

Female spiders ignore condition-dependent information from nuptial gift wrapping when choosing mates

Maria J. Albo^{a,b,*}, Søren Toft^a, Trine Bilde^a

^a Department of Bioscience, Aarhus University, Aarhus, Denmark

^b Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

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In many species, condition-dependent secondary sexual traits are important for female choice. In the spider *Pisaura mirabilis*, males offer females a nuptial gift (prey wrapped in silk) during courtship. Gift construction may involve high costs for males, and those in low condition invest less time and silk in wrapping the prey. We investigated how male condition and gift wrapping affect male reproductive success and whether females use the wrapped gift as an honest indicator of male condition. We experimentally manipulated male condition (satiated and starved males) and gift wrapping (well- and poorly wrapped gifts) and carried out experiments in a fully factorial design. We found that males in good condition were more successful in obtaining matings and obtained longer copulations than males in poor condition. In contrast, gift wrapping did not affect female mate choice. Only good-condition males obtained offspring. Gift wrapping is an honest indicator of male condition, but in spite of this females did not use this information in mate choice. We argue that because gift wrapping mainly functions to promote male interests, good-condition males would also be better at cheating the female, for example using wrapping to hide a worthless gift. Females should therefore evolve to ignore the wrapping information and instead base their mate choice decision on male traits that unequivocally benefit their own reproductive success. Our results are consistent with this prediction, as females discriminated males based only on their actual feeding condition, and this choice provided them with direct reproductive benefits.

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The ‘handicap hypothesis’ explains how secondary sexual traits, such as ornaments or behaviours, can be costly and honest signals for mate choice (Zahavi 1975; Zahavi & Zahavi 1997). Several examples verify that only males in good condition can efficiently perform and maintain their signals during courtship and mating; as a result males in poor condition are often rejected by females and suffer reduced reproductive success (Mappes et al. 1996; Andrade & Mason 2000; Ahtiainen et al. 2002; Kotiaho 2002; Engqvist & Sauer 2003; Hunt et al. 2004; Engels & Sauer 2006; Lomborg & Toft 2009). Condition-dependent secondary sexual traits may be influenced by food acquisition, as shown in the spider *Schizocosa ocreata* in which hair tufts on the front tibia are negatively affected by a low-quality individual diet (Uetz et al. 2002; Hebets et al. 2008). The tufts are an important part of the visual signal during courtship, and females preferentially select males with well-developed tufts (Uetz et al. 2002; Hebets et al. 2008). Similarly, only males in good feeding

condition can maintain high rates of abdominal ‘drumming’ during courtship in the spider *Hygrolycosa rubrofasciata* (Mappes et al. 1996) indicating high energetic costs of drumming (Kotiaho et al. 1998). As a result females prefer the most actively drumming males (Parri et al. 1997).

In the gift-giving spider *Pisaura mirabilis*, gift construction is affected by male feeding condition (Albo et al. 2011a). The nuptial gift consists of prey wrapped in silk and is constructed when males perceive sexual stimuli as contact pheromones associated with the female silk (Nitzsche 1988; Albo et al. 2011a). In this system, females prefer males that offer a nuptial gift during courtship and those males experience the highest reproductive success (Stålhandske 2001; Prokop 2006; Bilde et al. 2007). Sexual selection for producing nuptial gifts forces males in poor condition to construct a gift, but this behaviour is constrained and performed inefficiently, as these males spend less time and less silk in prey wrapping than good-condition males (Albo et al. 2011a).

Silk wrapping has an important function for males: it facilitates male handling and control over the gift as it allows the male a better grasp of the gift compared with an unwrapped insect (Andersen et al. 2008). A well-wrapped gift reduces the risk of the female running away with it before sperm transfer is completed. In

* Correspondence: M. J. Albo, Laboratorio de Etología, Ecología y Evolución, Instituto de Investigaciones Biológicas Clemente Estable, Avenida Italia 3318, Montevideo, Uruguay.

E-mail address: maria.albo@biology.au.dk (M. J. Albo).

addition, silk wrapping provides males with the opportunity to disguise the gift's content, which may vary from genuine nutritious insect prey to worthless items such as empty arthropod exoskeletons, and thus deceive the females (Albo et al. 2011b). Therefore, silk wrapping should act against female interests, unless females use information from the gift wrapping for mate choice. During courtship, females could visually evaluate mate quality by the amount and quality of the silk wrapping and prefer to mate with males that are able to offer well-wrapped gifts as an indication of their good condition. By manipulating gift colour, Stålhandske (2002) found that females are more attracted to bright than dark gifts, revealed by a reduced latency of gift acceptance.

Since silk wrapping has several functions for males, the fact that male condition is a limiting factor for silk wrapping raises the question whether females use gift wrapping as an honest signal of male condition. We experimentally manipulated male diet (to create males in good and poor condition) and gift wrapping (well-wrapped and poorly wrapped gifts), and carried out mating experiments in a fully factorial design. If females during courtship use information on the quality of gift wrapping as an indicator of male condition, males offering well-wrapped gifts should be more successful in obtaining matings than those offering poorly wrapped gifts, when male feeding condition is controlled for. Alternatively, female mate choice could depend on male condition itself or an interaction between both factors.

METHODS

We collected juvenile and subadult *P. mirabilis* spiders in April 2010 and 2011 at the Mols Laboratory in Eastern Jutland, Denmark. In the laboratory, spiders were housed individually in vials (30 ml) containing moist moss (*Sphagnum* spp.) and water was provided two to three times a week to maintain humidity. Males and females were raised at room temperature (24.0 ± 0.1 °C) and natural photoperiod. We fed individuals with house flies, *Musca domestica*, three times per week until maturation.

Male Condition and Gift Wrapping

To examine how male condition and gift wrapping interact and influence reproductive success we designed four experimental male groups, combining male feeding condition (satiated males = good-condition males and starved males = poor-condition males) and gift-wrapping quality (well-wrapped and poorly wrapped, see below). The four experimental groups were: 'GC-WW' consisting of good-condition males offering well-wrapped gifts ($N = 24$); 'GC-PW' consisting of good-condition males offering poorly wrapped gifts ($N = 20$); 'PC-WW' consisting of poor-condition males offering well-wrapped gifts ($N = 24$) and 'PC-PW' consisting of poor-condition males offering poorly wrapped gifts ($N = 25$).

We obtained differences in male condition by exposing males to two different feeding regimes after their maturation to adulthood. Males in good condition were satiated by receiving a house fly every day, while males in poor condition were starved by being fed one house fly in 3 weeks. Male condition index at the time of the experiment was calculated as the residuals of the body weight/cephalothorax width regression (Jakob et al. 1996), and was 0.009 ± 0.001 mg for good-condition males and -0.008 ± 0.001 mg for poor-condition males (mean \pm SE; $F_{1, 90} = 144.0$, $P < 0.0001$). As gift wrapping varies with male condition (Albo et al. 2011a) we used gifts constructed by males in good condition as well-wrapped gifts, and those constructed by males in poor condition as poorly wrapped gifts. In the GC-WW and PC-PW groups, we allowed the males to construct and offer their own gift to females. In the GC-PW and

PC-WW groups, we allowed GC and PC males to construct gifts and subsequently switched gifts between the groups, so that good-condition males offered poorly wrapped gifts produced by poor-condition males, and poor-condition males offered well-wrapped gifts produced by good-condition males. In this species, it is easy to remove a gift from a male using forceps, and males readily accept a nuptial gift offered in forceps. Only gifts typical of poor- and good-condition males (see below) were used for switching. We did not switch gifts between individuals of the GC-WW and PC-PW groups because Bilde et al. (2007) found no effects of gift switching on male behaviour. To ensure that gifts differed in wrapping quality between experimental groups, we compared gift construction behaviours between good- and poor-condition males. As indicators of wrapping investment we measured gift construction duration (time between first and last silk wrapping, including periods of gift handling without wrapping), the number and duration of silk-wrapping bouts (including only the time spent wrapping the prey), and gift colour was scored as 'black' or 'white' based on its appearance, reflecting the amount of silk. Gifts were classified as 'black' when the prey was visible through the silk and 'white' if it was not.

Mating experiments were performed in May–June after 3 weeks of the assigned feeding regime and were carried out in transparent plastic cages (22×17 cm and 6 cm high) with paper covering the bottom. A female was placed in the experimental cage at least 1 h prior to the experiment, allowing her to deposit silk threads. We then removed the female and introduced a male, thus exposing him to the female's silk, and the male was provided with a house fly for gift construction. Triggered by silk-borne female cues, males usually initiated gift construction immediately. Ten minutes after wrapping had terminated we assumed the gift construction was completed and carefully reintroduced the female into the experimental cage with the male ($t = 0$). In the gift-switched groups (GC-PW and PC-WW) we gently removed the gift from the male with forceps 10 min after the last silk-wrapping bout and offered him the replacement gift; subsequently the female was transferred to the experimental cage. All individuals used in the experiments were initially virgins and were not reused.

We registered male courtship and mating success. Courtship duration (min) was measured from when the male made contact with the female and offered the gift until the first pedipalp insertion. During mating, the male pushes up the female's abdomen and performs alternate pedipalp insertions into the female's sperm storage organs. After each insertion the male returns to a face-to-face position with the female, grabbing the gift with his chelicerae (Bristowe 1958). Mating duration was measured from the beginning of the first to the end of the last pedipalp insertion and included the time the male and female were in the face-to-face position and handled the gift. We classified individual insertions depending on their duration. 'Long insertions' lasted for at least 0.5 min while 'short insertions' were very brief, that is, less than 1 s. Expansions of the hematochoae (the structure that creates the pressure that injects the sperm into the female genitalia) were observed for both long and short insertions. Insertion duration was measured from pedipalp insertion until pedipalp disengagement, and the sum of all long insertion durations was considered the total insertion duration (probably equivalent to the time of sperm transfer). Short insertions were too brief to measure accurately and were not included in the total insertion duration; however, we counted them and compared their frequencies between groups.

Subsequent to the mating experiment, females were kept individually in the same vials and under similar condition as they were raised in, and all females were fed three house flies per week. Vials containing females that had produced an eggsac were placed under light bulbs 20 cm above the vials to increase the temperature to

26.7 ± 0.1 °C for 3 h at noon every day to enhance the hatching success of eggsacs. We measured reproductive fitness by counting the spiderlings emerging from the first eggsac produced by each female.

Statistical Analyses

Statistical analyses were performed using JMP 7.0 software (SAS Institute, Cary, NC, U.S.A.). Response variables were inspected for normal distribution of residuals and homogeneity of variance with Shapiro–Wilk and Levene tests, respectively. Dependent variables were analysed by fully factorial models including male condition, gift wrapping and their interaction. Continuous variables (courtship, mating and total insertion duration) were analysed with two-way ANOVA, number of insertions by two-way ordinal logistic fit, mating success by two-way nominal logistic fit, and number of spiderlings by a general linear model of the Poisson family (GLM-p). Since the data were collected over two seasons, all tests were initially made with year as a third factor, but it was in no case significant ($0.050 \leq P < 0.82$ for the variables shown in Table 1) and was therefore excluded in the final models.

RESULTS

Males in good condition spent longer on gift construction and silk wrapping, and they performed more silk-wrapping bouts than males in poor condition. Consequently, gifts of males in good condition appeared completely white compared with gifts of males in poor condition, which appeared black with little or no silk wrapping (Table 1). These results justify our use of the gifts from good-condition males as well wrapped and those from poor-condition males as poorly wrapped, respectively.

Male condition affected mating success significantly, as good-condition males were more successful in mating than poor-condition males ($\chi^2_1 = 14.9$, $P < 0.0001$; Fig. 1). There was no indication of an effect of gift wrapping ($\chi^2_1 = 1.8$, $P = 0.17$) or for a significant interaction between male condition and gift wrapping ($\chi^2_1 = 1.1$, $P = 0.27$). In the four treatment groups all males performed courtship; however, good-condition males courted females for a shorter duration and thus initiated mating earlier than poor-condition males (Table 2, Fig. 2a). Conversely, mating duration, total insertion duration and average insertion duration were longer for males in good condition than for males in poor condition (Table 2, Fig. 2b, c, d). Gift wrapping had no significant effect on courtship duration, mating success or insertion duration (Table 2).

We found that good-condition males performed a significantly higher number of long pedipalp insertions than poor-condition males (Table 2, Fig. 3a). Males in poor condition performed more short insertions (Table 2, Fig. 3b), and they had more difficulty

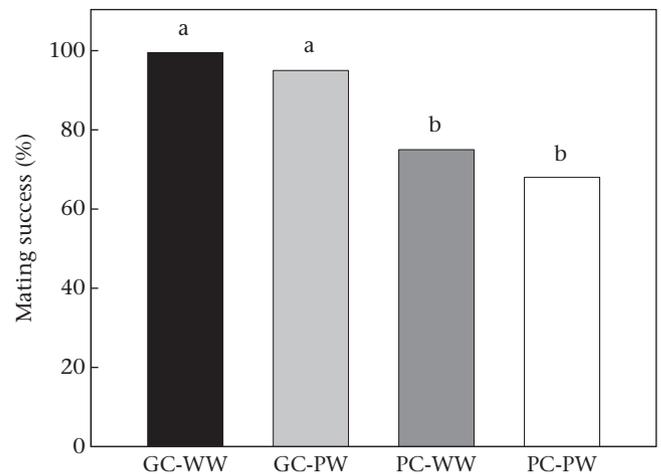


Figure 1. Male mating success in four experimental groups. GC-WW = good-condition males offering well-wrapped gifts to females, GC-PW = good-condition males offering poorly wrapped gifts, PC-PW = poor-condition males offering poorly wrapped gifts, PC-WW = poor-condition males offering well-wrapped gifts. Different letters indicate significant differences ($P < 0.05$) in pairwise chi-square tests.

maintaining the mating position and the hematodochal expansion during each pedipalp insertion than males in good condition. Gift wrapping did not affect male behaviours except for the number of short insertions (Table 2), where males offering poorly wrapped gifts performed significantly fewer short insertions independent of their condition.

Females mated with males in good condition produced on average 38.1 ± 6.3 spiderlings, whereas no female mated to a male in poor condition succeeded in producing spiderlings. There was no effect of gift wrapping on fitness (Table 2).

DISCUSSION

Our results confirmed the findings of Albo et al. (2011a) that gift-wrapping investment is an honest indicator of male condition, which reveals the actual feeding state of the male in *P. mirabilis*, as males in good condition produced well-wrapped gifts compared to males in poor condition. This may indicate that males in poor

Table 1
Nuptial gift construction by males in good and poor condition

	Gifts constructed by good-condition males (N=48)	Gifts constructed by poor-condition males (N=45)	Statistics
Gift construction duration (min)	10.7±5.5	5.5±3.8	$U=488.5$, $P<0.0001$
Silk-wrapping duration (min)	6.6±2.8	3.6±2.9	$t_{91}=5.85$, $P<0.0001$
No. of silk-wrapping bouts	3.7±1.5	2.5±1.5	$U=565.5$, $P<0.0001$
Gift colour (no. white/no. black)	45/3	1/44	$\chi^2=77.8$, $P<0.0001$

Statistical comparisons were performed using a Mann–Whitney *U* test, Student's *t* test and chi-square test.

Table 2
Effects of male condition, gift wrapping and their interaction on courtship and mating duration, total and average pedipalp insertion duration, number of long and short pedipalp insertions, and the average number of spiderlings produced in each experimental group

	N	Male condition (df=1)	Gift wrapping (df=1)	Interaction (df=1)
Courtship duration	78	$F=5.90$, $P=0.02$	$F=1.74$, $P=0.19$	$F=0.16$, $P=0.68$
Mating duration	78	$F=40.15$, $P<0.0001$	$F=0.0003$, $P=0.99$	$F=1.08$, $P=0.30$
Total insertion duration	63	$F=115.9$, $P<0.0001$	$F=0.01$, $P=0.91$	$F=1.83$, $P=0.18$
Average insertion duration	63	$F=6.58$, $P<0.0001$	$F=0.15$, $P=0.89$	$F=1.32$, $P=0.19$
No. of long insertions*	78	$\chi^2=21.96$, $P<0.0001$	$\chi^2=0.07$, $P=0.78$	$\chi^2=0.009$, $P=0.92$
No. of short insertions*	78	$\chi^2=47.78$, $P<0.0001$	$\chi^2=6.61$, $P=0.01$	$\chi^2=0.06$, $P=0.80$
No. of spiderlings*	78	$\chi^2=712.4$, $P<0.0001$	$\chi^2<0.0001$, $P=0.99$	$\chi^2<0.0001$, $P=0.99$

Statistical comparisons were performed using two-way ANOVA, ordinal logistic regression or GLM-p (*). Significant *P* values are shown in bold.

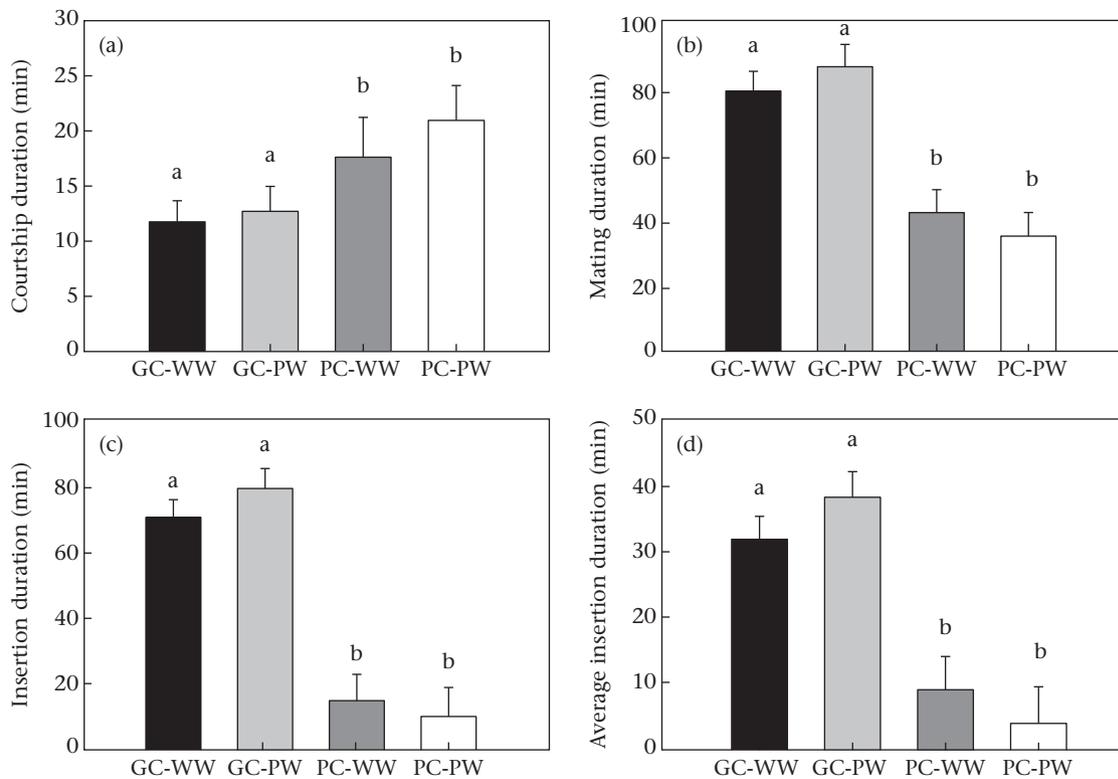


Figure 2. Male mating behaviours in four experimental groups (mean and SE). (a) Courtship duration, (b) mating duration, (c) total insertion duration and (d) average insertion duration per female in GC-WW (good-condition males offering well-wrapped gifts to females), GC-PW (good-condition males offering poorly wrapped gifts), PC-WW (poor-condition males offering well-wrapped gifts) and PC-PW (poor-condition males offering poorly wrapped gifts). Post hoc comparisons were performed using Tukey's test after one-way ANOVAs; different letters indicate significant differences ($P < 0.05$).

condition have high energetic or material costs of silk wrapping and/or are impaired in their ability to perform these behaviours; thus silk wrapping potentially can be used as an honest indicator in mate choice (Zahavi 1975; Zahavi & Zahavi 1997). However, *P. mirabilis* females did not use information revealed by the gift-wrapping trait in mating decisions. Mating success depended solely on male condition.

Previous studies have assigned several roles to the gift-wrapping trait that serve to promote male interests: gift wrapping in *P. mirabilis* may function to disguise a worthless gift (Albo et al. 2011b), facilitate male control over gift possession and thus over mating (Andersen et al. 2008), and prolong copulation duration (Lang 1996). These effects favour male interests and may lead to mating rates and durations that are suboptimal for females (Arnqvist & Rowe 2005). Females should thus evolve resistance to the gift-wrapping information (Bilde et al. 2007) and instead base their mate choice decisions on traits that directly and unequivocally benefit their own reproductive success. Our results are consistent with this argument. Evidently, females mated with good-condition males reproduced successfully, while those mated to poor-condition males did not; hence females gained direct benefits from choosing males in good condition.

Male feeding condition generally has strong effects on male courtship performance and female mate choice in many species such as crickets, scorpionflies, beetles and other spiders (Gwynne 1993; Mappes et al. 1996; Andrade & Mason 2000; Ahtainen et al. 2002; Kotiaho 2002; Engqvist & Sauer 2003; Hunt et al. 2004; Hoefler et al. 2008; Lomborg & Toft 2009). In fact, males often reveal information about their body condition by courtship intensity, for example by strong vibrations and displays (Mappes et al. 1996; Parri et al. 1997; Kotiaho et al. 1998; Schneider & Lesmono 2009; Byers et al. 2010) or by demonstrating individual

skills (Byers et al. 2010). In our study, males in good condition (whether with well- or poorly wrapped gifts) experienced shorter courtship and started mating earlier than males in poor condition, indicating that female acceptance is probably mediated by the male's active performance. A similar phenomenon was found in a wolf spider, in which female choice depended on aspects of male courtship, irrespective of male ornamentation (Shamble et al. 2009).

Male condition is also related to several advantages for males, for instance short courtships decrease the time exposed to predators and diminish the chances of attracting competitors (Kotiaho et al. 1998; Balsby & Dabelsteen 2005; Hoefler et al. 2008; Wilgers et al. 2009), whereas long matings increase sperm transferred by males and therefore the paternity in a sperm competition context (Simmons 2001). *Pisaura mirabilis* males in good condition obtained longer matings and were more successful than poor-condition males. Although we did not quantify it, we observed that males in poor condition were less able to reach female genitalia and had problems maintaining the hematodochae expanded during pedipalp insertions. Consequently, these males performed fewer and shorter insertions leading to a remarkably low fertilization success of zero. Sperm transfer in *P. mirabilis* is correlated with insertion duration (M. Albo, S. Toft & T. Bilde, unpublished data) and it is probably not accomplished during short insertions. Poor-condition males performed some long insertions although fewer than good-condition males and their average duration was shorter. Accordingly, they must be assumed to have transferred some sperm. Our results may therefore indicate that a threshold duration of long pedipalp insertions is required for enough sperm to be transferred to secure egg fertilization. Other explanations for the low success of poor-condition males are possible, for instance in poor-condition males the ability to transfer sperm may be

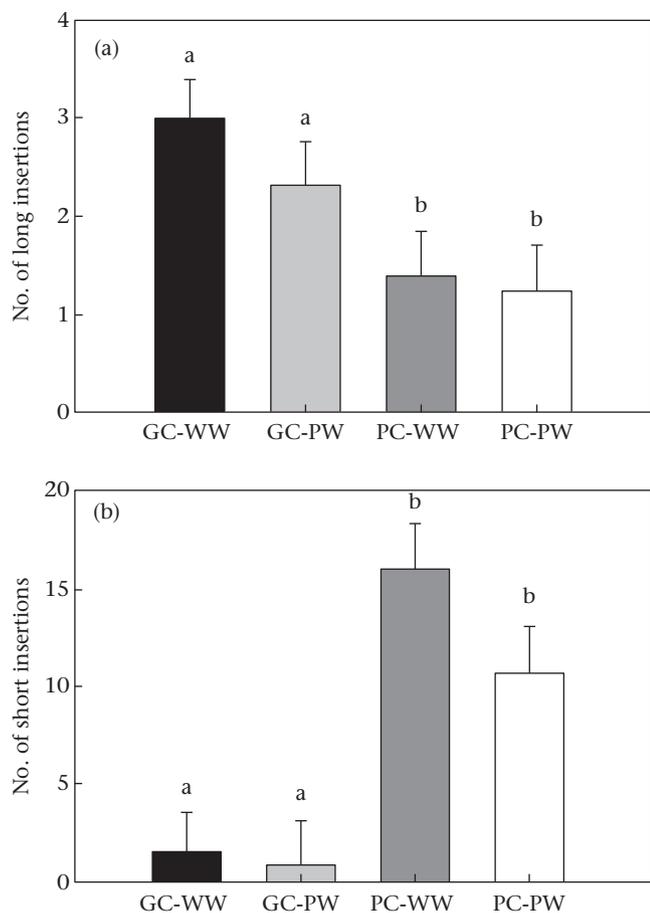


Figure 3. (a) Number of long pedipalp insertions (>0.5 min) and (b) number of short insertions (<1 s, mean + SE), in four experimental groups, GC-WW (good-condition males offering well-wrapped gifts to females), GC-PW (good-condition males offering poorly wrapped gifts), PC-WW (poor-condition males offering well-wrapped gifts) and PC-PW (poor-condition males offering poorly wrapped gifts). Post hoc comparisons were performed using Tukey's test after one-way ANOVAs; different letters indicate significant differences ($P < 0.05$).

impaired. They may also suffer from low sperm supply or other physiological deficiencies that restrict their success in sperm transfer (Proctor 1992; Andrade & Mason 2000) even if sperm is available. Alternatively, females may be capable of storing or using the sperm differentially depending on male condition. Whether male mating success was driven by female mate choice for males in good condition or lack of ability for males in poor condition to perform courtship, mating and sperm transfer, we conclude that male success depended on male condition and was independent of gift wrapping.

We note that gift wrapping affected only short insertions, and this effect was independent of male condition. Males with poorly wrapped gifts had fewer short insertion attempts. A possible explanation for this may be derived from the fact that it is more difficult for the males to control a poorly wrapped gift (Andersen et al. 2008). Short insertions indicate that the male also has difficulties with mating. With a poorly wrapped gift the male must divert more of his attention to gift control at the expense of his attention to mating (cf. Dukas 2004). If gift wrapping has any effects of prolonging mating duration or making the gift more attractive to the female (Lang 1996; Stålhandske 2002) these effects were overridden by the effects of differences in condition, which, admittedly, were here extreme. With smaller variation in male condition, as is probably the situation in nature, wrapping might possibly have an effect on male mating success.

In conclusion, offering a wrapped gift in *P. mirabilis* is not in itself sufficient to achieve a successful mating. Instead, it appears that male performance during courtship provides honest signals to the female about male quality, as is the case for many other animal species (Byers et al. 2010).

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