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Biometrical and behavioural associations with offering nuptial gifts by males in the spider *Pisaura mirabilis*

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Nuptial gifts are under strong selection in terms of female choice. It is hypothesized that nuptial gifts represent an honest signal resulting from the trade-off between self-maintenance and mating effort. Furthermore, nuptial gift size may correlate with certain personality traits, such as male fighting or hunting abilities. We investigated the nuptial gifts of a gift-giving spider, *Pisaura mirabilis*, consisting of both exogenous (prey) and endogenous (silk) components and their relationships to male biometry (the honest signalling hypothesis) and personality traits (the personality traits hypothesis). The gift's weight in the field was positively correlated with male size providing support for the honest signalling hypothesis. No differences in body condition and fluctuating asymmetry between males carrying and not carrying gifts in the field were found which does not support the honest signalling hypothesis. A substantial proportion of males offered worthless gifts that were smaller and lighter than genuine gifts. Reliable personality traits of males were not identified and no behavioural or survival differences between males carrying nuptial gifts, unwrapped prey and not carrying gifts in the field were observed. These results suggest that male size serves as an honest indicator of the exogenous component of the gift (i.e. the nuptial prey).

Nuptial feeding, the male's provision of nourishment to his mate before, during or after mating, occurs in many arthropods (Simmons & Parker, 1989; Thornhill & Alcock, 1983; Vahed, 1998, 2007), including certain spiders (reviewed by Albo, Toft, & Bilde, 2014). The nuptial gifts are variable including food items captured by the male, male glandular secretions, edible spermatophores and even the male's body parts (reviewed in Gwynne, 1997; Vahed, 1998, 2007). These donations can be endogenous resources produced by the males themselves, exogenous resources such as seeds or prey that males gather from the environment (Lewis & South, 2012) or a combination of both. The origin and maintenance of nuptial feeding may be explained by three hypotheses. The mating effort hypothesis suggests that the nuptial gift ensures a higher probability of mating and more successful sperm transfer. The paternal investment hypothesis suggests that the gift can increase the number and/or quality of the male's own offspring (Simmons & Parker, 1989; Vahed, 1998). These two hypotheses are not mutually exclusive, because successful sperm transfer is expected to precede the production of the male's offspring (Lewis & South, 2012). The third hypothesis suggests that nuptial gifts protect males against sexual cannibalism (Bristowe & Locket, 1926; Vahed, 1998), although experimental data have failed to find strong support for this hypothesis (Stålhandske, 2001; Prokop, 2006; Prokop & Maxwell, 2009; but see Toft & Albo, 2016).

Like many other sexual traits, nuptial gifts can act as reliable indicators of overall genetic quality, if (1) their production or maintenance is costly to the bearer in terms of reduced naturally selected fitness, (2) they depend on the phenotypic and genotypic condition of the male and (3) the cost of sexual traits is lower for males in good than poor condition (Bradbury & Vehrencamp, 2011; Grafen, 1990a, 1990b; Kotiaho, 2001). Indeed, nuptial gifts seem to be excellent examples for testing honesty, because most of them are easily observable which allows researchers to test for correlations with nonobservable male quality (Számadó, 2011). Empirical evidence, however, is scarce (Vahed, 2007). The number of salivary masses (i.e. endogenous nuptial gifts), for example, that male scorpionflies can produce during their lifetime correlates with their body condition, which, in turn, correlates with personality traits, such as fighting and foraging ability (Engels & Sauer, 2006; Sauer et al., 1998). The size of the nuptial gift also correlates with male

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immunocompetence (Fedorka, Zuk, & Mousseau, 2005; Kurtz & Sauer, 1999; Luong & Kaya, 2005). There is, however, a trade-off between immunity and reproductive effort in gift-giving species, as immune-challenged decorated cricket, *Gryllodes sigillatus*, males produced significantly smaller endogenous gifts than control males and males that synthesized more gifts had lower immunity (Kerr, Gershman, & Sakaluk, 2010). This suggests that at least endogenous nuptial gifts may serve as Zahavian handicaps (Kerr et al., 2010). If male immunocompetence, a cue of genetic quality, correlates with the size of the nuptial gift, it is also possible that gift-bearing males have low fluctuating asymmetry (FA) as the bilateral symmetry of physical traits reflects the individual's ability to resist pathogens (Møller, 2006; van Valen, 1962).

The degree to which a male can minimize costs associated with producing a nuptial gift may, however, vary greatly (Vahed, 2007). Exogenous token gifts of empid flies are, for example, probably less costly to males than endogenous large spermatophylaces produced by male bushcrickets, *Steropleurus stali*, which need about 3 days to produce a new spermatophylax after mating (Vahed, 1997). This suggests that exogenous and endogenous nuptial gifts may represent different physiological costs to males and their possible role as honest signals and/or in genetic superiority in mate choice needs to be investigated with respect to the type of gift.

Males of the nursery web spider, *Pisaura mirabilis*, often capture prey (various arthropods, i.e. the exogenous component), wrap them in silk (i.e. the endogenous component) and offer these gifts to females. Upon female acceptance, copulation occurs while the female consumes the gift (Austad & Thornhill, 1986; Bristowe & Locket, 1926). Nuptial feeding is under sexual selection as females manifest strong preferences for males offering gifts (Albo, Bilde, & Uhl, 2013; Prokop, 2006; Prokop & Maxwell, 2009; Stålhandske, 2001), particularly gifts of high quality (Albo, Winther, Tuni, Toft, & Bilde, 2011). The size and content of the gift may increase male fertilization success by extending female feeding and prolonging copulation duration (Albo et al., 2013; Albo, Winther et al., 2011; Andersen, Bollerup, Toft, & Bilde, 2008; Stålhandske, 2001). Furthermore, by consuming nuptial gifts, the female can obtain direct benefits in terms of acceleration of oviposition (Tuni, Albo, & Bilde, 2013), increased fecundity and increased egg hatching success (Drengsgaard & Toft, 1999; Toft & Albo, 2015).

It has been shown that *P. mirabilis* males in poor condition construct gifts less frequently, use less silk (Albo, Toft, & Bilde, 2011) and have lower reproductive success (Albo, Toft, & Bilde, 2012). We hypothesized that if the nuptial gift indeed represents an honest signal, the trade-off between self-maintenance (i.e. eating the prey) and mating effort is conditional and depends on the nutritional state of the male (honest signalling hypothesis, Zahavi, 1975). Data on possible honest signalling of nuptial gifts, however, primarily come from laboratory conditions (Albo, Toft et al., 2011, 2012; Macedo-Rego, Costa-Schmidt, Santos, & Machado, 2016) while data from the field are scarce (Albo et al., 2014; Prokop & Maxwell, 2012). We therefore focused our research on natural populations of *P. mirabilis*. First, we predicted that males offering gifts in the field have better body condition than males without gifts (Prediction 1). Second, we predicted that the size/weight of the gift correlates positively with the male's size (prosoma width), because body size has been suggested to be an uncheatable signal in sexual selection (Kokko, 1998; Prediction 2). Third, if males with gifts are of superior genetic quality (i.e. larger, heavier and in good body condition), then we predicted that they should be more symmetrical than males that do not carry gifts (Prediction 3), because only males that did not face developmental instability during development can afford nuptial gifts. Thus, male symmetry, a cue of genetic quality, is expected to be associated with carrying nuptial gifts. These predictions collectively suggest that low-quality males are not able to pay the costs associated with high signal quality (Zahavi, 1975). These predictions would be confounded, however, by the different ages of males with and without gifts in the field. To exclude the possibility that males without a gift found in the field were the youngest and not sexually active, we compared the life spans of males that were originally captured in the field both with and without gifts.

Given the expected correlations between the presence of a gift and male quality (e.g. Albo & Peretti, 2015; Engels & Sauer, 2006; Sauer et al., 1998; Vahed, 2007), it is possible that specific personality traits, for instance male aggression or mobility (Schuett, Tregenza, & Dall, 2010, personality traits hypothesis), are correlated with the presence of the nuptial gift. Personality is defined as behavioural differences between individuals that are consistent across time and context (Réale, Reader, Sol, McDougall, & Dingemanse, 2007) and has been documented in a number of vertebrates and invertebrates (Bell, Hankison, & Laskowski, 2009). The repeatability of certain behaviour is viewed as the first step towards investigating the genetic basis of behaviour (Dohm, 2002; van Oers, Drent, de Goede, & van Noordwijk, 2004). This suggests that low within-individual repeatability of behaviour may be caused by various nongenetic factors. Second, the personality traits should correlate with one other, within a single context (van Oers et al., 2004). A spider male, for example, can be repeatedly more mobile, aggressive or have a superior foraging strategy as these traits can be beneficial for obtaining nuptial gifts and finding potential mates. We predicted that the nuptial gift may be a cue of certain beneficial personality traits associated with offering nuptial gifts (Prediction 4). Mobility and prey-capturing abilities, in particular, may allow the male to quickly find and immobilize the prey. Aggression may allow the male to distract competitors and/or defend the nuptial gift against conspecifics and/or predators.

We tested two nonmutually exclusive hypotheses regarding the evolution of nuptial feeding. If the nuptial gift serves as an honest signal of male quality (the honest signalling hypothesis), males with large gifts are expected to have superior physical quality (i.e. be larger, more symmetrical) to males with small or no gifts. Furthermore, males that can obtain (large) nuptial gifts are expected to have superior personalities (the personality traits hypothesis) that allow them to find and secure gifts that enhance their reproductive success.

METHODS

Study Organism

Pisaura mirabilis (Pisauridae) is a common species living in abandoned grasslands and deciduous woods. In Central Europe, it has an annual life cycle (Buchar, Babrakzai, & Hodek, 1989): spiderlings hatch in the summer and reach maturity in the spring of the following year. Mature males can be found up until June, and some females can even be found up until the end of summer (P. Prokop, personal observation). When a male detects a receptive female's draglines, he catches a prey item and wraps it in silk (e.g. Albo, Toft et al., 2011; Andersen et al., 2008; Lang, 1996; Nitzche, 1988). The male then approaches the female and the female takes hold of the gift in her chelicerae. The male then inserts his pedipalp into the female's epigyne and transfers sperm while the female feeds on the gift (Bristowe, 1958).

Honest Signalling Hypothesis

Nuptial gifts in the field

To examine the contents of nuptial gifts in the field, we captured adult males ($N = 79$, about 5% of all found males escaped) which were found through visual searching in an open woodland site near Trnava, Slovakia (48°23′N, 17°34′E) on 11 May 2016 by the first author. This time is typically the peak mating season for *P. mirabilis* in Slovakia (Prokop & Maxwell, 2012), when males are most likely to be found carrying gifts in the field.

Searching and capturing occurred during daylight hours (0900–1800 hours). Upon capture, each male was isolated in a ventilated cup (0.3 litres) with wet cotton to maintain humidity. Each male was anaesthetized in the field with CO_2 immediately after capture, and the gifts were carefully removed from the males' chelicerae to avoid consumption of the gifts (Fig. 1). Gifts were maintained in Eppendorf tubes up until the following morning. The contents of the gifts were then examined through dissection under a binocular microscope in the laboratory. We classified the gifts according to Albo, Winther et al. (2011) as 'genuine' (containing fresh prey) or 'worthless' (containing prey leftovers; i.e. empty exoskeletons). Only gifts wrapped with silk were considered nuptial gifts, because in most cases males wrap the gift before mating (e.g. Andersen et al., 2008; Lang, 1996). We also recorded males with unwrapped prey and those without prey or a gift.

Biometrical associations with offering nuptial gifts

The following morning, all males and their nuptial gifts were brought to the laboratory, anaesthetized with CO_2, and prosoma width (to 0.01 mm) and body mass (to 0.0001 g) were measured. Gifts were weighed to 0.0001 g with an analytical balance (METTLER TOLEDO B-S type) and measured along the longest diameter to 0.01 mm with digital callipers. Gift volume (V) was measured as $V = 4/3 \times \pi + r^3$ where r represents the radius of the gift. After all the measurements, the spiders were housed outdoors in ventilated cups on private property in Trnava, Slovakia, protected from direct sunlight under a natural photoperiod and temperature. Individuals were fed ad libitum with dead house crickets, *Gryllus assimilis*, three times per week (ca. one adult cricket per feeding), and were misted with water once per day until death. All males were individually preserved after death in 92% ethanol. All field work and experiments were performed in compliance with Slovak laws.

Figure 1. An example of a *P. mirabilis* male carrying a nuptial gift (designated with an arrow) in the field.

Fluctuating asymmetry

FA refers to the subtle, random differences between the left and right values of otherwise perfectly symmetrical bilateral traits of organisms (Møller, 2006; van Valen, 1962). To assess the FA, the pedipalp tarsus ($N = 69$ males) and foreleg (only femur and patella, $N = 67$ males) were measured manually. Spiders with a damaged right or left pedipalp or foreleg were excluded from analyses. To assess the measurement error, the measurements were taken three times. First, the left tarsus was separated with forceps, precisely oriented (as in Fig. 2a), and photographed three times. The measurements were taken from the three photos. The same procedure was repeated with the right palpus. The leg measurement was performed in steps: the left leg was separated from the body, the coxa and tarsus were removed, and the leg was photographed three times in a horizontal position (Fig. 2b). Measurements were taken from the three photos. The same was repeated with the right leg. All measurements were completed with a ZEISS Stemi 2000-C binocular microscope with a mounted Micrometrics digital camera and Micrometrics SE premium program. To avoid inter-rater error, the second author performed all the measurements (Hubert & Alexander, 1995). FA of the pedipalp, femur and patella was defined as the mean length difference between the left and right sides.

Personality Traits Hypothesis

Behavioural tests

We assessed three different behavioural traits in all the spiders captured in the field: mobility, aggression and prey capture abilities. All the behavioural tests took place between 18 and 26 May 2016, from 0900 to 1600 hours, indoors at room temperature (typically 24 °C), 1 m from a window to mimic natural indirect light. At the start of each trial, the spider was placed on the floor of a terrarium or Petri dish (see below) covered with white absorbent paper which was replaced after each trial and the terrarium was cleaned with 92% alcohol to remove traces of conspecific cues. All

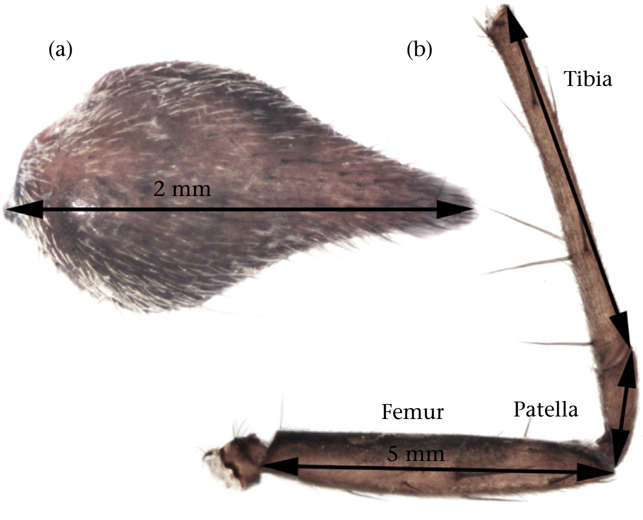

Figure 2. (a) The terminal segment of the palpus (tarsus). The double arrow designates the measurement taken. (b) The foreleg. The double arrows designate the measurements taken.

spiders were given approximately 120 s to acclimatize before observations began. All measurements were made three times (one per day). Male mobility was tested on days 1–3, aggression was tested on days 4–6 and prey capture abilities were tested on days 7–9. Each spider was tested once per day. The means from the measurements were subsequently used in statistical analyses. Three spiders that died from unknown causes before the experiments were completed and one spider that escaped were removed from the analyses. The final sample comprised 75 males.

Examining male mobility

For the mobility measurement, we followed the recommendations of Kotiaho, Alatalo, Mappes, and Parri (1999). Specifically, we divided the terrarium (30 × 20 cm and 20 cm high) into quarters and counted how many times a male entered a new section of the arena for 2 min, identically as Kotiaho et al. (1999). This number was used as the mobility index. Higher values indicated a higher mobility.

Examining male aggression

Aggression levels were assessed according to the methodology of Riechert and Johns (2003) and Grinsted, Pruitt, Settepani, and Bilde (2013), which was designed to mimic the approach of an unknown arthropod. A spider was placed in the centre of the terrarium (30 × 20 cm and 20 cm high) and touched on the chelicerae with a wooden stick (2 mm diameter, 30 cm length). We recorded and ranked the spider's response as follows: (0) huddle: the male pulled its legs against its body; (1) run: the male ran away from the wooden stick; (2) walk: the spider walked away from the wooden stick; (3) lurch: the male shifted forwards but did not initiate locomotion; (4) no response: the male did not exhibit any movement; and (5) raise: the male lifted one or more of its anterior legs (a threatening posture). Higher values indicate higher levels of aggression. The ranking of these behaviours was adopted from the work of Grinsted et al. (2013) and is applicable to *P. mirabilis* (P. Prokop, personal observation).

Examining male's prey capture abilities

We introduced each spider into an 18 cm petri dish and inserted one *Lucilia sericata* larva into the petri dish approximately 4 cm in front of the male. The petri dish was immediately covered by another petri dish to prevent the spider's escape. The mean length of the larvae (mm) ± SE was 11.27 ± 0.16 ($N = 5$) and the mean body mass (g) ± SE was 0.04 ± 0.001 ($N = 29$). Spiders were given a duration of 600 s to capture the prey following Royaute et al. (2015). We recorded latency to capture the prey with a stopwatch to the nearest 1 s. The trial was stopped as soon as the spider captured the prey or when 600 s was reached. The larva was removed from the spider's chelicerae by probing it with the tip of a small brush to standardize conditions between trials. We assigned a capture latency value of 600 s for spiders that failed to capture the prey. Higher values indicate a slower prey capture.

Statistical analyses

We compared the life spans of males that did and did not carry a gift with the Mantel–Cox test. Normality of the data was assessed with the Kolmogorov–Smirnov test. Male body mass and prosoma width were significantly correlated (Pearson correlation: $r_{79} = 0.71$, $P < 0.001$). We quantified male body condition as the residual of regression of body mass on prosoma width (Jakob, Marshall, & Uetz, 1996). Male body mass and body condition were also significantly correlated (Pearson correlation: $r_{79} = 0.7$, $P < 0.001$). A simple comparison of the means was made with a Student *t* test or ANOVA and if data were not normally distributed or when the sample sizes were low, a Mann–Whitney *U* test or Kruskal–Wallis ANOVA was performed. Categorical data were analysed with the Fisher's exact test.

To calculate the repeatabilities of male mobility, aggression and prey capture abilities, we followed the methods of Lessells and Boag (1987) using intraclass correlation coefficients, which were based on variance components derived from analyses of variance. Mean values obtained from behavioural tests (dependent variables) were Box–Cox ($x + 0.1$) transformed and normality was achieved. The influences of carrying a gift (the categorical predictor) and spider biometry (covariates) on behavioural scores were analysed with the multivariate analysis of covariance (MANCOVA).

RESULTS

Honest Signalling Hypothesis

Examining male gifts from the field

Of the 79 captured males, 17 were carrying nuptial gifts (wrapped items), 13 were carrying unwrapped prey and 49 had no gift or prey. From those with nuptial gifts, seven included worthless items. The edibility of these worthless gifts was probably limited. All the gifts contained the bodies of arthropods. The prey bodies were chewed and broken apart. Wrapped nuptial gifts seemed to be more frequently worthless (7 of 17, 41%) than unwrapped prey (0 of 13; Fisher's exact test: $P = 0.01$).

The gifts' longest diameter (mean ± SE = 3.36 ± 0.17 mm, range 2.36–6.04) and mass (mean ± SE = 0.0086 ± 0.0019 g, range 0.0005–0.0448) were significantly correlated (Pearson correlation: $r_{30} = 0.66$, $P < 0.001$). Nuptial gifts wrapped with silk ($N = 17$) were of a similar size (Mann–Whitney *U* test: $U = 110$, $P = 1.0$) and volume (Mann–Whitney *U* test: $U = 110$, $P = 1.0$) to unwrapped prey ($N = 13$), but were lighter (Mann–Whitney *U* test: $U = 63.5$, $P = 0.05$; Table 1). Considering only wrapped nuptial gifts, genuine wrapped gifts were heavier, larger and with greater volume than wrapped worthless nuptial gifts (Table 1).

Biometrical associations with offering nuptial gifts

Males with nuptial gifts did not differ significantly in body mass, prosoma width or body condition from males with unwrapped prey and from males without gifts (Table 2). Prediction 1 was not supported since it stated that males offering nuptial gifts in the field have better body condition than males without nuptial gifts.

For males with nuptial gifts, the gift weight was significantly correlated with prosoma width (Pearson correlation: $r_{17} = 0.58$, $P = 0.02$; Fig. 3). Male body mass and body condition did not correlate with gift weight (Pearson correlation: $r_{17} = 0.3$ and -0.13, $P = 0.23$ and 0.62, respectively). Nuptial gift size did not correlate with male prosoma width, body mass or body condition (Pearson correlation: $r_{17} = 0.44$, 0.04 and -0.34, $P = 0.07$, 0.88 and 0.19, respectively). Gift volume did not correlate with male biometry (Pearson correlation: $r_{17} = -0.37$–0.38, all Ps > 0.12). Prediction 2 received support, because larger males carried heavier gifts.

Table 1
Descriptive statistics for nuptial gifts from the field

	Nuptial gift		*U*	Unwrapped prey	
	Genuine	Worthless		Genuine	Worthless
Size (mm)	3.65±0.27	2.7±3.32	4[a]	3.49±0.24	–
Weight (g)	0.007±0.003	0.002±0.004	7[a]	0.013±0.008	–
Volume (mm^3)	27.24±7.37	10.62±8.81	4[a]	29.89±6.47	–
N	10	7	–	13	0

Numbers are means ± SE.

[a] $P < 0.01$; genuine and worthless nuptial gifts were compared with Mann–Whitney *U* tests.

Table 2
A comparison of males captured in the field

	Nuptial gift	Unwrapped prey	No gift	F
Body mass (g)	0.07±0.003	0.07±0.003	0.08±0.002	0.47
Prosoma width (mm)	3.38±0.05	3.44±0.06	3.44±0.003	0.55
Body condition	0.003±0.002	−0.002±0.002	0.0005±0.001	0.45
N	17	13	49	

Numbers are means ± SE.

Table 3
Descriptive statistics for behavioural tests

	Mobility	Aggression	Prey capture	N
Nuptial gift	0.77±0.09	2.73±0.26	190±35.41	15
Non-nuptial gift	0.78±0.09	3.10±0.28	165±38.0	13
No gift	0.80±0.05	2.73±0.15	142±20.0	47

Numbers are mean behavioural scores ± SE.

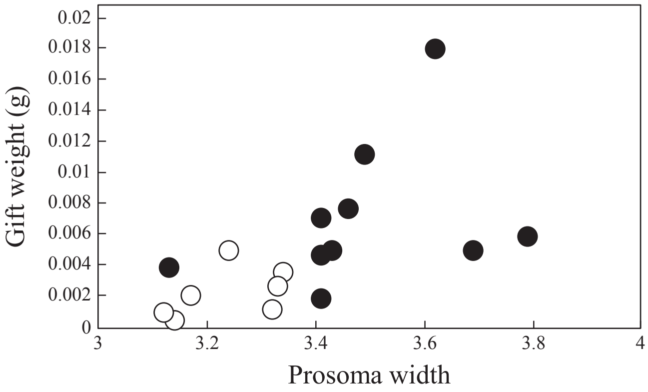

Figure 3. Relationships between prosoma width and nuptial gift weight (closed circles are genuine gifts; open circles are worthless gifts).

Fluctuating asymmetry (FA)

The measurements of both the femur and patella on the right and left foreleg ($N = 67$) as well as on the right and left palpus ($N = 69$) revealed asymmetry in *P. mirabilis* males. Wilcoxon matched-pairs tests revealed no significant differences in size between the right and the left size in any of the three measures of spider body parts (all $Ps > 0.17$, data not shown). The asymmetries were consequently not directional, but can be classified as FA.

There were no significant differences in fluctuating asymmetry of the femur (Kruskal–Wallis test: $H_2 = 0.13$, $P = 0.94$) and patella length (Kruskal–Wallis test: $H_2 = 3.28$, $P = 0.19$) between males carrying nuptial gifts ($N = 14$), unwrapped prey ($N = 11$) and not carrying gifts ($N = 42$). Similarly, palpus length asymmetry did not differ between males carrying nuptial gifts ($N = 14$), unwrapped prey ($N = 11$) and not carrying gifts ($N = 44$; Kruskal–Wallis test: $H_2 = 0.79$, $P = 0.68$). Prediction 3 was not supported, because males with nuptial gifts were not more symmetrical than other males.

Male life span

One male that escaped during experiments was removed from this analysis. The mean life span ± SE was 43 ± 1.94 days (range 10–103 days, $N = 78$). Males with nuptial gifts had a similar life span to males with unwrapped prey and males without gifts (Mantel–Cox test: $\chi^2_2 = 0.31$, $P = 0.86$).

Personality Traits Hypothesis

Repeatability of mobility (ANOVA: $F_{74,150} = 2.26$, $P < 0.001$), prey capture (ANOVA: $F_{74,150} = 1.68$, $P = 0.003$) and aggression (ANOVA: $F_{74,150} = 1.59$, $P = 0.009$) tests were low ($r_{75} = 0.30$, 0.19 and 0.16, respectively). Moreover, there were no correlations between these traits (all $r_{75} = -0.04$–0.12, all $Ps > 0.29$). The proportion of capture success in the prey capture experiment did not differ between spiders that carried nuptial gifts or unwrapped prey or did not carry gifts (Pearson $\chi^2_2 = 2.53$, $P = 0.28$). MANCOVA showed no significant influence of gifts on behavioural measures (Wilks's $\lambda = 0.96$, $F_{6,36} = 0.52$, $P = 0.79$; Table 3). The personality traits hypothesis was not supported, because males carrying gifts did not have greater mobility, prey capture and aggression than males that did not offer gifts or that offered unwrapped prey.

By analysing the same MANCOVA model, we further examined whether male biometry influences personality traits. Male body mass was not associated with behavioural measures (Wilks's $\lambda = 0.99$, $F_{3,68} = 0.33$, $P = 0.8$), but prosoma width revealed a significant association with the dependent variables (Wilks's $\lambda = 0.87$, $F_{3,68} = 3.3$, $P = 0.03$). In particular, males with larger prosomas were less mobile and took longer to capture prey ($\beta = -0.38$ and 0.34, both $P < 0.05$, respectively) than males with smaller prosomas. Aggressive behaviour was not influenced by prosoma width ($\beta = 0.06$, $P = 0.75$). When male body condition was inserted into the model instead of the prosoma width and body mass, there was no significant association between body condition and the dependent variables (Wilks's $\lambda = 0.99$, $F_{3,69} = 0.33$, $P = 0.8$).

DISCUSSION

This study examined two hypotheses regarding the evolution of nuptial feeding in *P. mirabilis* males. The honest signalling hypothesis suggests that the size of a male's ornament reflects his quality or condition (Johnstone, Rands, & Evans, 2009; Zahavi, 1975) and that honesty may be maintained by potential costs of cheating (Számadó, 2011). We found some support for this hypothesis as the size of the nuptial gifts in the field was dependent on male size: larger males carried larger and heavier gifts than their smaller counterparts. This provides support for the conditional dependence of gift construction in gift-giving spiders studied in the laboratory (Albo, Toft et al., 2011; Macedo-Rego et al., 2016) and for *Paratrechalea ornata* studied in the field (Albo, Melo-Gonzalez et al., 2014). Larger males can bear the costs of killing and carrying a larger prey by having, for example, more fat reserves (Aisenberg & Peretti, 2011). Such reserves would enable large males to avoid feeding on nuptial prey in contrast to small males and/or males in poor body condition. Prokop and Maxwell (2012) did not find significant correlations between male biometry and gift size probably because of differences between localities or years or lower sample sizes. The fixed body size of *P. mirabilis* depends on local differences in prey availability (P. Prokop, personal observation); thus, pooling data from two localities could have confounded the results of their study.

We found no differences between males whether they offered nuptial gifts or unwrapped prey or did not offer gifts in the field which is in agreement with Prokop and Maxwell (2012), but these results do not support the honest signalling hypothesis. In addition, males offering gifts were no more symmetrical than males not offering gifts suggesting that the presence of a gift is not associated with superior genetic quality. It does not seem, however, that males without gifts employ an alternative, ‘giftless’ mating strategy. Field observations would suggest that females never copulate unless the male offers a nuptial gift (Austad & Thornhill, 1986). Furthermore, nuptial gifts are necessary for mating in the study population (Prokop, 2006; Prokop & Maxwell, 2009) which makes it unlikely that males would pursue a dishonest, ‘giftless’ mating strategy. The ability of males to carry a gift may vary over the reproductive period, which may explain why we found some males without gifts, as we collected all the males on the same day.

Pisaura mirabilis females gain not only direct but also indirect benefits from mating in terms of increasing the probability of oviposition and egg hatching success (Tuni et al., 2013). Thus, females can be expected to prefer males of higher genetic quality or superior genetic compatibility (Jennions & Petrie, 2000). In this system, females probably select sexual signals that cannot be faked rather than potentially fakeable signals. Males use nuptial gifts to exploit the female‘s foraging motivation in order to copulate (Prokop & Maxwell, 2009; Stålhandske, 2002), but females should evaluate the male by his own size rather than by the size of his gift (Albo et al., 2012), which is easily faked (worthless gift; Albo, Winther et al., 2011). According to this scenario, both male size and maintenance of nuptial gifts are under strong sexual selection by females.

The donation of worthless gifts has been reported both in *P. mirabilis* (Albo, Winther et al., 2011; Nietzsche, 1988, 1999, this study) and in *P. ornata* (Albo & Costa, 2010; Albo, Melo-Gonzalez et al., 2014). Here we demonstrated that wrapped nuptial gifts seemed to be more frequently worthless than unwrapped prey. In agreement with Albo, Winther et al. (2011), we suggest that males may mask the gift content with additional silk, thereby manipulating female willingness to copulate. Even a short copulation with a female that is inspecting the content of the gift may result in successful sperm transfer (Nitzsche, 1999), suggesting that possible manipulation of the gift's content can provide a reproductive advantage for the male. This seems to be the case with small males which more often carry worthless, light gifts. Wrapping the gift with silk increases the gift's attractiveness to the female (Stålhandske, 2002), prolongs copulation duration (Lang, 1996) and facilitates male handling and control over the gift (Andersen et al., 2008). Donating worthless gifts, however, reduces male reproductive success (Albo, Melo-Gonzalez et al., 2014; Albo, Winther et al., 2011), suggesting that this cheap alternative mating strategy will not prevail over the donation of genuine gifts. There is a need, however, to examine whether silk production is a cheaper strategy for males than searching for prey before any conclusion can be made. Interestingly, Albo, Winther et al. (2011) found that males invest less time in the construction of worthless gifts and perform fewer wrapping bouts than with nutritious gifts. In their case, however, spiders were allowed to construct gifts when exposed to fresh female draglines containing pheromones attractive to males (Nitzche, 1988), while *P. mirabilis* males also construct gifts even in the absence of female cues (Lang, 1996). Males in the field may invest more energy in wrapping the prey in silk after partly eating it and, thus, the gift is less attractive to the female.

Another alternative is that males spend less effort in worthless gift construction if the female is in the immediate vicinity. Males instead invest more energy in adding silk to nutritious gifts to prevent the female stealing the valuable gift (Andersen et al., 2008).

We hypothesized that males offering nuptial gifts could have different personalities to those that did not offer gifts. However, we were unable to reliably identify personalities by measuring three different behavioural traits (mobility, aggression, prey capture ability) of *P. mirabilis* males under the standard conditions that were previously investigated in different spiders (Grinsted et al., 2013; Kotiaho et al., 1999; Royautte, Buddle, & Vincent, 2015). Certain behaviours that are more sensitive to environmental factors, particularly those influenced by energy needs, may be more variable and, thus, less repeatable (Bell et al., 2009). Male mobility and prey capture speed are possibly influenced by both prey type and hunger level, as these variables affect the prey capture behaviour of spiders (Aguilar-Argüello & García-Chávez, 2015; Gardner, 1965; Jackson, 2000), and the aggression of males could be influenced by the abundance of predators in their microhabitat (Huntingford, 1982). Possibly, the protocol for determining personality needs to be optimized for this species and behavioural tests should be repeated at longer intervals. Low within-individual repeatabilities, an absence of correlations between potential personality traits and the partial dependence of these behaviours on male biometry suggest the involvement of nongenetic factors (Bell et al., 2009; Grinsted et al., 2013; van Oers et al., 2004), although low repeatabilities do not preclude the possibility of additive genetic variation (Aragaki & Meffert, 1998). As males appeared not to differ in foraging ability, females probably do not use this to select males. Moreover, the lack of differences in biometry suggests that males offering gifts had similar feeding histories to those without gifts. Because no similar data are available from other gift-giving species, further research is required to identify personalities in arthropods with nuptial feeding.

Conclusion

Exogenous (dead prey) and endogenous (silk) components of nuptial gifts in *P. mirabilis* seem to be under different selection pressures, while the former shows an association with male size. It is possible that by selecting larger males, the female receives genes of males with superior genotypes (indirect benefits) as well as larger gifts (direct benefits). In contrast, wrapping worthless gifts provides an opportunity for males to deceive females by exploiting their visual and/or chemical preferences. Further research should experimentally investigate whether males invest more silk on small or worthless gifts to mask the gift's content and focus on possible predation costs of males with and without nuptial gifts. The advantages of male size and the possible role of spider personalities in the sexual selection of *P. mirabilis* requires further attention.

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