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ARTICLE

Male preferences for nuptial gifts and gift weight loss amongst the nursery web spider, *Pisaura mirabilis*

Pavol Prokop[1,2]

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Abstract

Sexual signals produced by males are costly. Thus, sexual selection may favour males who are able to minimise these costs, but are still reproductively successful. I investigated male preferences for large and small prey used to produce nuptial gifts, which serve as sexual signals in the nursery web spider, *Pisaura mirabilis*. Males showed strong preferences for large prey compared to small prey for gift production, which is likely to be more attractive for females and provide males with longer copulation. These preferences were strongest in the presence of female pheromonal cues. Unexpectedly, carrying nuptial gifts did not influence male mobility measured in a 5-min-long behavioural test. Both gifts carried by males and the intact gifts showed similar decreases in mass, suggesting that males did not actively suck the content of the gift. Wrapping the gift with silk did not effectively reduce the gift's dehydration, meaning that the function of the silk is not to protect the gift's contents. Males in poor body condition were more likely to feed on the prey before wrapping it. This is consistent with condition dependent signalling, as males in low condition are predicted to feed on the prey as they are not able to pay the cost of gift production. Males preferred large-sized prey for gift production and males in poor body condition reduced the cost of gift production by feeding on the prey, supporting the idea that nuptial feeding is condition dependent.

Keywords Honest signalling · Cheating · Nuptial feeding

Introduction

Zahavi (1975, 1977) proposed that ornaments are costly to produce; thus, only high-quality males can afford significant investment in them. The cost of the ornament is an honest signal of male quality, which may be used in female mate choice (Kotiaho 2001). There is definite evidence that ornaments are costly to produce (e.g., Verhulst et al. 1999; Mobley et al. 2018), that ornaments correlate with the individual's quality (e.g., Møller 1990; Emlen et al. 2012) and that females prefer males with larger ornaments (e.g., Andersson 1982; West 2002).

Nuptial feeding is the transfer of nutrients between a male and female during courtship or copulation (Thornhill and Alcock 1983; Simmons and Parker 1989). This phenomenon is widespread in animals (Vahed 1998, Tryjanowski and Hromada 2005), and research suggests that resource limitations play a major role in the production of nuptial gifts (Engels and Sauer 2006; Engqvist 2007; Immonen et al. 2009; Albo et al. 2011a; Macedo-Rego et al. 2016; Ghislandi et al. 2018). Gift-giving species are therefore excellent candidates for investigating condition dependent signalling, because a handicap could be the result of specific biological constraints that may result from resource-based trade-offs between self-maintenance and male mating effort (Számadó 2011; Macedo-Rego et al. 2016).

Male nursery web spiders, *Pisaura mirabilis*, carry gift items as they search for or court females (Van Hasselt 1884; Bristowe and Locket 1926; Austad and Thornhill 1986). Prey wrapping is elicited even in the absence of a female by female draglines which contain sexually attractive pheromones (Nitzsche 1988). The gift consists of an insect prey wrapped in white silk (e.g., Nitzsche 1988; Lang 1996; Stålhandske 2001; Prokop and Maxwell 2012; Ghislandi et al. 2017). Production of the gift increases male mating success by increasing probability of mating (Stålhandske

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✉ Pavol Prokop
pavol.prokop@savba.sk

[1] Department of Environmental Ecology, Faculty of Natural Sciences, Comenius University, Ilkovičova 6, 842 15 Bratislava, Slovakia

[2] Institute of Zoology, Slovak Academy of Sciences, Dúbravská cesta 9, 845 06 Bratislava, Slovakia

2001; Prokop 2006; Prokop and Maxwell 2009; Maxwell and Prokop 2018), prolonging copulation duration (Stålhandske 2001; Maxwell and Prokop, 2018) and increasing the amount of sperm transferred when males carry gifts (Albo et al. 2013). Wrapping a gift with silk extends female feeding duration and hence sperm transfer (Lang 1996), it disguises the gift's contents (Ghislandi et al. 2017; Prokop and Maxwell 2012) and may also facilitate handling and control over the gift by the male (Andersen et al. 2008; Hromada et al. 2015).

The exogenous (silk) and endogenous (dead prey) components of nuptial gifts enhance male mating success in *P. mirabilis*, but both seem to be costly to produce. Carrying nuptial prey reduces, for example, male running speed (Prokop and Maxwell 2012) and larger males in particular are able to produce larger gifts (Prokop and Semelbauer 2017). With respect to spider silk, poorly fed males constructed gifts less frequently, spent less time and used less silk than well-fed males (Albo et al. 2011a). Females seem to be unable to assess the value of the gift content, although they can shorten copulation duration when presented with a small or low quality gift (Albo et al. 2011b). Nuptial gifts of *P. mirabilis* males vary greatly in mass: large gifts can be 90 times heavier than small gifts (Prokop and Maxwell 2012; Prokop and Semelbauer 2017). This suggests that the degree to which males can minimise costs associated with creating, carrying or displaying nuptial gifts may vary greatly (Vahed 2007).

The use of variable nuptial gifts by *P. mirabilis* males opens the question as to whether nuptial gifts should be considered honest signals, because handicaps should be too costly to fake (Zahavi 1975, 1977; Johnstone and Grafen 1993; Kotiaho 2001) and the display of an ornament should be condition dependent (Kotiaho 2001; Roulin 2016). Furthermore, nuptial feeding can positively influence female fitness (reviewed by Maxwell and Prokop, 2018), suggesting that females prefer males with large gifts, but males can minimise costs of nuptial feeding by creating smaller gifts. Here, I am testing different predictions that relate to condition dependence and gift quality in *P. mirabilis*. Males in good condition are more likely to produce a nuptial gift than males in poor condition, because it is costly and therefore condition dependent to produce a gift (Prediction 1). Indeed, field research showed that larger males carried heavier nuptial prey than smaller males (Prokop and Semelbauer 2017) and carrying nuptial prey reduces male running speed (Prokop and Maxwell, 2012). In contrast, Ghislandi et al. (2018) did not find a positive association between production of nuptial gifts and male condition in the field. Males should show preference for large over small prey and, because large prey convey benefits in terms of longer copulations, preference is condition dependent and/or depends on presence of a female cue (Prediction 2). Males should wrap large prey in relatively more silk compared with small prey, and if wrapping is condition dependent, males in better condition should be able to apply more silk (Prediction 3). Males are more likely to hold a large prey as a nuptial gift after a period of 24 h than a small prey, because larger prey is reproductively more advantageous than small prey (Prediction 4). Carrying nuptial prey would impair male mobility. Therefore, males in good condition should be better able to maintain mobility when carrying prey (Prediction 5). The function of silk wrapping could be to reduce dehydration from the prey; I examined whether wrapping a gift with silk would prevent the gift from dehydrating over a period of 24 h.

Materials and methods

Study organism

The nursery web spider, *Pisaura mirabilis* (Pisauridae), is a common spider living in deciduous woods, meadows and abandoned grasslands. In Central Europe, spiderlings hatch in the summer and reach maturity in the spring of the following year (Buchar et al. 1989). Mating takes place roughly from mid April until the end of May, depending on climatic conditions (P. Prokop, personal observations). Males die soon after the mating season ends, while females continue with maternal care for the eggs and spiderlings (Austad & Thornhill, 1986). Sexually receptive females spread draglines with sexually attractive pheromones. After the male detects the draglines, he becomes sexually excited, catches a prey item and wraps it in silk (e.g. Nitzche 1988; Lang 1996; Andersen et al. 2008; Albo et al. 2011a; Tuni et al. 2013). The male then approaches the female and the female takes hold of the gift in her chelicerae. The male then inserts his right or left pedipalp into the female's epigyne and transfers sperm while the female feeds on the gift (Bristowe 1958).

Collection and male treatments

Subadult spiders ($N = 87$) were collected in April–May 2017 from various grasslands and small woods near Trnava, Slovakia (N 48°37, E 17°58). Each spider was individually kept in a ventilated 0.3-l glass jar with wet cotton to maintain humidity. Jars were placed outdoors on private property in Trnava, Slovakia (48°23′N, 17°35′E), protected from direct sunlight under a natural photoperiod and temperature. The individuals were sprayed with water daily and fed ad libitum 3 times per week with dead house crickets, *Gryllus assimilis* (ca. one adult cricket per feeding). In total, 80 males (an additional three males died) and four females moult ed into adulthood during May 2017. After the experiments finished, all the spiders were released near their sites of capture by early June 2017.

Female phermonones/gift size experiment

About 10–15 days post-moult, each male was randomly assigned four treatments: Large Prey × Presence of Female Pheromones (LP × PFP, *N* = 19), Large Prey × No Female Pheromones (LP × NFP, *N* = 22), Small Prey × Presence of Female Pheromones (SP × PFP, *N* = 20) and Small Prey × No Female Pheromones (SP × NFP, *N* = 19). "Large Prey" and "Small Prey" treatments refer to whether each male was offered a large [mean (g) ± SE = 0.02 ± 0.005, range 0.011–0.03, *N* = 41] or small [mean (g) ± SE = 0.006 ± 0.002, range = 0.002–0.009, *N* = 38, data for one male are missing] dead cricket nymph (*G. assimilis*) in treatment with presence (PFP) or absence (NFP) of female pheromones. Prey masses correspond with those found with males collected in the field (range 0.0005–0.045 g, Prokop and Maxwell 2012; Prokop and Semelbauer, 2017). Dead prey was used instead of live prey in order to standardise distance between the prey and the spider male. The presence of female pheromones was manipulated by random placing of one of two virgin females for 10 min in a glass terrarium (30 × 20 × 20 cm) that was lined with clean white paper. No female was placed in a terrarium in NFP treatment. The male was placed in the terrarium after the female was removed and allowed to habituate for 2 min. A large or small dead cricket nymph was then placed ~ 1 cm in front of the male's chelicerae. I observed male behaviour toward a dead cricket nymph; prey carrying or ignorance, prey wrapping or not wrapping, and male mobility. Although carrying dead prey is not a direct measure of the production of a nuptial gift, because the dead prey is not yet wrapped with silk, this behaviour was included in analyses because it is a prerequisite for production of a nuptial gift. Moreover, males do not always wrap dead prey with silk (e.g. Maxwell and Prokop 2012), so it is sometimes hard to recognise whether dead prey will be considered to be a nuptial gift by a male without additional wrapping with silk or not. Mobility was examined following Kotiaho et al. (1999) and Prokop and Semelbauer (2017); the terrarium was divided into quarters and how many times a male entered a new section of the arena was counted. This number was used as the mobility index. Since *P. mirabilis* males are known to exhibit moderate repeatability in their mobility across three trials (*R* = 0.30, Prokop and Semelbauer 2017), mobility was measured only once. Higher values indicated higher mobility. To visually isolate experimental males, I attached white paper to the external sides of each terrarium. Clean paper was replaced after each trial and the terrarium was cleaned with 92% alcohol to remove traces of conspecific cues.

After each trial, each male was returned to its housing jar. Each trial lasted 5 min and was conducted between 10:00 and 13:00. All these experiments refer to day 1. On the subsequent day (day 2), I inspected whether the male carried the gift and whether the gift was wrapped with silk. Intensity of silk wrapping was subjectively established on a three-point scale: unwrapped, partly wrapped with silk and densely wrapped with silk. Before the experiments, males were anaesthetised with CO_2. Prosoma width (to 0.01 mm) and body mass (to 0.0001 g) were measured with a digital calliper and an analytical balance (METTLER TOLEDO B-S type), respectively. Cricket nymphs used as nuptial prey were killed by freezing and weighed before and after the experiment. Experiments took place between 11 and 28 May 2017.

Experimentally manipulated weight losses in the nuptial gifts

Since males can feed on nuptial gifts before they are offered to the female (Ghislandi et al. 2017), it is impossible to separate the effects of male feeding and natural dehydration on the gift's weight. To address this issue, I also investigated weight losses in nuptial gifts in the absence of males. For the purposes of this study, unmanipulated gifts are defined as gifts produced and carried by males. Dead prey items, which were wrapped with silk by males (as well as unwrapped controls), removed from males' chelicerae and examined out of males, were defined as manipulated nuptial gifts. Cricket nymphs were assigned as large gifts [LG, mean (g) ± SE = 0.02 ± 0.001, range 0.011–0.029, *N* = 20] and small gifts [SG, mean (g) ± SE = 0.007 ± 0.0004, range 0.004–0.009, *N* = 20] in treatments. Half of the LGs and SGs were wrapped, and half were unwrapped. Wrapped gifts were obtained by giving dead cricket nymphs to males who were placed in a glass terrarium (30 × 20 × 20 cm) with one virgin female. After the male caught the prey item and wrapped it with silk, the gift was gently removed from his chelicerae with soft tweezers. Each gift was individually placed into a small plastic cup and placed in a refrigerator (+4 °C). Gifts belonging to the unwrapped treatment were not offered to the males. On the subsequent day at 10:00, all the gifts were placed on the bottom of a glass terrarium and remained intact at room temperature (~ 23 °C) for 24 h and weighed on an electronic scale again. Each male was used for wrapping a gift only once. All the males used in this experiment were those previously used in the female phermonones/gift size experiment and two virgin females which were not involved in any other experiment.

Statistical analyses

Gift acceptance (binomial dependent variable) was examined with logistic regression. Male mobility (continuous dependent variable) was examined with analysis of covariance (ANCOVA) where the male body condition was defined as the covariate. Male prosoma width and body mass were significantly correlated (Pearson correlation: $r = 0.90$, $P < 0.001$, $N = 80$). I quantified the male body condition as the residual of regression of body mass on prosoma width (Jakob et al. 1996). The subjectively rated intensity of gift wrapping (ordinal dependent variable) was examined with a generalised linear model (GLM) with ordinal probit distribution. Factors influencing weight loss (male condition, prey size, presence of female pheromones, gift acceptance within 5 min and ranked gift wrapping on day 2) of unmanipulated nuptial gifts (continuous dependent variable) were investigated with multiple linear regression. Experimentally manipulated weight loss in nuptial gifts was investigated with repeated-measures ANOVA where initial and final gift weights were defined as dependent variables. Mean ± standard error (SE) is reported for descriptive statistics. Normality of data was assessed via the Shapiro–Wilks test. Male mobility (how many times a male entered each of the four quarters) was Box-Cox $(x + 0.1)$ transformed and normality was achieved. Statistical tests were performed with the software Statistica (version 8, StatSoft 2007, Tulsa, OK, USA, http://www.statsoft.com). All tests were two-tailed.

Results

Is the production of a nuptial gift condition dependent?

Males which grasped the dead prey within 5 min were in better body condition (mean body condition ± SE = 0.0009 ± 0.002, $N = 30$ males) than males which did not grasp the dead prey (mean body condition ± SE = −0.0005 ± 0.001, $N = 50$ males). This partly supports the prediction that males in good condition are more likely to produce a nuptial gift than males in poor condition, because grasping dead prey is a prerequisite for gift production. The interaction term between male body condition and the presence of female pheromonal cues was significant (Table 1). This suggests that males in better body condition accepted gifts in the presence of female pheromonal cues more frequently than in the absence of female cues. In contrast, males in poor body condition showed no preferences for gifts with respect to presence/absence of female cues. The interaction term between gift size and male body condition was not significant.

Do males show preference for large over small prey?

A higher proportion of large prey (23/41) was accepted by males within 5 min than small prey (7/39). This supports the prediction that males should show preference for large over small prey. A higher proportion of dead prey was accepted within 5 min when female pheromonal cues were present (19/39) than when female pheromonal cues were absent (11/41) (Table 1). The interaction term between the presence of female pheromonal cues and gift size was not significant (Table 1).

Is large prey wrapped with more silk than small prey?

I continued with analyses of gift wrapping on a subsequent day (day 2, $N = 75$ gifts, an additional five gifts were completely consumed and not included in the analyses, see below). A total of 42 gifts were unwrapped, eight were partly wrapped and 25 gifts were densely wrapped with silk. Large gifts were wrapped with silk significantly more frequently than small gifts, but neither the presence of female pheromonal cues, nor male body condition was associated with wrapping gifts (Table 2). This supports the prediction that males should wrap large prey in relatively more silk compared with small prey. On the other hand, this prediction also suggests that prey wrapping is condition dependent and males in better condition should be able to apply more silk. No support for condition dependence was found. A higher proportion of large prey were wrapped when female pheromonal cues were present (15/19) than when female pheromonal cues were absent (11/21). No similar trends, however, were observed for small gifts. Only 3/18 small prey items were wrapped when female pheromonal

Table 1 Results of logistic regression (df = 1) on prey acceptance within 5 min by males

	Wald's χ^2	P
Intercept	3.23	0.07
Prey size	10.04	0.001
Male condition	5.60	0.02
Presence of female pheromones (PFP)	6.57	< 0.01
Prey size × male condition	1.72	0.19
PFP × male condition	4.69	0.03
Prey size × PFP	0.59	0.44

Table 2 Results of GLM with ordinal probit distribution on the intensity of prey wrapping

	df	Wald's χ^2	P
Intercept	2	11.46	0.003
Prey size	1	15.73	<0.001
Presence of female pheromones (PFP)	1	1.58	0.20
Male condition	1	0.53	0.47
Prey size × PFP	1	5.59	0.02
Prey size × male condition	1	3.18	0.07
PFP × male condition	1	5.64	0.02

cues were present and 4/17 when female pheromonal cues were absent. Males in better body condition wrapped large gifts with silk more when female pheromonal cues were present (mean body condition ± SE = −0.0003 ± 0.002, $N = 15$ males) than when cues were absent (mean body condition ± SE = −0.008 ± 0.004, $N = 4$ males). No similar trends were observed for males for small gift treatment in the presence of female cues (wrapped vs unwrapped gifts; mean body condition ± SE = −0.003 ± 0.005, $N = 3$ males and −0.004 ± 0.002, $N = 15$ males). In the absence of female cues, however, males which wrapped small gifts with silk were in poorer body condition (mean body condition ± SE = −0.005 ± 0.004, $N = 4$ males) than males which did not wrap gifts with silk (mean body condition ± SE = 0.007 ± 0.002, $N = 13$ males). The interaction term between gift size and male body condition was not significant (Table 2).

Is large prey carried by males more than small prey?

Five males (four from SG and one from LG treatment) consumed their gifts within 24 h and were removed from analyses. A higher proportion of large prey (21/40) were carried by males on a subsequent day (day 2) than of small prey (7/35) (Wald's $\chi^2 = 7.62$, df = 1, $P = 0.006$). Prediction 4 was supported. The marginally significant interaction term between the presence of female pheromonal cues and male condition (Wald's $\chi^2 = 3.68$, df = 1, $P = 0.055$) suggests that when female cues were present, a higher proportion of males (7/11) in better body condition (mean ± SE = 0.007 ± 0.002, $N = 11$) than males in poorer body condition (mean ± SE = −0.007 ± 0.001, $N = 26$, 9/26 males) carried gifts. When female cues were absent, however, males in poor condition (mean ± SE = −0.007, SE = 0.002, $N = 16$) tended to carry gifts more (7/16 males) than males in good body condition (mean ± SE = 0.01 ± 0.002, $N = 22$, 5/22 males). Influences of other variables, including interaction terms, were not statistically significant (all Wald's $\chi^2 > 0.025$, df = 1, all $P > 0.08$).

Does prey carrying impair male mobility?

Mean male mobility ± SE (how many times a male entered each of the four quarters) was 7.9 ± 0.61 (range = 1–23, $N = 80$). Male mobility was not influenced by prey acceptance, the presence of female pheromonal cues, gift size or male condition (covariate) (all $F_{1,69} > 0.049$, all $P > 0.54$). The interaction terms were also non-significant (all $F_{1,69} > 0.04$, all $P > 0.15$). This provides no support for the prediction that carrying nuptial prey would impair male mobility.

Does silk wrapping reduce dehydration from the unmanipulated gifts?

I hypothesised that the function of silk wrapping could be to reduce prey dehydration. Statistical analyses failed to support this hypothesis. Data on gift weight were missing for one spider, thus the following analyses are based on $N = 74$. Multiple regression with differences in nuptial gift weight loss (day 1 minus day 2) and independent variables listed in Table 3 resulted in a significant model [$R^2 = 0.73$, $F(5,68) = 37.64$, $P < 0.001$]. Gifts in LP treatment lost more weight than gifts in SP treatment (Fig. 1). However, relative weight losses (65% and 67%, respectively) were very similar between treatments. Gifts that were accepted by males within 5 min from the start of the experiment revealed a

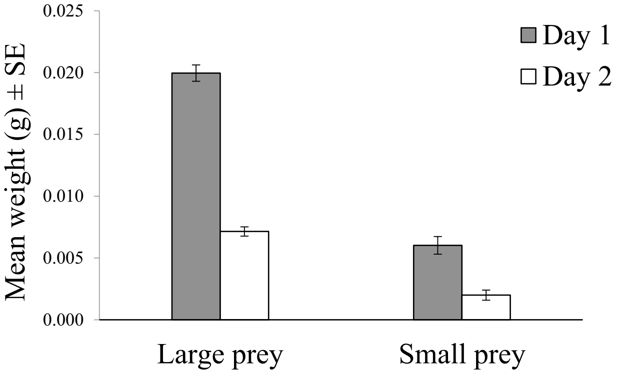

Fig. 1 Differences in the decrease in prey weight in unmanipulated gifts with respect to prey size

Table 3 Multiple regression on differences between unmanipulated nuptial gift weight between day 1 and day 2

	β	SE of β	B	SE of B	$t(68)$	P
Intercept			22.92	2.70	8.50	<0.001
Male condition	−0.04	0.07	−0.45	0.81	−0.55	0.58
Prey size	−0.78	0.08	−0.20	0.02	−10.16	<0.001
Presence of female pheromones	−0.02	0.07	−0.01	0.02	−0.33	0.75
Prey acceptance within 5 min	−0.18	0.07	−0.05	0.02	−2.41	0.02
Ranked prey wrapping on day 2	−0.04	0.07	−0.005	0.01	−0.51	0.61

slower weight drop than gifts which were ignored by males (Table 3). Other variables showed no significant influence on the gift's weight drop. Since wrapping the gift with silk did not influence weight loss, the dehydration hypothesis was not supported.

Does silk wrapping reduce dehydration from the experimentally manipulated gifts?

Repeated measures ANOVA revealed that LG were heavier than SG ($F_{1,36} = 169.7$, $P < 0.001$) and wrapped gifts were of similar weight to non-wrapped gifts ($F_{1,36} = 0.36$, $P = 0.55$). The interaction term was non-significant ($F_{1,36} = 0.03$, $P = 0.86$). This suggests that wrapping a gift with silk did not influence weight loss, thus the dehydration hypothesis was not supported.

Within-subject analyses showed that the gift's weight dropped significantly after 24 h ($F_{1,36} = 473.55$, $P < 0.001$). Relative weight losses of wrapped and unwrapped LG and wrapped and unwrapped SG were 60%, 64%, 68% and 51%, respectively. The interaction terms with gift size were significant ($F_{1,36} = 132.94$, $P < 0.001$), suggesting that weight drop was stronger for LG compared with SG (Fig. 2). The remaining interactions were not significant ($F_{1,36} > 0.02$, P's > 0.08).

Discussion

This study investigated some predictions derived from the hypothesis that honest signalling implies a cost to creating, carrying or displaying the trait. It was found that male preference for large dead prey is condition dependent. Female pheromonal cues stimulated gift production by males, but carrying nuptial prey did not impair male mobility. Contrary to expectations, gifts wrapped with silk did not show reduced dehydration compared with unwrapped gifts.

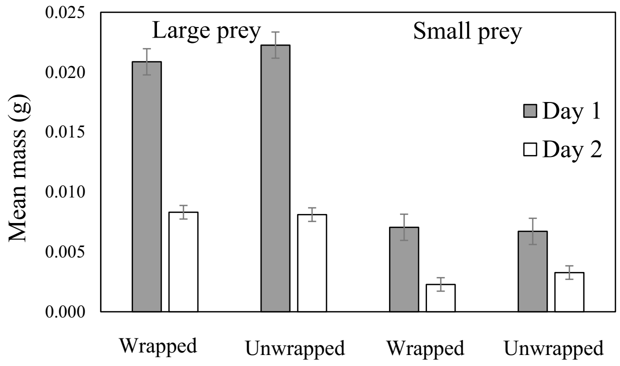

Fig. 2 Differences in experimentally manipulated nuptial prey weight losses with respect to prey size and wrapping

Male physical condition and carrying nuptial gifts

Carrying dead arthropods, which could be subsequently used as nuptial prey, was positively influenced by male physical condition. This finding is in agreement with honest signalling which predicts that only individuals in good physical condition can produce high-quality ornaments (Zahavi 1975; Kodric-Brown and Brown 1984; Kotiaho 2001; Weaver et al. 2017). Experimentally starved *Pisaura* males, for example, produce less silk for wrapping nuptial prey than well-fed males (Albo et al. 2011a; Ghislandi et al. 2017), supporting the condition dependence of nuptial feeding. If nuptial feeding is not costly to sustain, it would instead predict the carrying of dead arthropods irrespective of male physical condition because, for example, males in good condition carrying prey would be more successful mates (e.g., Stålhandske 2001; Albo et al. 2013) and males in poor body condition would gain body mass by feeding on prey (Albo et al. 2011a). In contrast to honest signalling, I found that males in poor body condition carried nuptial prey in the absence of female pheromones on day 2. This may suggest that males initially feed on prey and afterward wrap it with silk, which may partly support an opportunistic feeding strategy (Ghislandi et al. 2017).

Male preferences for gift size

Large gifts were immediately accepted by males and wrapped with silk more than small gifts. The strong preference for large gifts was also supported by observations on day 2, when males carried large gifts more frequently than small gifts. Production, maintenance and carrying large gifts are reproductively advantageous, but also more costly than production of small gifts, supporting the honest signalling hypothesis. On the other hand, even small gifts could be reproductively more advantageous than no gifts (e.g., Stålhandske 2001; Albo et al. 2011b; Maxwell and Prokop 2018). Notably, Bruun et al. (2004) did not find strong preferences for large nuptial prey in *P. mirabilis*, possibly because pheromonal cues which elicit male sexual behaviour (e.g., Nitzsche 1988; Albo et al. 2011b) were absent in their experiment. On the other hand, the present study did not investigate male preference in the classical sense, as males were not presented with a choice in each trial (see Bruun et al. 2004). Further research may benefit from simultaneous involvement of more and less beneficial prey to males.

More frequent wrapping of gifts with silk in the presence of female pheromones could be motivated by better control over nuptial prey (Andersen et al. 2008) and/or by expected prolonged female feeding duration and hence sperm transfer (Lang 1996). Gift carrying could be costly in terms of reduced running speed (Prokop and Maxwell 2012). Thus, strong preferences for large gifts, which provide the greatest mating effort for males (Stålhandske 2001; Bruun et al. 2004; Maxwell and Prokop 2018), is likely to be an honest signal rather than opportunism. On the other hand, research failed to show any differences in body condition between males who carried genuine, worthless gifts, or those who did not carry gifts at all (Prokop and Maxwell 2012; Ghislandi et al. 2017, Prokop and Semelbauer 2017). This argument casts doubt on the role of honest signalling in gift-giving species.

Male mobility and carrying nuptial prey

Male spider mobility is ultimately associated with male mating success (Kotiaho et al. 1998). Previous research showed that carrying a nuptial gift reduces male running speed (Prokop and Maxwell 2012), but also that males with and without gifts found in the field showed no differences in mobility measured under laboratory conditions (Prokop and Semelbauer 2017). This study revealed no negative impact of gift presence/size on male mobility, as could be expected according to the honest signalling hypothesis. Since any associations between male mobility and physical condition was not found, it is possible that longer experimental testing, ideally combined with field observations, would be necessary for more sensitive measurements of energetic costs from male mobility.

Gift construction in *P. mirabilis* is associated with a loss of the gift's weight (Ghislandi et al. 2017). I speculated that worthless gifts densely wrapped with silk could be a result of male motivation to prevent the remaining nuptial prey from dehydration. This hypothesis was not supported because both unmanipulated and experimentally manipulated gifts lost weight at similar rates irrespective of the presence of spider silk. Ghislandi et al. (2017) showed that heavier prey lost more weight and the same was true in the present experiment. This finding is extended to natural dehydration causing significant gift weight loss comparable with weight losses which occur after carrying a gift by the spider male. These findings imply that males conserve gift content for mating at least from a short-term perspective, which contributes to honest signalling.

Conclusions

Nuptial feeding in *P. mirabilis* is condition dependent and it is strongly stimulated by the presence of female pheromones. Male preference for large prey over small prey was documented by it being carried more frequently and the large prey being wrapped with silk. Males in poor physical condition could gain nutrition through prey ingestion, rather than producing a nuptial gift, hence they do not carry it around. The benefits of production of nuptial gifts together with female preferences for large nuptial prey maintain the occurrence of genuine nuptial gifts.

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Compliance with ethical standards Conflict of interest. The author has no conflict of interest to declare.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not refer to any studies with human participants performed by the author.

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