Nuptial gifts of male spiders function as sensory traps

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While nuptial food gifts come in various forms in arthropods, their evolutionary origins are unclear. A previous study on insects has shown that such gifts may arise as a sensory trap that exploits a female's underlying motivation to feed. Here I present independent evidence of a sensory trap in spiders. In certain visually oriented spiders, I suggest that males initially exploit the maternal care instinct by producing a nuptial gift that closely resembles the female egg sac. Males of the spider *Pisaura mirabilis* cover their prey gift with a silk layer, transforming it into a white round object. In a laboratory experiment I tested whether the colour of the gift affected the rate that females accepted males displaying their gifts. I found that the brighter and the more alike the nuptial gift to a female's egg sac, the faster the female responded by grabbing the gift. My results support the hypothesis that the nuptial gift in *P. mirabilis* works as a sensory trap.

Keywords: *Pisaura mirabilis*; sensory trap; spiders; nuptial food gifts; sexual selection

1. INTRODUCTION

The evolutionary origin and maintenance of nuptial gifts in insects are much-debated issues (Simmons & Parker 1989; Vahed 1998). Recently, Sakaluk (2000) suggested that nuptial food gifts in insects might evolve as a form of sensory trap (Christy 1995) that exploits the normal gustatory responses of females. Such a mechanism may explain the diversity of nuptial gifts, the post-copulatory mate choice occurring in gift-giving species, and why food gifts of certain species apparently provide no significant nutritional benefits to females (Sakaluk 2000). Here I present support for a similar sensory trap mechanism in another arthropod taxon (Araneae), which may explain why males of the spider *Pisaura mirabilis* (Pisauridae) add a cover of silk around their prey gifts.

Pisaura mirabilis is a hunting spider with unique courtship behaviour (Van Hasselt 1884). When the male becomes sexually mature he changes his behaviour towards prey. Instead of eating the prey he wraps it up with silk, transforming it into a white round parcel. Males do not wrap their prey to immobilize it; they start wrapping only after the prey is paralyzed (Nitzsche 1988; P. Stålhandske, personal observation). Prey wrapping is otherwise only found among web-building spiders (Foelix 1996). However, hunting spiders may fasten large immobilized prey items to the ground by some silk threads before the spider feeds (Nitzsche 1988; Foelix 1996). The *Pisaura* male carries the parcel in his chelicerae and when he meets a female he presents the gift to the female in a characteristic visual display. He tilts his body vertically downwards with the spinnerets resting on the ground and exposes the gift against his dark brown ventral side in a motionless display right in front of the female (Bristowe 1958).

A courtship is successful when the female grabs the gift (piercing the silk cover) with her chelicerae, and begins to eat it. While the female is eating, the male enters the mating position and transfers sperm (Van Hasselt 1884; Bristowe 1958).

Recent research indicates that the nuptial gift is maintained by sexual selection (Stålhandske 2001a): in mating experiments the presence and size of the nuptial gift influenced copulation duration and fertilization success, but female fecundity and spiderling size were not significantly affected.

The nuptial gift closely resembles the white round egg sac produced by the *Pisaura* female (Van Hasselt 1884; P. Stålhandske, personal observation). The female pierces the egg sac with her chelicerae and carries it continuously for three to four weeks (Austad & Thornhill 1986) until free-living spiderlings appear. The visual resemblance between the nuptial gift produced by the male and the egg sac produced by the female in *P. mirabilis* suggests a possible explanation for why males wrap their gifts. By producing a nuptial gift that mimics the egg sac *Pisaura* males may exploit the maternal instinct to recognize and clutch at white, round egg sacs. If so, the courting male can be said to make use of a sensory trap (Christy 1995), a mode of sexual communication in which male signals mimic stimuli to which females respond in other contexts and elicit female behaviours that enhance male fertilization success.

The sensory trap hypothesis predicts that male efforts to produce a gift that is close to an egg sac in colour and shape should be rewarded by fast female acceptance. To test this, I investigated female responses towards displaying males with natural white gifts, gifts painted brown and gifts painted extra white. Vision is vital for hunting spiders because they use motion, shape and size as cues in prey catching and courtship (Forster 1985; Foelix 1996). Because colour vision has not yet been established in spiders (Foelix 1996), I used brightness for comparison of gifts and egg sacs. However, if a female can identify her own egg sac, she cannot be 'trapped' by the nuptial gift. Therefore, I also tested if a female was able to recognize her own egg sac by discriminating against an egg sac produced by another female.

2. MATERIAL AND METHODS

(a) Collection and rearing conditions

Sub-adult spiders were collected in May 1999, from grasslands surrounding the Mols Laboratory close to Aarhus, eastern Jutland, Denmark. Initially, the spiders were kept individually in 30 ml plastic tubes. In the laboratory the spiders were housed individually in plastic terraria (16 cm × 10 cm × 9 cm). In each terrarium some woody branches and a vial containing water and moss (*Sphagnum* spp.) were provided. The spiders were kept at room temperature (ca. 20 °C) and at a natural photoperiod. They were fed *ad libitum* with laboratory-reared fieldcrickets, *Gryllus bimaculatus*.

(b) Mating experiments

Laboratory experiments were conducted between 14–20 June 1999. Eleven previously unmated males and 33 virgin females were used in the experiment. Each male was allowed to court three virgin females in random order in three separate trials. Observations on mating behaviour were made in transparent plastic terraria (45 cm × 27 cm × 14 cm). The inside bottom of each box was covered with paper towels. Each female was placed in a separate box one day before the mating experiment. While running and walking around the female produces drag-lines, which provide essential stimuli that the male uses to find the female. On the day of the experiment, the box was divided into two parts by a wall. The male was introduced to the part not occupied by the female. When the male touched the drag-lines made by the female, he showed 'sexual excitement' that included trembling of the palps and abdomen, jerking of the body, moving in jerks and rapid rubbing of the legs (Lang 1996). When the male exhibited these behaviours a prey item was given to him. The male immediately paralyzed the prey and started to wrap it up. I used laboratory-reared field crickets of equal size (mean = 15.5 mg; s.d. = 0.2; $n = 33$) as prey. When the male had finished wrapping the prey, I removed the gift from him with a pair of tweezers. The gift was manipulated in one of three ways, and the order of these treatments for each male was randomly assigned. One gift was painted brown (B) with watercolour, one gift was painted extra white (EW) with watercolour, and one was left unmanipulated, i.e. natural white (NW). All treatments were quickly dried with a hair-drier. The males always accepted the manipulated gift and as soon as the male started to show 'sexual excitement' again I removed the partition wall. The couple were followed continuously through the courtship, and in each courtship trial I recorded how long the male displayed his gift in front of the female before she grabbed it with her chelicerae.

(c) Egg sac recognition

I experimentally deprived 20 mated females of their newly produced egg sacs by anaesthetizing the females with carbon dioxide. This allows removal of the sacs without hurting the females. The day after taking the sacs they were returned to the females. Ten females were offered their own sac, while 10 females were offered an egg sac produced by another female. I held the sac in a pair of tweezers and gently dropped the sac 1 cm ahead of the female. When the sac hit the floor of the terrarium I measured the time until the female grabbed the sac with her chelicerae.

(d) Brightness measurements

By using a Colortron reflectance spectrophotometer (Light Source, San Rafael, CA, USA) (Hill 1998) I recorded reflectance spectra of freshly wrapped gifts treated as in the mating

Figure 1. Brightness (mean + s.e.) of B gifts ($n = 7$), NW gifts ($n = 27$), EW gifts ($n = 8$), and ES (egg sacs) produced by females ($n = 26$).

tance spectra of freshly wrapped gifts treated as in the mating experiment described above: B ($n = 7$), EW ($n = 8$) and NW ($n = 27$). I also recorded the reflectance spectra of 26 newly produced egg sacs (referred to as ES) and used brightness scores generated by the Colortron to compare gifts and ESs. The Colortron does not measure ultraviolet (UV) light (wavelength of less than 390 nm), to which at least some spiders may be sensitive (Yamashita 1985; Barth *et al.* 1993). Therefore, I checked a small sample ($n = 3$ for each group of objects) of ESs and manipulated and unmanipulated gifts by using a UV-VIS spectrometer (320–700 nm) (S2000, Ocean Optics Inc., USA). All objects reflected some UV light, but NW gifts and ESs reflected more than EW gifts and B gifts. However, this was not sufficient to alter the rankings of brightness as estimated by the Colortron spectrophotometer (390–700 nm), and hence does not affect the overall brightness similarities.

(e) Analysis

Statistical tests were performed using STATVIEW, v. 5.0 (SAS 1998). Some data were normally distributed but others were not, hence both parametric and non-parametric tests were used.

3. RESULTS

Brightness differed significantly among objects (figure 1; one-way ANOVA, $F_{3,64} = 188.3$; $p < 0.0001$). ESs and EW gifts were brighter than NW gifts, and NW gifts were brighter than B gifts. Multiple comparisons (according to Scheffé) revealed significant differences in five pairs (B versus NW; B versus EW; B versus ES; NW versus EW and NW versus ES; all pairs $p < 0.0001$), but not between EWs and ESs ($p = 0.94$).

All males were accepted as mating partners and allowed to copulate three times, but there was a significant difference among treatments in display time until the female grabbed the gift (figure 2; Friedman two-way ANOVA, $F_3 = 11.45$; $p < 0.01$). EW gifts were quickly accepted (median = 39 s; $n = 11$), NW gifts gave intermediate response rates (median = 197 s; $n = 11$), whereas B gifts had to be exposed for the longest time before acceptance (median = 383 s; $n = 11$). Multiple comparisons (according to Siegel & Castellan 1988) showed that there were

Figure 2. Male display time (median, 10, 25, 75 and 90 percentiles) of the nuptial gift in front of the female ($n = 33$) until acceptance. B ($n = 11$), NW ($n = 11$) and EW ($n = 11$). The display time for an egg sac (ES) ($n = 19$) held in a pair of tweezers until female acceptance is included in the graph for comparison.

significant differences between B gifts and EW gifts ($p < 0.05$) and between NW gifts and EW gifts ($p < 0.05$).

Females experimentally deprived of their egg sacs readily grabbed an egg sac when it was offered to them. In total, 19 out of 20 (95%) clutched at the sac. An offered sac was accepted after 16 s (median, $n = 19$; figure 2). There was no significant time difference between females accepting their own egg sac (median = 6 s; $n = 10$) and females accepting an egg sac produced by another female (median 16 s; $n = 9$; Mann-Whitney U -test, $p = 0.33$). All 19 females clung on to the egg sacs until I terminated the experiment, i.e. a period of 16 to 21 days.

4. DISCUSSION

As predicted from the sensory trap hypothesis, the visual appearance of the nuptial gift had a significant effect on the female response. The display time until the virgin female grabbed the gift was correlated with its brightness; the brighter the gift, the faster the female responded. The female response rate towards a displaying male may make the difference between whether a male mates or not because other males may disturb courtship in the field. A fast female response is also beneficial to a male because he starts sperm transfer almost immediately after the female accepts his gift (Stålhandske 2001a). Because males of *P. mirabilis* cover their prey gift with a layer of silk, the content and its value as a food item are concealed from the female. The size of the wrapped gift does not affect the rate of the female response towards a male (Stålhandske 2001a), but results presented in this paper show that the brightness of the silk cover does.

By painting a gift extra white, its brightness became similar to an egg sac and virgin females responded very quickly towards such egg-sac-like gifts. Maternal care of the egg sac is extended in *P. mirabilis* and the female continuously clings to her sac for several weeks. A female deprived of her egg sac immediately starts to search for it

and when found again she grabs it with her chelicerae (present study). There are at least three reasons why females who lose their egg sac suffer a severe reduction in fitness. First, in a field experiment it was found that unattended egg sacs were predated within 2–3 days (Stålhandske 2001b). Second, the development of eggs to spiderlings is dependent on female egg-sac care (Nitzsche 1999) and references therein). Third, spiderlings probably cannot emerge from the sac without help from the mother (Roberts 1995; Nitzsche 1999) and references therein). Consequently, this maternal care instinct, clinging to or searching for the sac, is under strong selection. A prerequisite is that a female can recognize an egg sac. Sacs are bright, round and motionless and such objects are presumably rare in this spider's natural environment. Hence it seems probable that selection has favoured a general preference (grabbing response) towards such objects. My findings support this idea; virgin females responded faster towards brighter gifts, mated females towards their own egg sac, but also towards a sac produced by another female.

A significant difference between the nuptial gift and the egg sac is that the contents of the former are eaten while those of the latter are not. Whether the female starts to eat a bright and round object may be governed by the female's reproductive state, because the onset of egg sac guarding has been found to be linked to oviposition (Horel & Gundermann 1992). Female size (measured as cephalothorax width) and condition (measured as weight) are factors that depend on food intake and are important for female survival and fecundity (Arnqvist & Henriksson 1997) and references therein). So it can be expected that as long as the female has not produced an egg sac, an initial grabbing response to a white round object is followed by a strong eating impulse.

Others have commented on the design of the gift in *P. mirabilis*. It has been suggested that wrapping makes it easier for the male to carry the prey, gives the prey more tensile strength, makes it possible to enlarge the gift by adding further prey and provides the female with essential substances (Nitzsche 1999), or to prolong the feeding time of females (Lang 1996), i.e. making the gift bigger by adding silk. While these hypotheses may partly explain the significance of prey wrapping in *P. mirabilis* they do not explain the results in the present paper. Neither do they explain why the male wraps the prey even when a female is right beside him, nor why, if the female does not respond, the male stops displaying and adds more silk to the gift before resuming courtship (P. Stålhandske, unpublished data). Furthermore, observations of sexually mature males wrapping other objects such as small flowers (Nitzsche 1999) and field-collected gifts containing no more than exoskeletons (Bristowe 1958; Nitzsche 1988; P. Stålhandske, personal observation) indicate that the wrapping of the gift rather than its content is of primary importance.

I suggest the following reasons for a sensory trap operating in *P. mirabilis*: (i) the female is under strong natural selection to care for her egg sac; (ii) the male produces a nuptial gift visually resembling an egg sac; (iii) the initial female response towards the gift is as if it was an egg sac and the more like an egg sac the gift is the faster

the female responds; and (iv) the female's response increases the male's chances of fertilizing eggs because: (i) sperm transfer starts almost immediately after the female grabs the gift (i.e. more females or eggs available per time unit) and (ii) such a response is also present in well-fed or already-mated females (Drengsgaard & Toft 1999; Stålhandske 2001b). Drengsgaard & Toft (1999) found that a predominantly first male sperm priority pattern was operating in *P. mirabilis* when females were mated with two males ($P_2 = 29.7\%$). However, when females mated with four males, the fertilization success of the last male was almost as high as in double-matings ($P_4 = 23.9\%$).

According to the sensory trap hypothesis females always benefit by responding to the model and they may often benefit by responding to mimetic courtship signals. If the response as a preference is costly, it may be maintained by frequent and strong selection for the response to the model (Christy 1995). In *P. mirabilis* the female may benefit because she gets a food item. However, recent work (Stålhandske 2001a) indicates that the size of this donation is of less importance to female reproductive success when females mate only once. Whether multiple matings are beneficial to females warrants further study.

Austad & Thornhill (1986) discussed why the nuptial feeding has not been observed in other spiders. Since then, two (Itakura 1993, 1998), or possibly three (Nitzsche 1988), more species have been found to use a wrapped prey gift in courtship. Together with *P. mirabilis* these species represent three genera within the same family. The mating behaviour of very few of the world's spider species is known in any detail, and this behaviour may eventually be found in a diversity of spider species (Austad & Thornhill 1986). However, if nuptial gifts evolve by the process of sensory exploitation, there is no reason to assume that males of different taxa will converge on the same mimetic signal in courtship (Sakaluk 2000). Comparisons between pisaurids and those 33 other families found in Britain and northern Europe (Jones 1983; Roberts 1995; Foelix 1996) show some unique traits for Pisauridae. Female pisaurids carry around the eggs, the egg mass is protected by a dense cover of silk and females hold the egg sac by piercing it with the chelicerae. This particular combination of characters may be prerequisites for the evolution of wrapped nuptial gifts.

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