Original Article

Silk wrapping of nuptial gifts aids cheating behaviour in male spiders

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Sexual traits, such as nuptial gifts, are costly and often condition-dependent. Males should be under selection to reduce these costs without impairing their reproductive success. Spider gifts consist of silk-wrapped food, but may also consist of worthless (non-nutritive) donations that successfully lead to mating, despite yielding shorter copulations. Worthless gifts may either represent a cheaper cheating strategy or the inability to produce genuine gifts due to resource limitations (i.e. poor body condition). Unless energetic constraints limit expenditure in silk, males should apply more silk to worthless gifts to compensate for their lower reproductive value. We ask whether in *Pisaura mirabilis* 1) worthless gifts are condition-dependent and 2) males strategically use silk based on gift type (genuine vs worthless). We tested whether male body condition explains the gift-giving strategy and compared silk amounts covering each gift type, in gifts collected from the field and produced in the laboratory by males given different feeding regimes. Our findings show that worthless gifts are not promoted by poor body condition or limited resources. They rather result from a cheating strategy evolved to opportunistically reduce the costs of genuine gifts while ensuring nutritional advantages, with cheaters gaining body mass. Males applied more silk to worthless gifts regardless of their body condition or feeding state, suggesting they can strategically adjust silk expenditure despite its costs. By masking gift contents and prolonging female feeding, silk is crucial for the maintenance of cheating, likely resulting from an evolutionary arms race between male deception and female assessment.

Key words: **deception, mating strategies, nuptial gifts, sperm competition.**

INTRODUCTION

Theory predicts that sexual traits (e.g. courtship displays) are honest indicators of males' underlying quality due to the costs associated to their production and maintenance (Zahavi 1975). The extent to which males invest in reproduction is therefore often affected by energetic resources, with males of higher body condition being better at expressing sexual traits (van Noordwijk and de Jong 1986). As it is in the male's best interest to optimize investment in current reproduction in order to allocate resources to future mating or other activities, males should be under selection to reduce some of these costs without impairing their overall reproductive success. Males, for example, can use cheaper mating strategies if there are limits to female accurate assessment of the quality of the information they convey (Dawkins and Guilford 1991). These strategies lead to male cheating behaviour if females do not receive the expected benefits

(direct or indirect) from their mate choice, with males saving energy at their own reproductive advantage (Johnstone and Grafen 1993; LeBas and Hockham 2005). Alongside cost-reduction in males, selection should favour accurate female mate assessment (Kokko et al. 2003), leading to a potential evolutionary arms race between selection for cheaper deceptive traits in males and resistance to such traits in females (Arnqvist and Rowe 2013).

Nuptial gifts, consisting of male donations of nutritious substances to females (Lewis and South 2012), are sexually selected traits particularly prone to male cheating (LeBas and Hockham 2005; Ghislandi et al. 2014). The gift may have several, non-mutually exclusive, functions: it is used by males to attract females, it secures sperm transfer, and may act as parental investment through nutrient-derived resources (Thornhill 1976a; Boggs 1995; Vahed 1998; Gwynne 2008). Invertebrates show a rich variation of gift types, ranging from oral or seminal male secretions (endogenous gifts) to food items captured or collected from the environment (exogenous gifts) (Lewis et al. 2014). Exogenous gifts are often polymorphic and may also consist of items with little or no nutritional value to females (i.e. plant parts, prey remains, and empty silk balloons), which nevertheless

successfully elicit female mate acceptance (Preston-Mafham 1999; Albo et al. 2011b). These types of donations generally reflect a reduction of male investment into reproduction from more costly to less valuable donations (from nutritious prey, to prey remains and worthless donations) (LeBas and Hockham 2005; Ghislandi et al. 2014). Hence, cheaper (worthless) gifts may either represent an opportunistic cheating strategy used by males to reduce the costs of mating or a consequence of facing unfavourable ecological conditions, for example when resources are lacking (Engqvist 2007; Albo et al. 2014; Ghislandi et al. 2014). Through cheaper donations, males enhance their reproductive success while minimizing the costs associated with producing a genuine gift, such as increased risk of predation while hunting for a prey to offer, missed foraging opportunity, or transportation costs (Boggs 1995). On the other hand, males attempting to use worthless gifts may incur fitness costs, derived by female mate rejection or reduced sperm transfer due to shorter copulation time (LeBas and Hockham 2005; Albo et al. 2011b).

The evolution of worthless gifts in spiders remains particularly intriguing. Male spiders offer a prey gift to the female during courtship and mating. Gift-offering enhances mate acquisition (Stålhandske 2001; Albo and Costa 2010) by exploiting female foraging motivation (Bilde et al. 2007). It also increases male fertilization success by prolonging female gift-consumption and concurrent sperm transfer (Drengsgaard and Toft 1999; Albo and Costa 2010; Albo et al. 2011b; Albo et al. 2013). In certain ecological contexts the gift may also function as paternal investment (Toft and Albo 2015). Males wrap their gifts in dense silk layers, an advantageous trait for males because it prolongs mating by increasing female feeding duration (Lang 1996; Albo et al. 2011b) and allows the male to strengthen hold of the gift, preventing mating interruptions (Andersen et al. 2008). Gifts may however range from edible intact prey, to worthless prey remains and plant parts (Stålhandske 2001; Albo et al. 2011b; Albo et al. 2014). Limited food availability and poor male body condition have been proposed to be the possible ecological drivers promoting the use of these worthless gifts (Albo et al. 2014; Ghislandi et al. 2014).

Disguising gift content with silk to lure females into accepting a gift that does not confer the expected food reward is suggested to play a key role in facilitating the use of worthless gifts (Albo et al. 2011b; Ghislandi et al. 2014). In the species Pisaura mirabilis, males offering worthless gifts are known to achieve similar mating success as of those offering genuine prey gifts, indicating that during courtship females are not able to assess the value of the gift content (Albo et al. 2011b). These males however experience on average 20% shorter copulations and reduced fertilization success, most likely due to female interruption of copulation once the silk layers covering inedible gift contents are consumed and the content unmasked (Albo et al. 2011b). Due to the importance of silk in serving the male's reproductive interest (Lang 1996; Andersen et al. 2008), males are expected to use silk strategically. Enhancing silk investment when offering worthless gifts would be particularly advantageous for males, not only to effectively mask worthless gift contents, but also to prolong female feeding and compensate for the otherwise shorter copulation achieved (Lang 1996; Andersen et al. 2008; Albo et al. 2011b). However, if gift-wrapping entails substantial energetic requirements due to costly silk proteins (Craig et al. 1999; Nentwig and Kuhn-Nentwig 2013), we would expect higher silk investment only in the case worthless gifts occur as a male cheating strategy. In contrast, if worthless gifts are condition-dependent limiting energetic resources may also constraint silk production.

By taking advantage of the silk-wrapped nuptial gifts of male Pisaura mirabilis we investigated 1) whether worthless gifts are condition-dependent and 2) whether males modulate silk investment based on their gift giving strategy (genuine vs worthless gifts). In a first study, we collected gifts from a natural population of spiders and scored them as genuine or worthless based on their contents, consisting respectively of intact prey (genuine) or prey leftovers and plant parts (worthless). We tested whether the use of worthless gifts is explained by variation in male body condition and compared the amounts of silk covering each gift type (genuine and worthless). In a second study we obtained gifts during laboratory trials by providing males with live prey, and scored whether a gift is worthless based on the extent males fed on prey prior to silk wrapping (i.e. prey weight loss). We experimentally manipulated male body condition by allocating males to high and low feeding regimes and tested whether food availability explained worthless gift production, and whether silk investment varied based on gifts' worthlessness. Unless the use of worthless gifts itself is condition-dependent and limits silk investment we expect males to cover worthless gifts in greater silk amounts compared to genuine gifts to compensate for their lower reproductive value.

METHODS
Field collected nuptial gifts

Collecting
Males carrying gifts were collected from a natural population of Pisaura mirabilis surrounding Ludwig Maximilian University of Munich (Germany) during May and June 2014 and 2015. On each day of collection, which occurred over a total period of 4 weeks at variable intervals, males were captured, placed in a vial (5 cm diameter, 10 cm height) covered with a sponge lid and given an individual ID. In order to avoid males' gift manipulation after capture, the gift was immediately removed from the males' mouthparts using forceps and placed in an Eppendorf tube labelled with the male ID. Males were brought to the laboratory, their body mass was weighted to the nearest 0.01 g using a digital scale (KERN PKT, KERN & SOHN GmbH, Balingen, Germany) and their cephalothorax width (used as a proxy for body size) measured to the nearest 0.01 mm using digital callipers (AEROSPACE, China). Animals were then released back to the study site. Gifts were frozen at −4 °C.

Scoring of gift content
Gifts were weighed to the nearest 0.001 g using a microbalance (Sartorius Supermicro S4, Sartorius AG, Göttingen, Germany.) and then placed under a stereomicroscope where the silk was gently opened using micro-dissecting forceps. The content of field-collected gifts was inspected and the gift was defined as genuine if containing intact prey, which did not appear to be dried out or eaten, and worthless if containing dried prey and prey leftovers (i.e. pieces of body parts or exoskeletons) or items such as seeds or plant parts. Gifts that contained more than one prey were classified as genuine where at least one of the items consisted of intact prey. If possible the Taxonomical group of the arthropod prey was defined. Gift contents were scored by the same observer (P.G.G).

Experimentally produced gifts

Animal rearing and treatment groups
Sub-adult spiders were collected during April 2014 from grass meadows described above, and were brought to the laboratory. They were reared at room temperature (approx. 25 °C) under natural photoperiod and were kept individually in plastic vials (5 cm

diameter, 10 cm height) covered with a sponge lid and with a bottom layer of moss that was kept wet by spraying water every second day. Spiders were fed regularly twice a week with 5–10 fruit flies (*Drosophila spp.*) or one prey consisting of a field cricket nymph (*Gryllus spp.*) or a housefly (*Musca domestica*). The occurrence of molted exoskeletons in the vials was noted every second day. Upon emergence to adulthood males were randomly assigned to one of the two feeding treatments, with males in the high food treatment (HF, *n* = 28) being fed an insect prey (fly or cricket) twice a week and those in the low food treatment (LF, *n* =17) being fed once a week with the same prey type.

Silk-wrapping trials

Males were used in experimental trials 12–14 days after reaching adulthood in order to ensure sexual maturity. Prior to each trial, male body mass and size was measured (as above). In order to elicit gift-wrapping behaviour we exposed males to female silk-draglines: we placed males into housing vials of sexually receptive females that were temporarily removed, or into transparent plastic boxes (7 cm height × 10 cm width × 10 cm depth) with a bottom layer of paper in which a female was previously housed for a minimum of 30 min. As soon as males showed signs of sexual stimulation (i.e. abdomen jerking and rubbing of the first pair of legs against each other) we placed a live cricket nymph of known weight nearby the spider using forceps and waited for the male to catch the prey. If males did not catch the prey within 20 min the trial was interrupted, males were returned to their own vial and the trial was repeated on the following day, for a maximum of 3 times. Similarly, trials were interrupted if males caught a prey but did not wrap it into a nuptial gift. Overall we obtained one gift from each male, 10 from the LF and 24 from the HF treatment.

For each male that produced a gift we measured latency to gift-wrapping, as the time spent from prey capture to start of silk wrapping, to account for possible manipulations of the prey prior gift construction. During gift-wrapping males move their body in rounds keeping their silk spinning organs (spinnerets) that are located at the underside posterior of their abdomen attached to the gift. Males may often interrupt this process, remaining motionless and/or picking up the gift it their chelicerae, producing distinct wrapping episodes. We measured the total gift-wrapping duration (seconds) as the sum of the duration of all wrapping episodes to correlate behavioural observations of silk wrapping to quantified silk measures. All time durations were measured using a CG-501 stopwatch (Genutek Electronics Co., Ltd, China). The trial was ended when males did not wrap for 10 consecutive minutes following the end of the last wrapping episode. The gift was then removed from the male using forceps and frozen at −4 °C.

At the end of the experiments, in order to evaluate male silk production without time constraints imposed by our experimental trials, a cricket nymph was placed inside the male's housing vial and on the following day we collected silk-wrapped gifts constructed overnight and stored them at −4 °C.

Silk measurements

Silk of nuptial gifts was measured from field-collected and experimentally produced samples. Silk was gently separated from the gift content using micro-dissecting forceps and placed in an Eppendorf tube. Silk measurements were conducted by modifying an existing protocol for this species (Lang 1996). The removed silk was heated for 1–2 h in a heating block at 100 °C and then stored in a desiccator (in dry atmosphere) for 12–36 h until it was weighed to the nearest 0.001 g using a Sartorius microbalance. All measurements were taken by the same observer (M.B.).

Statistical analyses

We estimated male body condition by calculating a body condition index measured as the residuals of a regression of body mass on body size (cephalothorax width) (Jakob et al. 1996).

Field collected nuptial gifts

We used Logistic regression to test whether male body condition has an effect on the gift-giving strategy used (genuine vs worthless gifts). To understand whether silk investment depends on the gift giving strategy used by males and is affected by body resources we used ANCOVA, testing for the effects of male body condition and gift type (genuine or worthless) on silk amounts covering gifts.

Experimentally produced gifts

We tested whether the applied food treatments (LF and HF) generated differences in male body condition index by using a *t*-test. To analyse whether feeding treatment (LF and HF) affected silk wrapping latency we used ANCOVA, including prey body mass as a covariate in the model to control for possible effects of prey size on male behaviour. We estimated weather a gift is worthless in terms of the extent to which males consumed the prey prior to silk wrapping. We therefore calculated prey weight loss as the differences in weight between prey body mass before the trial and the content of the nuptial gift after the trial (calculated as gift weight—silk weight). We used ANCOVA to test whether prey weight loss is affected by the food treatment (LF and HF), controlling for initial prey body mass. To ascertain whether regression-to-mean effects explain prey weight loss in respect to prior prey weight value we used Pitman's test for the equality of variances in paired samples (Kelly and Price 2005). To understand whether silk investment depends on the gift-giving strategy (worthlessness of the gift) and is affected by body resources we used ANCOVA, testing for the effect of feeding treatment (LF and HF) and prey weight loss on silk amounts covering gifts. Linear regression was used to assess whether the total duration of silk wrapping behaviour related to the amount of silk deposited by males. We also estimated the costs of gift production for males by measuring male body mass loss and used Linear Regression to assess whether such cost is related to cheating (prey weight loss). Finally, for gifts produced overnight without direct observations we tested differences in mean silk amount between LF and HF males using *t*-test.

Statistical tests were performed using the software JMP, Version 11 (SAS Institute Inc., Cary, NC). Appropriate data transformations were applied when residuals did not meet assumptions of normal distribution. Means are reported ± SE.

RESULTS

Field collected nuptial gifts

We collected a total of 113 nuptial gifts from the field (21 in 2014 and 92 in 2015), of which 41.6% (47) contained intact prey and were scored as genuine gifts, whereas 58.4% (66) contained dried and fragmented prey leftovers and plant parts and were scored as worthless gifts. Male body condition, calculated in 110 males, did not affect the mating strategy adopted (genuine vs worthless gifts) (Logistic regression, $\chi^2 = 0.12$, $n = 110$, $P = 0.72$).

Gift contents ranged from 1 to 4 items, with most gifts containing 1 (84%) and 2 (11.5%) items. In 79.7% of the cases, we found

arthropods (26.3% Dipteran, 21.8% Spiders, 19.1% Coleopteran, 16.4% Lepidoptera and 16.4% others), in 4.4% of plant parts and 15.9% of not identifiable items, the latter being scored as one item. The number of items found in gifts did not differ significantly between those scored as genuine and worthless (mean N items ± SE, genuine 1.19 ± 0.07 and worthless 1.25 ± 0.09; Wilcoxon, $Z = 0.74$; $n = 113$, $P = 0.45$). Gift weight was measured in 111 samples and we found that genuine gifts were significantly heavier than worthless gifts (mean ± SE (mg), genuine 13.93 ± 1.59 ($n = 64$) and worthless 5.76 ± 0.91 ($n = 47$); log-transformed, t-test, $t = -5.28$, df = 109, $P = <0.0001$).

Due to practical unfeasibility in isolating silk in 3 genuine gifts, silk weight was measured from 110 samples. We found that the amount of silk covering gifts varied significantly according to gift type, with higher amounts of silk being found on worthless compared to genuine gifts (log-transformed, ANCOVA, Gift type $F_{1, 104} = 4.39$, $P = 0.038$; Body condition $F_{1, 104} = 1.68$, $P = 0.19$; Figure 1).

Experimentally produced nuptial gifts

The food treatment applied had a significant effect on male body condition (mean body condition index ± SE, LF −7.49 ± 3.60 ($n = 10$), HF 3.98 ± 2.66 ($n = 24$); t-test; $t = 2.41$, DF = 32, $P = 0.022$). Neither feeding treatment nor prey body mass (measured in 27 trials) affected male latency to silk wrapping (log transformed, ANCOVA, Food Treatment $F_{1, 24} = 0.06$, $P = 0.79$; Prey weight $F_{1, 24} = 0.01$, $P = 0.93$). We measured prey weight loss in 23 gifts. Whereas prey generally lost weight, in 3 cases we measured an increase of prey body mass. This is most likely due to spiders' injection of digestive fluids that serve for liquefying the prey during feeding. We found that the feeding treatment given to males did not significantly affect prey weight loss (worthlessness of the gift) but heavier prey lost more weight (ANCOVA, log-transformed, Food Treatment $F_{1, 20} = 1.25$, $P = 0.27$, Prey weight $F_{1, 20} = 35.23$, $P < 0.0001$) and the correlation between change in prey mass and initial prey mass was not entirely driven by regression-to-mean effects (Pitman's test, $t = 18.98$, DF = 21, $P > 0.0001$).

We were not able to isolate silk from prey in 4 gifts, therefore silk weight was measured from 30 samples. We found higher amounts of silk on the gifts that were scored as worthless (higher prey weight loss), but not according to male feeding treatment (LF and HF) (square-root transformed, ANCOVA, Food Treatment $F_{1, 20} = 2.54$, $P = 0.12$, Prey weight loss $F_{1, 20} = 4.41$, $P = 0.048$; Figure 2). The total time males spent wrapping a gift in silk correlated significantly

with the total amount of silk measured (log-transformed, Linear regression, R2 = 0.42, $F_{1, 27} = 21.10$, $P = <0.0001$).

We estimated the costs of gift construction for males in terms of body mass loss (male weight prior—after gift construction). After gift construction 53.33% ($n = 16$) of the males increased their weight and 46.66% ($n = 14$) showed a decrease in body mass. We found that male body mass increase correlated positively with prey weight loss (Linear regression, R2 = 0.27, $F_{1, 21} = 9.11$, $P = 0.0065$).

Of the total of 45 males, 40 constructed gifts in their housing vials overnight, without direct observations. Gifts of HF males were covered in higher amounts of silk compared to LF males (mean ± SE (mg), HF 0.38 ± 0.05 ($n = 23$), LF 0.17 ± 0.03 ($n = 17$), t-test, DF = 38, $t = 2.68$, $P = 0.016$). We acknowledge that our experimental set up may explain the differences in average silk amounts measured from gifts produced during experimental observations (0.10 mg) and those produced without direct observations, in the laboratory (0.29 mg) and in the field (0.39 mg).

DISCUSSION

Energetic limitations have been suggested to play a major role in the production of nuptial gifts (Engels and Sauer 2006; Immonen et al. 2009; Albo et al. 2011a). However, unlike suggested for male spiders (Albo et al. 2014; Ghislandi et al. 2014), our study shows that limitation in male body condition or food resources does not promote the use of worthless gifts, consisting of less valuable food donations to females. In the field, males varying in their body condition were equally likely to carry genuine and worthless gifts. Similarly, males raised under high and low food regimes in the laboratory fed on prey prior to gift construction to an equal extent. We can therefore overall reject the hypothesis of worthless gifts deriving from the inability of poor quality males to produce genuine gifts. Worthless food gifts rather appear to result from a cheating strategy, evolved to opportunistically reduce the costs of mating while ensuring nutritional advantages. We indeed show that males producing worthless gifts increase their body mass from partially feeding on prey prior to gift construction. Short-term access to nutrients may promote male mating success through strengthened courtship effort and vigour, providing males with mating advantages that go beyond gift quality (Kotiaho 2002; Hunt et al. 2004; Shamble et al. 2009; Albo et al. 2012). Using a cheaper strategy would then be particularly valuable with increasing energy requirements necessary to overcome resistance of already mated females (Gabor and Halliday 1997;
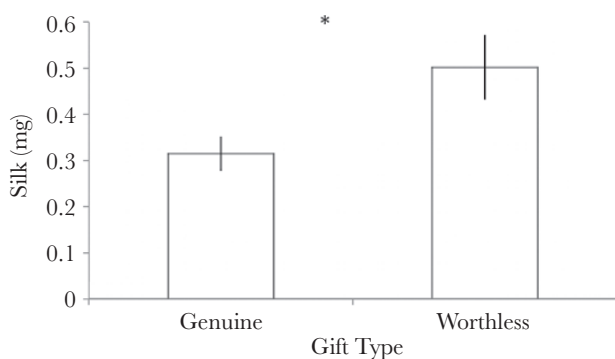
Figure 1
Amount of silk (mg) covering genuine (prey) and worthless (prey leftovers and plants) nuptial gifts collected from a natural population of the spider *Pisaura mirabilis*. *Denotes statistical significance.
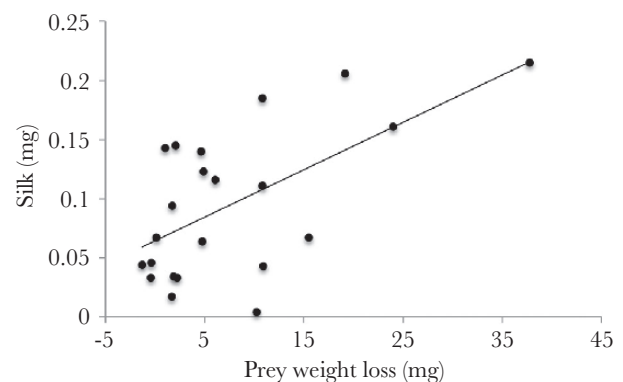
Figure 2
The amounts of silk (mg) covering experimentally produced nuptial gifts correlates linearly with the extent on which males fed on the prey prior to silk wrapping (prey weight loss).

Maklakov et al. 2003; Aisenberg and Costa 2005; Tuni and Bilde 2010), or to outcompete competitors (Hack 1997; Nitzsche 2011).

The finding that males producing worthless gifts fed to a greater extent on prey of higher body mass, further suggests that cheating may function to efficiently feed on larger and/or higher quality prey providing males of greater hunting abilities with the opportunity to gain nutritional benefits, while still being able to produce a gift that allows successful reproduction. This may also represent an effective male strategy to optimize the decreasing reproductive payoff of prolonged copulations in relation to the costs of not feeding on the prey. Males would indeed benefit from offering larger and more nutritive prey to females only if the extra copulation time achieved provides substantial fertilization advantages. If paternity gain is instead a decreasing payoff function of copulation duration (Parker 1970; Thornhill 1976b) feeding on larger prey and using prey of reduced size for mating, may allow males to outweigh the costs of a missed meal while ensuring sufficient sperm transfer for reproduction.

We also found that males producing worthless gifts apply more silk regardless of their body condition or feeding state, suggesting that they are not energetically limited in their ability to invest in the gift and can strategically adjust silk expenditure despite its costs (Albo et al. 2011a). The silk cover is instrumental for a successful cheating strategy as it prevents female pre-mating evaluation of gift contents; greater silk amounts covering worthless gifts will effectively disguise distasteful or inedible items to females. Additional silk wrapping may also be a means of extending inseminations in the face of the shorter matings yielded from worthless gifts, as extra silk layers will prolong female feeding duration and hence sperm transfer (Lang 1996). Silk itself is likely an important component of the nuptial gift as females ingest it, hence cheaters may provide extra silk to improve the nutritive value of worthless items (Craig et al. 1999; Wilder 2011). Finally, silk may also facilitate handling and control of smaller lower quality gifts (Andersen et al. 2008). Because of the lack of consensus on silk acting as a visual signal enhancing mate acceptance (Stålhandske 2002; Bilde et al. 2007; Albo et al. 2012), greater silk layers are suggested not to promote male mating success. For all the above-mentioned reasons, we suggest that males use higher silk investment to compensate for the lower reproductive value of worthless gifts. The finding that males that feed opportunistically on the prey to produce a worthless gift gain weight despite wrapping their gifts in more silk, further suggests that adding silk is not a costly compensation energy wise. We expect such compensation in gift quality however not to be complete, as achieving copulations equivalent in frequency and duration to those with genuine gifts would indicate that the worthless gifts may in turn have the potential to invade and replace genuine gifts (LeBas and Hockham 2005).

Nuptial gifts most likely evolved in the context of female foraging, with males providing extra nutrients to their mating partners while enhancing their reproductive success through improved fertilizations and increased female fecundity (Boggs 1995; Vahed 1998; Bilde et al. 2007). Male spiders may have originally benefited from investing in costly nutritive gifts at their own feeding expenses (Albo et al. 2009), with gift-giving becoming a trait strongly selected by females (Stålhandske 2001; Albo et al. 2013). Only subsequently, males may have evolved means to reduce the nutritional costs of gift production by lowering content quality in order to facilitate their own reproductive interests, yet still fulfilling female mate choice expectations (Sakaluk 2000; LeBas and Hockham 2005).

Once the gift quality is reduced, females are likely to suffer fitness costs from being deceived owing to reduced direct benefits (i.e. missed foraging opportunity), and are expected to be under selection to distinguish genuine from worthless gifts. In return, males might evolve more efficient traits, such as silk wrapping to prevent accurate female assessment. Females may instead become more resistant to the information carried by silk (Albo et al. 2012), potentially basing their reproductive decisions on other traits. Overall, this would generate an antagonistic arms race between males under selection to deceive and females under selection to evolve resistance to deception (Arnqvist and Rowe 2013).

Our study shows that the use of worthless gifts is well established in the population, occurring in 58.4% of the males in our field study (and 85% in laboratory trials). Similar frequencies are also described in natural populations of the Neotropical gift-giving spider *Paratrechalea ornata* (Albo et al. 2014). These high frequencies of worthless gifts are not explained by theory, which instead predicts cheating to occur at low incidence as the benefits of the strategy will decline with increasing frequency of cheats in the population (Dawkins and Guilford 1991; Johnstone and Grafen 1993). Our following reasoning may provide a possible explanation for such high levels of worthless gifts. The non-trivial nutritional benefits gained by cheaters together with the effectiveness of the strategy derived by silk-wrapping (worthless gifts are not rejected at higher rates), may allow males using worthless gifts to maintain overall high mating rates (LeBas and Hockham 2005; Albo et al. 2011b) at the costs of reduced paternity gained per mating (Albo et al. 2011b). Despite the fact that larger inseminations promote male success in sperm competition when females mate with multiple partners (Drengsgaard and Toft 1999; Simmons 2001), shorter copulations may not necessarily affect male lifetime reproductive success negatively. Theoretical models of sperm allocation predict that males should increase sperm investment when facing sperm competition risk, but should reduce sperm investment under high sperm competition intensity (Parker 1970; Parker and Pizzari 2010). Therefore under environmental conditions in which sperm competition is most intense (i.e. male biased sex ratios, high female re-mating rates) it may pay to reduce investment in gifts and hence sperm, as larger inseminations achieved through high quality gifts may not confer the fertilization benefits necessary to counterbalance the costs of mating. Under these circumstances males could enhance their reproductive success by ensuring mate acquisition through cheaper matings (worthless gifts, shorter inseminations) rather than investing largely in fewer costly encounters (i.e. genuine gifts, longer inseminations), with selection favouring cheating.

To conclude, genuine and worthless gifts may be maintained as alternative reproductive strategies, each of which maximizes male reproductive fitness under a specific set of circumstances (Oliveira et al. 2008). Whether these reflect changes in the competitive social environment (e.g. sperm competition intensity) or the quality of available prey remain interesting avenues for research. Silk wrapping, which increases assessment costs for females and compensates for the lower reproductive value of worthless gifts, facilitates the maintenance of the cheating strategy.

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