

## SHORT COMMUNICATION

## Empty nuptial gifts: a further step in the evolution of deception in spiders?

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**Abstract.** In the spider families Trechaleidae and Pisauridae, males offer nuptial gifts to females during courtship. Nutritive gifts contain recently caught prey wrapped in silk, while worthless gifts contain prey leftovers or plant parts. The presence of wrapped gifts is known in three out of 16 genera (*Paratrechalea* Carico, 2005, *Trechalea* Thorell, 1869 and *Trechaleoides* Carico, 2005) in Trechaleidae, suggesting that this sexual trait is of widespread occurrence in the family. Here, we report the presence of wrapped nuptial gifts in the genus *Paradossenus* F.O. Pickard-Cambridge, 1903. Males of *P. longipes* (Taczanowski, 1874) produce prey-gifts following the same sequence of behavioral units as described for other species of the family. More surprisingly, these males may also produce empty gifts consisting of a silken structure lacking contents. This is the first record of empty nuptial gifts in spiders. This novel male tactic may have evolved from worthless gifts as a further step in the evolution of deception in gift-giving spiders.

**Keywords:** Sexual selection, gift-giving behavior, alternative reproductive tactics, *Paradossenus longipes*, Trechaleidae

Nuptial gifts have been defined as materials beyond gametes transferred from one sex and consumed by the other (usually offered by males to females) during courtship and mating (Lewis & South 2012). This secondary sexual trait is widely recorded among insects, being present in 41% of the orders (~7% of the families), and occurs in many forms. Evidence indicates it has evolved independently in many groups, and that it may have positive, negative, or neutral effects on the reproductive success of both sexes (Vahed 1998; Gwynne 2008; Lewis & South 2012; Lewis et al. 2014). In spiders, fewer than 15 species from 5 families have been reported to have nuptial gifts, which are classified into three types: body parts, glandular secretions, and items wrapped in silk (Albo et al. 2014b). In some species of the families Trechaleidae and Pisauridae, males offer females a prey item during courtship which is usually wrapped in silk. If the prey is recently caught it will provide food for the female (nutritive gift), but sometimes the males wrap prey leftovers or plant parts, thus producing a deceptive worthless gift (Bristowe 1958; Costa-Schmidt et al. 2008; Albo et al. 2011, 2014a). Regardless of the gift content, males offering wrapped gifts increase both their chance to mate and mating duration compared to males without gifts (Stålhandske 2001; Albo & Costa 2010). However, nutritive gifts represent an important source of nutrients that improve females' fecundity (Toft & Albo 2015; Pandulli-Alonso et al. 2017).

Gift production behavior is highly ritualized and the process is conserved among species (Bristowe 1958; Costa-Schmidt et al. 2008; Albo et al. 2009). After capturing a prey or grabbing an inedible item, the male starts silk wrapping by adding silk threads to the substrate until a silken sheet has been formed (basal plate spinning). The prey or item is placed on the basal plate (item placement), which will then be covered with more silk (silk covering). The male manipulates the silk cover with his pedipalps (drumming), and eventually grabs the still unfinished structure with his chelicerae and lifts it from the substrate (gift grabbing). Finally, while holding it with the chelicerae he wraps the gift using his legs III to draw silk from the substrate (final manipulation). The complete process of nuptial gift construction includes several silk wrapping bouts and results in a round, white

package which the male carries in his chelicerae until offering it to a female. It is unknown if females consume the silk, but it has been suggested that silk wrapping of the gift is used by males to camouflage the content (Albo et al. 2011), to lure females (visually and chemically) during courtship (Brum et al. 2012; Trillo et al. 2014) and to have better control of the gift during the mating (Andersen et al. 2008).

The family Trechaleidae includes 16 genera and 120 species, most of which live associated with freshwater courses in the Neotropical region (Carico 2005; World Spider Catalog 2019). The presence of wrapped gifts is known in seven species from three genera: *Paratrechalea ornata* (Mello-Leitão, 1943); *P. azul* Carico, 2005; *P. galianoae* Carico, 2005; *Trechalea amazonica* F.O. Pickard-Cambridge, 1903; *T. tirimbina* Silva & Lapinski, 2012; *T. bucculenta* (Simon, 1898) and *Trechaleoides keyserlingi* (F.O. Pickard-Cambridge, 1903) (Costa-Schmidt et al. 2008; Albo 2009; Lapinski & Tschapka 2009; Silva & Lise 2009; Silva & Lapinski 2012; Trillo & Albo 2019). The genus *Paradossenus* F.O. Pickard-Cambridge, 1903 has been reported from much of South America while the species *P. longipes* (Taczanowski, 1874) occurs in most of Brazil and northern Uruguay (Carico & Silva 2010). This species is also semiaquatic and perches in riparian vegetation. Carapace length of individuals measure 3.5–3.9 mm. They are characterized by extremely long forelegs, which are approximately 1/3 longer than legs II and IV, while legs III are the shortest (Fig. 1) (Carico & Silva 2010). The reproductive behavior of *P. longipes* is undescribed, but we expected that silk wrapped nuptial gifts may be part of its courtship and mating as in other species of the family.

In order to examine whether *P. longipes* males produce wrapped nuptial gifts, we explored the presence of the trait in the field, and performed laboratory trials to study males' sexual behavior and potential variations in the content (nutritive and/or worthless). During 2012–2013, we visited a natural population of *P. longipes* at the locality of Maquiné (29.538900 S, 50.246200 W), Rio Grande do Sul, Brazil, searching for males with nuptial gifts. In addition, during November 2018, we found and collected five adult individuals (three



Figure 1.—Male of *Paradossenus longipes* (Trechaleidae), Maquiné Brazil. Photo: L.E. Costa-Schmidt.

females and two males) of *P. longipes* in Valle del Lunarejo (31.241 S, 55.882 W), Rivera Province, Uruguay. Spiders were transported to the laboratory and raised individually in plastic jars (8 cm diameter and 7 cm height) at room temperature averaging 21–23°C. Individuals were fed twice a week with houseflies (*Musca domestica*) and water was provided *ad libitum*.

We performed the behavioral experiments after 10 days of individuals' habituation to the laboratory conditions. Repeatedly and in random order, we exposed the two collected males to the three females totaling 16 trials. Following previous protocols (Albo & Costa 2010), we performed behavioral experiments in glass cages (30 × 14 cm base, 20 cm height) containing small pebbles as substrate and water in a Petri dish. It is known that chemical information in females' silk is an important stimulus for gift-giving males to initiate courtship and nuptial gift production (Lang 1996; Albo et al. 2009). Thus, in each case, we placed the female in the experimental cage for dragline deposition 24 h prior to the observations. The trials started by placing the male in the experimental cage with the female, and, once he started to court (displaying foreleg vibrations and tarsal rubbing), we offered him a housefly. If the male did not grab the housefly, we repeated the offer every 15 min until the male took it or stopped courting. The experimental cages also have dry exoskeletons from *Tenebrio molitor* larvae in order to allow males to wrap it and produce worthless gifts. Behavioral trials lasted on average 2.5 h. We registered and recorded whether or not the male wrapped the housefly in silk, the silk wrapping duration, and the number of silk wrapping bouts. We also registered whether or not the male offered the gift to the female, the mating occurrence, the number of pedipalp insertions, and the mating duration. Mating duration was recorded from pedipalp insertion until pedipalp disengagement, and was calculated as the sum of the duration of all insertions performed by the male. Once the behavioral experiments finished, we examined the nuptial gift contents under a stereomicroscope.

In the field, we found between 10 and 20 males carrying nuptial gifts during the night. We also observed 17 of those males courting

and offering the wrapped items, but only two successful matings. The sequence of behavioral units displayed during courtship and mating were the same as observed in the laboratory (details described below).

In 10 trials in the laboratory, males courted females and attempted to mate. In two trials, the male courted and mated without any gift for 0.4 and 0.3 min, performing 2 pedipalp insertions in each case. In the remaining 8 trials, males offered either a wrapped or unwrapped gift. Four involved the male grabbing the housefly and offering the unwrapped prey, while in two trials males captured the housefly and wrapped it in silk, performing four silk wrapping bouts during 13.2 min (only one case was possible to measure). The behavioral units in each wrapping bout were the same as the ones described for other gift-giving spiders: basal plate spinning, item placement, silk covering, drumming, gift grabbing, and final manipulation. Though offering a nutritive prey gift (wrapped or unwrapped), neither male succeeded to mate.

In the remaining two cases, the same male produced an empty nuptial gift, consisting of a silken ball without a content. In these trials, the male performed exactly the same sequence of gift construction behaviors as when having a housefly, except for the item placement. The construction of the empty gifts lasted 9.1 and 5.9 min, involving two and one wrapping bouts, respectively (supplementary video I, online at <http://dx.doi.org/10.1636/JoA-S-19-019.s1>). We verified the absence of gift content by opening the wrapped package under the stereomicroscope (Fig. 2A). In both cases, the male offered the empty gift but only in one trial did the female accept to mate (Fig. 2B; supplementary video II, online at <http://dx.doi.org/10.1636/JoA-S-19-019.s2>). The mating duration was 3.7 min and included 30 pedipalp insertions—15 for each side.

In all cases during gift offering, the males vibrated their body against the substrate, drumming with the whole body, a feature not observed for other Trechaleidae species yet. Once the female grabbed the gift with her chelicerae, the male mounted her, starting a series of alternately right and left pedipalp insertions into her genital tract.

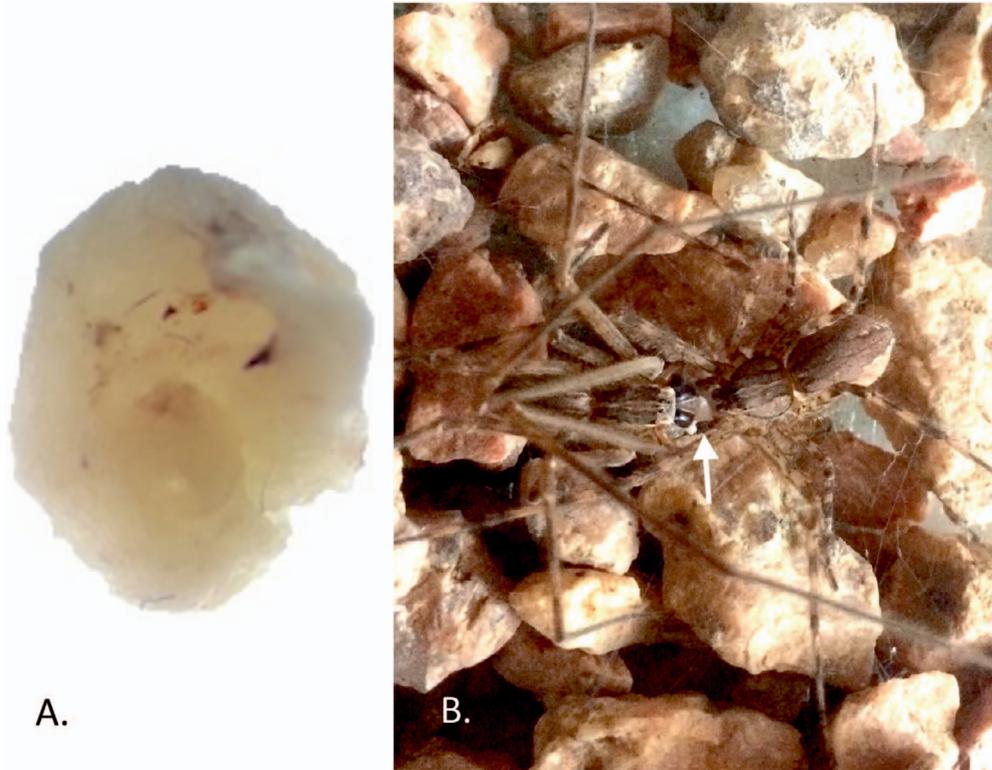


Figure 2.—A. Empty nuptial gift produced by *P. longipes* male and dissected under the stereomicroscope. B. Female (right) and male (left) grabbing the empty nuptial gift (indicated by an arrow) during courtship. Photos: M.J. Albo.

After each insertion, the male returned to a face-to-face position with the female but did not grab the gift with his chelicerae. However, the male held the gift with the tarsal claws of his legs III during the entire mating.

We also observed that males changed tactics along consecutive trials. For instance, one male mated without a gift, while in the following two trials, he produced an empty wrapped gift. The other male produced a wrapped gift with a housefly in the first two trials, but in the third he offered an unwrapped fly.

Here, throughout field and laboratory studies we report for the first time the presence of wrapped nuptial gifts in *P. longipes*, adding a new genus with this male secondary sexual trait to the three already described (*Paratrechalea*, *Trechalea* and *Trechaleoides*) in the family Trechaleidae (Costa-Schmidt et al. 2008; Albo 2009; Lapinski & Tschapka 2009; Silva & Lise 2009; Silva & Lapinski 2012; Trillo & Albo 2019).

Surprisingly, *P. longipes* males may also produce empty nuptial gifts consisting of a silk ball with no content. Until now, the existence of both nutritive (prey) and worthless (prey leftovers) gifts were known from two nuptial gift-giving spiders, the trechaleid *Paratrechalea ornata* (Albo et al. 2014a) and the pisaurid *Pisaura mirabilis* (Clerck, 1757) (Albo et al. 2011). In both species, females accept the two types of gift with the same frequency during courtship, and it has been suggested that they cannot recognize the gift content at this stage (probably because the silk camouflages it). In our observations, *P. longipes* males were better at obtaining matings when offering empty gifts than when offering wrapped prey gifts. Though this may be due to few observations, it is also possible that males producing empty gifts invest more in silk wrapping than those producing prey gifts (silk wrapping bouts average: 5.2 and 3.3 min, respectively), and thus, they may be better at luring females for mating. Although males were also successful in mating without offering a gift, this occurred only in the first behavioral trial.

For producing worthless nuptial gifts, spider males wrap inedible items in silk. The absence of content and the resulting empty gifts found in *P. longipes* represent another alternative reproductive tactic not previously documented for gift-giving spiders. Nitzsche (2011) mentioned a possible case in *Thaumasia argenteonotata* (Simon, 1898) (Pisauridae). Apparently, there is only a single similar case from the animal kingdom, which is the empty silk balloons produced by dance fly males (Empididae) (Cumming 1994; Sadowski et al. 1999). In this insect family, different species have nuptial gifts ranging from intact prey to inedible items to empty silk balloons. In contrast, individual males from *P. longipes* and other gift-giving spiders can vary the gift content and alternately produce wrapped or unwrapped gifts (Albo et al. 2014b).

It would be relevant to understand the potential advantages for males of producing the different types of wrapped gifts – nutritive, worthless, and empty – as alternative tactics, and the reproductive consequences in terms of mating access, mating duration and ultimately the fertilization success. It would also be interesting to evaluate the existence of a trade-off between investing in gift content and in the amount of silk. It seems clear from our data that males are able to adjust their tactic along the consecutive mating attempts. Empty nuptial gifts could be used to reduce the time spent in searching for an item. On the other hand, males deposit large amounts of silk on empty gifts, perhaps to compensate the lack of content. New studies using controlled experimental groups will bring the information necessary to understand the effect of empty nuptial gifts on the reproductive success of both sexes in *P. longipes*.

The existence of empty nuptial gifts in a trechaleid species opens bright avenues for studying the evolution of this sexual trait within the family. We assume the nutritive gift to be the ancestral state of the gift trait from which worthless gifts have evolved due to an interplay between sexual selection and selective pressures from various

ecological conditions. Empty gifts are likely derived from worthless gifts and may represent a further step in the evolution of deception.

#### ACKNOWLEDGMENTS

We thank Laura Montes de Oca for her help with spider and prey maintenance and to Laura Rengifo-Gutierrez for her help with photo and video editing. We are especially indebted to Dr. Søren Toft, two anonymous reviewers and editor Dr. Thomas Jones for constructive comments on the manuscript and language revision of the final version. MMV, MG, CPP were funded by Comisión Sectorial de Investigación Científica (CSIC). MJA was funded by Sistema Nacional de Investigadores (SNI), Agencia Nacional de Investigación e Innovación (ANII). LECS received financial support from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Fondo para la Investigación Científica y Tecnológica (FONCYT), and Secretaría de Ciencia y Tecnología (SECYT-UNC) of Argentina. We thank Sebastián Horta and Sistema Nacional de Areas Protegidas (SNAP) for allowing us to carry out this research at Lunarejo, Uruguay.

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*Manuscript received 17 April 2019, revised 18 December 2019.*

#### SUPPLEMENTARY MATERIALS

Supplementary Video I.—Empty nuptial gift production. First, the male deposits silk threads forming the basal plate on the substrate (time: 0'00"–0'27"). Second, the male performs silk covering (time: 0'28"–0'55"), drumming, gift grabbing and final manipulation (time: 0'55"–1'06"). Note that the behavioral unit “prey placement” is absent. Video: M. Martínez-Villar and M. Germil. Online at <http://dx.doi.org/10.1636/JoA-S-19-019.s1>

Supplementary Video II.—Female (above) and male (below) *P. longipes* during mating with an empty nuptial gift. The male offered the gift during courtship and once the female grabbed it, the male initiated sperm transfer. He mounted (time: 0'00"–0'12") the female performing alternate pedipalp insertions (time: 0'15"–0'41", 0'51"–1'12"). During mating, the male held the gift with the third pair of legs. After each insertion, the male returned to a face-to-face position with the female. Note that the behavior of grabbing the gift during the face-to-face position is absent. Video: M. Martínez-Villar and M. Germil. Online at <http://dx.doi.org/10.1636/JoA-S-19-019.s2>