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No Evidence for the Sensory Trap Hypothesis during Courtship in the Gift-Giving Spider *Pisaura mirabilis* (Clerck, 1757) (Araneae: Pisauridae)

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Abstract: Males of a gift-giving spider *Pisaura mirablis* silk-wrap prey and offer it a nuptial gift to the female during courtship. The sensory trap hypothesis proposes that males exploit the maternal care instinct of females by a close resemblance to a wrapped gift with an egg sac. We predict that if the sensory trap hypothesis works, then females should not feed on egg sacs and should adopt and carry them after copulation finishes. There were no differences in mating behaviour in terms of latency to copulation, copulation duration, wrapping prey/egg sacs with silk or with the likelihood of holding gifts/egg sacs by females after copulation. Females consumed approximately 23% of the egg sacs during copulation (mean = 0.016 g, 95% CI [0.01–0.02]). None of the females who received an egg sac during mating continued to care for it. We conclude that the production of gifts by males correlates with female foraging needs, and the silk wrapping of prey during courtship in *P. mirabilis* did not evolve as a sensory trap.

Key words: nuptial feeding, spider mating behaviour

Introduction

No animals have an unbiased sense of the world around them.

The sensory trap hypothesis suggests that males exploit an existing female preference used in non-sexual contexts and use these signals during reproduction (Christy 1995, Endler & Basolo 1998, Sakaluk 2000, Christy et al. 2003, Ryan & Cummings 2013). Males in this process can gain control over mating(s) at the expense of female fitness (Sakaluk 2000, Arnqvist & Rowe 2005). In the course of coevolutionary processes between the sexes, females adapt to resist manipulation by males (Arnqvist 2006, Sakaluk et al. 2006) while males respond to these counteradaptations by the production of more exaggerated sexual signals (Holland & Rice 1998, Arnqvist & Rowe 2005, Garcia & Ramirez 2005).

The nursery web spider *Pisaura mirabilis* (Clerck, 1757) has an extraordinary mating system, where males silk-wrap prey and constitute a nuptial gift, which they consequently offer to the female during courtship. The female feeds on the gift while mating. After the production of the egg sac, the female does not feed and carry over it for about three weeks (Austad & Thornhill 1986, Stålhandske 2001a). Wrapping gift with the silk prolongs copulation duration (Lang 1996, Maxwell & Prokop 2018), entices acceptance of the gift (Beyer et al. 2021) and increases male control over nuptial gift as a prevention against its stealing by the female

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(Andersen et al. 2008). Stålhandske (2002) found that gifts that were painted extra-white with watercolour were accepted more readily by females than unmanipulated gifts or gifts painted brown. Spectral reflectance in her study showed that extra-white gifts resembled natural egg sacs, suggesting that males wrap gifts with silk to exploit maternal care instincts. If gift wrapping serves as sensory trap, then female fitness could be impaired through suboptimal mating rates or post-copulatory exploitation (Sakaluk 2000, Arnqvist & Rowe 2005).

In this study, we examined the sensory trap hypothesis in *P. mirabilis*. We hypothesise that if wrapped gifts resemble egg sacs, then offering an egg sac by the male to the female in the course of courtship should trigger female maternal care, i.e. adoption and carrying the egg sac after copulation. Because maternal care inhibits female feeding behaviour, acceptance of an egg sac instead of nuptial prey should not result in its consumption.

Materials and Methods

Study organism

The nursery web spider *Pisaura mirabilis* (Pisauridae), is a common spider that occurs in meadows, abandoned old fields and deciduous forests. In former Czechoslovakia, spiderlings hatch in the summer and reach maturity in the spring of the following year (Buchar et al. 1989). Mating takes place in April and May, with the male approaching the female and offering a nuptial gift (an arthropod prey wrapped in silk). If the female accepts the nuptial gift, she starts to feed on it while the male copulates (Bristowe 1958).

Collection and maintenance

Subadult females (N = 40) and males (N = 40) were collected in April–May 2017 from various grasslands and small woods near Trnava, Slovakia (N 48°37, E 17°58). Each spider was individually kept in a ventilated 0.3-l plastic jar with wet cotton to maintain humidity. Jars were placed in the laboratory at constant 20°C and 12:12 h L:D regime with 85-90% humidity. The individuals were sprayed with water daily and fed ad libitum three times per week with dead house crickets *Gryllus assimilis* (ca. one adult cricket per feeding). In total, 37 males and 37 females (additional six individuals died) moulted into adulthood during May 2022. Additional 40 females were captured and maintained in the same way as described above; they were mated with 40 males and allowed to produce egg sacs. One- to three-days old egg sacs were removed from female chelicerae using CO_2 anaesthesia and stored in a freezer (-8 to -10°C). Each spider was used only once. After the experiments finished, all the spiders were released near their sites of capture and no later than June 2023.

Experiments with nuptial gifts

About 10–15 days post-moult, each male was randomly assigned to one of two treatments, i.e. Experimental (N =21) and Control (N = 16). Males in the experimental treatment were offered an egg sac removed from the refrigerator two hours before the experiment and placed at room temperature. The males in the control treatment received dead cricket nymphs (*G. assimilis*) of a mass similar to nuptial gifts collected in the field (range 0.0005–0.045 g, Prokop & Maxwell 2012, Prokop & Semelbauer 2017).

Each experiment began by placing of one virgin female for 10 min in a glass terrarium (30 × 20 × 20 cm) lined with clean white paper. The male was placed in the terrarium and offered a dead cricket nymph or an egg sac from tweezers. We recorded the overall time the male spent wrapping the gift with silk, the latency to copulation since the beginning of the experiment and the duration of the copulation to the nearest minute. After copulation was completed, we recorded whether the male or female held the nuptial gift/egg sac in the chelicerae and whether the females continued to care for the egg sac. Clean paper was replaced after each trial and the terrarium was cleaned with 92% alcohol to remove traces of conspecific cues.

After each trial, female behaviour toward egg sacs were observed for four hours and we recorded whether the female started to carry over it. The males were immediately returned to their housing jars. Three trials from the control group and three trials from the experimental group were terminated because the males did not respond to nuptial prey/egg sacs. The occurrence of copulation between the experimental (86%) and control group (81%) was not significantly different (Fisher exact test, P = 1.0). Each trial was conducted between 08:00 and 13:00.

Before the experiments, all individuals were anaesthetised with CO_2. The width (to 0.01 mm) and body mass (to 0.0001 g) were measured with a digital calliper and an analytical balance (KERN ABS 80-4N), respectively. Body condition was calculated using residuals of regression of body mass on prosoma width (Jakob et al. 1996). Female body measurements (body mass, prosoma width, body condition) did not differ significantly between the two treatment groups (M-W U tests: U = 91, 116

Table 1. Descriptive statistics for mating behaviour in the nursery-web spider *P. mirabilis*. Values are means ± 95% CI measured to the nearest minute.

	Wrapping gift	Start of copulation	Copulation duration
Control (nuptial prey)	3.15 (1.85–4.45)	32.07 (22.03–42.13)	51.08 (34.54–67.61)
Experimental (egg sac)	1.83 (0.98–2.69)	25.44 (17.82–33.07)	38.50 (25.57–51.43)
Test statistic	U = 72	U = 87.5	t(29) = 1.30
P	0.07	0.25	0.20

and 86, all P > 0.22). Male body measurements did not differ among treatment groups (M-W U-tests: U = 102, 113 and 92, all P > 0.32).

Cricket nymphs used as nuptial prey were killed by CO_2 and weighed before the experiment. The egg sacs were weighed before and after the experiment to show whether the females consumed parts of them or not. Nuptial prey is notoriously consumed by females during copulation (e.g., Austad & Thornhill 1986, Bilde et al. 2007, Prokop & Maxwell 2009), thus we did not weight nuptial gifts after experiments. All experiments took place between 18 May and 7 June 2023.

Statistical analyses

The data distribution was checked with the Shapiro-Wilk test. Parametric tests (t-test for independent samples), as well as non-parametric tests (Mann-Whitney U-test, Spearman correlation) were used to analyse the data. The frequency of holding nuptial gifts and egg sacs by males were analysed with Fisher exact test. All statistical tests were two-tailed and analyses were made with Statistica ver. 12.0.

Results

Egg sacs (M = 0.077, 95% CI [0.063 – 0.091]) were significantly heavier than nuptial prey (M = 0.022, 95% CI [0.02 – 0.025]) before the start of the experiment (M-W U-test, U = 0.00, P < 0.001). Egg sac weight decreased significantly after mating (Wilcoxon matched-pairs test, Z = 3.72, P < 0.001) and females consumed 0.016 g (95% CI [0.01 – 0.02]) of the egg sacs, which constituted about 22.7% of the egg sac content (95% CI [15.14 – 30.22]). Egg sac consumption was not related to female body condition (Spearman r = 0.29, P = 0.24). There were no differences between the experimental and control groups in the total time that the males spent wrapping gift to the silk, latency time since before the start of copulation and copulation duration (Table 1). Four out of 18 males (22%) in the experimental treatment did not wrap cocoons at all, while all males (13/13, 100%) in the control treatment with nuptial prey did so (Fisher exact test, P = 0.12). After copulation has finished, females held gifts (11/13, 85%) or egg sacs (11/18, 61%) in most trials. Males held gifts after copulation in 18% (2/11) in the control treatment and in 28% (5/18) in the experimental treatment. Two egg sacs were left completely unattended in two experimental trials. When excluding the last two trials from the analyses, differences in holding gifts/egg sacs by females were not different with respect to treatment (Fisher exact test, P = 0.41). None of the females continued to carry the egg sac and all of them were later abandoned on the same day.

Discussion

This study examined the sensory trap hypothesis as a possible evolutionary origin of silk wrapping gifts by males of *P. mirabilis*. There were no differences in mating behaviour between females receiving nuptial gifts or egg sacs, nor was there any evidence for triggering maternal instinct caused by the acceptance of egg sacs that contradicted with the sensory trap hypothesis.

The results of our experiments are similar to those of Bilde et al. (2007), who showed that the wrapped or unwrapped housefly offered by males of *P. mirabilis* resulted in copulatory success, as did trials with egg sacs. Interestingly, males with egg sacs added more silk to their gifts/egg sacs than males with prey already wrapped with silk. Our results showed the reverse trend: males tended to add less silk to egg sacs (and less frequently), albeit not statistically significantly, in comparison with arthropod prey. We suggest that a non-significant tendency to decrease silk investment when offering an egg sac could be explained by their large size; egg sacs are several times larger (Bilde et al. 2007) and heavier (this study) than nuptial prey in natural conditions. Given that production of nuptial gifts is costly for males (Ghislandi et al. 2017, Prokop & Okrouhlík 2021), any silk investment in extraordinarily large egg sacs must create additional time and energy costs for courting by males of *P. mirabilis*.

In contrast to Bilde et al. (2007), we weighed egg sacs before and after the experiment to examine the consumption rates (if any) of females during copulation. Our measurements showed that the mean female consumption rate in egg sacs was 0.016 g. This value falls well within the range of weights of nuptial gifts found in the study area (Prokop & Maxwell 2012, Prokop & Semelbauer 2017). It suggests that males of *P. mirabilis* optimise gift weight in order to satiate female feeding requirements. Although larger gifts are beneficial to males in terms of prolonged copulation duration (Stålhandske 2001b, Maxwell & Prokop 2018), their handling is costly in terms of reduced running speed (Prokop & Maxwell 2012).

Most importantly, our observations did not show any attempts by females to adopt and carry egg sacs offered by males under experimental conditions. Interestingly, females of *P. mirabilis* (Stålhandske 2002) as well as female wolf spiders (Culley et al. 2010, Ruhland et al. 2017, Berry & Rypstra 2021) are able to adopt and carry over someone else's egg sacs. All our trials resulted in the abandonment of partially consumed egg sacs, again rejecting the sensory trap hypothesis. Notably, we ran several additional trials using non-virgin females as well as females experienced in carrying egg sacs; the results were identical to those of the experiments with virgin females described in this paper. These anecdotal observations further add to the absence of exploitation of maternal instinct by males of *P. mirabilis.* Finally, a greater willingness of food starved females to copulate (Bilde et al. 2007, Prokop & Maxwell 2009) provides further evidence that males use nuptial feeding to exploit female foraging motivation rather than maternal instinct.

In conclusion, we did not find any evidence supporting the idea that silk-wrapped prey of *P. mirabilis* exploited female maternal instinct. Instead, female foraging responses were triggered by nuptial prey and by egg sacs similarly. Females were apparently unwilling to adopt egg sacs, at least when they were sexually stimulated by males. The evolution of silk-wrapping of nuptial prey could be influenced by sexual conflict but not by sensory traps.

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