Why Do Males of the Spider *Pisaura mirabilis* Wrap Their Nuptial Gifts in Silk: Female Preference or Male Control?

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Abstract

Males of the spider *Pisaura mirabilis* present a nuptial prey gift to the female during courtship as a mating effort. The gift is usually round and wrapped in white silk. It was suggested that the wrapped gift functions as a sensory trap by mimicking the female's eggsac implying that males exploit the female maternal care instinct and not her foraging motivation in a sexual context. The shape of the gift (round) and appearance (white) should then increase female acceptance of males. We tested these predictions experimentally and found that neither gift shape (round or oblong) nor silk wrapping (wrapped or unwrapped) facilitated female acceptance, in contrast unwrapped gifts were accepted faster than wrapped ones. Instead, we found that silk wrapping benefited the males because it significantly decreased the risk of females stealing the gift without copulation and consequently directly increased male mating success. Large oblong gifts were difficult for males to handle during copulation, resulting in shorter copulations for oblong vs. round gifts. Thus, round gifts were not preferred by the females but were beneficial to the males. Our results indicate two adaptive benefits to males of wrapping the nuptial gift: to reduce the risk of losing the gift to females without copulation, and make it possible to reshape an oblong prey into a round gift that facilitates the male's access to the female's genitalia. Our results suggest that the male gift wrapping trait may be selected though sexual conflict over remating rate.

Introduction

Some arthropods use nuptial gifts in connection with mating. The diversity of these gifts is vast and they may take the form of insect prey, spermatophores, saliva, parts or even the whole body of the male (Thornhill & Alcock 1983, reviewed by Vahed 1998). Several hypotheses can explain the adaptive significance of nuptial gifts in arthropods: (1) the nuptial gift acts as parental investment (Thornhill 1976a), (2) the nuptial gift acts as mating effort (Kessel 1955; Thornhill 1976b) and (3) the nuptial gift protects the male from sexual cannibalism (Kessel 1955). Nuptial gifts in spiders are rare (Bristowe 1958), but they are a characteristic part of courtship and mating in the nursery web spider *Pisaura mirabilis* (Bristowe & Locket 1926). At adulthood the male wraps an insect prey in white silk and carries it in his chelicerae while searching for a mate (Bristowe 1958). The male courts the female by presenting the prey in a characteristic display. When the female accepts the gift and is busy eating it, the male mates with her while maintaining contact with the gift with a silk thread and a leg (Bristowe 1958; Stålhandske 2001; Bilde et al. 2007). In *P. mirabilis*, there is little evidence for paternal investment, suggesting that the nuptial gift may function as a male mating effort (Stålhandske 2001; Bilde et al. 2007). Females almost

obligatorily require a nuptial gift to accept copulation, hence there is strong sexual selection on the gift giving behaviour (Stålhandske 2001).

Sakaluk (2000) suggested that nuptial food gifts have evolved as a form of sensory trap. A sensory trap may affect mate choice when male courtship signals mimic stimuli to which females respond in non-sexual contexts. These stimuli cause a response in the female which increases the male's fertilization rate (Christy 1995). Males that present nuptial gifts exploit the female's gustatory responses in a sexual context to obtain copulation (Sakaluk 2000). Because the process only requires that the male elicits a gustatory response from the female, the exact nature of the phagostimulatory material may be largely a matter of chance. This also offers a possible explanation for the variety of nuptial gifts in arthropods (Sakaluk 2000).

For the spider *P. mirabilis*, Stålhandske (2002) presented the hypothesis that the nuptial food gift functions as a sensory trap that exploits the female maternal care instinct. Stålhandske (2002) justified this hypothesis with the gift's resemblance to the female's eggsac, which is round, covered with white silk, and carried in the chelicerae as the gift. She showed that females accepted the gift faster with increasing brightness (whiteness) of the gift, suggesting that brighter gifts resembled eggsacs more and hence were more attractive to females. Bilde et al. (2007) tested other predictions of the eggsac hypothesis but were unable to confirm them. On the contrary, their results supported the alternative hypothesis that the gift exploits the female's gustatory responses. For example, hungry females were much more likely to accept a gift and copulate than satiated females. However, they provided no explanation for the particular feature of the spider nuptial gift that the eggsac hypothesis was erected to explain: why the males wrap the prey in a dense silken cover, seemingly hiding its nature as a food gift.

In this paper, we present a test of predictions of the eggsac hypothesis and of an alternative hypothesis to explain why males wrap the gift. If the male wraps the gift in white silk to mimic the female eggsac, the more resemblance the nuptial gift has with a female's eggsac the faster she is expected to accept it. Other aspects than colour should also matter, e.g. the shape of the gift. The eggsac is spherical while prey comes in many shapes. According to the eggsac hypothesis, we expect the females to prefer a round gift over a gift with any other shape. If, in contrast, it is the female's gustatory response that the male exploits in a sexual context, the resemblance of the gift to an eggsac should not be decisive for female acceptance. Rather the female foraging motivation should influence acceptance. In this case, we would expect that the volume of the prey would have a larger influence on the female acceptance than the shape of the gift (Lang 1996). We tested the effect of gift shape and volume on female acceptance in an experimental set-up where males presented a round or an oblong prey gift to the female.

If the nuptial gift exploits the female gustatory response (Bilde et al. 2007), the wrapping of the prey in white silk must have other functions than imitating the female's eggsac (Lang 1996). One possibility is that the male wraps the prey in silk to maximize control over the fate of the gift. Silk wrapping may function to facilitate the grip of prey in the chelicerae while searching for mates or during gift presentation (Bilde et al. 2007). However, males are particularly at risk of losing the prey to the female during copulation, where she can steal the gift without mating (Stålhandske 2002). This is because during mating the male must release the hold of the gift by the chelicerae and rely on prey contact via a silk thread and a leg claw. We tested the hypothesis that by wrapping the prey the male gains better control over it and can prevent females from stealing it without copulating. This was performed by comparing gift acceptance and male mating success in experiments where males presented wrapped or unwrapped prey gifts to the females.

Materials and Methods

Sub-adult *P. mirabilis* were collected 4 May 2006 from grazed grasslands surrounding the Mols Laboratory close to Århus, eastern Jutland, Denmark. The spiders were kept individually in plastic tubes (3 cm in diameter and 7 cm in height) where the bottom was lined with moist *Sphagnum* spp. The spiders were kept at room temperature (approx. 20°C) and on a natural photoperiod. They were fed every other day with one housefly (*Musca domestica*) from laboratory cultures and watered once a week. The two experiments were conducted sequentially.

Effect of Gift Shape

Upon maturation to adulthood, we switched the spiders between containers placing the males in the female tubes, to promote male gift-wrapping. We expected that pheromones from the female silk would initiate male gift wrapping behaviour (Lang

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1996). After the switching, we gave the male a prey either in form of a mealworm (as an oblong gift, n = 13) or a housefly (as a round gift, n = 13). Courtship experiments were conducted in transparent plastic terraria (17 × 17 × 10 cm). The bottom of each box was covered with paper towels. A female was placed in a terrarium 10 min prior to the experiment. While walking around she produced draglines, which are essential stimuli for the male in search of a mate (Stålhandske 2001). Then the male was introduced to the terrarium. When he sensed the female draglines, he displayed sexual excitement, which included trembling of the palps and abdomen, jerking of the body, moving in jerks and rapid rubbing of the legs (Lang 1996), after which he presented the gift to the female.

During the experiment, we observed the spiders continuously. We measured the time from the start of the display until the female accepted the gift (presentation time). Then, we measured the duration of the copulation (copulation time) of the first palp insertion. When sperm transfer with one pedipalp was completed, we separated the spiders and removed the gift which was measured with electronic calipers (length and diameter to nearest 0.1 mm). Subsequently the gift volume was calculated, the oblong gift as a cylinder ($V = \pi \times r^2 \times l$) and the round as a sphere [$V = (4/3) \times \pi \times r^3$] where r is the radius and l the length. The projected area of the gifts was calculated to investigate the effect of perceived gift area when viewed frontally, i.e. from the female's perspective, on presentation and copulation time (oblong gifts: $r \times l$; round gifts: $\pi \times r^2$). For oblong gifts, this projection method was used as males presented oblong gifts in such an angle that it was viewed by females from the side.

Gift volume was log-transformed and presentation time was square-root transformed to comply with the criteria for normal distribution of residuals and variance homogeneity. Statistical tests were preformed using ANCOVA testing the effect of shape and volume (covariate) and their interaction using JMP, SAS Statistical Institute.

Effect of Silk Wrapping

The spiders were kept and fed as described above. The male spiders were given a housefly. Half of them (n = 17) were permitted to wrap the fly and the other half (n = 17) were not. We prevented the wrapping by introducing the male to female terrarium immediately after he got the prey. Experiments were performed as described above: First, we placed the female in a terrarium and after 10 min we introduced the male. We observed the female behaviour when the male was introduced. When mating display started, we measured presentation time until female acceptance, the time from female acceptance until copulation was initiated and we recorded whether the female monopolized the gift without copulation. The experiment was terminated before copulation took place.

Results

Effect of Gift Shape

We found no significant effect of gift shape on presentation time (ANCOVA, $F_{3,25} = 2.96$, p = 0.05; effect of shape, p = 0.96) (Fig. 1a); however, there were

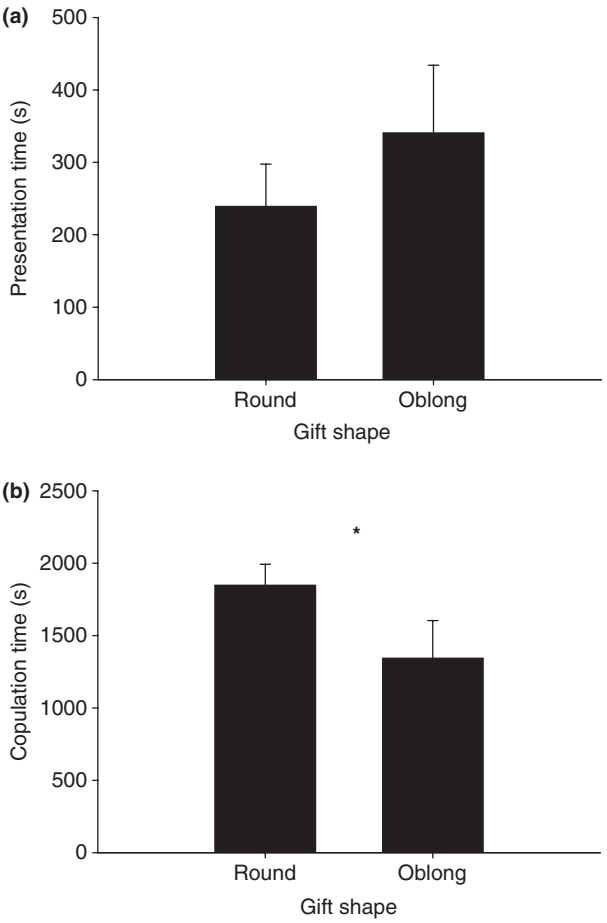

Fig. 1: In mating experiments, *Pisaura mirabilis* males presented a round or an oblong nuptial gift to a female, and the time recorded from the gift presentation time until the female accepted the gift was recorded (a), and of copulation duration, (b) in mean seconds + SE (*p < 0.05).

significant effects of gift volume (log volume, p = 0.01) and of the volume × shape interaction on presentation time (p = 0.01; Fig. 2a). For oblong gifts, presentation time decreased with increasing volume, whereas this was not the case for round gifts hence the strong interaction between volume and shape (Fig. 2a). Gift shape influenced copulation duration, as males presenting round gifts had significantly longer copulations than males with oblong gifts (ANCOVA, $F_{3,25} = 2.45$, p = 0.08; effect of shape, p = 0.04; Fig. 1b). We found no overall significant relationship between gift volume and copulation time (volume: p = 0.08). Copulation time for oblong gifts tended to decrease with increasing volume while remaining constant for round gifts, resulting in a significant volume × shape interaction (p = 0.04; Fig. 2b). This means that for oblong gifts, increasing volume had a positive influence on the female acceptance (faster acceptance), but a negative influence on copulation time (shorter copulation time), while these effects were not found in round gifts. Oblong gifts had a mean projected surface of 7.9 + 0.54 SE mm^2 and round gifts of 11.4 + 1.62 SE mm^2. There was a strong correlation between gift volume and projected area (log-transformed, $F_{1,25} = 607.33$, $p < 0.0001$). ANCOVA, therefore, provided similar results as reported above, the shape of the gift did not influence presentation time ($F_{3,25} = 2.96$, p = 0.05; effect of shape, p = 0.84), whereas presentation time decreased with increasing projected area (effects of log area, p = 0.018; shape × area interaction, p = 0.016). Copulation time was longer for round gifts than for oblong gifts (ANCOVA $F_{3,25} = 2.45$, p = 0.08; effect of shape, p = 0.04), with no clear effects of area (log area, p = 0.19). Copulation time decreased with increasing area for oblong gifts, while it increased for round gifts (shape × area interaction, p = 0.05). As the data showed large variation, nonlinear relationships cannot be excluded regardless that assumptions of normality and variance homogeneity were fulfilled.

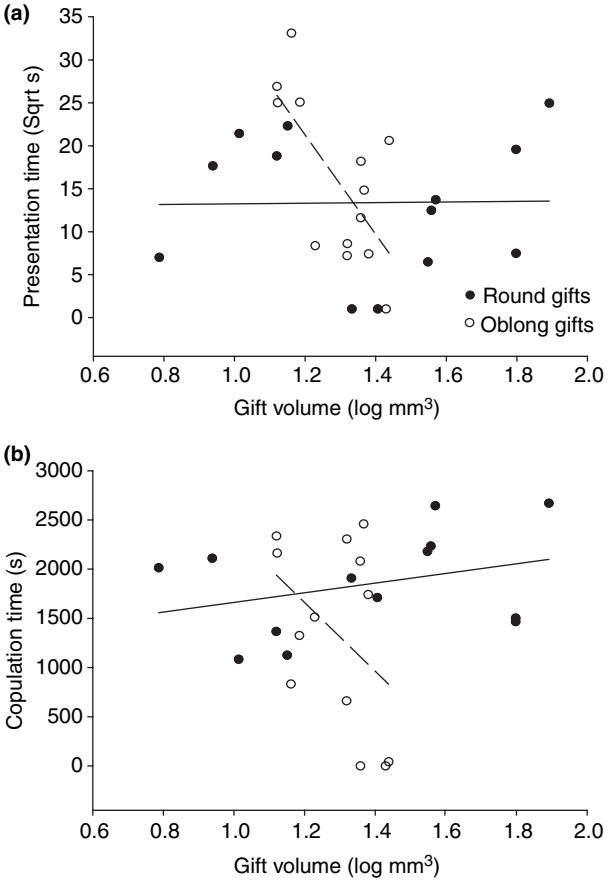

Fig. 2: Regression plot of the relationship (a) between gift volume (log mm^3) and presentation time (sqrt seconds), and (b) gift volume (log mm^3) and copulation time (seconds) in mating experiments where *Pisaura mirabilis* males presented either round or oblong nuptial gifts to females. Round gifts are black circles and solid regression line, oblong gifts are white circles and broken regression line.

Effect of Silk Wrapping

Presentation time was significantly longer for a wrapped gift in comparison with an unwrapped gift (ANOVA: $F_{1,33} = 9.28$; p = 0.004; log-transformed data; Table 1). There was no significant difference in the time from female acceptance until copulation was initiated ($F_{1,19} = 2.57$; p = 0.12). The prediction that it would be more difficult for the female to steal a wrapped gift without copulation than an unwrapped gift was confirmed: significantly more males that presented unwrapped gifts lost their gift without mating than males presenting wrapped gifts ($\chi^2 = 3.95$; p = 0.04; n = 34; Fig. 3a). As a consequence, the

Table 1: Data on gift presentation time, time from female acceptance to copulation initiation, and the proportion of females that attacked males in mating experiments where *Pisaura mirabilis* males presented either silk wrapped or unwrapped nuptial gifts (n = 34)

	Wrapped gift	Unwrapped gift
Presentations time in seconds (SE)	485 (150)	86 (36)**
Time from gift acceptance to copulation seconds (SE)	315 (63)	509 (130) ns
Sexual cannibalism (%)	0	17.6*

ns, not significant.
*p < 0.05; **p < 0.01, see text for details.

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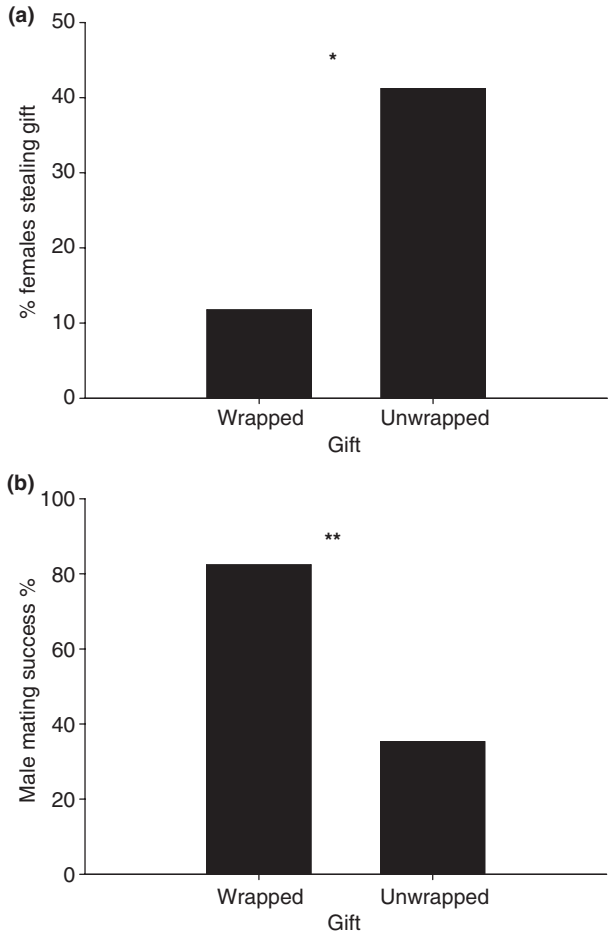

Fig. 3: (a) The proportion of females that took the gift and ran away without copulation. (b) The mating success of males (%) in mating experiments where *Pisaura mirabilis* males presented either silk wrapped or unwrapped nuptial gifts to females (*$p < 0.05$; **$p < 0.01$).

probability of achieving copulation was significantly higher for males presenting a wrapped gift than an unwrapped gift ($\chi^2 = 8.15$; $p = 0.004$; Fig. 3b). There were three incidents of sexual cannibalism, which all occurred when an unwrapped gift was presented ($\chi^2 = 4.45$; $p = 0.03$; Table 1).

Discussion

The hypothesis that *P. mirabilis* males produce a white and round nuptial gift to mimic an egg sac, predicts that the appearance of the male's gift (colour and shape) influences female acceptance and hence male copulation success (Stålhandske 2002). Our data showed that females do not require the nuptial gift to be wrapped in white silk, indeed acceptance of the gift was faster when an unwrapped prey was presented, confirming a previous similar finding (Bilde et al. 2007). It is possible that females accepted unwrapped gifts faster because the prey insect was not disguised and could immediately be recognized as food. Hence, wrapping of the prey in white silk represents a potential cost to the male, which are therefore expected to be balanced by considerable benefits. We did not find evidence for faster acceptance of round gifts as opposed to oblong gifts when controlling for gift volume. A significant interaction between shape and volume indicated that presentation time for an oblong gift decreased with an increasing volume suggesting that females accepted larger gifts faster. However, presentation time for round gifts was more or less independent of gift size. A similar interaction was seen when analysing how the two types of gifts might be perceived by females upon frontal presentation: presentation time decreased for oblong gifts with increasing area but not for round gifts. Overall, the data on presentation time and hence gift acceptance refute the eggsac hypothesis (Stålhandske 2002) as neither white silk wrapping nor round shape caused faster gift acceptance.

A test of the effect of gift shape on copulation duration showed that round gifts resulted in longer copulations than oblong gifts, and the effect of volume depended on the shape of the gift. When an oblong gift was presented the copulation time became shorter with increasing volume. We noted that an oblong gift actually was an obstacle for the male: it appeared to hinder male's access to the female's sperm storing organs. Copulating males would attempt to reach sideways past the gift to the female's epigyne with his pedipalps (the sperm transfer organs) while holding on to the gift with a leg or the spinnerets. Males would keep contact with the gift to secure that the female did not run off with it and to sense female feeding behaviour during sperm transfer (Bilde et al. 2007). However, when presenting a large and oblong gift it was difficult for the male to hold on to the gift and access the epigyne because the long ends literally were in the way. For this reason, when the male finally succeeded in initiating the copulation, it sometimes became very short. It appeared that males were unable to maintain control over gift and copulation when presenting large oblong gifts. Round gifts could easily be handled also when the gifts were large. These observations indicate strong selection for round gifts, which facilitate male handling and control during copulation. Our results clearly indicate that gift shape is a decisive factor for successful copulation

for other reasons than imitating an eggsac. Incidentally, oblong natural prey like crane flies or caterpillars is bent before wrapping to produce a round gift (S. Toft, pers. obs.). However, the long gifts (mealworm) used in this experiment could not be bent as they have a relatively hard cuticle compared to oblong prey of other taxa. This is likely the explanation why mealworms were difficult for the males to handle and impeded copulations mechanically. While the use of two different prey types were necessary for examining the effect of gift shape on female acceptance, we can not rule out an effect of prey species on our results. However, we have no indication that prey species *per se* influences female acceptance, because males in nature present a taxonomic broad variety of prey species (Nitzsche 1988; S. Toft, pers. obs.).

That silk wrapping is not essential for gift acceptance raises the question of why the male wraps the gift in white silk? We provide evidence to support that wrapping aids male control over the gift during courtship and copulation. We showed that females succeeded in stealing an unwrapped gift more often than a wrapped gift. Prey wrapping facilitate the grip of the gift in the chelicerae during mate search (Gilbert & Rayor 1985), and helps to retain control prior to and during copulation (Bilde et al. 2007). While females may benefit from a meal without accepting sperm, males always loose if females monopolize their gift without copulating (Thornhill & Alcock 1983). This potential conflict between the sexes over mating exerts strong selection on males to keep control of the gift until sperm transfer is completed. Furthermore, the wrapping also forms the prey into a uniform sphere, which facilitates male access to the female's copulatory organs as suggested above.

We propose that gift wrapping is under strong selection to facilitate male control over courtship and mating, which means that selection acts on males to maintain control over the gift and not on female preference for white silk. In addition, a positive relationship between silk wrapping and female consumption time results in longer copulation duration (Lang 1996), and the positive relationship between copulation duration and sperm transfer directly provides males a paternity advantage in sperm competition (Drengsgaard & Toft 1999). Males and females do not necessarily share a common interest over mating frequency, suggesting a potential for conflict (Andersson 1994; Arnqvist & Rowe 2005). A previous study showed that satiated females were less likely to remate than starved females, indicating that the nuptial gift functions as a male mating effort to achieve copulations (Bilde et al. 2007). Furthermore, it was shown that males have evolved thanatosis – death feigning in conjunction with gift presentation – as a male mating effort that increases male mating success when paired with already mated, resistant females (Hansen et al. 2008). Hence, gift wrapping may result from the co-evolution of male and female traits resulting from sexual conflict over remating rate.

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