



## Aversion for bitter taste reveals sexual differences in alimentionation strategies in a praying mantis



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Insects, as well as vertebrates, possess morphological, physiological and behavioural sexual dimorphisms. Because they are commonly bigger and produce eggs, female insects usually require more and specific energy intake. In addition to quantitative and qualitative requirements in food for reproduction, animals also have to avoid eating lethal toxins. The praying mantis *Tenodera aridifolia* is a good model to investigate sexual differences in feeding behaviour because its sexual dimorphism is marked in terms of morphology and behaviour. Here, we observed that females ate approximately four times as much prey as males. We then investigated the attacking and feeding behaviours of praying mantises by presenting mealworms injected with bitter solutions (quinine hydrochloride dihydrate or denatonium benzoate at 50 or 500 mM) as prey. We observed that males had a low level of acceptance for bitter prey: unlike females, they reduced consumption of mealworms injected with 50 mM of these bitter solutions. However, they showed higher motivation (unlike females, their rate of attack on prey increased when they reduced their consumption of mealworms). This difference in ingestion between the sexes did not seem to be due to different sensitivities for these bitter solutions (there was no detectable difference between the sexes in time taken to drink drops of these bitter solutions). Instead, this seems related to males and females having different feeding strategies based on different nutritive requirements. The possible effects of nutritional composition of prey on avoidance behaviours in predatory insects are discussed.

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Differences between male and female animals (sexual dimorphism) are observable in many taxa, from insects to vertebrates, and take different forms: morphological, physiological and behavioural (Darwin, 1871; McPherson & Chenoweth, 2012). It is relatively easy to distinguish both sexes in insects based on morphological differences such as the segmentation and differentiation of their abdomen (e.g. Brown, 1975; Ross & Cochran, 1960) or their antennae (e.g. Carle, Yamawaki, Watanabe, & Yokohari, 2014; Rospars, 1988). Furthermore, Darwin (1871) was the first to observe that female insects are 'commonly' larger than males (e.g. Eisenberg, Hurd, & Bartley, 1981; Testa, Ghosh, & Shingleton, 2013; Vollrath & Parker, 1992; but see Leimar, Karlsson, & Wiklund, 1994), and put forward the theory of 'fecundity advantage' involving natural selection for larger females. However, this theory is not applicable to every species (Shine, 1988), and it is currently assumed that the size of a given species depends on the lifestyle

and mating behaviour for each sex (McPherson & Chenoweth, 2012; Shine, 1989; Vollrath & Parker, 1992).

Physiologically, insects produce hormones that differ between the sexes (for review Nüssel & Winther, 2010), which undoubtedly involves sexual differences in feeding behaviour. It is well known that hormones are at the base of anatomical changes (Rembold, Czoppelt, & Rao, 1974) such as the production of eggs in females (Bownes, 1989; Dhadialla, Carlson, & Le, 1998; Postlethwait, Bownes, & Jowett, 1980). This oogenesis requires more and specific energy intakes for females (Foster, 1995; Gordon, 1968). Thus, females eat more food than males in some species such as fruit flies (Wong, Piper, Wertheim, & Partridge, 2009) and spiders (Givens, 1978), or have specific requirements for reproduction, such as blood feeding in mosquitoes (Foster, 1995). In general, the quality and quantity of eggs produced in insects depend on the body mass of females (Birkhead, Lee, & Young, 1988; Leather, 1988; Maxwell, Gallego, & Barry, 2010; Wickman & Karlsson, 1989) and on the quantity of food ingested (Barry, 2013; Eisenberg et al., 1981; Terashima & Bownes, 2005). High nutrient intake also reduces the period before oviposition (Matsura & Morooka, 1983), and favours the attraction of males (Barry, 2010). But, although the

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quantity ingested is important, the quality of food (e.g. macronutrients: proteins versus lipids) is also important for reproduction and growth in insects (e.g. Wilder, Holway, Suarez, & Eubanks, 2011), affecting the number of eggs produced (Barry, 2010; Barry & Wilder, 2013), the period before oviposition (Wilder & Rypstra, 2008) and the attraction of males (Barry, 2010). In other words, both food quantity and quality are directly related to reproductive success.

In addition to being selective for macronutrients, animals have to avoid ingesting toxins, which induce malaise and vomiting (Davis, Harding, Leslie, & Andrews, 1986) and can lead to death. They are relatively easy to detect because they are usually associated with a bitter taste (Glendinning, 1994). However, even when toxins are easily detectable, animals continue to include toxic food in their daily diet (Provenza, Villalba, Dziba, Atwood, & Banner, 2003; Skelhorn & Rowe, 2006) or use strategies to reduce their intake of toxins (e.g. Bernays & Chapman, 1994) in order to benefit from the nutrients that food contains. Thus, there is a trade-off between the benefit of nutrients for survival and the risk of malaise. For example, when their nutritional demands are high, birds ingest more toxic mealworms (Barnett, Bateson, & Rowe, 2007). Hence, if there are sexual differences in nutritional requirements, there should be sexual differences in feeding strategies regarding bitter and possibly toxic food. However, little attention has been given to this point.

The praying mantis is an insect predator that might be a good model to investigate sexual differences in feeding strategy and its neural bases, for the following reasons. First, it is an insect with marked sexual dimorphism in terms of morphology and behaviour: as Prete (1999) has described, adult female mantises are generally larger, stronger and heartier eaters than males (Matsura & Inoue, 1999). Second, it is easy to observe their feeding and predatory behaviours and their predatory attacks in laboratory conditions. Finally, they possess a simple nervous system as in other insects (Menzel, Lebouille, & Eisenhardt, 2006). Although it has been assumed that female mantises eat more prey than males (e.g. Prete, 1999), few data have been provided concerning the quantity of food ingested daily at adulthood for both sexes. Additionally, little is known about their feeding responses to bitter and possibly toxic food and more specifically about sexual differences in aversion for food.

The present study tested for sexual differences in aversive feeding behaviours in praying mantises. We hypothesized that higher nutritional requirement in female mantises makes them accept more bitter prey than males. To test this hypothesis, we presented to praying mantises *Tenodera aridifolia* prey that were injected with different bitter solutions (quinine and denatonium benzoate) at two different concentrations (low and high). In an additional experiment, we examined the difference in taste sensitivity between the sexes by measuring the time spent ingesting these bitter solutions at different concentrations.

## METHODS

### Subjects and Housing

In total, 101 adult praying mantises *T. aridifolia*, 48 females and 53 males, were used. We collected oothecae in Fukuoka (Japan) on grassland near Tachibana mountain (+33°40'46.7", +130°28'6.20"), and bred the nymphs obtained to adulthood as previously described (e.g. Sato & Yamawaki, 2014). During breeding, the mantises were kept at 25 ± 3 °C and in a 12:12 h light:dark photoperiod (light phase: 0900–2100 hours). Until the third instar, the individuals were kept together in a plastic box (40 × 23 cm and 25 cm high) provided with mesh walls inside for moulting and with

aeration at the top. During this time, the mantises were fed with fruit flies, *Drosophila melanogaster*, three times per week, in addition to water ad libitum. After the third instar, each individual was isolated and placed in similar plastic boxes that were partitioned into nine compartments (13 × 7 cm and 25 cm high). From this moment, the mantises were fed with crickets, *Acheta domesticus*, ca. 5–20 mm long, three times per week, and the top of the box was sprayed with water after food was given. Finally, at adulthood, each individual was placed in an individual box (15 × 10 cm and 20 cm high) and received the same diet as previously.

### Experiment 1: Decision Making to Ingest Bitter Prey

In this first experiment, 73 mantises were used: 41 males and 32 females. The experimental procedure was executed every other day, i.e. 1 day of experimentation followed by 1 day without experimentation, and it consisted of three consecutive sessions (Fig. 1a): free-feeding, acclimation and bitter stimuli presentation.

In the free-feeding session, the mantises received crickets ad libitum in their cage on 3 experimental days in order to normalize their level of satiation.

In the acclimation session, to acclimate the mantises to manual feeding and to quantify daily food intake, the mantises received mealworms that were not manipulated for 3 experimental days. The mantises received a single trial per experimental day. A trial consisted of placing a mantis in a cage surrounded by white boards to prevent any visual disturbance, and to present prey in front of them (Fig. 1b). The mantises were acclimated for 30 min before starting the presentation of prey in a room kept at approximately 25 °C. Then, the mantises were offered a single mealworm (*Tenebrio molitor* larvae, ca. 15 mm long) every 2 h for the males (four times per trial) and every 30 min for the females (16 times per trial; Fig. 1a). Each mealworm was fixed to the end of a fishing line and moved manually towards the mantis. If the mantises did not attack the prey within 30 s, the prey was withdrawn.

In the bitter stimuli presentation session (2 experimental days), the mealworms were injected and coated with either water or a bitter solution (100 µl): each mantis received only water-injected mealworms or only bitter mealworms in a day. To counterbalance effects of prior experience, half of the mantises received water-injected mealworms during the first day and bitter mealworms during the second day and the other half were treated in the reverse order. We investigated the effects of bitter solutions with four different conditions as follows: denatonium benzoate (DB; Tokyo Chemical Industry, Tokyo, Japan) or quinine hydrochloride dihydrate (Kanto Chemical Co., Tokyo, Japan) at high (500 mM) or low (50 mM) concentrations and we compared the results with the water-injected mealworms. Both DB and quinine have been used as bitter substances in many gustatory studies (e.g. Meunier, Marion-Poll, Rospars, & Tanimura, 2003; Spector & Kopka, 2002).

In both acclimation and bitter stimuli presentation sessions, the behaviour of the mantises was recorded using a video camera (30 frames/s) placed at the top. We recorded the number of mealworms that was attacked and the number that was fully or partially eaten. In addition, we measured the shaking and wiping behaviours during the 20 s after a prey was caught. These behaviours were considered as reactions to bitter substances (see below).

### Experiment 2: Sexual Dimorphism in Sensitivity for Bitter Solutions

To test for sexual dimorphism in gustatory sensitivity for bitter solutions, we measured the time required to ingest bitter solutions in 28 mantises (16 females and 12 males). After 2 days of food deprivation, we fixed the mantises on their back on supports using dental wax. Then, we placed one drop (10 µl) of solution on the

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