

Condition dependence of male nuptial gift construction in the spider *Pisaura mirabilis* (Pisauridae)

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Abstract *Pisaura mirabilis* males offer a prey wrapped in silk as a nuptial gift that functions as a male mating effort. If nuptial gift construction is costly, males in poor feeding condition would invest less in this behaviour than males in good condition. We investigated frequencies and characteristics of gift construction in males under different sexual stimuli and different feeding conditions. We analysed gift construction behaviours of 17 males exposed sequentially to three treatments: female silk (S), female silk plus female (SF) and no female cues (control; C). The same individuals were first tested when in good feeding condition (young/satiated) and subsequently in poor feeding condition (old/starved). A separate group in good feeding condition controlling for effects of male age was also tested (old/satiated). Presence of female cues (S and SF) elicited much stronger gift construction response in males compared with the control group. Both groups of satiated males constructed nuptial gifts more frequently than starved males, spending more time on gift construction and using more silk. Our findings show that poor feeding condition affects pre-copulatory gift construction behaviour. Nuptial gift construction may be an honest indicator of male condition and therefore a target of female choice.

Keywords Indicator trait · Handicap hypothesis · Gift construction · Male quality · Nuptial gift · Sexual selection · Spiders

Introduction

Sexual selection theory predicts the development of secondary sexual characters (weapons, ornaments, courtship behaviour) that allow individuals to obtain high reproductive success, even against their own survival success (Darwin 1871). In general, males compete for access to females and invest heavily in particular morphological traits and behaviours that increase their chances of being selected by females (Andersson 1994). Zahavi's (1975) "good genes" or "handicap" principle predicts that such sexual traits are costly and honest indicators of male condition, allowing females to distinguish between males of good and poor quality. Males in poor energetic and physical condition would not be able to maintain those traits and will be rejected by females, while males in good condition will have higher reproductive success (Andersson 1986, 1994). Several external factors can affect male physical condition, e.g. diseases or parasites. In invertebrates, it has been demonstrated that poor feeding condition or poor nutritional balance can reduce a male's reproductive success, in some cases as a result of female preference (Mappes et al. 1996; Ahtiainen et al. 2001; Andrade and Mason 2000; Kotiaho 2002; Engqvist and Sauer 2003; Hunt et al. 2004; Lomborg and Toft 2009).

Typically, pre-copulatory courtship is one of the behaviours required for species recognition, as well as for mate evaluation and choice (Andersson 1994; Alcock 1998). Nuptial gifts in insects increase male attractiveness during courtship and mating (Boggs 1995; Vahed 2007;

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Gwynne 2008) and could be markers of male quality (Zahavi and Zahavi 1997; Simmons et al. 1998; Engels and Sauer 2006). Nuptial gifts are presented in the form of captured prey, regurgitation, glandular or salivary fluids, or specialized male body parts, which are donated to the females during courtship and mating (Thornhill 1976; Boggs 1995; Sakaluk 2000; Vahed 1998, 2007). In spiders, the nuptial gift-giving trait of *Pisaura mirabilis* (Pisauridae) has been studied extensively (Bristowe 1968; Austad and Thornhill 1986; Lang 1996; Drengsgaard and Toft 1999; Stålhandske 2001, 2002; Bruun et al. 2003; Prokop 2006; Bilde et al. 2006, 2007; Andersen et al. 2008; Hansen et al. 2008; Prokop and Maxwell 2009), and a similar behaviour has been studied in *Paratrechalea ornata* (Trechaleidae) (Costa-Schmidt et al. 2008; Albo et al. 2009; Albo and Costa 2010). In *P. mirabilis*, females exert strong preference for a nuptial gift. Stålhandske (2001) observed that, although males may acquire copulation without offering a gift, the presence of a gift greatly increases mating success and also facilitates male mating position, and importantly keeps the female occupied by feeding during the mating. The gift thus functions as a male mating effort, and larger gifts promote longer copulations and more fertilized eggs than small gifts (Austad and Thornhill 1986; Lang 1996; Stålhandske 2001; Bilde et al. 2007; Andersen et al. 2008).

The prey offered by *P. mirabilis* males is usually wrapped in white silk, and males display characteristic gift construction behaviour. Prey wrapping is elicited even in the absence of a female by sexual stimuli such as female silk (Nitzsche 1988), and courting males that are initially rejected by a female usually perform additional bouts of gift wrapping and are often eventually accepted (Bilde et al. 2007). Copulation duration is positively correlated to the amount of silk applied to the gift (Lang 1996). Several hypotheses have been put forward to explain the function of silk wrapping; among these, it was suggested that silk functions to avoid prey disintegration during handling, or to allow the males to pack more than one prey within a gift and thus increase the gift size (Austad and Thornhill 1986; Lang 1996). Stålhandske (2002) found that the white colour of the wrapped gift was attractive to females, whereas this hypothesis was refuted when females accepted wrapped and unwrapped gifts equally (Bilde et al. 2007). Andersen et al. (2008) showed that silk wrapping reduces the risk of females escaping with the gift before sperm transfer has been completed, because the silk facilitates male control over the gift during copulation. These findings indicate conflict between male and female interests in a situation where the partners trade food for sex and vice versa.

A previous study suggested that the silk investment was unlikely to confer high costs to the male, because male

feeding condition seemed not to influence gift construction (Lang 1996). However, others have suggested general costs associated with silk production in spiders (Craig 2003). Furthermore, for a male in poor feeding condition there is a trade-off between wrapping and eating, because eating the prey may alleviate male hunger and secure longer reproductive life. The aim of this study is to investigate the rates and characteristics of gift construction in males of *P. mirabilis* under different sexual stimuli and different feeding conditions. Following the handicap model (Zahavi 1975), if gift construction is costly, only males in good condition will be able to perform gift construction and produce an attractive gift. We predicted that feeding condition would affect male gift construction behaviour so males in poor feeding condition would wrap a prey as a nuptial gift less frequently, and invest less time and silk in producing the gift.

Materials and methods

Collection and breeding

We collected juveniles and subadults of *P. mirabilis* in April 2009 at the Mols Laboratory near Aarhus, Denmark. In the laboratory the spiders were housed individually in vials (30 ml) containing moist moss (*Sphagnum* spp.), and water was provided daily. Males and females were raised in separate rooms, kept at room temperature (on average 20°C) and at natural photoperiod. Individuals were fed with houseflies (*Musca domestica*) three times per week until maturation. Experiments were carried out in transparent plastic cages (22 × 17 × 6 cm³) with paper-covered bottom in May–June 2009. All individuals used in experiments were initially virgins.

Experimental design

Nitzsche (1988) showed in *P. mirabilis* that female silk triggers male nuptial gift construction. We analysed gift construction behaviours of initially 17 males exposed sequentially but in random order to three treatments (following Albo et al. 2009): female silk (S), female silk plus female (SF) and control, i.e. no female cues (C). In a first period we carried out 51 trials using males in good feeding condition, whereas in a second period the same tests were carried out with the same males but now being food deprived and in poor feeding condition (see below). Prior to and during the first period the males were fed one housefly (*Musca domestica*) three times per week for 10 days following the moult to maturity, and the three trials were conducted within the next 10 days (Fig. 1). For each trial, a different female was used to provide cues

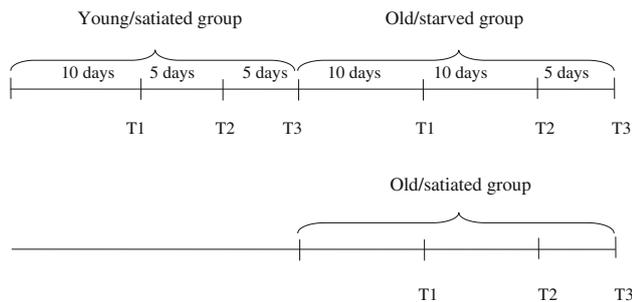


Fig. 1 Schedule of the experimental blocks and the time of each test (T). Males in good feeding condition (3 house flies weekly) were exposed to each test (T1, T2 and T3) with an interval of 5 days. Subsequently, feeding was reduced to one fruit fly during 10 days, and the test T1 was performed again. We reduced feeding for another 10 days before carrying out T2. After this, males were deprived flies for 5 days and exposed to T3. Old/satiated males were of similar age as the starved males, but were kept under good feeding condition and exposed to similar tests as starved males to control for male age

(chemical and visual cues) in the S and SF trials. In both treatments, a female was placed in the experimental cage at least 1 h prior to the experiment, allowing her to deposit silk threads. At the beginning of a trial the male was given a live housefly and immediately (i.e. before gift construction) transferred to the experimental cage. In the S treatment the female had been removed before introduction of the male. In the SF treatment the female was placed in a vial at one end of the cage. The vial was closed with mesh allowing male and female contact but preventing mating. In the C treatment the male was placed in a clean arena without any female cues.

We repeated the experiments in a second block using the same males but being subject to poor feeding condition. This allowed us to determine if the males were able to modify their behaviour according to their feeding state and the stimuli received. During the 10 days between the first and second block of tests, the 17 males were fed only one fruit fly each (*Drosophila melanogaster*). The interval between the first two tests was 10 days but only 5 days between the second and third test due to increasing male mortality (Fig. 1). The males were again exposed consecutively to the three treatments (S, SF and C) in random order.

To account for the effect of male age on male responses during the second block of tests, we raised another group of 10 males under good feeding condition and exposed them to the same three treatments (S, SF and C) at the same age as starving males in the second block of tests (Fig. 1). We weighed the males at this stage of the experiment; mean \pm SD weight of the starved males was 72.2 ± 10.0 mg and of the old/satiated males was 84.3 ± 19.0 mg, suggesting a weight loss of 14% of body mass in the starvation treatment.

Gift construction

The duration of each trial was 30 min, but if nuptial gift construction had been initiated within this period, the observations continued until nuptial gift construction was completed. We registered occurrence, latency and duration of gift construction, number of silk wrapping bouts and total duration of silk wrapping. The 'latency of gift construction' was defined as the time from when the male was placed in the test box until he initiated silk wrapping. The 'gift construction duration' was the time between first and last silk wrapping (including periods of gift handling and carrying without wrapping). The 'silk wrapping duration' included only the time spent wrapping. As an estimate of the amount of silk deposited we measured the number of silk wrapping bouts a male performed, and classified the gifts according to their colour: black (no or little silk) and white (much silk). To determine if males had eaten of the prey, the dry weight of fly gifts among groups in the S and SF treatments, and of unwrapped flies from the control treatment C, was determined by placing flies in a vacuum oven (Struers Heraeus) at 60°C for a minimum of 3 days and then weighing them on a Mettler A30 (0.0001 g) balance. Differences in dry weight of flies/gifts amongst males of different condition and age would indicate whether males had fed on the flies rather than using them for construction of gifts.

Statistical analyses

Statistical analyses were performed using JMP 7.0 software (SAS Institute) and the Past statistical package (Hammer et al. 2003). We tested for normal distribution of residuals and homogeneity of variance with Shapiro–Wilk and Levene tests, respectively. For comparing mean values, we performed two-way analysis of variance (ANOVA); post hoc analyses were performed with Tukey test. Number of silk wrapping bouts was treated as an ordinal variable and analysed with two-way ordinal logistic fit. Chi-square test and Fisher exact probability test were used for comparison of frequencies.

Results

Gift construction frequencies

Whether starved or not, all males responded similarly to the treatments (S, SF, C): we recorded a high frequency of gift construction in the presence of silk and silk + female, but a lower frequency when there were no female cues ($\chi^2_{\text{young/satiated}} = 31.4$, $p < 0.0001$, $df = 2$; $\chi^2_{\text{old/starved}} = 5.66$, $p = 0.06$, $df = 2$; $\chi^2_{\text{old/satiated}} = 17.9$, $p < 0.0001$,

$df = 2$; Fig. 2). Because of the absence of significant differences between S and SF treatments in all three experimental groups, we combined the data from S and SF to perform comparisons among groups (Fig. 2). The two groups of satiated males constructed gifts with similar frequency (90% and 91%, respectively), which was significantly higher than that of starved males (54%) ($\chi^2 = 12.9, p = 0.001, df = 3$). Starved males that did not construct a gift remained motionless while eating the prey. These results show that the lower gift construction

frequency in starved males was due to poor feeding condition rather than to age.

Gift construction duration

We did not find differences in the effect of female cues (S and SF) on the latency of gift construction, the duration of construction or the duration of silk wrapping (Table 1). We found an overall higher number of silk wrapping bouts when both silk and female stimuli were available (SF), although in the pair-wise comparisons this was significant only in the young/satiated group (Table 1). For three variables: latency of gift construction, duration of silk wrapping and number of silk wrapping bouts, there were no effects of feeding condition and age. However, starved males showed lower gift construction duration than the males from both satiated groups (Table 1). These results show that some aspect of gift construction behaviour depends on feeding condition rather than on age.

Gift colour

Nuptial gift construction differed qualitatively between satiated and starved males. We observed (but did not quantify) that starved males performed slower movements when sensing the female silk threads as well as when they wrapped the prey (deposition of silk for the basal plate and silk covering of the gift, see Nitzsche 1999) than satiated

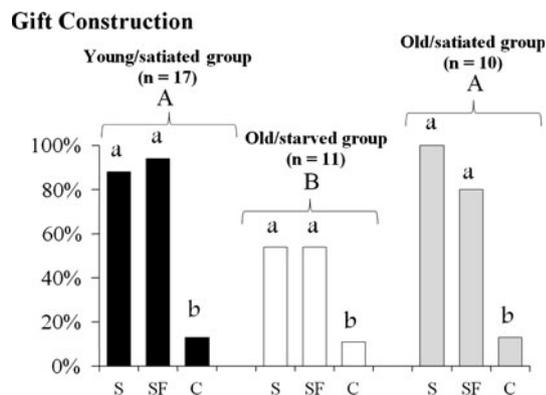


Fig. 2 Gift construction frequencies (percentages) observed in three treatments from each group. S with female silk, SF with silk and female, C control, without female cues. Small letters compare treatments (S, SF and C); capital letters compare age/feeding groups. Different letters indicate significant differences ($p < 0.05$), post hoc comparisons with chi-square test and Fisher’s exact test

Table 1 Mean \pm standard deviation (SD) (in minutes) latency and duration of nuptial gift construction, and the number of wrapping bouts and duration of silk wrapping

	Young/satiated group		Old/starved group		Old/satiated group		Statistics		
	S (N = 15)	SF (N = 16)	S (N = 6)	SF (N = 6)	S (N = 10)	SF (N = 8)	Treatment (df = 1)	Group (df = 2)	T \times G interaction (df = 2)
Latency of gift construction ^a	6.4 \pm 5.6	4.5 \pm 4.3	4.1 \pm 3.0	2.9 \pm 3.0	3.0 \pm 0.9	6.4 \pm 10.4	$F = 0.05$ $p = 0.83$	$F = 0.75$ $p = 0.47$	$F_2 = 1.83$ $p = 0.17$
Gift construction duration ^a	12.4 \pm 9.6	13.8 \pm 7.4	5.5 \pm 2.9	5.2 \pm 2.0	9.2 \pm 32.1	14.8 \pm 7.3	$F_1 = 1.83$ $p = 0.18$	$F_2 = 5.52$ $p = \mathbf{0.006}$	$F_2 = 0.62$ $p = 0.54$
Duration of silk wrapping ^a	4.7 \pm 2.4	5.7 \pm 2.4	4.3 \pm 2.1	5.0 \pm 1.9	4.9 \pm 2.4	4.5 \pm 1.8	$F_1 = 1.68$ $p = 0.20$	$F_2 = 0.57$ $p = 0.56$	$F_2 = 0.53$ $p = 0.59$
Number of silk wrapping bouts ^b	2.7 \pm 0.8 a	3.7 \pm 1.3 b	2.7 \pm 0.5	3.0 \pm 1.0	2.7 \pm 1.1	2.8 \pm 1.0	$\chi^2 = 4.9$ $p = \mathbf{0.027}$	$\chi^2 = 4.6$ $p = 0.10$	$\chi^2 = 0.1$ $p = 0.95$

Small letters compare treatments (S and SF); capital letters compare age/feeding groups. Different letters indicate significant differences ($p < 0.05$)

^a Analysed by two-way ANOVA followed by Tukey tests for significant effects

^b Analysed by ordinal logistic fit followed by pair-wise χ^2 tests between treatments of each group

males. This was especially the case with males in the worst physical condition [the two last assays (T2 and T3) with starved males (cf. Fig. 1)]. Gift colour varied between white and black (Fig. 3) in all groups. We observed a higher absolute number of black gifts (less silk) in the starved group compared with both satiated groups ($\chi^2 = 4.1, p = 0.04, df = 1$), indicating that males in poor feeding condition deposited less silk.

Gift weight

Table 2 shows gift dry weights in S and SF treatments and the dry weight of the prey without silk in C (where males did not construct gifts), for males in the three groups. The significant treatment effect and the post hoc comparisons showed that C males consumed a larger fraction of the flies offered compared with males in S and SF. The significant group effect indicated that only old-satiated males refrained from eating from the flies in the control treatment.

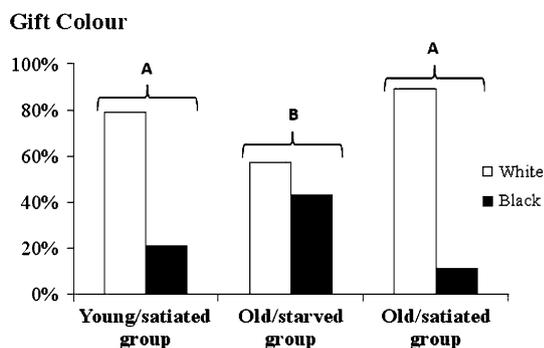


Fig. 3 Frequencies of gift colours—white and black (percentages)—in the three groups: young satiated males ($N_{white} = 27, N_{black} = 7$), old/starved males ($N_{white} = 8, N_{black} = 6$), old/satiated males ($N_{white} = 16, N_{black} = 2$). Different letters indicate significant differences ($p < 0.05$). Post hoc comparisons with chi-square test

Discussion

Our data show that the presence of female silk alone triggered nuptial gift construction in *P. mirabilis* males to the same extent as when the female was also present. This is in accordance with observations by Lang (1996) for this species, and by Albo et al. (2009) for *Paratrechalea ornata*, and with field observations that males construct and carry the gift when searching for females. The data in general support the hypothesis that gift construction in the absence of a female is advantageous for the male, as it allows him to court the female immediately by offering the gift once a female is encountered. However, female presence had some effect on male construction decisions by increasing the number of silk wrapping bouts. This may reflect that gift wrapping is costly for males, so they delay investment in silk wrapping until the female is close. In accordance with this hypothesis, males of *P. mirabilis* and *P. ornata* carrying prey without silk usually start silk wrapping once they are confronted with a female (Bilde et al. 2007; Albo and Costa 2010). Moreover, if males are initially rejected by females they perform additional wrapping bouts before repeated courtship and mating attempts (Bilde et al. 2007). Contrary to the observations in *P. ornata* (Albo et al. 2009), males of *P. mirabilis* may construct gifts in the absence of female cues (C treatment), although at much lower frequency than when female cues are present. We also observed males constructing gifts in their breeding vials (M.J. Albo, personal observations). As males and females were all virgin, and they were raised in separate rooms, we can exclude that previous experience or airborne pheromones could act as triggers of gift construction. Consequently, gift construction may be a spontaneous behaviour associated with sexual maturity, which is however strongly enhanced by external stimuli (female cues), suggesting that males adaptively adjust their behaviour in response to ecological conditions.

Our data show that feeding condition in *Pisaura mirabilis* males may considerably affect pre-copulatory gift

Table 2 Dry weight values (mean \pm SD, in milligrams) of the gifts from the S and SF treatments, and the prey without silk from the C treatment, of males from the three age/feeding groups

	S	SF	C	Statistics	Post hoc
Young/satiated group (Ysat)	3.0 \pm 0.6 (N = 9)	3.0 \pm 0.8 (N = 9)	1.8 \pm 0.5 (N = 7)	Treatment (df = 2) F = 7.7, p = 0.001	S = SF > C Osat > Osta = Ysat
Old/starved group (Osta)	3.6 \pm 0.1 (N = 6)	2.9 \pm 0.8 (N = 6)	2.2 \pm 0.3 (N = 5)	Group (df = 2) F = 9.9, p = 0.0002	
Old/satiated group (Osat)	3.9 \pm 0.9 (N = 5)	4.0 \pm 0.7 (N = 4)	3.7 \pm 0.1 (N = 4)	T \times G interaction (df = 4) F = 0.99, p = 0.42	

Statistical comparisons were performed using two-way ANOVA; post hoc test were performed with Tukey test

construction behaviour. Poor feeding condition resulted in lower frequency of nuptial gift construction and lower amount of silk invested in gift wrapping. Also Nitzsche (1988) suggested an effect of feeding rate on the frequency of nuptial gift construction in *P. mirabilis*. In addition, in our experiments, poorly fed males invested less time overall in gift construction than satiated males, whether young or old. This did not involve less time for deposition of silk, as duration of wrapping was similar among groups, but less time manipulating and carrying the gift while the male sensed the female silk threads. Nevertheless, the differences in gift wrapping performance among groups suggest that less silk is used by males in poor condition, as the proportion of “black” gifts with less silk cover was much higher among males in poor condition. Lang (1996) suggested that starved males could compensate by spending more time in silk wrapping. We failed to confirm this; instead we found that the starved males reduced their overall time investment (although not their wrapping time) in the gift.

This study indicates high sexual selection on male silk deposition and prey wrapping, because even under very poor feeding condition, some males invested in prey wrapping and nuptial gift construction. The gift/prey weight data indicate a conflict in the males about investment in mating (producing a gift) or own survival (eating the prey), resulting in a compromise in both young-satiated and old-starved males. This agrees with earlier observations that recently moulted males prioritize own feeding and initiate gift construction only after several days of feeding, once they are in good feeding condition and in the presence of female cues (Nitzsche 1988). Old-satiated males, on the other hand, seem to invest the whole fly for the gift, reflecting that they are under no pressure to feed and best enhance their reproductive success by offering a large gift, i.e. by not eating any of the gift.

Differences in diet among individuals may not only affect survival, development, maturation time and final adult size, but also reproductive behaviour and the development and characteristics of secondary sexual traits (Anderson 1974; Uetz et al. 2002; Toft and Wise 1999; Walker et al. 2000; Lomborg and Toft 2009). Indeed, it has been suggested that the “tufts” on the forelegs of the spider *Schizocosa ocreata* and the percussive “drumming” by the spider *Hygrolycosa rubrofasciata* vary according to male feeding condition. These traits are also important traits in female mate choice and may thus be honest signals of male quality (Mappes et al. 1996; Parri et al. 1997; Uetz et al. 2002). Though still able to maintain minimal normal activities, spiders under natural conditions often starve (Anderson 1974; Walker et al. 2000); therefore the investment in gift construction could be an indicator of male quality in *P. mirabilis*. In spite of some contradictions

in the literature, silk wrapping seems to give males several reproductive advantages, influencing female mate acceptance, promoting longer copulations and consequently higher fertilization success (Lang 1996; Stålhandske 2002; Bilde et al. 2007; Andersen et al. 2008). Hence, males able to invest more in gift construction and therefore able to offer well-wrapped gifts would indicate to females that they are good hunters and also are in good physical condition. Such males may be favoured in female mate choice. Further studies evaluating female–male interactions and the role of gift structure on female choice are needed to further validate this hypothesis.

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