

Mutual benefit from exploitation of female foraging motivation may account for the early evolution of gifts in spiders



Maria J. Albo^{a, b, *}, Nuria Macías-Hernández^{b, c, 1}, Trine Bilde^b, Søren Toft^b

^a Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

^b Department of Bioscience, Aarhus University, Aarhus, Denmark

^c Departamento de Biología Animal, Edafología y Geología, Universidad de La Laguna, Tenerife, Spain

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Male exploitation of female sensory or motivational biases has been proposed to account for the early evolution of nuptial gift-giving behaviour. The hypothesis is supported if females of a species positioned early in a clade respond positively to sexual signals from males of more recent species in the clade, and if these signals are not included in the courtship repertoire of its conspecific males. We tested whether such a scenario may apply to the evolution of gift-giving behaviour in the spider family Pisauridae. Presumably, the Canarian endemic *Cladycnis insignis* diverged on an early branch from the clade that includes the well-known nuptial gift-giving species *Pisaura mirabilis*. We first showed that the natural courtship and mating in *C. insignis* does not include gift-giving behaviour. Second, by staging female *C. insignis* with gift-carrying males of *P. mirabilis*, we found that these females accepted the gift and allowed the males to attempt mating. The duration of heterospecific 'matings' was much longer than conspecific matings (45–50 min versus ca. 1 min). Thus, there is scope for exploitation of the females' foraging motivation through a behavioural switch from courting without a prey gift to courting with a prey gift. Such a switch would initially have brought huge fitness benefits to these males in terms of greatly increased mating duration (advantage in sperm competition) and protection against aggressive females (shield effect), and also a benefit to the females from increased food supply.

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The function and maintenance of nuptial gift-giving behaviour has been well studied in several species of invertebrates, including insects and spiders (Albo, Toft, & Bilde, 2014; Lewis & South, 2012; Vahed, 1998). Among species, large variation exists in the form of the gift and in the way it is transferred to the females. Commonly, studies report fitness benefits of offering and receiving nuptial gifts, although it is also known that some gifts can have negative or neutral effects (Lewis & South, 2012). The remarkable variety of forms and corresponding effects suggests that the male trait has evolved independently in many taxa. Although some hypotheses for the evolution of nuptial gift-giving behaviour have been discussed for decades, few studies have focused on the origin of nuptial gifts. This is partly due to lack of complete phylogenies of taxa including both gift- and non-gift-giving species, but often also due to lack of knowledge of the sexual behaviour of the species that lack the trait.

Two hypotheses have been considered for the origin of nuptial prey gifts. In cannibalistic species they may result from natural selection as a protection strategy against sexual cannibalism (Bristowe, 1958; Kessel, 1955; Toft & Albo, 2016), or against any potentially harmful aggression from females also in nonpredatory species (Kuriwada & Kasuya, 2012). The gift may simply act as a physical shield against female attacks (Toft & Albo, 2016). Nuptial gifts are also considered to have arisen under sexual selection, commonly stated as a source of conflict between sexes (Basolo, 1990; Bilde, Tuni, Elsayed, Pekar, & Toft, 2007; Christy, 1995; Ryan, Fox, Wilczynski, & Rand, 1990). Under this idea, males may exploit the females' sensory system by imitating/using signals that are attractive to females due to natural selection (e.g. prey signals in predators). Male sensory exploitation has been suggested for several animals (Basolo, 1990; Christy, Backwell, & Schober, 2003; Madden & Tanner, 2003; Proctor, 1991), including gift-giving species, such as crickets and spiders (Bilde et al., 2007; Sakaluk, 1984, 2000; Stålhandske, 2002). Three main criteria have been suggested for the coevolution of male traits and female preferences (Basolo, 1995). First, females prefer the trait; second, the trait must be absent in the ancestral clade; and third, in phylogenetically basal species where the males provide no gifts, the females may have a preference for it.

* Correspondence: Maria J. Albo, Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318, Montevideo, Uruguay.

E-mail address: mjalbograna@gmail.com (M. J. Albo).

¹ N. Macías-Hernández is now at the Finnish Museum of Natural History, Pohjoinen Rautatiekatu 13, 00100 Helsinki, Finland.

Nuptial gifts are known in a few spider species where the males wrap prey or some non-nutritive items in silk and offer this gift package to the females during courtship (Albo, Winther, Tuni, Toft, & Bilde, 2011; Albo et al., 2014; Bristowe & Locket, 1926; Costa-Schmidt, Carico, & De Araújo, 2008; Itakura, 1993, 1998; Nitzsche, 2011; Silva & Lise, 2009). In the family Pisauridae, four genera (*Pisaura*, *Perenethis*, *Thaumasia* and *Tinus*) have been reported to have prey gifts (cf. Nitzsche, 2011), of which the species *Pisaura mirabilis* is the most extensively studied. By offering nutritive nuptial gifts males of this species obtain more and longer matings (Stålhandske, 2002), while by mating with multiple gift-giving males, females increase their fitness through both direct and indirect benefits (Toft & Albo, 2015; Tuni, Albo, & Bilde, 2013). The origin of this trait is unknown and, so far, there is no complete phylogeny for the family, but nevertheless it seems possible that gift giving has originated independently in separate clades (Albo et al., 2017). There is evidence suggesting that prey gift-giving behaviour currently attracts females by exploiting their foraging motivation (Bilde et al., 2007; Toft & Albo, 2015), and at the same time the males protect themselves from aggressive and potentially cannibalistic females (Toft & Albo, 2016). Often, an attacking female's mouthparts becomes embedded in the gift, and the situation is transformed into gift acceptance, followed by courtship and mating (Toft & Albo, 2016).

To test the hypothesis that sensory exploitation underlies the evolution of nuptial gift-giving behaviour in pisaurid spiders, we must study the behaviour of females of species from a position in the phylogeny that diverges from the line leading to gift giving prior to the occurrence of that trait. Here we consider the species *Cladycnis insignis* (Lucas 1838), which is the single species in the genus and endemic to the Canary Islands (World Spider Catalog, 2017). This species presents morphological similarities to *P. mirabilis* but have longer legs, especially in males (Fig. 1). Pilot observations suggested that nuptial gift-giving behaviour is absent in *C. insignis* (M. J. Albo, personal observations). If confirmed, two

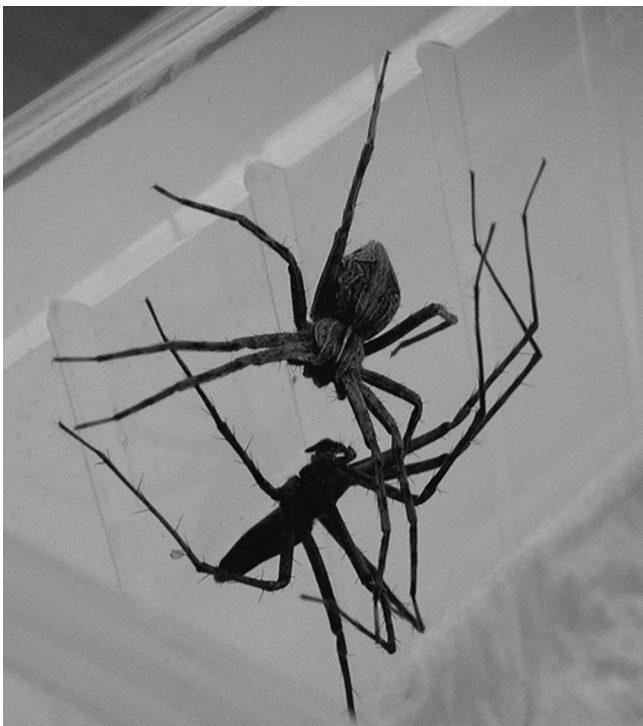


Figure 1. *Cladycnis insignis* female (above) and male (below). Photo by S. Toft.

evolutionary paths are possible: either the genus descended from nuptial gift-giving species and the male trait was lost, or it belongs to a clade within the family with no gift-giving ancestors. The latter hypothesis is favoured by a preliminary molecular phylogeny (Albo et al., 2017) indicating that *Cladycnis* is more basally derived in the family than *Pisaura*. Here, we first investigated by observations whether *C. insignis* males present a prey gift as part of their behavioural repertoire. Second, we presented *C. insignis* females with a *P. mirabilis* male holding a nuptial gift and recorded their response to this 'novel' (from the female's point of view) male trait. If nuptial gifts exploit the female sensory system, *C. insignis* females should accept the nuptial gifts even though the trait is absent in this species. Additionally, we tested whether prey wrapping might have been essential for the early evolution of nuptial gift giving. There is evidence suggesting that wrapping of the nuptial gift evolved through sexual conflict after the trait was genetically fixed (Albo et al., 2011; Andersen, Bollerup, Toft, & Bilde, 2008; Brum, Costa-Schmidt, & Mellender de Araujo, 2012; Stålhandske, 2001; Trillo, Melo-González, & Albo, 2014). Thus, we did not expect differences in females' responses to males with wrapped and unwrapped gifts. We discuss possible evolutionary paths for the early evolution of prey gifts in pisaurid spiders.

METHODS

Spider Collection, Maintenance and Common Experimental Procedures

We collected juveniles, subadults and adults of *C. insignis* spiders in April 2012 and 2013 on Tenerife (28°32'7"N, 16°17'48"E, 880 m) and El Hierro (27°47'10"N, 17°56'15"E, 1008 m), Canary Islands, Spain. For the experiments in 2014 we used offspring of mated females from 2013 raised to adulthood during the intervening year. During all years, we also collected subadults of *P. mirabilis* from meadows at Mols Laboratory (56°13'34"N, 10°35'20"E, <5 m), Denmark, and raised them to adulthood. In the laboratory, we housed spiders individually in 30 ml vials containing moist moss (*Sphagnum* spp.) and raised them at natural photoperiod in a climate room averaging 24.5 °C (0.2 SE). We provided water twice a week to maintain humidity and spiders were fed individually with laboratory-raised house flies, *Musca domestica*, three times per week. Once the spiders reached adulthood, we waited at least 2 days before setting up experiments. Most of the individuals used in the experiments were initially virgins, although we also used some adults collected from the field. We controlled for any effects by including this variable (female status) in the statistical analyses of the data.

For behavioural observations, we followed a protocol used for the Scandinavian population of *P. mirabilis* (Bilde, Tuni, Elsayed, Pekár, & Toft, 2006; Bilde et al., 2007), by carrying out experiments in transparent plastic cages (9 × 9 × 5 cm) with the bottom covered by paper. Females were placed in the experimental cage at least 30 min prior to the experiment, allowing them to habituate and to deposit silk threads, which are important stimuli for male courtship in spiders (Gaskett, 2007; Schulz, 2004), including pisaurids (Arnqvist, 1992; Lang, 1996; Roland & Rovner, 1983). Afterwards, we added the males and recorded all behaviours (see details for each experiment below). We finished experiments 10 min after a mating was completed, or after approximately 40 min if no mating occurred. All animals were used only once.

Testing Male Nuptial Prey-giving Behaviour

Here we examined the natural *C. insignis* sexual behaviour and the potential male use of prey gifts during courtship and mating. We

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