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Biol. Lett. 2006 **2**, 23-25

doi: 10.1098/rsbl.2005.0392

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Death feigning in the face of sexual cannibalism

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Pre-copulatory sexual cannibalism by females affects male and female reproductive success in profoundly different ways, with the females benefiting from a meal and the male facing the risk of not reproducing at all. This sexual conflict predicts evolution of traits to avoid cannibalism and ensure male reproductive success. We show that males of the nuptial gift-giving spider *Pisaura mirabilis* display a remarkable death feigning behaviour—thanatosis—as part of the courtship prior to mating with potentially cannibalistic females. Thanatosis is a widespread anti-predator strategy; however, it is exceptional in the context of sexual selection. When the female approached a gift-displaying male, she usually showed interest in the gift but would sometimes attack the male, and at this potentially dangerous moment the male could ‘drop dead’. When entering thanatosis, the male would collapse and remain completely motionless while retaining hold of the gift so it was held simultaneously by both mates. When the female initiated consumption of the gift, the male cautiously ‘came to life’ and initiated copulation. Death feigning males were more successful in gaining copulations, but did not have prolonged copulations. We propose that death feigning evolved as an adaptive male mating strategy in conjunction with nuptial gift giving under the risk of being victimized by females.

Keywords: sexual cannibalism; sexual conflict; cannibalism avoidance; thanatosis; male mating strategy

1. INTRODUCTION

Pre-copulatory sexual cannibalism affects male and female reproductive success in dramatically different ways and represents the ultimate sexual conflict (Parker 1979; Partridge & Hurst 1998). The consumption of a potential mate prior to insemination may be an adaptive female foraging strategy solely on a nutritional basis (Newman & Elgar 1991). While providing the female with a meal, pre-copulatory cannibalism is obviously non-adaptive for males who face the risk of not reproducing at all. This sexual conflict has been suggested to result in antagonistic coevolution of traits, involving the evolution of male traits aimed at reducing the risk of sexual cannibalism. Yet, there is little empirical evidence for such traits.

The nuptial gift-giving spider *Pisaura mirabilis* displays a striking death feigning behaviour—

thanatosis—as part of courtship. Death feigning concurrent with nuptial gift presentation is a novel behaviour and previously undescribed in *P. mirabilis* (Bristowe 1958; Stålhandske 2001). Thanatosis is a widespread anti-predator strategy in which the potential prey freezes or plays dead to avoid the attention of the predator (Edmunds 1974). We propose that death feigning in conjunction with the nuptial gift evolved as an adaptive male mating strategy to overcome the risk of sexual cannibalism.

2. MATERIAL AND METHODS

Sub-adult *P. mirabilis* (Clerck) were collected in April 2004 from a grass meadow in the eastern part of Jutland, Denmark. The spiders were kept individually in vials (3 cm in diameter, 7 cm in height) supplied with wet fresh *Sphagnum* moss as a substrate at room temperature (approx. 20 °C) and at natural photoperiod. Each individual was fed twice a week with two to three houseflies (*Musca domestica* L.) obtained from a laboratory culture and were assigned for experiments when they reached adulthood. Experiments were performed in transparent plastic terraria (17×17×10 cm) with *Sphagnum* moss. A female was transferred to the terrarium approximately 15 min prior to the mating experiment and subsequently a male holding a nuptial gift was introduced and female and male responses were recorded.

The nuptial gift offered to females during courtship is usually a prey item wrapped in silk. We quantified death feigning in mating experiments where males presented different nuptial gift types to unmated females. Nuptial gifts were a silk wrapped fly or an unwrapped fly (*M. domestica*) or a conspecific eggsac $n=14$, 27 and 16, respectively. These gift types were chosen to alter the size and appearance of gifts which may result in differences in prevalence for thanatosis; hence, eggsacs are larger than flies and silk wrapped gifts may be more attractive than unwrapped gifts (Stålhandske 2002).

In a second experiment, we tested whether death feigning was influenced by female hunger state (females were fed either three or six flies per week) and mated state (virgin or single-mated) in a full factorial two-factor design ($n=68$). Males presented wrapped flies as gifts.

3. RESULTS

When courting a female, the male performed his remarkable display, presenting the nuptial gift in the chelicerae while raising the body to a near-vertical position with the front legs held above the head and the tip of the abdomen touching the ground (illustrated in Bristowe 1958). In this position, the male's body was partly hidden behind the gift that may possibly act as a shield. When the female approached, she usually showed interest in the gift but would sometimes attack the male, and at this crucial point the male could ‘drop dead’. When entering thanatosis, the male, while still holding the gift with his chelicerae, would extend his legs backwards and remain completely motionless in a stretched out posture. The gift was held simultaneously by both mates and sometimes the female dragged the immobile male around when carrying the gift along with her. When the female initiated consumption of the gift, the male, ‘came to life’ and cautiously moved under her into the mating position and initiated copulation. The male kept contact with one leg on the nuptial gift during copulation, seemingly in an attempt to sense female activity.

The mean proportion of death feigning males in the first experiment was 32% and did not significantly differ between nuptial gift type (21% for wrapped fly, 31% for unwrapped fly and 44% for eggsacs; generalized linear model (GLM), binomial errors, $p=0.25$).

In the second experiment, 51 females (75%) accepted the nuptial gift, and thanatosis occurred in 43% of these encounters with no significant effect of female hunger state or mated state (proportion of males performing thanatosis on encounter with: virgin starved females 44%, $n=18$; virgin satiated females 33%, $n=12$; mated starved females 25%, $n=8$; mated satiated females 62%, $n=13$; GLM, $p=0.26$).

All males that played dead prior to copulation succeeded in copulating with the female compared to 58% of the males that did not perform thanatosis (GLM; $p=0.0018$, $n=51$). All males, including those that did not death feign, courted the female and offered the nuptial gift in the attempt to mate; hence death feigning increased male mating success. No effect of death feigning was found on copulation duration ($p=0.32$).

Females frequently interrupted copulations and could be aggressive towards males while attempting to depart with the gift. In response to interruptions, the male retained hold of the gift with his chelicerae and entered thanatosis (82%, $n=28$). When the female resumed consumption, the male resumed copulation. Sexual cannibalism occurred in 4% of the mating trials and occurred exclusively during pre-copulatory courtship.

4. DISCUSSION

Death feigning males were more successful in gaining copulations but did not achieve longer copulations, signifying a function of this behaviour in overcoming the risk of approaching a potentially dangerous mate. We suggest that death feigning evolved as an adaptive male mating strategy under the risk of being victimized by females prior to insemination.

Sexual cannibalism is prevalent among Arachnids and well known in the family Pisauridae (Zimmerman & Spence 1989; Elgar 1992). Studies in a related species indicate that females most commonly attack during pre-copulatory courtship and that the male is killed in 5–10% of these attacks (Arnqvist & Henriksson 1997), imposing continual selection on males to evolve counter strategies (Dukas 2001). Pre-copulatory sexual cannibalism may result from selection for high levels of aggression towards prey (Arnqvist & Henriksson 1997; Johnson 2001), because large body size in females is associated with high fecundity (Newman & Elgar 1991). Under this scenario, sexual cannibalism evolves as a female foraging strategy which is not necessarily adaptive when viewed solely in the context of mating. Aggression towards a potential mate may result from 'spillover' of high levels of aggression towards food that is favoured in previous life-history stages (Arnqvist & Henriksson 1997).

Surprisingly, the evolution of male traits that reduce the risk of sexual cannibalism has previously been rejected on the basis of few observed cannibalistic incidents (Austad & Thornhill 1986; Cumming 1994; Stålhandske 2001). The idea behind this argument was that if cannibalism is rare, it is not a strong selective force. However, the argument can be reversed: any non-zero risk of death prior to

insemination creates selection on males to evolve counter strategies (Edmunds 1974; Dukas 2001). Such strategies reduce the risk of being cannibalized, and therefore frequent cannibalistic events are not expected. It remains inherently difficult to identify the evolutionary origin of an observed trait, yet we propose that the risk of cannibalism has shaped the evolution of male counter adaptations. The current male mating strategy may result from coevolutionary processes where traits that reduce the risk of cannibalism ultimately facilitate copulations. Furthermore, few cannibalistic attacks in previous studies of *P. mirabilis* were possibly an experimental artefact, since the females were well fed (Austad & Thornhill 1986; Stålhandske 2001) which would reduce female attack propensity (Polis 1981; Andrade 1998).

In cannibalistic species, it is frequently seen that males reduce the likelihood of female attack by postponing mating until the female is engaged in prey consumption (Fromhage & Schneider 2005 and references therein; see also Arnqvist *et al.* 2003). In *P. mirabilis*, males offer a nuptial gift, which in itself could be a mating effort that reduces the risk of cannibalism (Bristowe 1958), and death feigning males remain attached to the gift. This coupling of traits suggests a concerted evolution of nuptial gifts and thanatosis as male strategies to reduce pre-copulatory sexual cannibalism. It appears that the strategy of *Pisaura* males is to direct female attention to the gift prey while entering thanatosis until the female chelicerae are engaged in feeding and pose no danger. In support of this notion, thanatosis was very frequent (82%) when females interrupted copulations and attempted to run away with the nuptial gift. Females could attack the males when interrupting copulations. Death feigning males remained attached to the gift and resumed copulation when the female resumed consumption. Copulation duration is positively correlated to sperm transfer and fertilization of eggs (Stålhandske 2001), signifying the interest of males in completing sperm transfer following interruption.

Death feigning is exceptional in the context of sexual selection. We are aware of one example of thanatosis performed by female robber flies to avoid male harassment (Dennis & Lavigne 1976). Lawrence (1992) describes that male mantids sometimes freeze at a distance from the female when they are moving away from her after mating is completed, which could be a post-copulatory cannibalism avoidance behaviour. Pre-copulatory death feigning as in *P. mirabilis* appears to be an extraordinary adaptation in a sexual context.

Not all males in the experiments death feigned; one possible explanation could be that playing dead is a high-risk/high-reward strategy which is not always beneficial. Death feigning as an anti-cannibalism adaptation helps to reduce the overall risk of eliciting aggression by females but might at the same time increase the risk of being victimized if attacked. This would imply that death feigning males increase their chance of achieving copulations, but also face a higher mortality risk if the female attacks. Under this scenario, the choice of strategy is not obvious

and will critically depend on confounding factors such as the number of future mating opportunities males get.

We thank Göran Arnqvist for valuable comments on the manuscript.

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