Thanatosis as an adaptive male mating strategy in the nuptial gift–giving spider *Pisaura mirabilis*

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Males and females often experience different optima in mating rate, which may cause evolution of female resistance to matings and male counter adaptations to increase mating rate. Males of the spider *Pisaura mirabilis* display a spectacular mating behavior involving a nuptial gift and thanatosis (death feigning). Thanatosis in a sexual context is exceptional and was suggested to function as an antipredation strategy toward potentially cannibalistic females. If thanatosis serves as a protection strategy, males should death feign in response to female aggression or when they are more vulnerable to attack. We tested these predictions in a factorial design: males that were handicapped (1 leg removed) and hence vulnerable and control males were paired with females that were more or less aggressive intrinsically (measured toward prey). In mating trials, we recorded the tendency of males to death feign, copulation success, and copulation duration. In addition, we investigated the effect of female mating status (virgin or mated) on these male mating components. Intrinsically aggressive females showed increased mating aggression toward males. Neither female aggressiveness, mating status, nor male vulnerability increased the propensity of males to perform thanatosis. Instead, death-feigning males were more successful in obtaining copulations and gained longer copulations. Hence, our results suggest that thanatosis functions as an adaptive male mating strategy to overcome female resistance. All males were capable of performing thanatosis although some males use it more frequently than others, suggesting a cost of death feigning which maintains the variation in thanatosis during courtship. *Key words:* coevolution, death feigning, male mating effort, nuptial gift, polyandry, sexual cannibalism. *[Behav Ecol 19:546–551 (2008)]*

INTRODUCTION

Usually females invest more energy and resources into gamete production and offspring care than males (Trivers 1972). While males increase their reproductive success by mating with multiple females, 1 mating is usually enough to ensure the fertilization of a female's eggs. Nevertheless, polyandry is widespread also in organisms where males seemingly invest only gametes (Birkhead and Møller 1998), and polyandrous females may obtain material or genetic benefits which increase their survival, fecundity, or offspring fitness (Andersson 1994; Arnqvist and Nilsson 2000). However, polyandry can be costly (Arnqvist and Rowe 2005), and the relative costs and benefits to females of polyandry can lead mated females to become choosier toward additional males (Andersson 1994; Gabor and Halliday 1997; Maklakov et al. 2003). This may result in a coevolutionary arms race, where females evolve resistance and males evolve traits to increase their chance of additional matings (Andersson 1994; Holland and Rice 1998; Arnqvist and Rowe 2005).

Males of the polyandrous spider *Pisaura mirabilis* (Pisauridae) (Clerck 1757) has a remarkable mating behavior, which includes the use of a nuptial gift and performance of thanatosis—a death-feigning behavior, where the male can fake dead and later come back to life to continue courtship or mating (Bilde et al. 2006). The male performs a characteristic courtship display while he offers the gift to the female (Bristowe 1958). If the female accepts the gift she consumes it, and while the female is occupied eating the gift, the male initiates sperm transfer. At times, during mating the female interrupts the

copulation and the male may perform thanatosis and later continue copulation when the female resumes consumption of the gift. This may happen several times during a mating session (Bilde et al. 2007).

Nuptial gifts are a strategy for males to achieve reproductive benefits (Thornhill and Alcock 1983), and several hypotheses have been put forward to explain the adaptive significance of these gifts. First, the nuptial gift can represent paternal investment (Trivers 1972). Second, the nuptial gift can represent male mating effort by luring the female into mating (Thornhill 1976). Finally, the nuptial gift can protect the male from sexual cannibalism (Kessel 1955). In *P. mirabilis*, Staalhandske (2001) showed that the nuptial gift is maintained by sexual selection because females require a gift to accept a mating and that the gift is a male mating effort that can lure the female into mating. Nevertheless, it is possible that the gift-giving and death-feigning behaviors originally evolved as male adaptations to avoid being cannibalized (Kessel 1955; Fromhage and Schneider 2005). Sexual cannibalism is common in Pisauridae and also occurs in *P. mirabilis* (Elgar 1992; Elgar and Schneider 2004; Bilde et al. 2006). Thanatosis is a widespread antipredation strategy for avoiding the attention of a predator, where the prey simply freezes or plays dead (Edmunds 1974, Reitze and Nentwig 1991, Miyatake et al. 2004). However, thanatosis is exceptional in the context of sexual selection (Bilde et al. 2006). Thanatosis in *P. mirabilis* seems to be possible only when males hold on to the gift and therefore likely evolved subsequently and in close conjunction to the gift-giving trait, and both behaviors were suggested originally to function as cannibalism-avoidance traits (Bilde et al. 2006, 2007). However, these studies did not demonstrate reduced aggression or cannibalism toward death-feigning males, perhaps, because incidents of sexual cannibalism were low. Interestingly, males that performed thanatosis had an increased mating success. It is therefore possible that thanatosis

has evolved into a male mating effort (Bilde et al. 2006, 2007). Which factors elicit thanatosis in males and how it influences male mating success and risk of cannibalism are therefore still open questions. Furthermore, we lack information on whether death feigning is a polymorphic behavioral trait which is used facultatively under specific circumstances.

Sexual cannibalism in *P. mirabilis* occurs prior to mating, which is paradoxical as the male risks zero fitness and the female reduces her own chances of reproducing. Elgar (1992) proposed 3 possible explanations for precopulatory sexual cannibalism. First, sexual cannibalism can be explained as an adaptive female foraging strategy; however, there is little evidence to support this hypothesis (Staalhandske 2001; Elgar and Schneider 2004). Second, it can be explained by females showing extreme discriminatory aggression toward males they reject as potential mates (Prenter et al. 2006). Third, Gould (1984) proposed sexual cannibalism to be the result of mistaken identity. Before realizing the value of the males as mates, intrinsically aggressive females accidentally attack males as prey by mistake. Later, this mistaken-identity hypothesis was revised by Arnqvist and Henriksson (1997), who suggested a nonadaptive model for the evolution of precopulatory sexual cannibalism. This model described sexual aggression toward mates as a spillover of high aggression levels in earlier life stages toward prey. The model predicted that the most aggressive juvenile females would achieve more food and greater adult size, become more fecund, and be more aggressive toward mates as adults. However, in the adult life stage, the spillover of high aggression is not beneficial for either sex as they run the risk of not reproducing at all (Arnqvist and Henriksson 1997).

In the study presented here, we investigated the function of thanatosis experimentally. We tested the alternative hypotheses that thanatosis functions as an anticannibalism strategy or as a mating effort in a 2-factorial design, where female intrinsic aggressiveness and male vulnerability to attack was varied. If precopulatory sexual cannibalism in *P. mirabilis* results from aggressive spillover, there should be genetic differences in aggressive behavior in females. We predicted that males should increase the frequency of thanatosis when faced with more aggressive females or when they were more vulnerable to attack. Alternatively, if death feigning is a male mating effort, thanatosis should increase male mating success and not vary with risk of cannibalism. The 2 hypotheses are not mutually exclusive, and they both predict that all males should be able to death feign. We, furthermore, tested whether female mating status had an effect on the frequency of thanatosis and male mating success as females were expected to become choosier when mated. Hence, we predicted a higher mating success and lower frequency of thanatosis when males were presented with virgin females compared with mated females. In a second experiment, where males were presented with different virgin females, we investigated whether all males are capable of performing thanatosis.

MATERIAL AND METHODS

Study animal

The polyandrous nursery-web spider *P. mirabilis* (family Pisauridae) has a mating behavior that includes the use of a nuptial gift which is unique among spiders. When the male reaches adulthood, he will start wrapping prey into a white parcel with fine threads of silk instead of consuming it. The gift is held in the chelicerae of the male. When presented with a female, the male starts rubbing his legs against each other and shaking the abdomen and body. The male raises his body and front legs to a vertical position displaying the nuptial gift to the female. If the female accepts the gift, she slowly moves forward toward the male and grabs the gift with her chelicerae. When the female starts consuming the gift, the male will turn around until his cephalothorax is situated opposite the ventral side of the abdomen of the female. Here, the male initiates sperm transfer by coupling his pedipalp with the epigyne of the female. The male is capable of performing thanatosis before, during, and after copulation. When thanatosis is elicited, the male holds on to the gift with his chelicerae but otherwise remains completely motionless with his legs fully extended while being dragged over the substrate by the female (Bilde et al. 2006).

Female aggressiveness and male vulnerability

Juvenile *P. mirabilis* were collected on 10 and 25 October 2006 on a meadow at the Mols Laboratory, Eastern Jutland, Denmark. The spiders were individually kept in vials of 2 cm in diameter and 6 cm in height with a charcoal and plaster of paris substrate in the bottom to maintain humidity. Subadult spiders were transferred into larger vials (3.5 cm in diameter, 8 cm in height) with fresh peat moss (*Sphagnum* sp.) in the bottom. The animals were kept at approximately 25 °C and a 12-hour photoperiod in an air-conditioned room. They were fed 2–3 times a week with a varied diet of fruit flies (*Drosophila melanogaster*), houseflies (*Musca domestica*), and crickets (*Gryllus bimaculatus*). In order to synchronize size and molting, some spiders were kept between 1 and 2 months in a refrigerator at 10 °C.

Approximately 3 days after the final molt, we performed aggression assays to test the assumption that the level of female aggressiveness is intrinsic. Females were placed individually in a petri dish (9 cm in diameter, 1.5 cm in height), and subsequently, a fly was released directly opposite to the spider. The time which it took for the spider to attack the fly was recorded. If no attacks were observed after 10 min, the test was stopped. The females were subsequently divided into 2 groups. Females that attacked the fly in less than 11 s were termed aggressive, and females taking longer than 50 s to attack the fly were termed less aggressive. Females falling in the intermediate interval were excluded from the experiments.

To vary male vulnerability, approximately half of the males ($N = 44$) were experimentally handicapped in the subadult state. They were anesthetized with carbon dioxide and had 1 front leg removed. When these males became adult, at times, the dissected leg would be regenerated but it would appear thinner and smaller than the rest of the legs. The remaining males ($N = 66$) were used as controls.

Mating experiments were conducted from 31 January to 23 April 2007 in transparent terraria (diameter 13.5 cm, height 7 cm) with white paper towels as substrate. A female was first presented with a male 9 ± 3 days after reaching adulthood. A randomly chosen female was placed in the terrarium, and after appoximately 10 min, a male with a gift was placed in the terrarium and the time noted. We recorded courtship and mating behaviors including thanatosis and female mating aggression (attacks and/or cannibalism). We distinguished between precopulatory and postcopulatory thanatosis. Precopulatory thanatosis was defined as thanatosis performed prior to copulation. Postcopulatory thanatosis occurred after the copulation was initiated if a female interrupted the mating or after copulation was terminated.

Death feigning and copulation duration was recorded. Trials where copulation was not initiated within 30 min were stopped and the individuals were later attempted mated again with a different mate until copulation was attained. In order to detect the effect of female mating status, we repeated the experiments while reversing male order so the females were

mated with 2 different males with an interval of 1 week (7 ± 3 days).

Statistical test were performed with JMP 6. Data that did not fulfill the criteria of normality and variance homogeneity were transformed. We analyzed effects of female aggressiveness, male handicap, and female mating status and their interactions on components of male mating behavior in a full factorial analysis of variance (ANOVA) model. We included all interaction terms and removed the nonsignificant terms from the model reporting the results from the reduced models.

Ethical note

We considered leg loss a natural event because this phenomenon is widespread in wolf spiders in the field when subject to attack from predators (Brueseke et al. 2001; Brautigam and Persons 2003). Therefore, we did not consider the experimental removing of 1 leg as an unnatural trauma to the spider.

Behavioral polymorphism in thanatosis

Spiders used in this experiment were captured on 7 and 13 May 2006 on a grass meadow at the Mols Laboratory in Jutland, Denmark. Only juvenile and subadult specimens were collected.

Twenty males and 60 virgin females were used in the experiment. They were maintained in the laboratory at room temperature (21 ± 3 °C) and a natural photoperiod. They were kept individually in vials (3 cm in diameter, 7 cm in height) supplied with fresh peat moss (*Sphagnum* sp.). The spiders were fed a mixed diet with laboratory reared houseflies (*M. domestica*) and different insects of similar size, which were captured in nature by sweep netting a grass field. The spiders were fed an insect approximately 3 times per week. When males started wrapping their prey as nuptial gifts, they were ready to be used in the experiment. Females were regarded as sexually mature, when they reached adulthood and the epigyny was fully developed.

Mating trials were performed following the protocol described above between the 12 and 28 June 2006. Each male was presented with 3 different virgin females sequentially with an interval of 7 ± 3 days. We recorded the proportion of males that death feigned when presented with the first, second, and third female, respectively, and noted the identity of deathfeigning males to investigate the capability of individuals to perform and repeat thanatosis behavior. We analyzed the frequency of thanatosis in relation to sequential mating number (1, 2, or 3) and male ID using a mixed-effect model with mating number as fixed factor and male ID as random factor.

RESULTS

Female aggressiveness and male vulnerability

Females previously classified as aggressive (toward prey) showed higher levels of mating aggression toward males than less-aggressive females (Table 1, Figure 1). In addition, mated females were more aggressive during mating than virgins. Neither intrinsic aggressiveness nor female mating status influenced the propensity to death feign. There was a marginally significant effect of male state (handicapped or control) on the propensity to feign death as control males death feigned at a higher frequency than handicapped males (Table 2, Figure 2). The aggressiveness × handicap interaction term influenced the frequency of thanatosis (Table 2), as control males death feigned at a high frequency in trials with nonaggressive females and handicap males showing the opposite trend (Figure 2). In addition, a significant interaction effect

Table 1

Effects of female intrinsic aggressiveness, male handicap state, and female mating status on female mating aggression

Factor versus mating aggression	χ^2	P
Intrinsic aggressiveness	10.23	0.0014
Handicap	0.40	0.5281
Female mating status	3.93	0.0475

of handicap state × female state on thanatosis was found (Table 2) as control males increased the frequency of death feigning when faced with mated females (Figure 3).

We found no main effect of intrinsic aggressiveness and female mating status on male mating success. However, handicap status in males influenced mating success (Table 3), where control males were more successful in obtaining copulation than handicapped males (Figures 4 and 5). The intrinsic aggressiveness × handicap interaction affected mating success as control males achieved a higher mating success with nonaggressive females than handicapped males (Table 3, Figure 4). A similar effect of state × handicap interaction was seen when control males achieved more matings than handicapped males in trials with mated females (Table 3, Figure 5).

Overall, males performing thanatosis were more successful in achieving copulations than those which did not (χ^2 = 81.67; $P < 0.0001$) (Figure 6). Precopulatory thanatosis was a highly significant predictor for acquiring matings; hence, males performing precopulatory thanatosis achieved a higher mating success than males which did not or showed postcopulatory thanatosis (χ^2 = 22.75; $P < 0.001$, 89% of males performing precopulatory thanatosis achieved copulation compared with 40% males that did not). When analyzing the effect of thanatosis in trials where females interrupted copulation, we found that a higher proportion of the males performing thanatosis after the first female interruption (100%) than the males which did not death feign at this point (82%) were able to resume copulation (χ^2 = 9.76; $P = 0.0018$).

Death-feigning males achieved longer copulations (Mean ± standard error (SE) = 1589.02 ± 115.80 s) than males which did not (mean ± SE = 914.74 ± 145.94 s) (ANOVA: F_1 = 13.65; $P = 0.0004$). When analyzing only interrupted matings, total copulation duration also increased when males performed thanatosis ($F_{1,77}$ = 5.9713; $P = 0.0169$).
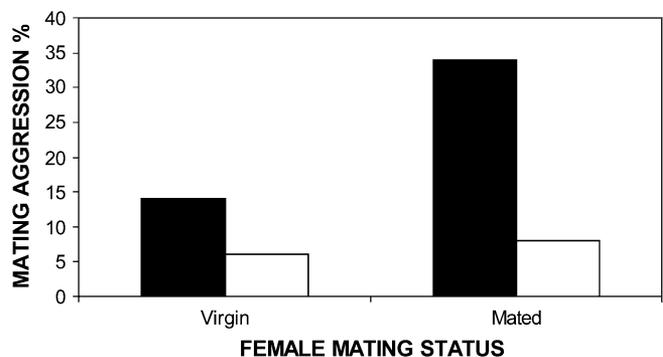

Figure 1
Percentage of females showing mating aggression in intrinsic aggressive and less-aggressive females in trials with virgin and mated females. Filled bars, aggressive; open bars, less aggressive.

Table 2

Effects of female intrinsic aggressiveness, male handicap state, and female mating status on proportion of males performing thanatosis

Factors versus thanatosis	χ^2	P
Intrinsic aggressiveness	0.04	0.8463
Female mating status	1.06	0.3021
Handicap	3.81	0.0511
Female mating status × handicap	4.20	0.0404
Intrinsic aggressiveness × handicap	13.80	0.0002

A total of 313 mating trials were observed during the experiment. In only 2.5% of these trials did the female kill the male; this number was too low to analyze statistically.

Behavioral polymorphism in thanatosis

The frequency of males that death feigned increased from the first to the second and third mating trials (Figure 7A) and all the tested males performed thanatosis at least once (Figure 7B). Five males performed thanatosis in all trials, 4 males in 2 out of 3 trials and 11 males only once. The analysis showed a significant effect of both male ID (random) ($\chi^2 = 30.50; P = 0.0457$) and of trial number ($\chi^2 = 8.74; P = 0.0126$) on the likelihood of death feigning.

DISCUSSION

In accordance with the aggressive spillover hypothesis (Arnqvist and Henriksson 1997), females that were aggressive toward prey showed significantly more mating aggression toward males than less-aggressive females. If thanatosis functioned as anticannibalism strategy, males that were faced with aggressive females should show higher propensity to feign death; however, in mating trials, we found no main effect of intrinsic aggressiveness on thanatosis. Assuming that handicapped males were more vulnerable to attack than control males, we expected vulnerable males to be more likely to death feign than control males. We found no evidence that vulnerable males increased the frequency of thanatosis toward aggressive or mated females; on the contrary, control males feigned death more often than handicapped males. Neither aggressiveness of females nor vulnerability in males increased the propensity to death feign; overall, therefore, there was very little evidence to support thanatosis as a strategy to reduce the risk of cannibalism by females.
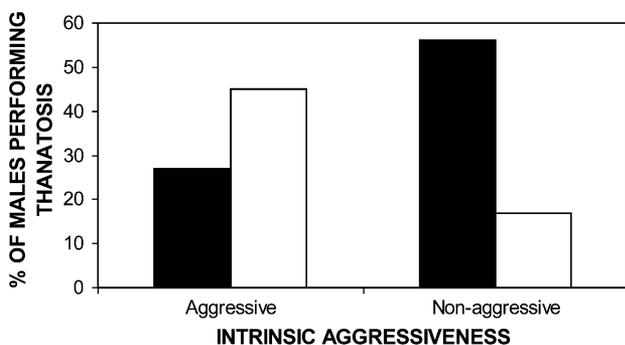

Figure 2
Percentage of control and handicapped males performing thanatosis in trials with intrinsic aggressive and less-aggressive females. Filled bars, control group; open bars, handicapped group.
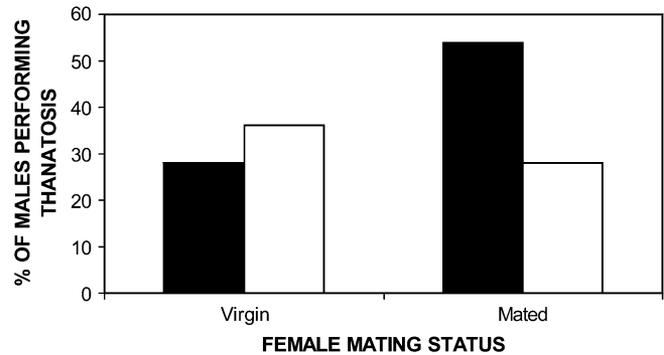

Figure 3
Percentage of control and handicapped males performing thanatosis in trials with virgin and mated females. Filled bars, control group; open bars, handicapped group.

Control males showed an increase in frequency of thanatosis when paired with nonaggressive females, indicating that male mating effort may better explain the observed pattern. Males performing thanatosis achieved significantly higher mating success than males that did not. The finding that precopulatory thanatosis was the most decisive factor in acquiring copulations strongly supports the mating effort hypothesis. In addition, copulation duration was longer in matings involving death feigning. Drengsgaard and Toft (1999) showed a positive correlation between copulation duration and the percentage of fertilized eggs in *P. mirabilis*, providing males obtaining long copulations an advantage in sperm competition. Hence, death feigning may increase male reproductive success through prolonged copulations.

Females may interrupt the copulation and attempt to escape with the gift (Staalhandske 2001). Males performing thanatosis during interruptions increase their chance of continuing copulation and thus gained prolonged total copulation duration compared with males not performing thanatosis on female interruption. These findings are in accordance with the results by Bilde et al. (2006, 2007), who found increased mating success in males performing thanatosis, although they did not record an effect of thanatosis on copulation duration.

We expected that mated females might become choosier toward additional males (Andersson 1994; Gabor and Halliday 1997). In *Dolomedes* spiders (also Pisauridae), Johnson (2001) showed that mated females attack courting males more often than virgin females. Mated females are not necessarily as dependent on achieving copulation as virgin females because they are most likely already fertilized. Indeed, mated females showed higher mating aggression than virgin females in our experiments. However, all together males did not show increased tendency to perform thanatosis toward mated females as would be expected if thanatosis was an antipredation strategy. The significant female state × male handicap interaction was mainly caused by an increase in thanatosis of control

Table 3

Effects of female intrinsic aggressiveness, male handicap state, and female mating status on male mating success

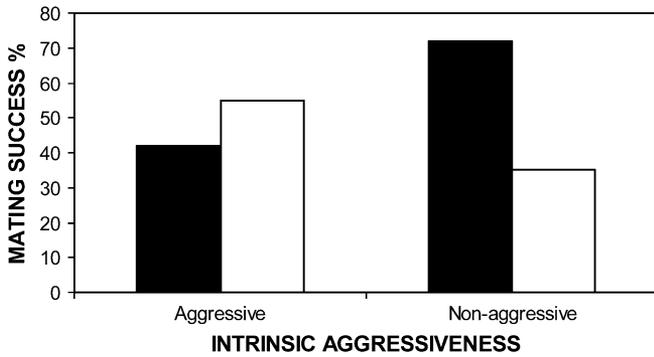| Factors versus mating success	χ^2	P
Intrinsic aggressiveness	0.39	0.5328
Female mating status	2.20	0.1377
Handicap	5.85	0.0156
Female mating status × handicap	12.25	0.0005
Intrinsic aggressiveness × handicap	9.85	0.0017

Figure 4
Percentage of mating success in control and handicapped males in trials with intrinsic aggressive and less-aggressive females. Filled bars, control group; open bars, handicapped group.

males toward mated females. This result suggests that when confronted with mated females that are more reluctant to mate, males are forced to invest more in the activity that increases their mating success.

Handicapped males had a lower mating success than control males experiencing a clear reproductive disadvantage. Our data suggest that handicapped males may not be capable of investing as much in mating effort as control males, for example, if handicapped males were less capable of death feigning than control males. This explanation was supported by the fact that handicapped males were less likely to be accepted by females than control males. Whether the decrease in acceptance of handicapped males was caused by reduced capability to perform courtship behavior would require further studies. A characteristic presentation of the gift seems crucial for obtaining copulations (Staalhandske 2001; Prokop 2006; Prokop P, personal communication).

If thanatosis functions as a male mating effort, all males should be able to feign death. The results from our second experiment support this prediction as all males performed thanatosis at least once during 3 mating trials. Nevertheless, not all males death feigned in every trial as we found individual male differences in the frequency of performing thanatosis. There was a tendency for males to increase the likelihood of death feigning after their first mating. That thanatosis gives males a reproductive advantage and all males are capable of death feigning begs the question why all males do not death feign as an integrated part of courtship behavior. One explanation may be that there are costs of death feigning suggesting a behavioral trade-off. Perhaps, there are energetic costs
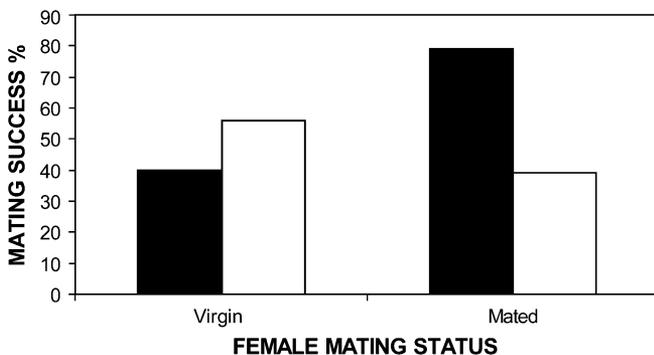

Figure 5
Percentage of mating success in control and handicapped males in trials with virgin and mated females. Filled bars, control group; open bars, handicapped group.
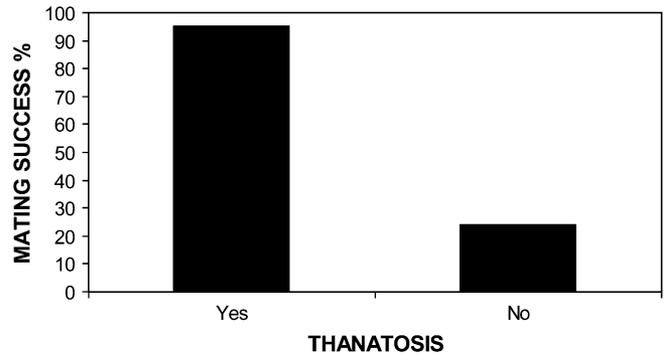

Figure 6
Percentage of males achieving copulation comparing presence and absence of thanatosis.

of death feigning or risks of injury when males are dragged over the substrate. Spiders use hydrostatic pressure to stretch their legs (Foelix 1996), and during thanatosis, the legs are stretched while the male is immobile implying an active performance. Alternatively, once feigning death, males might reduce their chances of escaping should the female perform an unexpected attack (Bilde et al. 2006). Evidence in support of costs of thanatosis was seen when handicapped males were less able to perform thanatosis than control males. Simultaneously, handicapped males obtained fewer matings compared with control males. In summary, our data clearly support that thanatosis primarily functions as an adaptive male mating strategy which increases male mating success and copulation duration. Thanatosis may entail energetic and other costs, which result in the observed behavioral polymorphism in the frequency of performing thanatosis.

It is possible that death-feigning behavior originally evolved as a male counter strategy to sexual cannibalism, similar to opportunistic matings with feeding females or the provision of nuptial gifts to distract female attention from males as prey (Kessel 1955; Fromhage and Schneider 2005, and references
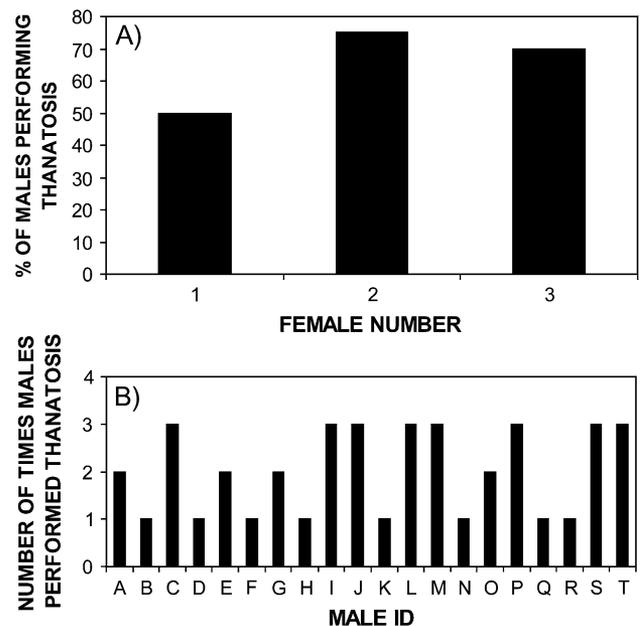

Figure 7
(A) Frequency of males performing thanatosis and (B) the number of times specific males death feigned when a male was presented with a virgin female in 3 successive mating trials.

therein). Thanatosis appears to be obligatorily coupled to gift-giving behavior and thus most likely evolved after the gift-giving trait. Coevolution between the sexes may have lead females to expect a gift from males and evolve resistance to unnecessary matings by attempting to steal the gift and escape without copulation. Thanatosis would allow males to keep contact with resistant females and hence increase male mating success, thus evolving into an adaptive male mating strategy.

FUNDING

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