging from light to dark tan which increases crypticity against visually oriented predators (Opell 2001). *Hyptiotes cavatus* (Hentz, 1847) constructs egg sacs in the form of convex and cryptic plates that are attached directly to the branches (Opell 1984). Construction of a stalk to suspend the egg sac or even use of a substrate to attach the egg sac are also characteristic behaviors, which widely vary across spider species (Nielsen 1932). For instance, *Mecynogea lemniscata*

(Walckenaer, 1842) and *Argiope aurantia* Lucas, 1833 (Araneidae) build silk structures on their egg sacs that allow the sac to be suspended, possibly to provide protection against predators (Hieber 1992). *Deinopis* sp. (Deinopidae) builds a peduncle, allowing the egg sac to suspend in midair to possibly restrict access to certain groups of natural enemies (Barrantes et al. 2014).

Maternal care after oviposition is another behavior that varies among spider species. Several female spiders remain close to their eggs until or even after hatching (Gillespie & Spagna 2009). This behavior is common among different spider groups. For example, in the jumping spider *Psecus chapoda* (Peckham & Peckham, 1894) (Salticidae), the female remains with her egg sac and defends her offspring against generalist predators (Viera & Romero 2008). The females of the funnel spider *Aglaotenus lagotis* (Holmberg, 1876) (Lycosidae) carry their eggs adhered to the spinnerets and held by the last pair of legs. After emerging from the eggs, spiderlings migrate to the dorsal region of the body of the mother, who regurgitates food for them, increasing the survival rate of offspring (Stefani et al. 2011). The orbicular spider *Uloborus glomosus* (Walckenaer, 1842) (Uloboridae) lays its eggs in a vertical chain in the center of the web. Females remain close to the egg sacs until spiderlings emerge, while she feeds normally and maintains her web (Cushing & Opell 1990). However, some females abandon their egg sacs immediately after oviposition (Foelix 2011).

In oviparous species without post-ovipositional maternal care, eggs are vulnerable to attack by natural enemies and are exposed to the external environment (Torres-Campos et al. 2016). These factors have driven the evolution of the “be prepared” strategies (Hamdoun & Epel 2007; Gillespie & Spagna 2009), involving the coevolution of maternal oviposition behaviors (e.g., site selection) (Touchon & Warkentin 2008; Moura et al. 2011; Schulze & Jansen 2012) with egg and

egg sac morphology and physiology (e.g., color, patterns, or temperature tolerance). For instance, some spiders construct a nest or a shelter made of leaves, debris, or silk, which may reduce the rate of offspring predation by preventing natural enemies from visually detecting or accessing the egg sac or spiderlings (Konigswald et al. 1990; Toyama 1999; Zanatta et al. 2016).

Spiders of the family Deinopidae are commonly called “ogre-faced” spiders. They are also known for producing cribellate capture threads and having a unique prey-capturing strategy (net-casting behavior) (Blamires et al. 2017). Currently, the family Deinopidae comprises 67 described species in only three genera. (1) *Asianopis* Lin & Li, 2020 is endemic to Asia, with seven described species. (2) *Menneus* Simon, 1876 is distributed in Africa and Oceania, with 14 representative species. (3) *Deinopis* MacLeay, 1839 is distributed in Asia, Oceania, Africa, and America, with 46 described species, 9 of which are found in Brazil (World Spider Catalog 2020). *Deinopis* cf. *cylindracea* C. L. Koch, 1846, species study, was recorded by Koch (1846) only in Colombia; however, there have been no studies on the natural history of this species. Deinopid spiders construct egg sacs which are perhaps the densest egg sac structures with the hardest external layer (Baum 1937; Coddington et al. 2012; Barrantes et al. 2014). The females do not remain with the egg sacs during embryogenesis. However, there are no detailed descriptions of egg sac construction behavior for many species. In one of the remnants of Atlantic Forest in southeastern Brazil, we observed females of *D.* cf. *cylindracea* moving and covering their egg sacs in litter. These observations suggest that this behavior is not random but rather a characteristic of the species. Thus, the aim of this study was to describe the egg sac construction behavior of *D.* cf. *cylindracea* and the camouflage characteristics of the egg sac when left without the female’s active protection.

METHODS

Sampling.—In March 2015, we collected 11 gravid females of *D.* cf. *cylindracea* from the trunks of a native tree, *Plinia cauliflora* (Mart.) Kausel [1956] (Myrtaceae). We noted that these spiders were very frequently found on this tree (Ponte et al. 2020). These trees were planted along trails or around forest clearings near the Ecological Station at Serra do Japi about 40 years ago at a site called Monte Horebe, and all trees are of similar height. The Ecological Station at Serra do Japi (23°12’S to 23°21’S and 46°30’W to 47°05’W), Jundiá Municipality, São Paulo, Brazil. This area of the Atlantic Forest is primarily covered by seasonal mesophyll forest (Morellato 1992). *Deinopis* cf. *cylindracea* presents distinct population dynamics, with adults occurring mainly in late summer and autumn (Ponte et al. 2020). *Deinopis* cf. *cylindracea* was identified by Jonathan A. Coddington.

Egg sac construction in the field and laboratory observations.—We described the egg sac construction behavior, egg sac deposition, and egg sac structure based on observations of females in the wild as well as of females collected and maintained in cages under laboratory conditions. Our observations were incidental, both during the day and at night, but mainly during the night, as *D.* cf. *cylindracea* is nocturnal. Laboratory conditions included a natural light

cycle, approximately 14:10 hrs light:dark, and temperature and humidity around 26°C and 60%.

To characterize the use of debris during oviposition, we conducted laboratory observations of gravid females collected from the field. Gravid females could be distinguished based on the expanded abdomen. We kept these females ($n = 11$) in separate cages under laboratory conditions. Of the 11 cages used, five measured $24 \times 24 \times 30$ cm and six measured $17 \times 17 \times 25$ cm. We covered the floor with sand, then leaves and dry branches (hereafter referred to as “litter elements”) from the same environment from which the specimens were collected were spread evenly along the sides. We designed the layout in such a way that the movement of litter by the spider, if any, would be evident.

We performed the analysis of movement of litter elements using photographs of the cage floor. We took a photograph before placing the gravid female on the floor to highlight the original organization of the added litter elements and another after oviposition by the female. In addition to litter elements, we provided other elements required for web construction and hunting. We included a vertically positioned branch in a sand-filled glass cup, which was placed on a galvanized sheet to provide a smooth horizontal surface. The spiders used the vertical branches as support to hang and built the web directed at the smooth surface of the tile. A wet cotton ball placed in each cage provided hydration. The spiders were kept in the experiment cages for 45 days, until all data were collected. During that time, we fed the spiders with ants of the genus *Camponotus*.

After the experiment, we collected some egg sacs ($n = 9$) from the cages and dissected under a stereoscopic microscope to examine their structure. We measured egg sac diameter and counted the eggs.

RESULTS

Egg sac construction and deposition.—The initial process of egg laying and egg sac construction was not observed, which probably consists of laying the eggs on a basal plate and wrapping the eggs and cover plate (Foelix 2011). Observations began during the process of applying the outer layer of the egg sac, which would be in contact with the external environment. While producing this outer layer, the female maintains the egg sac in her ventro-abdominal region (Figs. 1a, b). The egg sac is attached at one point to a support thread (Figs. 1a, c), which is a thread of uniform thickness and not a reinforced thread, as seen in *Deinopis subrufa* Koch, 1878, which keeps the egg case permanently suspended after construction (Baum 1937). This thread provides temporary support for the egg sac during construction as well as for the female, who holds on to it with her first pair of legs.

The female applies the outer layer of silk by bending her abdomen toward the egg sac such that the spinnerets are in contact with the sac. The spinnerets release silk fibers that coat the egg sac (Fig. 1b); the female controls the application site on the surface by turning the egg sac with the second, third and fourth pairs of legs as well as the pedipalps. At the end of the application of this layer, the female leaves the egg sac hanging by the support thread and positions herself in the web to which this thread is connected, such that the anterior part of her body is facing downward and her front legs are facing

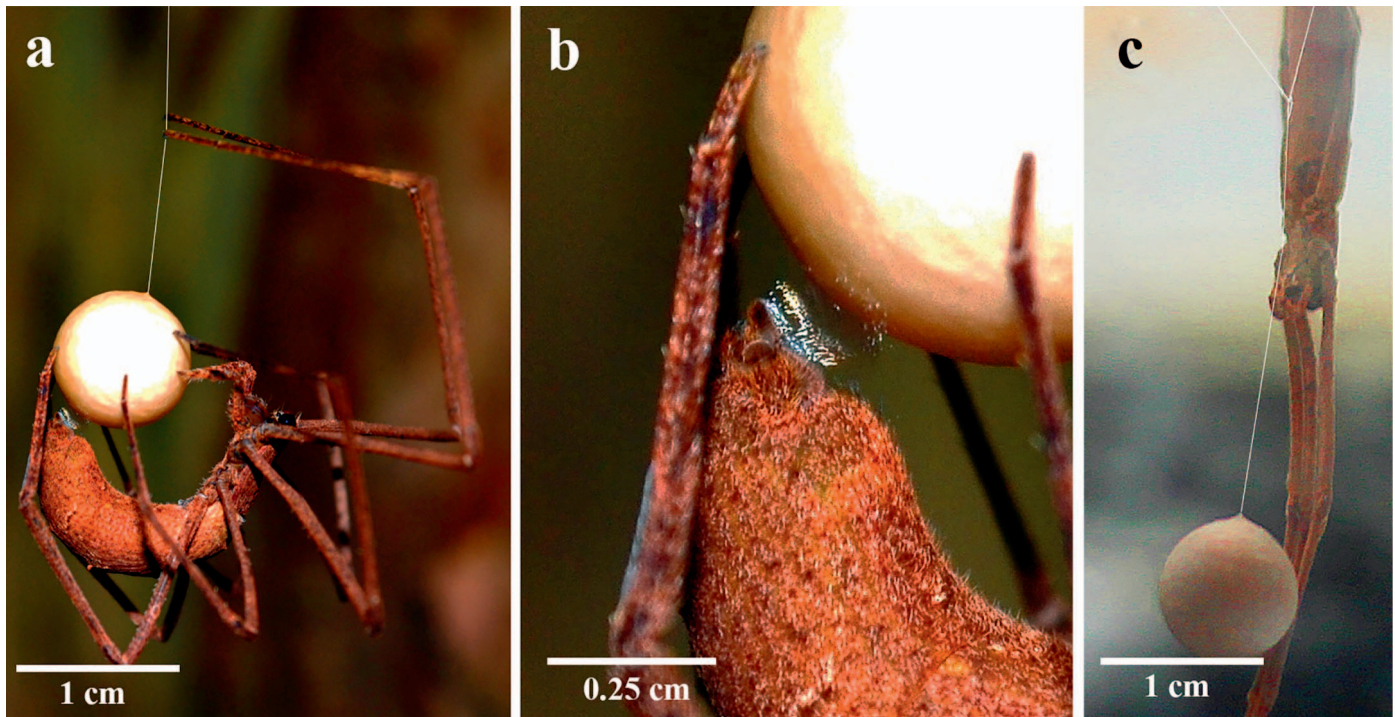


Figure 1.—A *Deinopis* cf. *cylindracea* female constructing an egg sac (a). Application of web covering the egg sac (b). Female positioned next to the newly built egg sac (c). The web threads shown in (a) and (b) were enhanced by photograph manipulation software to facilitate visualization.

the egg sac (Fig. 1c). For about 30 minutes, the egg sac remains hanging until the threads that constitute the outer layer are partially dry. At the end of construction of the outer layer, the egg sac appears clear whitish. As the female waits by its side, the egg sac gradually darkens, turning brownish.

On the same night of constructing the egg sac, the female begins the process of its deposition. After the egg sac is partially dried, the female cuts the support thread, holds it, and takes the egg sac to the floor hanging it by this thread (Fig. 2a). As she approaches the floor holding the thread, she repeatedly pulls and releases the thread causing the egg sac to strike the floor at different locations below her, until she permanently attaches the egg sac in one of these locations, and then she starts to cover it up. At some point this thread must be cut, as it is not visible on the egg sac after it is covered. During covering behavior, the posterior legs of the female are attached to the support thread that is attached to the web — the same thread that was used to support the egg sac. Standing over the egg sac deposited on the floor, the female uses the two pairs of front legs to search the floor for litter elements near the egg sac (see supplemental Video S1, online at <https://doi.org/10.1636/JoA-S-20-077.s1>). She joins small portions of litter elements using few silk threads and places them on the egg sac. She repeats this behavior using litter elements placed increasingly away from the egg sac, until it is fully covered (Figs. 2b, 3)

In the hours following the deposition and covering, the egg sac undergoes a further change in color and shape, until it reaches a dark brown hue with small concavities on the outer layer, similar to a golf ball (Fig. 2b).

Laboratory observations.—Egg sac construction, deposition, and covering behaviors were observed in all females subjected to laboratory experimentation in cages ($n = 11$). Of the 11 females, three deposited two egg sacs each, and the remaining deposited only one egg sac each. In the experiment, all 11 females covered the egg sacs produced in the cages, indicating that females actively used the litter elements (Fig. 3). We also observed that the egg sacs were mostly deposited in the corners of the cage ($n = 13$), and only one egg sac was deposited away from the edge (Fig. 3).

After covering the egg sac, two females altered the construction site of their hunting webs and positioned themselves above the site where the egg sac was deposited and covered, remaining armed with the capture web above the egg sac for the next two days, even during the daytime. On the third night after egg sac deposition, the females returned to the original web-building sites at the center of the cage.

The egg sac of *D. cf. cylindracea* was almost spherical and measured on average 8.3 ± 0.3 mm SD on the long axis and 7.6 ± 0.1 mm SD on the short axis ($n = 9$) (Fig. 4a). This difference in the long axis may be related to the point of attachment of the silk thread from which it was originally hung. Structurally, the egg sac is composed of a very hard outer silk layer and an internal web pouch (flocculent silk) in which the egg cluster is deposited and from which the spiderlings emerge (Fig. 4a). Hatched egg sacs had on average 69 ± 18 SD spiderlings ($n = 7$; Fig. 4b), while the non-hatched ones had on average 89 ± 24 SD eggs ($n = 2$; Figs. 4c, d). Only one egg sac was partly hatched, with 62 eggs and 16 spiderlings.

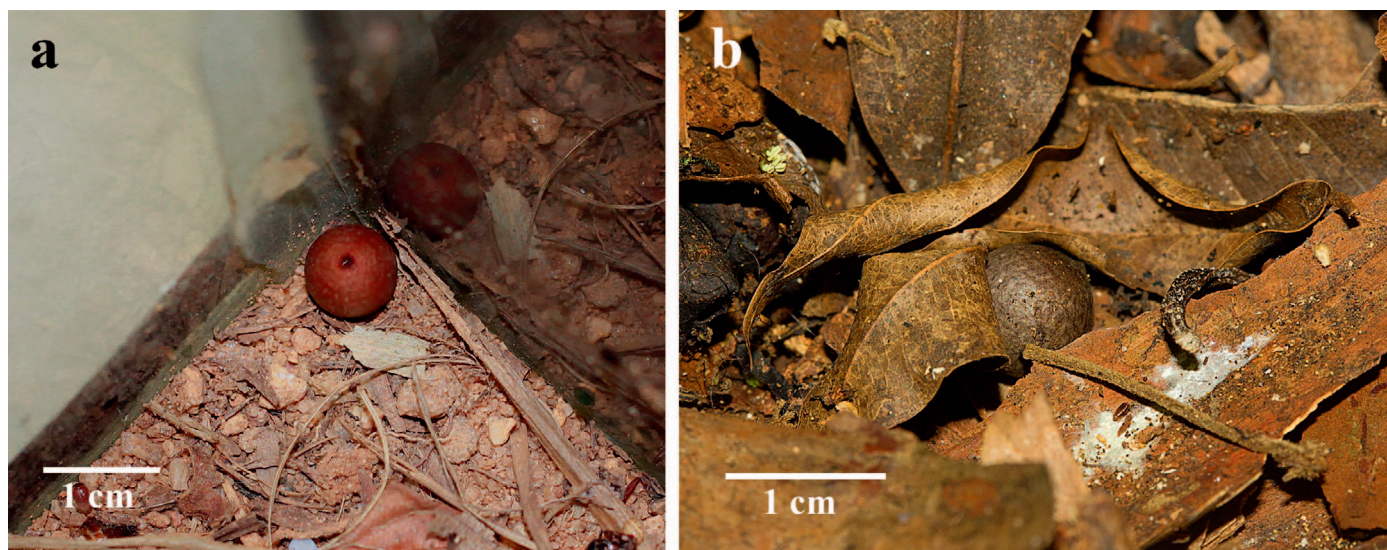


Figure 2.—Egg sac deposited in the soil of the cage (a) and covered by litter in the field (b)

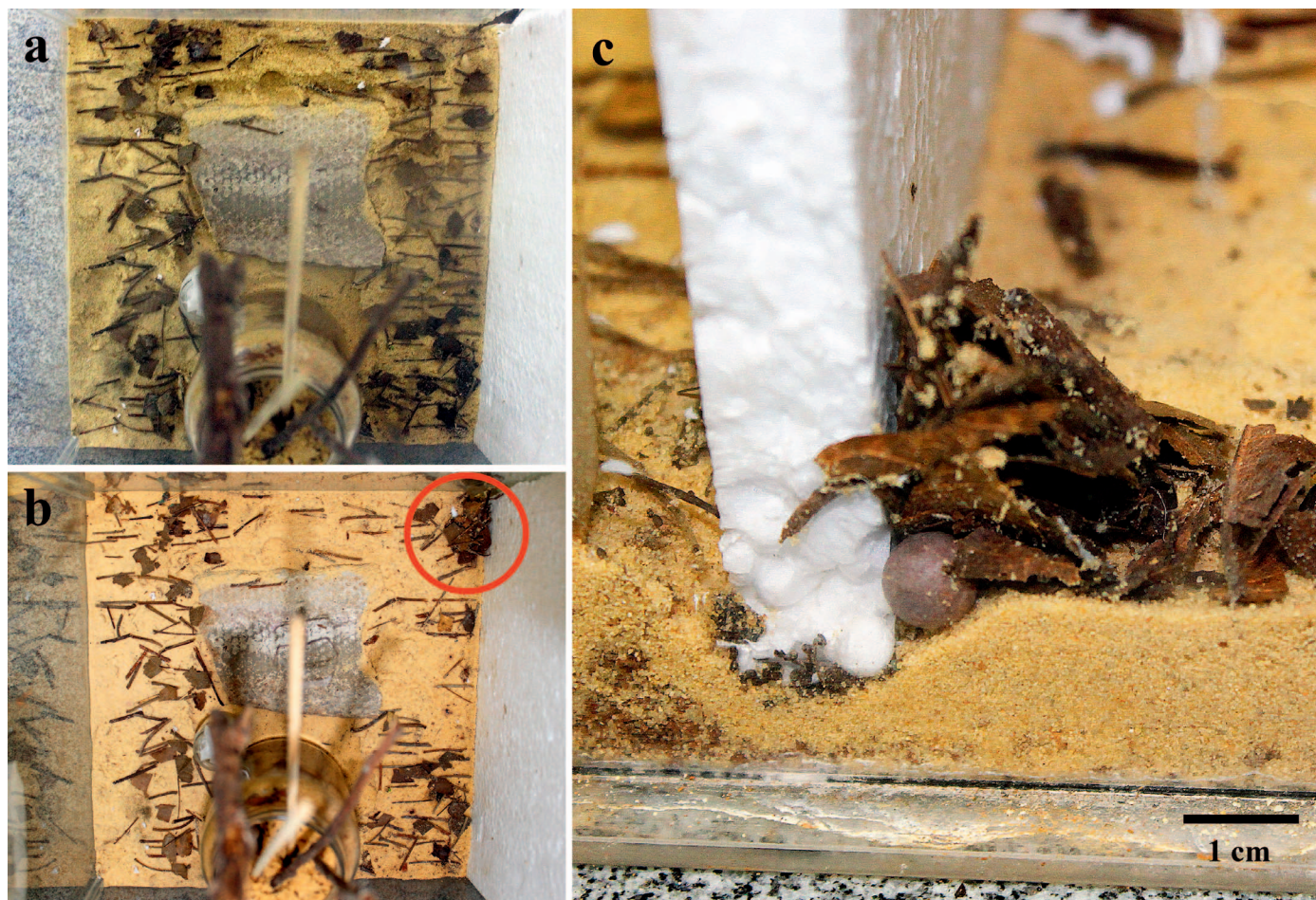


Figure 3.—Laboratory experiment confirmed active litter use to cover the egg sac. (a) Photograph before oviposition. (b) Photograph after covering the egg sac. The egg sac in the upper right corner is marked (circle). (c) Egg sac deposited in the corner of the cage and covered with leaves and sticks

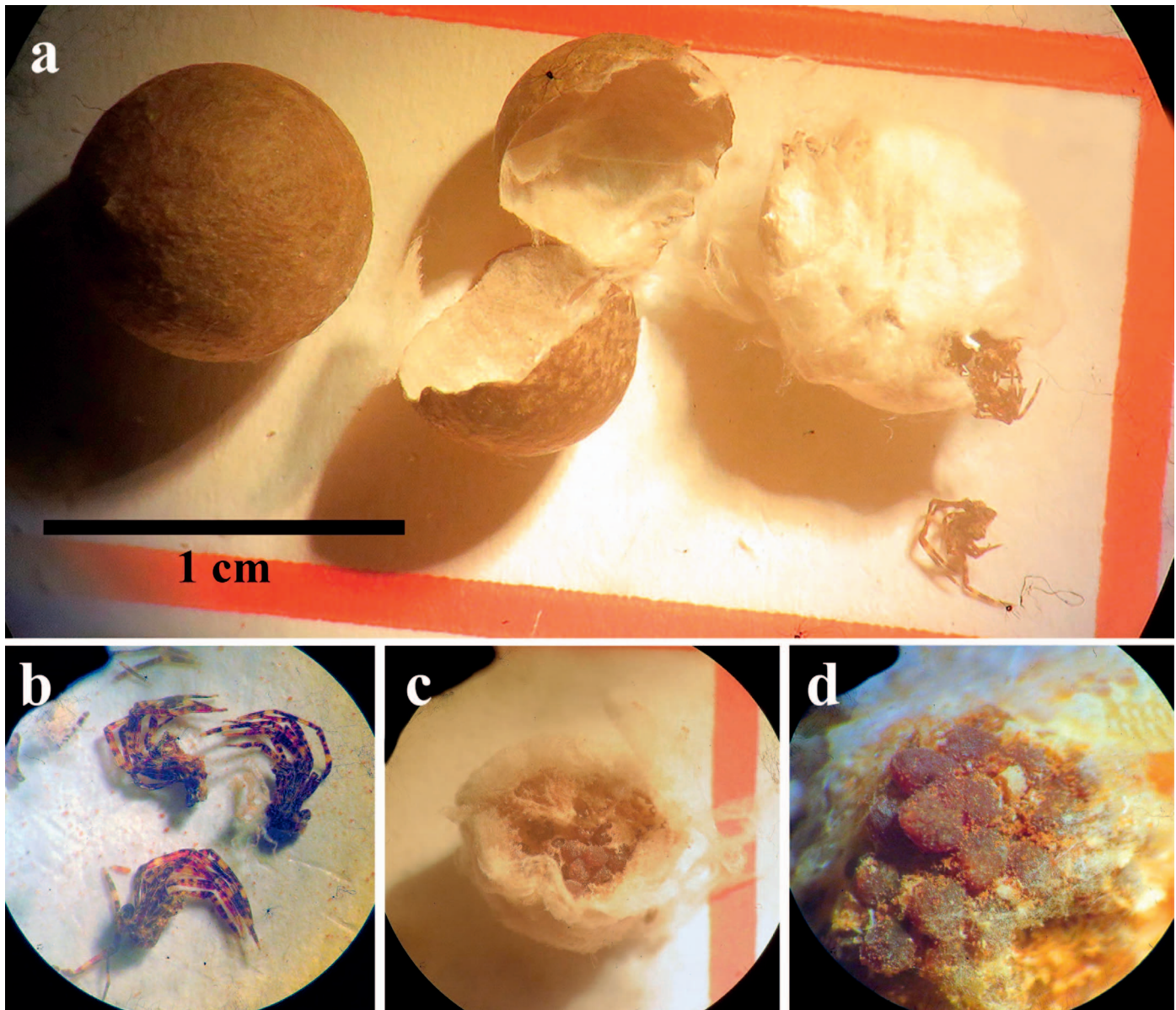


Figure 4.—Structure of the egg sac of *Deinopis* cf. *cylindracea* showing (a) from left to right, the intact egg sac, the outer protective layer, and the inner web pouch with an opening, with spiderlings at and just below outside the opening. (b) Egg sac with spiderlings. (c) Inner web pouch with spherical unhatched eggs. (d) Egg cluster inside the web pouch.

In the field, seeds and dried fruits of *Plinia cauliflora* (Myrtaceae) were found throughout the litter under these plants. These were similar in appearance and size (~7 to 8 mm) to the egg sacs of *D. cf. cylindracea*.

DISCUSSION

In this study, we describe the structure of egg sac of *D. cf. cylindracea* and steps in its construction. The outermost layer was quite compact and composed of a dense silk layer. However, upon opening the egg sac, an internal pouch was observed in which the egg cluster was directly deposited. Coddington et al. (2012) described the typical structures of egg sacs of *Menneus* species (Deinopidae), which also consist of two layers: an outer layer of densely woven thin threads and

an inner more compact layer without discernible threads. Our description of the outermost layer of egg sac in *D. cf. cylindracea* is similar to that reported by Coddington et al. in *Menneus*; however, the inner layer of egg sac in *D. cf. cylindracea* differs from that in *Menneus*, as it is composed of a soft, flocculent silk in which the eggs are embedded. Hajer et al. (2009) observed the ultrastructure of threads in the egg sac of *Theridiosoma gemmosum* (L. Koch, 18770 (Theridiosomatidae) and suggested that the flocculent silk layer may be an effective barrier against specialist parasitoid wasps with long ovipositors to parasitize cocoons. Hieber (1992) also observed the same inner layer in *Mecynogea lemniscata* (Walckenaer, 1841) and *Argiope aurantia*, and reported that flocculent silk could restrict the entry of specialist egg predators such as ichneumonid wasps or mantispid mantidflies. Although the

egg sac construction behavior was recorded here only for the outermost layer, the description of the behavior in the studied species resembles the descriptions in other *Deinopis* species reported by Barrantes et al. (2014).

The egg sacs produced by *D. cf. cylindracea* were spherical and dark brown, which are characteristics resembling a drying fruit of *Plinia cauliflora* observed in litter; these could be associated with egg sac camouflage. According to Endler (1978), an animal is camouflaged when it resembles a part of the background, which could be the case regarding the resemblance of *D. cf. cylindracea* egg sac to *Plinia cauliflora* seeds, which are specifically abundant only in the study location. However, future specific experiments are necessary to establish this camouflage hypothesis. Several egg sacs that appear brown to the human eye show a relatively high UV reflectance, e.g., *Peucetia viridans* (Hentz, 1832) and *Deinopis* sp.; species that can perceive UV wavelengths would likely be able to distinguish between brown egg sacs with low and high UV chroma. In contrast, silk of the egg sacs of spiders in Uloboridae, (the sister family of Deinopidae) such as *Zosis geniculata* (Olivier, 1789), have low UV reflectance and high red reflectance (Barrantes et al. 2013). High red reflectance of egg sacs has presumably evolved within these families to reduce the visual contrast of the egg sacs against the background, as they blend in with the surrounding structures of similar coloration.

The brown color and spherical shape of egg sacs recorded in *D. cf. cylindracea* have also been observed in other *Deinopis* and *Menneus* species (Baum 1937; Coddington 2005; Coddington et al. 2012; Barrantes et al. 2013, 2014) and may be a conserved trait at the family level (Coddington et al. 2012).

Our results corroborate the observations of Coddington (2005) that females of *D. cf. cylindracea* actively cover the egg sacs placed in litter using different elements, such as leaves and dry branches. The reproductive period of our Deinopidae species spans between March and July; therefore, the egg sac is deposited in autumn, remains intact covered in litter through the cold and dry winter, and finally hatches in late winter and spring, with young spiderlings emerging in early summer (the wettest and hottest period of the year) (da Ponte et al. 2020). According to Baum (1937), the spiderlings abandoned the egg sac after placing a moist cotton in the cage, suggesting that after a dry period, rains may be an important cue for the emergence of spiderlings from the egg sac.

The covering of an egg sac with litter elements can also act as a form of camouflage to hide the characteristics of its shape (Toft & Lubin 2018). Similar results were recorded in *Paratrachelas maculatus* (Thorell, 1875) (Trachelidae). In this spider, at the end of egg sac construction, the female added black sand and soil particles on the external side to decrease its detection by visually oriented predators (Bauer et al. 2019). Another behavior that exemplifies the use of substrate, such as leaves, as a strategy of egg sac concealment was observed in *Pozonia nigroventris* (Bryant, 1936) (Moya et al. 2010). The female of this species collects a leaf from the forest floor and uses this as a wrapper in which she lays her eggs. As soon as she finishes oviposition, the female folds the leaf and secures it with silk threads, sealing the package, and then transports it to the forest floor. The egg mass wrapped in a dead leaf in the litter is very well camouflaged, and this can protect it from

large animals, such as birds looking for food on plants, although this would expose the eggs to another set of potential predators, such as ants on the forest floor (Hieber 1992). In our behavioral observations, 10 of the 11 females of *D. cf. cylindracea* deposited their egg sacs in the corner of the terrarium, possibly because egg sacs deposited near structures such as tree trunks or shrub stems may be better protected; however, this behavior needs to be further investigated as only one egg sac was discovered by the tree trunks where the spiders were found.

According to Baum (1937), egg sacs of *D. subrufa* were parasitized by Hymenoptera. However, the hard and hidden egg sac of *D. cf. cylindracea* would be protected from parasitoids. In addition to covering the egg sac, two females positioned themselves on top of the egg sac; however, whether the presence of female would decrease predation or parasitism of the eggs was not tested in this study. This behavior of females positioning themselves near the egg sac is the first record for a deinopid species from South America. Maternal care along with egg sac, which acts as a physical barrier to eggs, does not always provide sufficient protection against specialist predators or parasitoids. Barrantes et al. (2014) recorded pupae of an unknown egg predator within the egg sac of *Deinopis* sp. In other species of spiders, predation of up to 100% of eggs by wasps of the subfamily Cryptinae (Ichneumonidae), regardless of maternal care (Villanueva-Bonilla et al. 2016; Sobczak et al. 2020), is commonly reported.

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SUPPLEMENTAL MATERIALS

Supplemental Video S1, Female *Deinopis* cf. *cylindracea* behavior with egg sac. Available online at <https://doi.org/10.1636/JoA-S-20-077.s1>

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