



Copulation reduces the duration of death-feigning behaviour in the sweetpotato weevil, *Cylas formicarius*

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Although there have been numerous studies on the effects of mating history on mating behaviour, few studies have reported the relationship between mating history and other contextual behaviours such as foraging and predator avoidance. We examined the effect of mating history on death-feigning behaviour (an antipredator behaviour) in the sweetpotato weevil. Because mating behaviour can be divided into phases, we examined the effects of encounters with the opposite sex, copulation and insemination success on death-feigning behaviour. For females after copulation and males after multiple copulations the duration of death-feigning behaviour was reduced, whereas encounters with the opposite sex had no effect. Insemination success did not affect the duration of death feigning in males, but inseminated females reduced the duration of death feigning. We discuss the implications of these results for the effect of mating history on this antipredator behaviour.

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In the field of sexual selection, a large number of studies have shown that mating history affects mating behaviour such as male–male contests (Kendall & Wolcott 1999), female mating receptivity (reviewed in Simmons 2001; Arnqvist & Rowe 2005), mating preference (e.g. Kodric-Brown & Nicoletto 2001; Uetz & Norton 2007) and copulation duration (Ortigosa & Rowe 2003). However, the effect of mating history on the other contextual behaviours, such as foraging and predator avoidance, has not been extensively studied. Because the expression of certain traits including behaviour requires investing resources, an increase in the trait would result in a decrease in the resources available for other traits (Stearns 1992; Roff 2002). If mating behaviour changes as a consequence of mating history, one can expect other behaviours to change as well. For example, mated females will increasingly invest in foraging and predator avoidance because they do not need additional sperm. To understand the adaptive evolution of certain behaviours, the relationship between different contextual behaviours should be examined.

Predation is a major selective force in the evolution of the morphological, physiological and behavioural traits of animals, and predator–prey coevolution can lead to an evolutionary arms race (Abrams 2000; Lima 2002). Antipredator behaviours have a strong effect on fitness (Ruxton et al. 2004). Death-feigning behaviour (thanatosis, tonic immobility) is an antipredator behaviour found in mammals (Francq 1969), birds (Sargeant & Eberhardt 1975), fishes (Howe 1991), reptiles (Gehlbach 1970; Gerald 2008; Gregory 2008) and insects (Edmunds 1974). Although the adaptive significance of death-feigning behaviour has long remained unstudied as a subject of evolutionary biology, the behaviour has recently been empirically determined to be an antipredator adaptation in the red flour beetle, *Tribolium castaneum* (Miyatake et al. 2004), in nymphs of the damselfly *Ischnura elegans* (Gyssels & Stoks 2005) and in the pygmy grasshopper, *Criotettix japonicus* (Honma et al. 2006). Furthermore, this behaviour is used against cannibalistic mating partners in the nursery web spider, *Pisaura mirabilis* (Bilde et al. 2006; Hansen et al. 2008). Regrettably, it is difficult to quantify investment in antipredator behaviours. However, it is easy to measure the investment in death-feigning behaviour, for example, by considering the intensity of this behaviour (e.g. occurrence and duration) as an investment in predator avoidance. The intensity of death-feigning changes with external and internal

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conditions, including temperature (e.g. Larsen 1991; Gerald 2008; Miyatake et al. 2008), light–dark conditions (Miyatake 2001a), starvation (Acheampong & Mitchell 1997; Miyatake 2001b), behaviour before being startled (i.e. walking, resting and feeding; Miyatake 2001a) and body size (Hozumi & Miyatake 2005; Gerald 2008). Mating history will also affect death-feigning behaviour. Investment in death feigning reduces mating opportunities, whereas a shorter duration of death feigning may raise predation risk (i.e. there is a trade-off between death feigning and mating). Individuals are expected to adopt an optimal duration of death feigning that balances mating opportunity with predation risk. Therefore, plasticity in the death-feigning behaviour dependent on mating history will be adaptive. However, no study has examined the relationship between death-feigning behaviour and mating history.

The sweetpotato weevil, *Cylas formicarius* (Coleoptera: Brentidae), shows death-feigning behaviour (Sherman & Tamashiro 1954; Miyatake 2001a, b) and is therefore a good model animal for study. Its predators include wasps, mites and mice (Reinhard 1923; Cockerham et al. 1954; Sherman & Tamashiro 1954); ants, stinkbugs, geckos and wandering spiders have also been observed as predators on Okinawa Island, Japan (D. Haraguchi, unpublished data; K. Yasuda, unpublished data). When adult weevils are startled by an external stimulus, they fall from the leaves or stems of host plants (e.g. sweet potato, *Ipomoea batatas*, railroad vine, *Ipomoea pes-caprae*, and blue morning glory, *Ipomoea indica*) to the ground and either feign death in a state of extreme rigidity or quickly escape. A death-feigning weevil is difficult to identify because of its dark coloration. Thus, for the sweetpotato weevil, such behaviour is a defensive strategy that has evolved to reduce a predator's interest, and hence allows escape.

Mating behaviour can be divided into several phases, such as encounter with the opposite sex, courtship, copulation, insemination and postcopulatory interaction (e.g. Alexander et al. 1997), each of which can affect death-feigning behaviour. In the present study, we examined the effects of encounters with the opposite sex, copulation and insemination success on the duration of death-feigning behaviour in sweetpotato weevils to explore the effect of mating history on such behaviour. The effects of copulation and insemination success can be discriminated in this species because insemination does not often occur even when copulation is successful (T. Kuriwada & K. Shiromoto, unpublished data). Male weevils can mate four or five times in a single night (Sugimoto et al. 1996), and thus sperm depletion by insemination during one mating episode may not have a strong effect on male death-feigning behaviour. Conversely, encounters with females would have a stronger effect on such behaviour in males. Recently mated males are more eager to mate than unmated males because they have a perception of both high mate encounter rates and a high possibility of mating (e.g. Ortigosa & Rowe 2003; van Son & Thiel 2006). When a male perceiving many mating opportunities invests more resources and time in mating behaviour, the duration of death-feigning behaviour is shortened because of a trade-off between mating and death feigning (i.e. weevils are immobile while feigning death). On the other hand, insemination success would have a strong effect on female death-feigning behaviour. Female weevils release a sex pheromone to attract adult males (Heath et al. 1986) and mate with them from evening to midnight (Sakuratani et al. 1994). Remating by females is probably very rare because secretion of the sex pheromone ceases after mating (Sugimoto et al. 1996). Therefore, insemination would increase the duration of death-feigning behaviour because inseminated females would benefit less from additional mating and hence will reduce their investment in mate searching, and invest more resources and time in death-feigning behaviour.

METHODS

Insects and Culture

We mainly used wild sweetpotato weevils in this study; however, we also used mass-reared weevils as mating partners of the focal weevils in experiment 2 because we were concerned that we would not be able to obtain sufficient numbers of wild weevils. In May 2008, we collected infested sweet potato roots from Yomitan Village, Okinawa Island, Japan, to obtain a wild strain. Approximately 300 adult weevils that emerged from the collected roots were placed in a plastic container (215 × 150 mm and 80 mm high) containing sweet potato roots (approximately 400 g) under the following conditions: 25 ± 1 °C, 70–90% relative humidity and a photoperiod of 14:10 h light:dark (lights on: 0400–1800 hours). We used the progeny (F₁) of these adult weevils. The mass-reared strain originated as adults collected from Yomitan Village in October 1997. We reared the weevils on sweet potato roots at 25 ± 1 °C and a photoperiod of 14:10 h light:dark for 70 generations at the Okinawa Prefectural Plant Protection Center (OPPPC). We replicated the experiments twice by using weevils from separate containers.

Observation of Death-feigning Behaviour

We observed death-feigning behaviour in 11–16-day-old adult weevils. We weighed each weevil (±0.1 mg) using an electric balance (Libror AEX-120; Shimadzu, Kyoto, Japan) 5 h before observation. We then individually placed all weevils from both strains into the wells of 24-well multiplates (As One Corp., Osaka, Japan). This step was necessary to avoid disturbance by other weevils, which usually reduces the duration of death-feigning behaviour (Miyatake 2001a). We induced the death-feigning behaviour by lifting each weevil by its thorax with forceps and then dropping it back into its well from a height of 2 cm. We recorded the duration of death-feigning behaviour using a digital video camera (GR-DF590; Victor, Yokohama, Japan) for 120 min, and defined it as the time between the dropping of a weevil into its well and the detection of its first visible movement. If the beetle did not respond, we repeated the stimulus (i.e. lifting and dropping) three times. If the weevil failed to respond on all three occasions, we considered the insect nonresponsive and recorded the duration of death-feigning behaviour as 0.1 s. In this study, few weevils performed more than 120 min of death-feigning behaviour [three males (2.1%) and two females (1.3%) in experiment 1; five males (5.3%) and five females (4.9%) in experiment 2], and the durations of the death feigning were recorded as 7200 s (i.e. 120 min). We started all the trials at 1530 hours, corresponding to early evening in the field (i.e. approximately 2 h before lights off).

Experiment 1: Effect of Copulation and Insemination

In this experiment, we compared the duration of death-feigning behaviour between virgin weevils and weevils that had copulated by dividing the experimental males and females into two groups (i.e. virgin and copulation) and measuring the duration of death-feigning behaviour on the next day. We maintained the weevils in the virgin group under the conditions described earlier until experimentation, and allowed adult weevils (10–15 days of age) in the copulation group to mate only once during the mating trial. We placed each focal male and focal female for mating in a petri dish (3.5 cm in diameter × 1 cm height) with a small piece of sweet potato root (approximately 1 g). To measure the copulation duration of the pairs, we observed them until matings occurred or for 60 min, and then discarded the unmated pairs. We measured the

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