

## Evolution of deceit by worthless donations in a nuptial gift-giving spider

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**Abstract** Males of the nursery web spider *Pisaura mirabilis* usually offer an insect prey wrapped in white silk as a nuptial gift to facilitate copulation. Males exploit female foraging preferences in a sexual context as females feed on the gift during copulation. It is possible for males to copulate without a gift, however strong female preference for the gift leads to dramatically higher mating success for gift-giving males. Females are polyandrous, and gift-giving males achieve higher mating success, longer copulations, and increased sperm transfer that confer advantages in sperm competition. Intriguingly, field studies show that approximately one third of males carry a worthless gift consisting of dry and empty insect exoskeletons or plant fragments wrapped in white silk. Silk wrapping disguises gift content and females are able to disclose gift content only after accepting and feeding on the gift, meanwhile males succeed in transferring sperm. The evolution of deceit by worthless gift donation may be favoured by strong intra-sexual competition and costs of gift-construction including prey capture, lost foraging opportunities and investment in silk wrapping. Females that receive empty worthless gifts terminate copulation sooner, which reduces sperm transfer and likely disadvantages males in sperm competition. The gift-giving trait may thus become a target of sexually antagonistic co-evolution, where deceit by worthless gifts leads to female resistance to the trait. We discuss factors such as female mating rate and intensity of sperm competition that may shape the evolution of male deception, and how ecological factors may influence the evolution and maintenance of worthless gifts as an evolutionarily stable alternative mating strategy by frequency dependent selection [*Current Zoology* 60(1): 43–51, 2014].

**Keywords** Sexual selection, Sexual conflict, Nuptial gift, Worthless gift, Polyandry, Polymorphic trait, Sperm competition

Mating systems where males offer nuptial gifts to females to acquire matings and prolong copulations are common in a number of arthropod species (Boggs, 1995; Vahed, 1998). The nuptial gift is typically offered to a female during courtship or copulation and may take very different forms such as captured prey, regurgitated food, glandular and salivary secretions, spermatophores and substances in the ejaculate, or body parts (Vahed, 2007; Vahed, 1998). Examples include the spermatophylax in gryllids and tettigonids (Orthoptera), large spermatophores in butterflies (Lepidoptera), or insect prey in dance flies (Diptera), hangingflies, scorpionflies (Mecoptera) and some spiders (Bristowe and Lockett, 1926; Costa-Schmidt et al., 2008; Vahed K, 1998). Gifts can function as a male mating effort to attract mates, facilitate copulation, and increase sperm transfer to counter the effects of sperm competition, or as parental investment by increasing female fecundity or offspring survival, or they can provide protection against sexual cannibalism (Simmons and Parker, 1989; Thornhill,

1976b; Vahed, 1998). The benefits accrued by males are not mutually exclusive and may act in concert. What is common among the different strategies is that males exploit female foraging motivation in a sexual context (Bilde et al., 2007).

Males are expected to increase reproductive success by increasing the number of mates (Bateman, 1948) and are therefore under selection to evolve traits that increase the probability of attracting females. Nuptial gifts may represent such a trait, by increasing the chance of achieving a copulation. Females, on the other hand, may evolve to mate multiply to acquire direct benefits in the form of nutrients from the gift. While male exploitation of female foraging motivation can lead to a higher than optimal mating rate for females (Arnqvist and Rowe, 2005), females may solicit multiple matings and acquire improved fertility or offspring viability (Arnqvist and Nilsson, 2000; Simmons, 2005). Polyandrous mating systems impose strong selection on males to secure paternity in sperm competition. On the one hand, this fa-

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vours investment in a trait that females prefer, such as a nuptial gift. On the other hand, it may select for male traits that secure copulations and increase fertilization success at low cost. Although gift offering may notably increase male mating success, males must also pay the costs associated with gift-giving such as increased risk of predation while hunting for prey to offer, by producing energetic secretions (Simmons, 1990), or by 'giving up' entire body parts to the female (Fedorka and Mousseau, 2002). If gifts are costly, the cost-benefit ratio may favour evolution of deceit by offering 'cheap' gifts, for example ones that have already been consumed, or just a token item that can be found and offered to females as a genuine gift (LeBas and Hockham, 2005; Preston-Mafham, 1999). Furthermore, if deceit is hard to detect, for example if it is disguised, males can exploit the female preference before she realizes that the gift is worthless and responds by rejection.

In this context, deception could be a highly attractive strategy for males: it increases mating success by exploiting the female foraging motivation while reducing the costs associated with acquiring a 'genuine' gift (LeBas and Hockham, 2005; Preston-Mafham, 1999). Deceit could evolve when there is strong female preference for gift giving males and when there is intense intra-sexual competitive interactions over females. This is expected in polyandrous mating systems, in species where females are the limiting sex, if resources are lacking and male-male competition reduces the availability of prey for gifts, or if costs associated with genuine gifts construction are particularly high. However, offering worthless gifts is presumed to generate conflict between the sexes, as females will be lured into mating without the expected nutritional reward. Females may then evolve resistance to the trait, which in turn reduces male fitness. The evolution of deceit through worthless gift-giving behaviour may therefore lead to sexual antagonistic coevolution (Arnqvist and Rowe, 2005; Gwynne, 2008; Vahed, 2007).

## 2 Nuptial Gift-giving Spiders

Gift-giving behaviour in spiders is relatively rare and is best known in two families, the Global Pisauridae and the New World Trechaleidae. It has been described in the following species: the pisaurid *Pisaura lama* (Itakura, 1993), *Perenethis fascigera* (Itakura, 1998), *Pisaura mirabilis* (Bristowe and Locket, 1926), and *Thaumasia sp.* (Nitzsche, 1988) and the trechaleid *Paratrechalea ornata* and *Paratrechalea azul* (Costa-Schmidt et al., 2008), *Trechalea amazonica* (Silva and

da Lise, 2009). Males of the spider *Pisaura mirabilis* (Clerck, 1757) use insect prey wrapped in white silk as a nuptial gift. However, in some populations males frequently carry nuptial gifts with no nutritional value consisting of silk wrapped empty arthropods exoskeletons or even plant fragments (Bristowe, 1958; Nitzsche, 1988), and males succeed in luring females into mating by the use of such inedible donations (Albo et al., 2011). The mating behaviour of *Pisaura mirabilis* has been extensively studied and is an emerging model for understanding the evolution of nuptial feeding (Bilde et al., 2007), and for investigating how male-female interactions drive the evolution of deceit through worthless gift donation.

## 3 The Nuptial Gift-giving Spider

### *Pisaura mirabilis*

The nursery web spider *Pisaura mirabilis* is a hunting spider with Palearctic distribution, and the female builds a nursery web where she tends her brood. Males court females by offering a nuptial gift that consists of an insect prey wrapped in silk, and upon female acceptance copulation occurs while the female consumes the gift. Gift-giving behaviour is under sexual selection by strong female preference for the nuptial gift (Bilde et al., 2007; Stålhandske, 2001). Males appear to exploit female foraging motivation in a sexual context as hungry females mate more frequently than satiated females (Bilde et al., 2007), the gifts therefore acts as a strong driver of female re-mating propensity (Tuni and Bilde, 2010). A study by (Stålhandske, 2001) failed to detect direct fitness benefits derived from the nutrients of a single gift, but it is possible that females that mate 4 times or more gain direct benefits through nuptial feeding (Albo and Toft, personal communication, Tuni et al., 2013), therefore that the gift could also function as a paternal investment.

There is ample evidence that the gift functions as a mating effort by increasing male mating success dramatically, and prolonging the duration of sperm transfer by keeping the female occupied by feeding during copulation (Albo et al., 2011; Andersen et al., 2008; Stålhandske, 2001). The feeding time dictates copulation duration, therefore larger gifts promote longer copulations (Lang, 1996; Stålhandske, 2001). Since sperm transfer in this species is positively related to copulation duration (Albo et al., 2013), the duration of gift-consumption is ultimately expected to correlate positively with a male's fertilization success (Drengsgaard and Toft, 1999). Females of this species are known to

mate multiply (Tuni et al., 2013, Tuni and Bilde, 2010), therefore nuptial gifts that prolong copulation should confer advantages in sperm competition to males (Simmons, 2001). However, gift donation is not a fixed precondition of mating and *P. mirabilis* males are able to mate without gifts. Laboratory studies show that mating success for males without a gift reaches approximately 40% (Albo et al., 2011; Stålhandske, 2001). Males that mate without a gift suffer from significantly shorter copulations (approximately 30% of the total copulation duration of a male offering a genuine gift), and their reproductive fitness is dramatically reduced probably due to limited sperm transfer (Albo et al., 2011).

#### 4 Deceit by Worthless Gifts

Nuptial gift construction is costly for males, as it requires time and energy invested in prey capture, production of venom to kill the prey, lost foraging opportunities (Albo et al., 2011), transportation costs associated to carrying the weight of the gift while mate searching (Prokop and Maxwell, 2012) and silk investment for gift-wrapping (Lang, 1996). These costs could potentially favor deception as a very attractive strategy for males, if deception secures mating through exploitation of the female foraging motivation, thereby increasing male fitness without bearing the costs of producing a genuine gift. Indeed, *P. mirabilis* males can offer worthless gifts to females. Worthless donations may consist of inedible items such as empty insect exoskeletons (i.e. a previously sucked out prey), or even plant parts wrapped in silk and offered by males during courtship in a similar way as genuine gifts (Bristowe, 1958; Ghislandi and Albo, personal data). An experimental study showed that males that offered worthless donations were equally successful in gaining matings as males offering genuine nutritional gifts (Albo et al., 2011). Deceiving males, however, suffered from shorter copulation duration as females terminated copulation sooner compared to copulations with males offering nutritious gifts. This indicates female ability to assess the lack of nutritional value of the gift during gift consumption. Shorter copulations and reduced sperm transfer will inevitably disadvantage deceptive males in sperm competition (Drengsgaard and Toft, 1999). However, females probably sense the absence of nutrients to feed on only after regurgitating digestive fluids (Albo et al., 2011), which gives males the advantage of transferring sperm before the deceit is revealed and copulation terminated. Males are therefore likely to benefit from worthless gifts through elevated mating success even if

they experience reduced competitiveness under sperm competition.

A strong female preference for the gift-giving trait together with the substantial investment in gift construction by males in this system may have promoted the evolution of deceit in the form of worthless nuptial gifts. Females that mate with deceptive males, on the other hand, will experience costs associated with the energetic expenditure in digestive fluids production and regurgitation feeding on an inferior gift, in addition to possible costs of polyandry (Tuni et al., 2013).

#### 5 Silk Wrapping

One of the intriguing traits in *P. mirabilis* males is the wrapping of nuptial insect prey in white silk. This display occurs even without the presence of a female and is induced by perceived sexual stimuli, such as contact pheromones on female silk threads (Albo et al., 2011; Nitzsche, 1988). Therefore, in the field males are observed carrying the gift in their chelicerae while searching for females (Prokop and Maxwell, 2012) to be able to promptly perform courtship once a female is encountered (Austad and Thornhill, 1986). Gift-wrapping was proposed to have multiple functions. Stålhandske (2002) found that gift brightness due to silk threads increased gift attractiveness for females, as females accepted experimentally brightened gifts faster. She suggested that females are caught in a sensory trap where the white rounded nuptial gift offered by males exploit the female maternity instinct by mimicking the female egg sac (Stålhandske, 2002). However, direct tests using female egg sacs as nuptial gifts demonstrated that there was no significant difference between female acceptance rate of wrapped and unwrapped gifts or eggsacs, rejecting the sensory trap hypothesis (Bilde et al., 2007). Unwrapped gifts were actually accepted faster than wrapped ones suggesting that the prey insect is immediately recognized as food by females when it is unwrapped (Andersen et al., 2008; Bilde et al., 2007). Nevertheless, a male that is initially rejected by a female will add more silk wrapping to the gift in a highly ritualized mode, and by adding more silk threads and pursuing the female the gift is usually subsequently accepted (Bilde et al., 2007). This could also function as a male mating effort, for example if freshly deposited silk acts as a vehicle for chemical communication through male deposited pheromones that females could use in male assessment (Brum et al., 2012).

It was also shown that silk wrapping facilitates male gift control during copulation by drastically reducing

the risk of losing the gift to females (Andersen et al., 2008). Once females accept the nuptial gift, males ‘secure’ it with a silk thread and by holding onto the gift with the claws of the third pair of legs (Ghislandi and Albo, personal data), which facilitates some control over what is happening with the gift during sperm transfer. Males perform alternate pedipalp insertions into the females’ epigyne and transfer sperm to sperm storage organs situated ventrally on the abdomen. Between each insertion, the male returns to a frontal position and grasp the gift in his chelicerae, whilst females keep on feeding on it. During such mating interruptions, *P. mirabilis* females often try to escape with the gift. In this context silk wrapping facilitates male control over the gift because it allows a stronger hold with the chelicerae compared to an unwrapped prey and females as a result are less likely to steal the prey (Andersen et al., 2008; Hansen et al., 2008). The gift wrapping behaviour of prey is known from other spiders in a foraging context (Gilbert and Rayor, 1985), however in *P. mirabilis* it is only seen in males in a sexual context.

## 6 Silk Wrapping Facilitates Deceit

In addition to the obvious benefits to males of increasing their control over the gift during copulation, and in adding silk to prolong the time it takes for females to consume the gift, silk wrapping plays a crucial role in the evolution of deceit by worthless gifts. Silk wrapping allows males to disguise the gift content, and to gain matings by exploiting the female preference for the gift without paying the full costs of gift construction, i.e. prey capture and lost foraging opportunities. Deceiving males successfully use gift-wrapping to mask a worthless gift and lure females into mating as shown by the high gift acceptance rate of females courted by males offering worthless gifts (Albo et al., 2011). Silk wrapping may initially have evolved to immobilise live insect prey and facilitate transport of the captured prey in web building or cursorial spiders (Gilbert and Rayor, 1985). The function of silk wrapping in aiding control of the gift during courtship and copulation (Andersen et al., 2008), and in disguising the content of worthless donations are therefore likely derived functions.

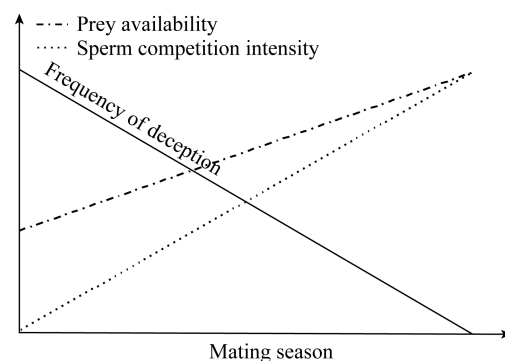
## 7 Thanatosis

Another intriguing and highly unusual behaviour in *P. mirabilis* males is a form of ‘thanatosis’ or ‘death feigning’ behaviour that frequently occurs when females interrupt matings and attempt to run away with the nuptial gift. Under these circumstances males death feign by

stretching-out their legs and literally hang on to the gift with their chelicerae while females move around without losing grip of the wrapped prey (Bilde et al., 2006). When the female resumes gift consumption males ‘come back to life’ and continue sperm transfer. Thanatosis behaviour dramatically increases male mating success by allowing males to complete or prolong copulation, and therefore functions as a male mating effort (Bilde et al., 2006; Hansen et al., 2008). The specific mechanism underlying the elevated mating success of death feigning males is unknown, however, the trait is polymorphic both within individuals and populations, suggesting a cost of death feigning for males (Hansen et al., 2008). Silk wrapping is decisive for retaining the grip of the gift by death feigning males so they do not lose it to females without copulation (Andersen et al., 2008). The evolution of gift-wrapping and thanatosis strongly indicate conflict of interests between males and females, as females attempt to steal the gift without copulations, whereas death-feigning males succeed in overcoming female resistance.

## 8 The Maintenance of Deceit as a Polymorphic Trait

A basic question is whether deceit by worthless gift donation is a plastic polymorphic trait that males can make use of opportunistically, or whether it is genetically fixed (Oliveira et al., 2008). If deceit is a plastic trait, we would expect males to choose a strategy depending either on cues in the environment, for example prey availability or female mating status (Fig. 1), or according to an internal threshold, for example his body condition or whether he has previously mated. If the alternative strategy (deceit) is condition-dependent, the



**Fig. 1** The frequency of worthless gifts (solid line) is expected to decrease with increasing sperm competition intensity (dotted line) and prey availability (dashed line) over the course of the mating season

The Y axis represents the frequency of deception in relation to prey availability and sperm competition intensity.

threshold that determines the switch from one strategy to another could be environmentally dependent, for example depending on what strategy other males in the population use (Maynard Smith, 1982; Parker, 1970a; Parker and Simmons, 1994). The threshold for the switch from one strategy to another may in itself be genetically determined and therefore subject to respond to inter-sexual and intra-sexual selection. Although probably less likely (Gross, 1996), it is also possible that worthless donation is a fixed genetic trait, where males present either genuine or worthless donations depending on their genotype. Even if worthless donation is a recessive trait, it would be maintained in the population in heterozygotes. These questions are challenging, and careful experiments where males are tested in different contexts for consistency of the occurrence of deceit would be necessary to provide some answers. Regardless whether the alternative strategy arises from a proportion of individuals showing the alternative trait, or from individuals changing between strategies in response to some threshold, the evolutionary explanation for the maintenance of the alternative trait in a population relies on equal fitness pay-offs of both traits (Maynard Smith, 1982).

Given the conflict of interests between the sexes that worthless donations reinforce, one of the most pertinent questions to ask is whether deception is maintained as an evolutionarily stable strategy (ESS) in natural populations. First it is important to note that deceit with worthless gifts varies among populations. A study of a Danish population showed that 38% of nuptial gifts collected in the field were worthless donations that contained a non-nutritious insect exoskeleton wrapped in silk (Albo et al., 2011). Sampling of males with gifts in the field in a following year showed a similar proportion of worthless gifts in this population (Ghislandi and Albo, personal data). A study from a Slovakian population however, showed that all field-collected nuptial gifts were genuine and consisting of fresh insect prey (Prokop and Maxwell, 2012). We are therefore faced with multiple problems: does the frequency of worthless gift donations vary consistently within and among populations and temporarily over years? What causes differences in deceit among populations? How is variation maintained within and among populations? Differences in frequency in occurrence of worthless gifts suggest that ecological conditions result in differential selective forces among populations that result in the observed divergent patterns. In the following sections

we will propose and discuss some of the relevant ecological conditions that are likely to influence the evolution of deceit, and whether frequency dependent selection is likely to maintain worthless gifts as ESS.

## 9 Sperm Competition Intensity

The proportion of females that mate multiply and the number of mating partners females have are factors that determine the intensity of sperm competition, which may interact with male deception (Parker, 1970b; Parker and Simmons, 1994). Due to the costs of worthless gift donations for males in terms of shorter copulations (Albo, 2011), it is possible to formulate the hypothesis that this strategy should be less common when the frequency of polyandry is high and sperm competition is most intense, as deceiving males would lose paternity in competition with males offering genuine gifts (Fig. 1). This hypothesis rests on the assumption that deceit is a plastic trait. If populations differ in the intensity of sperm competition, we would therefore predict that deceit by worthless gifts should be more frequent when sperm competition is low or intermediate. However, the opposite prediction can also be made: under strong sperm competition deceiving males benefit from securing even a small share in paternity. Also, male-male competition may lead to higher pressure on the local prey population and reduce the availability of prey for gifts, which could also favour male deception.

Female mating frequency is known to undergo temporal changes, as sperm competition intensity is expected to be highest at the end of the breeding season (Parker, 1970b; Simmons et al., 2007). Consequently, the pay-off of deceit may change over the course of the mating season. To understand how sperm competition intensity shapes the frequency and maintenance of deceit among and within populations, data on natural mating rates in multiple populations and throughout the season are needed. One possibility for the maintenance of polymorphism in the nuptial gift-giving trait is frequency dependent selection, where differences in selective pressure over the mating season favours different male strategies. This hypothesis could be tested by determining female natural mating rates and the associated fitness pay-off of male strategies to determine whether sperm competition risk is related with the expression of male deception in a consistent pattern (Fig. 1).

## 10 Male Condition and Prey Availability

Males may need to partition their energetic invest-

ment between reproduction and survival, and males in poor feeding condition may preferentially invest in nutrition rather than mating opportunities (i.e. eat rather than wrap the prey). Young adult males for example are known to feed on caught prey for several days and initiate gift construction only when they are in good feeding condition (Nitzsche, 1988), whereas old satiated males are less likely to feed on gifts and instead donate the entire prey to the female investing exclusively in reproduction (Albo et al., 2011). Males in poor body condition may therefore use 'empty' prey as nuptial gifts and thereby donate previously eaten meals with no nutritional value to the female. A reuse of inedible gifts is known in the empidid dance fly *Rhamphomyia sulcata* (Le Bas and Hockham; 2005, 2005), whereas in the hanging fly *Bittacus appicalis* males try to retrieve the gift after copulation to use it in the next mating attempt (Thornhill, 1976a). Male hunting abilities may also be compromised by poor body condition, leading males to construct gifts using dead insect carcasses found on the ground or even plant fragments such as seeds or small leaves (Albo et al., 2011; Ghislandi, personal data). The latter explanation for the use of worthless gifts would allow females to assess male hunting ability and use genuine gifts as an indicator of high quality.

Also prey availability may influence the frequency of male deception. When prey is abundant, honest donations may be the most common strategy, whereas under low prey availability, deception may be favoured due to the scarcity of food. Prey abundance in temperate climates is expected to increase in parallel to the mating season (in Denmark from May–July) (Wolda, 1988), suggesting that deceit might be favoured early in the season when prey availability is lower (Fig. 1). Studies quantifying the frequency of deceit by males in natural populations in relation to male body condition and prey availability are needed to investigate these hypotheses.

## 11 Female Counter-Strategies against Deceit

Deception should be costly for females, as females that mate with males donating a worthless gift obviously gain no nutritional benefits and may suffer from costs of mating, such as disease transmission, exposure to predators, and possible physical injuries (Arnqvist and Rowe, 2005; Knell and Webberley, 2004). Females should therefore evolve mechanisms to counter manipulative strategies, as for example the ability to discriminate between nutritious and non-nutritious gifts.

Pre-copulatory gift discrimination does not occur in this system, females mate acceptance does not vary much among males with gifts that vary in their wrapping state (wrapped vs unwrapped) (Bilde et al., 2007), and quality of wrapping (well vs poorly wrapped gifts) (Albo et al., 2012), or shape (round vs oblong) (Andersen et al., 2008), as long as a gift is presented. However, males offering worthless gifts experience approximately 30% shorter copulation duration compared to males donating a genuine gift, as females interrupt the copulation sooner when feeding on a worthless gift (Albo et al., 2011). Female control over mating duration may therefore be considered a female counter strategy that favours males that donate nutritious gifts. However, females are able to discriminate the gift's value (if the content of the gift is genuine or not) only after digestion of the external silk layers has started. In a study of worthless gifts that consisted of a cotton ball, the gift was wet when mating was terminated, indicating that regurgitation of female digestive fluids had occurred (Albo et al., 2011). Therefore deceit seems to be a trait it is difficult for females to evolve resistance to, given that sperm transfer is already initiated once it is discovered. However, if the cost of mating is high, frequent encounters with worthless gifts could lead to a co-evolutionary arms race resulting in reduced female preference for nuptial gifts and ultimately a loss of function of the nuptial gift in mate acquisition (Arnqvist and Rowe, 2005).

## 12 Post Copulatory Female Choice

While pre-copulatory mate choice based on gift quality seems unlikely here, females may evolve post copulatory mate choice through preferential use of sperm from males offering genuine gifts (Birkhead and Pizzari, 2002; Eberhard, 1996). Recent evidence shows that polyandrous *P. mirabilis* females gain indirect benefits in the form of enhanced egg hatching success (Tuni et al., 2013). Furthermore, females store more sperm from males that offer a gift compared to gift-less males, indicating the ability of females to strategically store sperm in response to gift presence (Albo et al., 2013). In many invertebrate systems where females store sperm from multiple partners mate choice occurs via selective control of sperm stores in the female spermatheca, as described in crickets (Bretman et al., 2004), dung flies (Bussiere et al., 2010) and spiders (Welke and Schneider, 2009). Whether females differentially store sperm from males offering genuine compared with worthless gifts is not known, however, if the trait has a genetic basis females that favour males with genuine gifts may derive

indirect fitness benefits (Bilde et al., 2008; Tuni et al., 2013). This also applies if the threshold for switching between genuine and worthless gifts has a genetic basis, in which case the threshold would come under selection by female preference.

If polyandrous females derive indirect benefits by cryptically favouring sperm from males that offer genuine nutritious gifts, they may counter the costs of accepting worthless gifts. Alternatively, by favouring males with high mating success (either honest or deceptive) females may gain 'sexy sons' provided the trait conferring high mating success has a genetic basis. The latter could lead to run-away sexual selection predicting fixation of the most successful trait (Fisher, 1930), however the presence of the polymorphism renders this scenario less likely.

### 13 Female Preference for High Condition Males

As gift construction is costly, females may evaluate their partners depending on gift quality. Albo et al. (2011) showed that males in good body condition (well fed males) were investing significantly more in gift construction than males in poor condition (starved males), suggesting that females can use gift-wrapping as an honest signal of male quality. However, an experimental study showed that females do not choose males based on gift 'quality' as an indicator, where a well wrapped gift would be a signal of a male in good condition. Instead, females ignored the gift signal and chose males in good condition regardless of the quality of the gift they presented (Albo et al., 2012). As silk can be used to mask the gift content, this finding is consistent with the hypothesis that *P. mirabilis* females may have evolved to ignore the gift as a quality signal (Arnqvist and Rowe, 2005), and instead screen males based on copulatory courtship performance. Males may then be evaluated based on their courtship abilities, such as condition dependent vibrations (Hunt et al., 2004; Kotiaho, 2002; Lomborg and Toft, 2009).

### 14 Deception as an Evolutionarily Stable Strategy

A trait that confers fitness benefits is expected to out-compete a less advantageous trait and become fixed in the population (Maynard Smith, 1982; Maynard Smith and Price, 1973). Since the majority of *P. mirabilis* males do not offer worthless gifts, this may indicate that deception is an alternative strategy maintained by

frequency dependent selection or condition dependence (Oliveira et al., 2008). As discussed above, some important factors influencing the prevalence of deceit may be the degree of polyandry and sperm competition in the population, and prey availability, which influences both male and female body condition (Fig. 1). These factors are likely to change over the mating season, such that deceit is favoured early in the season where prey availability and sperm competition are expected to be lowest, but selected against late in the season where prey availability and sperm competition increase (Fig. 1). This scenario would explain the existence of worthless gift donations by frequency dependent selection at least in some populations. Insect prey availability is expected to increase over the course of the season in the temperate Palearctic distribution of *P. mirabilis* (Wolda, 1988). However, our lack of knowledge on how the level of polyandry, body condition and prey availability interact to shape mating preferences leads us to present these hypotheses with caution. More studies are needed on whether deceit is repeatable and fixed in certain frequencies, or whether it is variable and context dependent, to understand male deceptive behaviour as an alternative mating strategy.

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