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

TRINE BILDE*, CRISTINA TUNI*, REHAB ELSAYED*, STANO PEKAR† & SØREN TOFT*

*Department of Ecology & Genetics, Aarhus University
†Institute of Botany & Zoology, Masaryk University

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.

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

Correspondence: T. Bilde, Department of Ecology and Genetics, Aarhus University, Ny Munkegade 540, 8000 Aarhus C, Denmark (email: trine.bilde@biology.au.dk). S. Pekar is at the Department of Zoology & Ecology, Masaryk University, Kotlarska 2, 611 37 Brno, Czech Republic.

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

carrying wrapped flies as nuptial gifts. In the treatment where males presented unwrapped flies, we removed the wrapped fly as described above and introduced a live fly to the male which he subsequently killed. When introduced to the female, the male would display the fly unwrapped or wrap a few threads of silk around the fly and then initiate courtship, but he did not wrap it in a dense layer of silk as would be necessary to conceal the fly. In the treatment where males presented wrapped flies these were previously wrapped by the males, and were removed and given back as a control for gift removal. Males were then introduced to the arena containing the female.

In all three treatments series we recorded components of male and female behaviour: the proportion of males adding silk threads to the gift (never wrapping the fly entirely in dense white silk once in contact with the female) before presentation; the proportion of males presenting the gift; the proportion of females accepting the gift (acceptance after the male's first or subsequent presentations, respectively); the proportion of rejected males adding more silk threads to the gift (if the nuptial gift was not accepted on first presentation males would add more silk threads and make a new attempt); the presentation time (duration of time for which the gift was displayed until female acceptance); and the copulation duration. We recorded whether females consumed the gift during copulation and any incidents of sexual cannibalism; finally, we measured the diameter of eggsacs and of wrapped flies (± 0.01 mm), using electronic callipers.

Hunger Level and Mating Status

Our aim in this experiment was to test whether hunger state and mating status of the female influenced male mating success. We manipulated female hunger level (food deprived versus satiated, $N = 30$ in each group) and mating status (virgin versus single mated 1–2 days before the experiment, $N = 15$ in each group). Food-deprived females were kept without food 3–4 days before the experiment, whereas satiated females were fed with three flies the day before the experiment. Males presented wrapped flies as nuptial gifts in all trials. For each mating trial we recorded similar variables as described above.

Statistical Analyses

For all data analysis we used statistical methods within R (R Development Core Team, www.R-project.org). Most of the data were processed to generalized linear models (GLM) with an appropriate error and link function. For counts we used the Poisson family (GLM-p), for proportions the binomial family (GLM-b) and for continuous data the gamma family (GLM-g) as the variance increased with the mean. To correct for overdispersion, we applied the quasi-Poisson family (GLM-qp) for counts and the quasibinomial family (GLM-qb) for proportions. The minimum adequate model was obtained by using a deletion procedure based on F tests (gamma models) and chi-square tests (other models). The parameters were estimated from the minimal model and differences between them were compared with the t statistic (Crawley 2002).

RESULTS

Gift-switching Experiment

When males were placed in the terrarium with the female, they initiated courtship behaviour and displayed the nuptial gift in front of the female. Male wrapping behaviour prior to gift presentation and the likelihood that the males presented the gift to females did not vary significantly with gift type (Table 1). Female acceptance of the gift after the first or subsequent presentation also did not differ significantly between treatment groups. Only 23–52% of the males succeeded in copulating upon the first attempt to present the nuptial gift. Rejected males usually added more silk threads to the gift and subsequently presented the gift to the female again. Males with eggsacs or unwrapped flies were more likely to add silk to their gift than males with wrapped flies (Table 1). Overall, copulation success was similar across treatment groups. The time from initiation of gift display until female acceptance varied between treatments: wrapped flies were presented for significantly longer than the eggsacs and unwrapped flies before being accepted (Table 1). We found no treatment effect on copulation duration, which was similar for the three gift types.

Copulation always occurred in conjunction with consumption of the gift by the female. Females fed on all gift items including eggsacs although they did not always consume them entirely. In several trials, the female succeeded in taking the nuptial gift and consuming it without copulating (eggsacs 22%, wrapped flies 14%, unwrapped flies 23%). Sexual cannibalism of males occurred in 4% of the trials ($N = 63$) prior to copulation. There were no incidents of postcopulatory cannibalism.

Eggsacs ($\overline{X} \pm \text{SE} = 15.5 \pm 0.34$ mm in diameter) were significantly larger than wrapped flies (3.55 ± 0.28 mm in diameter ANOVA: $F_{1,7} = 13.32$, $P = 0.01$); hence the volume of eggsacs was three times larger than that of wrapped flies.

Hunger Level and Mating Status

Two-factor analysis showed that female hunger level was the decisive factor for gift acceptance and male mating success (Table 2). Food-deprived females were much more likely to accept the nuptial gift and copulate than satiated females regardless of their mated status. When satiated, virgin females were more likely to accept the nuptial gift and to copulate than mated females (Table 2). We found no significant effect of female status on the likelihood of males to wrap and present the nuptial gift. However, the time from gift presentation to acceptance was shorter when males courted food-deprived females than satiated females, with no effect of mating status or their interaction. Total copulation duration was longer with mated females than with virgin females but did not vary with their nutritional state. Mated females

Table 1. Outcome of mating trials where males presented either an eggsac, a fly wrapped in silk or an unwrapped fly as a nuptial gift to the female

Response variable	Nuptial gift type			Statistic	P
	Eggsac	Wrapped fly	Unwrapped fly		
Males add silk before presenting (%)	38 (16)	57 (14)	63 (27)	GLM-b	0.272
Males present gift (%)	76 (21)	93 (15)	90 (27)	GLM-b	0.263
Females accept first presentation (%)	38 (16)	23 (13)	52 (27)	GLM-b	0.220
Males add silk threads to gift after rejection (%)	100 (10)[a]	44 (9)[b]	85 (13)[a]	GLM-b	0.010
Females accept second presentation (%)	60 (10)	56 (9)	38 (13)	GLM-b	0.545
Males wrapped overall (%)	69 (16)	64 (14)	85 (27)	GLM-b	0.249
Female acceptance of gift (%)	75 (16)	62 (13)	70 (27)	GLM-b	0.733
Copulation success (%)	65 (17)	62 (13)	52 (27)	GLM-b	0.669
Presentation time s, median (range)	212 (0−1800)[a]	900 (50−3060)[b]	480 (5−1200)[a]	GLM-g	0.006
Copulation duration s, median (range)	780 (120−2280)	1290 (360−2700)	1110 (240−2100)	GLM-g	0.259

Sample sizes are given in parentheses. Different superscript letters indicate significant effects of gift types in post hoc comparisons (*t* statistics).

interrupted copulations more frequently than virgin females, with no effect of hunger state or their interaction.

DISCUSSION

Females accepted unwrapped flies as frequently as wrapped gifts (fly or eggsac) and male mating success and copulation duration were comparable across treatments. Males did not attempt to wrap unwrapped flies in a dense, white silk layer prior to gift presentation. Instead they would add a few silk threads which did not cover the fly, suggesting that wrapping the prey in a dense white silk layer is not a precondition for males to acquire copulations. Females were as likely to feed on eggsac gifts as they were to feed on flies. Hence, females reacted to the eggsacs as food and did not show brood-caring behaviours. As a consequence, presentation of eggsacs as nuptial gifts did not provide males with a mating advantage and the display of unwrapped gifts was not disadvantageous, suggesting that eggsac mimicking, and hence exploitation of the maternal care instinct, is not the proximate mechanism of gift wrapping.

If silk wrapping per se were decisive for male mating success, wrapped gifts would be predicted to be accepted faster than unwrapped gifts. However, presentation time for wrapped flies was significantly longer than for eggsacs and unwrapped flies. There was a tendency for females to accept eggsacs faster than flies, and this nonsignificant relation could be interpreted in favour of the maternal care instinct (Stålhandske 2002). An alternative explanation for this observation is that eggsacs were larger gifts than flies and females prefer large gifts (Stålhandske 2001); this explanation is supported by the finding that females fed on the eggsacs. The female's foraging motivation and the male's sperm transfer rate, which is positively correlated with gift size, would both exert selection on larger gifts to be attractive (Drengsgaard & Toft 1999; Bruun et al. 2004).

In the food manipulation experiment we found that hungry females were much more likely to accept a gift and copulate than satiated females. In contrast, mating status (virgin versus mated) was a much weaker predictor of mating success although, when satiated, mated females were the least likely to accept the gift and mate. This result is consistent with previous findings, that the female's hunger state influences mating decisions (Le Pape 1974; Thornhill 1984). Indeed, females often attempted to steal the gift and escape to feed on it without mating. Consequently, the female's hunger state has a strong influence on her propensity to mate and therefore ultimately on male mating success. Our results lend no support to the idea that the nuptial gift in *P. mirabilis* evolved as a sensory trap by mimicking an eggsac. In contrast, they strongly favour exploitation of the female's foraging motivation as the true context for the maintenance of the nuptial gift.

The crucial question remains: what is the function of prey wrapping? In spiders, prey wrapping is a vital component of predatory behaviour. It functions to facilitate prey handling (Gilbert & Rayor 1985), to immobilize prey (e.g. Binford & Rypstra 1992), to protect the spider against dangerous prey (e.g. Malli et al. 1998), to preserve prey for later consumption (e.g. Griffiths et al. 2003) and to facilitate transport while holding on to the prey (Robinson & Olazarri 1971). For example, in canopy-foraging lycosid spiders (Rovner & Knost 1974), a sister group of the Pisauridae (Coddington & Levi 1991), prey wrapping facilitates handling and transport and is considered an adaptive strategy to reduce the risk of losing prey (Gilbert & Rayor 1985). These functions of prey wrapping are particularly beneficial in nuptial gift-giving species, where males hold the prey in their chelicerae while actively searching for females.

Table 2. Outcome of mating trials where males presented a fly as a nuptial gift to females of different mating (virgin or mated once) and nutritional status (food deprived or satiated)

| Response variable | Virgin females | | Mated females | | | P | | |
	Food deprived	Satiated	Food deprived	Satiated	Statistic	Interaction	Effect of nutritional state	Effect of mated state
Males wrap before presenting (%)	50 (22)	47 (17)	15 (20)	44 (16)	GLM-b	NS	NS	NS
Males present gift (%)	83 (23)	76 (21)	74 (23)	70 (23)	GLM-b	NS	NS	NS
Females accept first presentation (%)	40 (20)	38 (16)	41 (17)	0 (14)	GLM-b	0.006		
Males wrap more (%)	50 (12)	44 (9)	60 (10)	29 (14)	GLM-b	NS	NS	NS
Females accept second presentation (%)	64 (11)	33 (9)	60 (10)	29 (14)	GLM-b	NS	0.04	NS
Males wrapped overall (%)	59 (22)	59 (17)	40 (20)	50 (16)	GLM-b	NS	NS	NS
Female acceptance overall (%)	71 (21)	56 (16)	76 (17)	29 (14)	GLM-b	NS	0.01	NS
Copulation success (%)	67 (21)	50 (16)	76 (17)	29 (14)	GLM-b	NS	0.009	NS
Presentation time s, median (range)	180 (5−2940)	273 (5−3000)	123 (5−1200)	570 (10−3600)	GLM-g	NS	0.03	NS
Copulation duration s, median (range)	480 (60−1556)	390 (120−1380)	900 (5−2040)	960 (240−1680)	GLM-g	NS	NS	0.03
Interruptions (number, range)	0 (0−2)	0 (0−2)	1 (0−5)	0.5 (0−5)	GLM-qp	NS	NS	0.04

Sample sizes are given in parentheses.

The quantity of silk used in prey wrapping is positively correlated with copulation duration (Lang 1996), imposing sexual selection for gift wrapping. Nitzsche (1988) showed that nuptial gifts can consist of several small prey types held together with silk and wrapped in a coherent round parcel. Current selection would thus favour silk wrapping to increase the gift size and increase copulation time and hence sperm transfer (Stålhandske 2001).

Derived functions of prey wrapping may include manipulation of the female's reproductive behaviour by chemical substances in the silk, for example sex pheromones (Schulz & Toft 1993; Arnqvist & Rowe 2005). Our results showed that wrapping was not decisive for male mating success, yet we found that rejected males added silk threads to unwrapped flies and eggsacs more frequently than to previously wrapped flies. These were the two gift types that were not already wrapped with male silk. When adding silk, the male wrapped only a few silk strands around the prey which did not change the appearance of the gift. This behavioural pattern would be consistent with the presence of substances in the silk aimed at enticing females to accept the gift and to copulate.

While we argue that the ancestral function of prey wrapping should be sought in prey handling, we do not exclude alternative explanations. For example, males could use wrapping to disguise worthless gifts, as seen in the empidid flies (LeBas & Hockham 2005). In this case, we should expect to find males with worthless tokens inside the silk. Few and anecdotal reports of such findings from laboratory studies do exist (Stålhandske 2002); however, examination of 85 (Nitzsche 1988) and 26 (S. Toft, personal observations) field-collected gifts showed that all contained genuine prey. Males collect and offer nutritional prey, as would be expected in a system where the male's mating success depends on the female's foraging motivation.

An additional reason to believe that nuptial gifts exploit the female's foraging motivation stems from the perhaps prematurely dismissed idea of nuptial feeding having evolved as an antipredatory strategy against aggressive and cannibalistic females (Austad & Thornhill 1986; Stålhandske 2002). Precopulatory sexual cannibalism is well known in the family Pisauridae, including *P. mirabilis* (Arnqvist 1992; Elgar 1992; Drengsgaard & Toft 1999; Johnson 2001). When presenting a gift during courtship, *P. mirabilis* males frequently enter thanatosis (death feigning; Bilde et al. 2006), which is a well-known antipredator behaviour in animals (Edmunds 1974; Cloudsley-Thompson 1995), but is rare in a sexual context (Dennis & Lavigne 1976; Lawrence 1992). Males enter thanatosis when the female is approaching the nuptial gift, which is also when males are at most risk of a potential cannibalistic attack. When the female starts eating the gift, the male initiates copulation. Death-feigning males remain attached to the gift and this direct coupling suggests that the risk of precopulatory sexual cannibalism has influenced the concerted evolution of nuptial gifts and thanatosis as male counterstrategies (Bilde et al. 2006). This hypothesis also suggests another function of prey wrapping specific to the mating context, that is, to ease male control over the gift after it has been taken by the female. The 'cannibalism avoidance' hypothesis for the function of nuptial gifts has been rejected on the basis of few observed cannibalistic incidents (Austad & Thornhill 1986; Cumming 1994;

Stålhandske 2002). The fact that precopulatory sexual cannibalism is rare, however, does not reduce its selection force; on the contrary, frequent cannibalistic events would not be expected because of the evolution of male traits to counter the risk (Edmunds 1974; Dukas 2001; Fromhage & Schneider 2005). Hence, in cannibalistic species, males exploit the female's foraging motivation and reduce the likelihood of females attacking by postponing mating until the female is feeding on a prey (Prenter et al. 1994; Elgar & Fahey 1996; Elgar & Schneider 2004; Moya-Laraño et al. 2004; Fromhage & Schneider 2005; see also Arnqvist et al. 2003).

We suggest that cannibalism avoidance favoured the origin of nuptial gift giving by exploitation of the female's foraging motivation. The coevolution of male traits and female mating preferences would cause females to evolve to expect a gift (Stålhandske 2001). While the nutritional benefit of a single gift may be questionable (Stålhandske 2001), the female could benefit from accepting several gifts and multiple copulations, gaining either direct material benefits or other benefits such as increased fertilization success of eggs (Drengsgaard & Toft 1999). Hence, nuptial feeding would appear to represent sexual cooperation in this species. However, the silk wrapping of the gift could become subject to other selection forces as a target of conflict between male and female interests. Silk wrapping probably aids male control of the gift, it facilitates thanatosis which increases the likelihood of male copulation and it increases copulation duration, factors that are obviously in the male's interest (Lang 1996; Bilde et al. 2006). In contrast, the silk wrapping prolongs the feeding time for the female and could lead to suboptimal mating rates or copulation duration, which may be costly for the female while providing males with an advantage in sperm competition (Simmons 2001; Arnqvist & Rowe 2005).

Acknowledgments

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