



## Nuptial gifts of male spiders: sensory exploitation of the female's maternal care instinct or foraging motivation?

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Nuptial feeding can evolve as sensory traps where the male exploits the female's foraging motivation in a sexual context. The nuptial prey gift of the nursery-web spider *Pisaura mirabilis* is wrapped in white silk, and it has been suggested that males initially exploit the maternal care instinct by producing a nuptial gift that resembles the female's eggsac. In mating experiments we examined whether males exploit the female's foraging motivation or the female's maternal care instinct. We carried out a gift-switching experiment, where males presented an eggsac, a wrapped fly or an unwrapped fly as nuptial gifts. Females fed on eggsacs as well as on prey gifts. Mating success was similar for males with both wrapped and unwrapped gifts, indicating that wrapping per se does not increase male mating success. In a food manipulation experiment, we investigated the effect of the female's hunger level on male mating success. Hungry females were more likely to accept a gift and copulate; hence the female's hunger state is decisive for male mating success. Our results strongly suggest that the female's foraging motivation is the true context for the maintenance of the nuptial gift.

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Among the arthropods, the diversity of nuptial gifts offered by males to the female during courtship or copulation is remarkable, including prey items, spermatophores and substances in the ejaculate that can be more or less nutritious, but also gifts that can be completely worthless nutritionally (Thornhill 1976a; Vahed 1998; LeBas & Hockham 2005). The proximate routes by which a male receives reproductive benefits are: (1) through paternal investment, that is, if the gift enhances the reproductive output of the female with which he mates (Trivers 1972; Simmons & Parker 1989); (2) through mating effort, where the gift functions to entice the female into mating, ultimately increasing sperm transfer and providing the male with an advantage in sperm competition (Thornhill 1976b; Sakaluk

1984); and (3) through protection against sexual cannibalism by directing the attention of the female towards the gift which increases the male's chance of successful mating (Kessel 1955; Bristowe 1958; see also Arnqvist et al. 2003). All of these explanations assume that females receive direct benefits from the nuptial gift, which ultimately enhances male reproductive success (Thornhill & Alcock 1983; Andersson 1994; Boggs 1995). It is therefore assumed, implicitly or explicitly, that the mating strategy of the gift-giving male relies on exploitation of the female's foraging motivation. Sakaluk (2000) suggested that the nuptial food gift functions as a sensory trap if it exploits the pre-existing motivation of the female to feed in such a way that the male succeeds in fertilizing more eggs than he would have done otherwise. The sensory trap assumes that the female's preference under exploitation is currently advantageous to her outside the context of mate choice and is therefore not readily selected against (Thornhill & Alcock 1983; Sakaluk 2000; West-Eberhard 2003).

During courtship, males of the spider *Pisaura mirabilis* (Clerck 1757) offer females a nuptial gift that consists of

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a prey item that they have previously captured and wrapped in silk (Bristowe 1958). The nuptial gift in *P. mirabilis* is a sexually selected male trait that is maintained because it facilitates copulation and prolongs sperm transfer (Stålhandske 2001). The gift, a white round parcel, is carried by males in their chelicerae and displayed in front of the female until she accepts it. Once the female grasps it with her chelicerae and starts eating it, males enter the mating position and begin copulation. The spectacular trait of gift wrapping led Stålhandske (2002) to suggest that the nuptial gift of *P. mirabilis* functions as a sensory trap by imitating a female eggsac. Females produce a white round eggsac consisting of silken layers and carry it for several weeks in their chelicerae. The argument is that by wrapping the prey, males produce a nuptial food package that resembles an eggsac that the females carry and care for. Thereby, males are thought to exploit the female's maternal care instinct to recognize and accept an eggsac, an instinct that is assumed to be present before she herself produces an eggsac. This 'eggsac hypothesis' assumes that the natural prey insect is disguised with silk wrapping when the gift is presented and that males, at least initially, exploit the maternal care instinct rather than the female's foraging motivation. The exploitation of the female's maternal care instinct would imply that females react to a nuptial gift as an eggsac and not as food. Consequently, this hypothesis would assume that there has been a disruption of the original coupling between a food gift and the female's foraging motivation and the evolution of a correlation between the gift and the maternal care instinct.

We examined whether the nuptial gift of *P. mirabilis* males exploits the foraging preference or the maternal care instinct of females. Christy (1995) proposed comparing the male's signal (wrapping behaviour—eggsac mimicking) and the model stimulus (the eggsac) experimentally as the appropriate test for sensory exploitation. We therefore investigated the effect of gift wrapping per se on female acceptance and male mating success. In a gift-switching experiment, we replaced a wrapped prey with either an eggsac or an unwrapped prey gift, and compared the female's response and the male's mating success on presentation of either an eggsac, a wrapped prey or an unwrapped prey. If the function of prey wrapping is to mimic an eggsac (Stålhandske 2002), males should wrap the prey gift (the signal) to imitate an eggsac (the model stimulus) before presenting it and females should be less likely to accept unwrapped gifts than wrapped (Christy 1995). Furthermore, females should not consume the nuptial gift but rather care for it. Males will court females while presenting an unwrapped prey as a nuptial gift (Nitzsche 1988). The presentation of unwrapped prey therefore provides the opportunity to decouple the effect of the prey gift per se from the effect of wrapping.

In a second experiment, we investigated the effect of the female's nutritional status (food deprived or satiated) on her response to the nuptial gift and the male's mating success. If females perceive the nuptial gift as an eggsac rather than a food item, they should respond to the nuptial gift in a similar way regardless of their nutritional state. An influence of the female's hunger state on the male's mating success would suggest exploitation of the

female's foraging motivation rather than the maternal care instinct. In this second experiment we also investigated the effect of female mating status as we conducted the experiment in a two-factor design using virgin and single-mated females within each treatment group (satiated and food deprived).

## METHODS

*Pisaura mirabilis* is a nursery-web spider belonging to the family Pisauridae and is widespread across Europe. In Denmark, adults appear in May and females lay eggs at the beginning of June. Spiderlings hatch in July–August and reach adulthood 2 years later.

We collected juveniles and sub-adult spiders between 17 and 25 April 2004 from a cattle-grazed meadow at the Mols laboratory in the eastern part of Jutland, Denmark. The spiders were kept individually in vials (3 cm in diameter, 7 cm in height) supplied with wet, fresh *Sphagnum* moss as a substrate at room temperature (approximately 20°C) and at the natural photoperiod. Individuals were fed twice a week with two or three house flies, *Musca domestica* L., each, obtained from a laboratory culture, and were assigned for experiments when they reached adulthood. All laboratory experiments were conducted between 17 May and 28 June 2004. Individual spiders were used in only one trial.

### Gift-switching Experiment

We transferred females to transparent plastic terraria (17 × 17 cm and 10 cm high) approximately 15 min before each mating trial. The female would walk around leaving draglines on the substrate which elicits male courtship behaviour upon contact (Nitzsche 1988). We investigated the mating success of males given an eggsac ( $N = 21$ ), a wrapped housefly ( $N = 15$ ), or an unwrapped housefly ( $N = 27$ ) to present to the female during courtship. Wrapped flies were completely wrapped in dense silk layers (Nitzsche 1988) as were the eggsacs. In contrast, unwrapped flies usually had no threads of silk and were hence recognizable as flies. Approximately 10 days before the trials we mated several females which subsequently produced eggsacs. We obtained eggsacs from these females by anaesthetizing them with carbon dioxide and carefully removing the eggsac with a paint brush and soft forceps. In the field, males carry a wrapped nuptial gift while searching for females, and in the laboratory satiated males wrapped prey flies when kept in their rearing vials. In all gift-switching trials, we used males that were already holding a wrapped prey which we gently removed with brush and forceps.

In the eggsac treatment, we displayed an eggsac, held in forceps, in front of the male for 1–2 min, if necessary dropping it on the substrate a few cm from the spider until he grabbed it in his chelicerae. Rapid display of the eggsac after we removed the fly increased the likelihood of males accepting and holding the eggsac in a similar way as the wrapped fly. We introduced the male into the terrarium containing a female immediately after he accepted the eggsac. Upon sensing the female the male initiated courtship behaviour, which appeared identical to that of males

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