

Extreme male mating behaviours: anecdotes in a nuptial gift-giving spider

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Summary

Nuptial gifts may serve to increase male mating success, copulation duration, and fertilization success, as is known for the nuptial feeding spider *Pisaura mirabilis* Clerck, 1757. In this species, strong sexual selection for the gift-giving trait may lead to male strategies, such as gift enlargement or thanatosis behaviour (death feigning), which ultimately maximize male fitness. In laboratory trials, we observed male gift enlargement by inclusion of an autosomal (self-amputated) limb, female consumption of male soma during copulation, and high-injury risk thanatosis in which a male feigned death while still in copula and only attached to the female with his pedipalp, instead of hanging onto the gift with the chelicerae as is performed in a typical thanatosis. Although the observations are anecdotal, we propose functional hypotheses for these traits in the context of extreme male mating effort and cannibalism avoidance, which are characteristics of the mating system of this species. Sexual selection and sexual conflict are major evolutionary forces that shape a variety of morphological, behavioural, and physiological traits (Parker 1979). Males must compete intra-sexually over access to females or inter-sexually to attract females, and have evolved traits that serve to increase their reproductive success (Andersson 1994).

Introduction

In mating systems in which access to females is limited and competition among males intense, males may adopt extreme mating strategies, in which female monopolization and paternity assurance is often achieved at the expense of the male's own survival (Schneider & Fromhage 2010). Self-sacrifice, in which males feed themselves to females is one of the most severe forms of extreme male mating behaviour. Male Australian red-back spiders, for example, perform a 180° somersault into the female's mouthparts during mating, a behaviour that facilitates cannibalism, and is adaptive for males as it increases their paternity (Andrade 1996). Breakage of male copulatory organs during mating, resulting in male death or functional sterility, is also common in various spider species (Schneider & Fromhage 2010). Similarly, in bees and certain ants, males die by breaking off their abdomen during mating (Boomsma, Baer & Heinze 2005).

To out-compete rivals, males may adopt other mating strategies, such as providing nuptial gifts, which are nutritional donations offered to females during courtship or mating that attract partners, facilitate copulation, and

increase sperm transfer (Vahed 1998). Gifts may consist of captured prey, seminal substances transferred during copulation, or even somatic gifts, consisting of specialized body structures on which females feed. Male ground crickets, for example, possess spurs on their hind legs that females chew on during mating (Mays 1971), whereas male dwarf spiders possess a dorsal cephalic elevation from which secretory glands produce a substance taken up by females during mating (Kuntz, Garbe & Uhl 2012). Although females in some species may benefit from nuptial gifts, there is much scope for sexual conflict, as males may manipulate females into re-mating rates below their optima (Arnqvist & Rowe 2005).

Male nuptial gifts in the form of captured prey are relatively rare in spiders (Albo, Toft & Bilde 2013), and occur in the Palaearctic *Pisaura mirabilis* Clerck, 1757 (Araneae: Pisauridae). Males of this species offer a silk-wrapped insect prey during courtship. Upon female gift consumption, the male enters the mating position and inserts his pedipalp into the female's epigyne. The gift, which exploits the female foraging motivation in a sexual context (Bilde *et al.* 2007) is under strong sexual selection, as gift-less males suffer from decreased mating success (Stålhandske 2001; Albo *et al.* 2011). The gift functions as a male mating effort by increasing male mating success, assuring sperm transfer, and prolonging copulation duration, which correlates positively with male fertilization success (Stålhandske 2001; Albo *et al.* 2011). Control over the gift during mating is of crucial importance as females often attempt to steal the gift and then avoid or interrupt copulation. Silk wrapping facilitates male gift control during courtship and copulation, and reduces the risk of losing the gift to the females (Andersen *et al.* 2008). Males may also overcome female resistance by performing thanatosis (death feigning) (Bilde *et al.* 2006; Hansen *et al.* 2008), a stereotyped behaviour in response to female attempts to escape with the gift. When females cease eating and try to take the prey, males stretch-out their legs and hang motionless onto the gift with their chelicerae (mouthparts), while being dragged by the female. Once females resume gift consumption, males insert their pedipalp and resume sperm transfer (Bilde *et al.* 2006; Hansen *et al.* 2008). These behaviours strongly suggest conflicting interests over mating rate and mating duration between the sexes (Arnqvist & Rowe 2005). This scenario is further supported by the male ability to deceive females into mating using worthless or inedible silk-wrapped items as gifts (Albo *et al.* 2011).

Material and methods

Here, we describe the methods adopted to raise the spiders and the observations recorded during experimental trials. We collected *Pisaura mirabilis* spiders at juvenile stages in April 2013 from Mols, near Aarhus (Denmark), and from Merlino, near Lodi (Italy). Specimens were housed individually in 30 ml vials containing moist *Sphagnum* moss in the laboratory at Aarhus University, Denmark. Individuals were fed three times per week with green-bottle flies (*Lucilia* spp.), house flies (*Musca domestica*) and crickets (*Gryllus* spp.). Water was provided daily. Spiders were raised at room

temperature (on average 20°C) and natural photoperiod. Once individuals reached sexual maturity (approximately 14 days after their final moult) they were assigned to mating experiments. Mating trials took place in transparent plastic terraria (19 × 19 × 15 cm) in which females were allowed to walk and leave draglines for approximately 1 hour before the start of the trial in order to stimulate a sexual response in males. Prior to the mating experiments, males were given a fly (*Lucilia* sp.) to wrap with silk as a nuptial gift, and were subsequently introduced to the female. During a total number of 250 experimental trials we observed the following behaviours.

Results

Gift enlargement via male limb autotomy

An adult male was observed performing autotomy (self-amputation) of one of its legs (3rd pair) by literally pulling its leg off with its chelicerae, and fixing it with multiple silk threads to the nuptial gift it had previously constructed by wrapping a fly in silk. This behaviour occurred when the male was alone in its vial prior to contact with a female.

Since it was not possible to determine whether the leg had previous damage or was completely functional, different costs could have been involved in the described autotomy.

Soma-consumption by females during copulation

During an experimental trial in which we paired a non-virgin female with a gift-less virgin male, we observed the female feeding on the male's leg during copulation. As previously reported for gift-less males (Albo *et al.* 2011), the male courted the female by repeatedly vibrating his abdomen, bouncing towards and around the female, and finally pushing up the female to reach her ventral epigyne. After four minutes of courtship the male inserted his right palp in the female's epigyne. At this stage, the female bit the male's leg, and started feeding on a droplet of emerging hemolymph that was clearly visible on the female's chelicerae. The male did not escape but remained motionless and continued copulation for 10 minutes; during this time the female fed on the male's limb.

Pedipalp insertion during thanatosis

In two mating trials we observed gift-giving males *in copula* with virgin females performing thanatosis without removing their pedipalp from the female's epigyne. In the first trial, the female attempted to avoid copulation and escape with the gift once the male assumed the mating position and inserted his pedipalp. In the second trial, the female attempted to take the gift and interrupt copulation after 20 minutes of male pedipalp insertion. In both cases, the female's movements triggered thanatosis: males stretched out their legs and hung motionless, anchored on the gift with their chelicerae, and were transported by the females

through the experimental arena. Notably, these males did not disengage their pedipalp from the female's epigyne and, once the female started moving, they remained suspended from the female's body with the pedipalp still inserted. One of the males did not fix his chelicerae to the gift, which is how males usually remain attached during thanatosis (Bilde *et al.* 2006), and was dragged solely attached by his palp. In both cases, once females stopped moving and restarted gift consumption, copulation was resumed and sperm transfer was clearly occurring, as the haematodocha of the inserted palp was pulsating.

However, it was not possible to determine whether during these unusual thanatosis males were transferring sperm while dragged in the mating arena or if they interrupted sperm transfer until the females stopped moving.

Discussion

Limb or caudal self-amputation (autotomy) is known as a defensive strategy to counteract predation or negative consequences of appendage damage in several taxa, including arthropods (Maginnis 2006; Fleming, Muller & Bateman 2007). In spiders, autotomy is recorded across several families and is known to have very marginal costs, by not reducing locomotor or prey-capture ability (Brueseke *et al.* 2001), competitive fights over prey, or development (Johnson & Jakob 1999), and male's mating success (Brautigam & Persons 2003). These relatively negligible costs, suggesting that one or two limbs can be sacrificed with very little negative effect, have led to the spare limb hypothesis for this taxonomic group (Fleming, Muller & Bateman 2007). Although autotomy has been observed in spiders in a sexual scenario, as described for *Tidarren cuneolatum* males which amputate one of their palps a few hours after the penultimate moult and insert a single palp during copulation (Knoflach & Van Harten 2000), it has never been documented in the context of nuptial gift construction.

In addition to the insect prey, *Pisaura mirabilis* males are known to include several elements in the nuptial gift via silk wrapping, e.g. nutritionally worthless items such as sucked-out insect carcasses, plant parts or seeds, or a combination of these (Albo *et al.* 2011). This creates the potential to enlarge the gift prior to encounters with females. Since gift consumption predicts copulation duration, larger gifts lead to longer copulations and consequently larger transfer of ejaculate, representing a remarkable advantage in sperm competition (Lang 1996; Stålhandske 2001; Albo *et al.* 2011). Males should, therefore, be under strong selection pressures to donate large gifts. Due to the low costs of leg loss, inclusion of an autotomized leg to the nuptial gift should increase gift size and, ultimately, lead to fertilization advantages at low expense for the male. This prediction, however, relates to a hypothesis that remains to be tested. What triggered leg autotomy in our laboratory trial (e.g. disease, chemical stimulation from cues of conspecific, inadequate size perception of the nuptial gift) also remains unknown and should be subject to further investigations.

Low costs of appendages loss may also explain female limb consumption during copulation. During our observation, leg consumption seemed to replace the function of gift

consumption by allowing the male to copulate while the female was motionless and occupied by feeding. Gift-less males are known to suffer from reduced mating success and shorter copulations, which translates into lower sperm transfer and fertilization success (Stålhandske 2001; Albo *et al.* 2011). Thus, allowing the female to feed on one leg may serve to prolong copulation duration, and ultimately to increase male reproductive success.

Providing the female with a nuptial gift may also function to reduce the risk of cannibalism (Fromhage & Schneider 2005). In *Pisaura mirabilis*, sexual cannibalism, in which a female kills and consumes the male, occurs in 1.2–4% of laboratory trials (Bilde *et al.* 2006; Hansen *et al.* 2008), suggesting that the trait may have evolved as a cannibalism avoidance strategy. Cannibalistic attacks may result in the male surviving while the female consumes part of the male, most commonly a leg (Bilde *et al.* 2006). However, cannibalistic attacks usually occur either pre- or post-mating and not concurrent with sperm transfer. To our knowledge, sperm transfer during soma consumption that does not include killing and consuming the mate as observed here, has so far only been seen in species with specialized body structures such as dorsal cephalic secretions (Mays 1971; Kuntz, Garbe & Uhl 2012). Intriguingly, autotomy in *Pisaura mirabilis* may serve both as a substitute for a nuptial gift to facilitate sperm transfer and as a cannibalism avoidance behaviour, in which the male's leg has acquired alternative functions in a sexual context.

Thanatosis is an adaptive male mating strategy that allows males to increase their reproductive success by remaining in contact with resistant females (Hansen *et al.* 2008). During thanatosis the male fixes his chelicerae to the gift and remains motionless, with his legs stretched out and un-inserted pedipalps raised. Not removing the pedipalp from the female epigyne may be advantageous for males if it allows sperm transfer during female movements, or to resume sperm transfer more promptly once the female stops moving. The suggested mechanism of sperm transfer relies on capillary forces (Foelix 2011), and whether transfer is possible during thanatosis remains unclear. Nevertheless, by engaging in such behaviour, males may face severe injury risks, as pedipalp damage or breakage could limit their current and future reproductive success. Whether death feigning while the male is *in copula* with the female is an adaptive strategy that increases sperm transfer, similar to the somersault behaviour of red-back spiders (Andrade 1996), remains to be explored.

To conclude, whilst the functional significance of the extreme male mating behaviours reported here awaits further study, we believe our observations represent intriguing examples of male alternative mating strategies, providing a basis for further investigations. We hypothesize that the reproductive advantages of the gift-giving trait and thanatosis favour the evolution of extreme male mating behaviours such as those reported here.

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