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# Behavioral comparison in males of two praying mantis species of the same genus, *Hierodula patellifera* and *H. chinensis* (Mantodea: Mantidae: Hierodulinae) in Japan, in response to the conspecific or allospecific species of calling females and females' headspace crude extract.

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## Abstract

For many years, only one species of praying mantis in the genus *Hierodula*, *Hierodula patellifera* Serville, had been recorded in Japan. In recent years, however, *Hierodula chinensis* Werner, a larger species than *H. patellifera* Serville, has been discovered in Japan, and observations and collections in Japan have increased rapidly. There are reports that in some areas, *H. patellifera* became locally extinct due to the invasion of *H. chinensis.* Since females of *H. patellifera* attract conspecific males by volatile with characteristic calling behavior, a sex pheromone-mediated reproductive interference may exist between the two species.

Both males of *H. patellifera* and males of *H. chinensis* were strongly attracted to conspecific females and crude headspace extract from conspecific females, while they were not attracted to females of allospecific species or crude headspace extract from allospecific females. These results indicate that sex pheromone-mediated reproductive interference may not exist between *H. patellifera* and *H. chinensis*.

## Key words

communication interference, interspecific competition, mating behavior, volatile pheromone

## Introduction

In Japan, only one species of praying mantis belongs to the genus *Hierodula*, *Hierodula patellifera* Serville, had been recorded for many years. In recent years, a large previously-unknown *Hierodula* sp., which has a distinctly different morphology from *H. patellifera*, have been discovered in various regions of Japan (Fujino et al. 2010, Yoshitsuru 2013, Mano and Uno 2014, Aiba 2015, Ohgushi et al. 2015, Matsumoto et al. 2016, Nakamine 2016). Though the identity of this species had been a mystery for a long time, recently, Yamasaki et al. (2022) identified this species as *Hierodula chinensis* Werner by comparison with type specimens, and then Ioka et al. (2022) also reported the same result.

It is not clear whether *H. chinensis* is a native or alien species. However, certainly, the species is rapidly expanding its distribution into areas where only *H. patellifera* has previously been observed (Mano and Uno 2014, Matsumoto 2016, Karube and Kaga 2019).

Mano and Uno (2014) and Yoshitsuru (2014) in Aichi Prefecture, and Takahashi and Kishi (2016) in Kanagawa Prefecture each reported that *H. patellifera* distributed in these areas had disappeared only a few years after *H. chinensis* was first found there. These reports indicate that the invasion of *H. chinensis* into areas where this species had not been collected before may lead to rapid local extinction (or extreme decline) of *H. patellifera*.

When an organism expands its habitat to a new niche, an interspecific competition with a closely related predecessor species would occur, and then often resulting in the local extinction of either of the species in a pair (McClure 1984, 1989, Snyder and Evans 2006, Liu et al. 2007, Kenis et al. 2009).

There have been a series of reports in recent years that reproductive interference is more important than resource competition in these exclusive interactions that occur only among closely related species (Gröning and Hochkirch 2008, Burdfield-Steel and Shuker 2011, Takakura and Fujii 2010). Reproductive interference, unlike resource competition, is more likely to occur between closely related species that use similar species and/or heterosexual recognition signals in their mating behavior, thus reasonably explaining the dramatic exclusive distributions and character displacements seen only among closely related species. (e.g., Kishi et al. 2009).

In many cases, reproductive interference is unilateral, and upon secondary contact, the effect on the other species is asymmetric (Gröning and Hochkirch 2008). As a result, there is positive feedback on the effects of reproductive interference as only one species reduces its population (Kuno 1992, Söderbäck 1994, Yelenik and D'Antonio 2013). Due to its positive frequency dependence and its self-reinforcing impact by positive feedback, the reproductive interference can exclude either of the species in a pair far more easily than ordinary resource competition does (Kuno 1992, Nishida et al. 2012). In a competition between nonrelated combinations of species, either it takes a long period for one species to become extinct or extinction does not occur. And only density dependence is detected in these interspecific competitions, not frequency dependence [*Rhizopertha dominica* (Fabricius) (Coleoptera: Bostrichidae) and *Sitotroga cerealella*; Crombie 1945, *S. cerealella* and *Sitophilus zeamais* (Motschulsky) (Coleoptera: Curculionidae); Arbogast and Mullen 1987]. On the other hand, Levin and Anderson (1970) simulated competition between closely related species for pollination and showed that in competition between closely related species, one species often becomes extinct within a short period and that frequency dependences were detected in this competition. Ayala (1971) and DeBenedictis (1977) demonstrated these hypotheses in competition experiments with two fruit fly species *Drosophila pseudoobscula* Frolova and *D. willistoni* (Sturtevant) (Diptera: Drosophilidae), and Kishi et al. (2009) also showed similar results using two bean beetle species *Callosobruchus chinensis* Linnaeus and *C. maculatus* (Fabricius) (Coleoptera: Chrysomelidae).

These characteristics of reproductive interference can well explain the mechanism by which invasive alien species displace native species in a short period, and such cases have been rapidly accumulating in recent years (Dame and Petren 2006, Liu et al. 2007, Takakura et al. 2009, Matsumoto et al. 2010, Nishida et al. 2012, 2014).

Fea et al. (2013) pointed out that *Orthodera novaezealandiae* (Colenso) (Mantodea: Mantidae: Orthoderinae), the only native praying mantis in New Zealand might decline their population by an invasive alien praying mantis *Miomantis caffra*

Saussure (Mantodea: Miomantidae: Miomantinae). The sex pheromone produced by *M. caffra* females has a cross-attraction activity to males of *O. novaezealandiae*, and the males were more attracted to *M. caffra* sex pheromone than conspecific sex pheromone even though the two species belong to the different superfamilies. In addition, *O. novaezealandiae* males attracted by *M. caffra* females were frequently preyed upon by the females. These facts indicate that *O. novaezealandiae* is affected by reproductive interference from *M. caffra*, both by misdirected attraction and predation.

It is known that females of *H. patellifera* secrete sex pheromones to attract and mate with males of the conspecific species (Ferez 2005). The sex pheromone-based mating behavior of *H. patellifera* may be the cause of the drastic decline in the *H. patellifera* population due to the invasion of *H. chinensis*, as for example *O. novaezealandiae* is affected by reproductive interference from *M. caffra*.

In this study, we investigated whether pheromone-mediated reproductive interference exists between two closely related species, *H. patellifera* and *H. chinensis*. First, we observed whether the mating behavior of *H. chinensis*, like that of *H. patellifera*, attracts males by females showing a characteristic calling posture. Then we examined whether males of both species are attracted to the conspecific/allospecific females that show the calling posture and their crude headspace extracts.

## Materials and Methods

### *Insects*

The last instar nymphs of *H. patellifera* and *H. chinensis* were collected from June to August in 2017, 2018, 2019, and 2020. All collection sites were included in Tottori Prefecture, Japan; *H. patellifera* were collected at coppices in Tottori City and Misasa Town, and *H. chinensis* were collected in the campus of Tottori University (35.5152°N, 134.1733°W). The last instar nymphs often rested on leaves with a large surface area at a height of more than 1 m above the ground surface. The nymphs were directly collected with an insect net (net: Nylon net 50 cm white, Takimichi Insects, Osaka, rod: Shiga Aluminum Short, 149 cm height, Takimichi Insects). If the nymphs were in high or narrow places where the insect net could not reach, a hard plastic net (50 mm x 200 mm) attached to the tip of a fishing rod (H.B. Concept Hibiki Casting Game-DX 30-450 KW-2378, Takamiya Co. Fukuoka) was held out in front of a nymph, and when the nymph climbed up the net, the nymph was pulled back to the hand and collected by the insect net. The collected nymphs were reared in plastic cages (235 mm x 155 mm x 185 mm height, Clean Case S, Sanko Shokai Co., Osaka) under laboratory conditions (25±2°C, 14:10 L:D photoperiod). The nymphs and resulting adults were supplied *ad libitum* fresh water and nymphs of some prey orthopteran insects [*Blatta lateralis* (Walker) (Blattidae), *Oxya yezoensis* Shiraki (Acrididae), *O. japonica* (Thunberg), *Acrida cinerea* (Thunberg) (Acrididae)].

### ***Male responses to a female show a calling posture***

The response of adult males of *H. patellifera* and *H. chinensis* to adult females of each species which showed a calling posture was observed. Males were released into a net chamber of 90 cm × 45 cm × 45 cm, and after 10 min, a net chamber (30 cm cubic) containing one virgin female (12-36 days old) was placed 1 m away from the net chamber of the male (Fig. 1). A blind net was placed between the male and female net chambers to prevent seeing the female by the male. A fan (YLR-C30, Yamazen Co., Osaka) was used to continuously blow air (0.22 m/s) so that the female's net chamber was upwind. The net chamber containing the males was divided into 6 compartments with markers every 15 cm (Figure 1). In preliminary experiments, males began moving around 5 minutes after females showed calling behavior. Then, under conditions in which the males could not see the females, they stopped moving approximately 15 minutes later. Therefore, the plots where males were present when the females showed a calling posture and after 15 minutes were recorded, respectively. The definition of calling posture showed by females followed a description of calling behavior by Perez (2005); i.e., the female begins to curl her abdomen, flexing it away from the folded wings, exposing its dorsal intersegmental membranes with keeping the legs in the same position. Perez (2005) also reported that when females showed a calling posture and released sex pheromones to attract males from a distance, which was also shown in our preliminary experiments. For the *H. chinensis* females, when they showed a posture similar to the calling behavior of *H. patellifera* females, we assumed that this was the calling behavior of this species and tested them in all experiments. Movements by males toward the female were considered positive values, and movements in the opposite direction to the female were considered negative values. Seventeen *H. patellifera* males and 10 *H. chinensis* males were used. In all males of both species, 8 replications to *H. patellifera* females and 6 replications to *H. chinensis* females with showing calling postures were recorded. Experiments were conducted 2-4 hours from the start of the scotophase at laboratory conditions (25±2°C, 14:10 L:D photoperiod). The approaching distance (-6 ~ +6) by males of both two species to conspecific or allospecific females which showed calling posture were analyzed using Mann-Whitney *U* test. These analyses were performed with R version 4.0.1 (R Development Core Team 2021).

### ***Collection of crude headspace extracts***

A single virgin female of *H. patellifera* or *H. chinensis* was placed in a desiccator (GL32 DURAN®, Sibata Scientific Technology Ltd., Saitama). When the female showed a calling posture, clean air was supplied from one of the cocks in the desiccator, and the volatiles released by the female was collected by a 60 mg (ca. 0.5 mL) of adsorbent (Tenax® TA, GL Sciences Inc, Tokyo) placed on the other cock. The collection was carried out under laboratory conditions (25±2°C, 14:10 L:D photoperiod) for 3 hours from 2 hours after the start of the scotophase when calling postures of each species were frequently observed. The collected volatiles were extracted from the adsorbent with 2.0 mL EtOAc and collected in a glass vial. Then EtOAc was removed from the extract under a gentle nitrogen stream, and the residue was re-eluted with 100 μL of hexane per 1 FEh (= crude headspace extract). The extracts were kept at -20°C before bioassays.

***Male responses to crude extract***

A single male of *H. patellifera* or *H. chinensis* was placed on a horizontal surface and waited for the male to stand still, and then a fan was used to blow air (0.22 m/s) to the male. Crude extracts from *H. patellifera* or *H. chinensis* females (1 female equivalent × 3 hours: 3.0 FEh) were applied onto a filter paper and placed the filter paper to 1.0 m upwind of the male. Male responses to the filter paper were observed for 5 min. In preliminary experiments, males that responded positively to the filter papers began moving as soon as the filter papers were presented and reached the proximity of the filter papers in approximately 5 min. The distance walked by the males was recorded with positive values for movement towards the filter paper and negative values for movement in the opposite direction. Five males of each species were used in the experiment, respectively.

## Results

### ***Male responses to a female show a calling posture***

*H. patellifera* females showed a calling posture similar to that reported by Perez (2005) during the scotophase, and the conspecific males were attracted to the females in the preliminary observation. Though Perez (2005) reported only the calling behavior of *H. patellifera* females, we observed that the calling behavior of *H. chinensis* was like that of the former; conspecific males were attracted to the females which show this posture. Males of *H. patellifera* and *H. chinensis* both approached conspecific females showing a calling posture but were not attracted to allospecific females. In both species, males that responded to the calling behavior of females started to move around 5 minutes after the females showed the calling posture. The males firstly rocked their bodies vertically without moving their legs. Then the males moved toward the female, shaking their heads from side to side. During the series of behaviors, *H. patellifera* males occasionally stopped walking and showed the characteristic behavior of shaking their body in small increments (juddering movement, *sensu* Perez 2005), while no *H. chinensis* males did show this behavior.

When a female of *H. patellifera* (conspecific) or *H. chinensis* (allospecific) showing a calling posture was presented to *H. patellifera* males upwind of the males and out of sight of the males (Fig. 1), the males significantly approached to females of the conspecific species than to allospecific females (Fig. 2; Mann-Whitney $U$ test, $U$ =

2,660.0, $p < 0.001$). *H. patellifera* males responded generally positively to the conspecific females: 11 of 17 males approached the females and 3 of 17 moved away from the females (Fig. 2). The 17 males approached the females by an average of 1.15 ± 0.30 compartments (mean ± SE, $N = 8$). In contrast, the males showed no clear attraction/avoidance response to the allospecific females and only 1 of 17 males moved away from the allospecific females (-0.09 ± 0.19 compartments, $N = 6$).

Under the same conditions as for *H. patellifera* males, when a female of *H. chinensis* (conspecific) or *H. patellifera* (allospecific) showing a calling posture was presented to *H. chinensis*, the males also significantly approached females of the conspecific species than to allospecific females (Fig. 3; Mann-Whitney *U* test, $U =$ 1,012.5, $p < 0.001$) as the same as *H. patellifera* males. *H. chinensis* males also responded generally positively to conspecific females: all 10 males approached the females (Fig. 3). The 10 males approached the females by an average of 1.52 ± 0.26 compartments ($N = 6$). In contrast, the males showed no clear attraction/avoidance response to the allospecific females (0.01 ± 0.12 compartments, $N = 8$).

### ***Male responses to crude headspace extract from females***

In both species, stationary males showed clearly positive responses only to crude headspace extracts from conspecific females, and no response to crude headspace extracts from allospecific females or control. Three of 5 *H. patellifera* males and 2 of 5 *H. chinensis* males contacted the crude headspace extract within 5 minutes. The average distance walked by males of *H. patellifera* and *H. chinensis* was 90.6 ± 9.1 cm and 84.6 ± 6.0 cm, respectively (Fig. 4). Three of 5 *H. patellifera* males showed juddering movement, but *H. chinensis* males did not. The males of both species moved toward the crude headspace extract by shaking their heads from side to side. In contrast to the response to females under calling posture, males began to shake their heads and started moving soon after the crude headspace extract was presented to the males.

## Discussion

Males of both *H. patellifera* and *H. chinensis* responded positively to conspecific females showing a calling posture and to crude headspace extracts from the female. However, in both species, males did not respond to allospecific females or crude headspace extracts (Figs. 2, 3, 4). These indicate that females of both species showing calling behavior secrete volatile sex pheromones that specifically attract only conspecific males, respectively.

The fact that males of *O. novaezealandiae* are misattracted to and preyed upon by females of *M. caffra* (Fea et al. 2013), probably be due to a lack of overlap in the native distributions of the two species (Patal and Singh 2016). In China, where *H. chinensis* was originally described, the distributional ranges of *H. chinensis* and *H. patellifera* were overlapped (Wang et al. 2020, Liu et al. 2021), and at least as far as we have observed in Tottori Prefecture, *H. patellifera* was collected simultaneously whenever *H. chinensis* was collected (in this study). Therefore, there must be some reproductive isolation mechanism between these two species, e.g., sound, vision, volatile/contact/trail pheromones.

Reproductive isolation related to sex pheromones in insect species that exists among closely related species includes, for example, differences in compounds, number of compounds, and/or their blend ratios in the sex pheromones [e.g., *Adoxophyes* spp. (Lepidoptera: Tortricidae); Tamaki et al. 1971a, 1971b, Yang et al. 2009], differences in the time of mating [e.g., *Ostrinia* spp. (Lepidoptera: Crambidae); Ishikawa et al. 1999, *Virbia* spp. (Lepidoptera: Erebidae); Allison and Cardé 2016], differences in the seasonal prevalence of adult emergence [e.g., *Inurois* spp. (Lepidoptera: Geometridae); Yamamoto and Sota 2012, Yamamoto et al. 2016], and differences in microhabitat [e.g., *Yponomeuta* spp. (Lepidoptera: Yponomeutidae); Hendrikse and Vos-Bünnemeyer 1987, Löfstedt et al. 1991, Menken et al. 1992]. *H. patellifera* and *H. chinensis* are both arboreal, and with adults emerging from mid-summer to late autumn. And courtship and mating in both species occur primarily in trees (Perez 2005, Nakamine 2016). In addition, females of both species showed calling behavior throughout the scotophase in the laboratory conditions. Therefore, the two species which are sexually matured are not isolated by the time of mating, adult emergence, or microhabitat. These suggest that volatiles secreted by females of *H. patellifera* and *H. chinensis*, respectively, may play an important role in the reproductive isolation of both species in the field.

Invasive generalist predators are known to have a variety of negative impacts on native biota (e.g., Snyder and Evans 2006). The invasion of *H. chinensis* into areas originally inhabited exclusively by *H. patellifera* poses several risks that could drastically reduce *H. patellifera* populations. Three possible direct negative effects of *H. chinensis* on *H. patellifera* populations are resource competition, reproductive interference, and intraguild predation. If *H. patellifera* was eradicated within 2-3 years following the invasion of *H. chinensis* (Mano and Uno 2014, Yoshitsuru 2014, Takahashi and Kishi 2016), it is unlikely that this dramatic turnover (local extinction or niche partitioning) was the result of simple resource competition, and that either reproductive interference from *H. chinensis* to *H. patellifera* and/or unilateral intraguild predation of *H. patellifera* by *H. chinensis* had occurred.

Assuming that *H. patellifera* receive some reproductive interference from *H. chinensis*, this study rejects the possibility that female sex pheromones are the cause of this interference. However, if either or both *H. patellifera* and *H. chinensis* use means other than female sex pheromones in combination to seek out and mate with the opposite sex, there is a possibility for some reproductive interference between the two species. The microhabitat of both species overlaps, and the seasonal occurrence of adults of both two species overlaps as well. This means that if adults of both species encounter each other in the field with a high probability, it is possible that the wrong courtship and/or mating may occur between them. However, we have not yet been able to verify whether the misidentification occurs and it is enough of a reproductive interference to reduce the *H. patellifera* population.

If intraguild predation exists between *H. patellifera* and *H. chinensis*, it is possible that *H. chinensis* could cause a sharp decline in *H. patellifera* population. Intraguild predation relationships are often determined by relative body size, with larger predators typically prey on other smaller species (Turner and Polis 1979).

Snyder and Hurd (1995) conducted a competition experiment in which they manipulated the timing of hatching of each of the sympatric mantid species *Tenodera angustipennis* Saussure and *T. sinensis* (Saussure), and they concluded that the coexistence of both species through niche partitioning that shifts phenology is more influenced by intraguild predation than by resource competition. Rose and Hurd (2016) also studied local populations of both species continuously over 7 years and revealed that the two factors, intraguild predation, and an egg parasitoid wasp *Podagrion mantis* parasitize only the oothecae of *T. angustipennis*, have caused a gradual decline in *T. angustipennis* populations.

In Japan, *H chinensis* hatches earlier than *H. patellifera*, and adults also emerge earlier (Yamasaki, personal observation). In addition, the body size of both males and females of *H. chinensis* is larger than that of *H. patellifera*. These two factors indicate the possibility that *H. chinensis* unilaterally preys on *H. patellifera* in both species, which share a common microhabitat.

In conclusion, the possibility of sex pheromone-mediated reproductive interference between *H. patellifera* and *H. chinensis* was considered unlikely. However, this study did not identify sex pheromone components that would be present in crude headspace extracts from females of both species; identification of these components would lead to additional insights. Careful observation is needed that what kind of interspecific relationship exists between *H. patellifera* and *H. chinensis*, and whether *H. patellifera* always faces local extinction when *H. chinensis* invades.

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## Figure legends

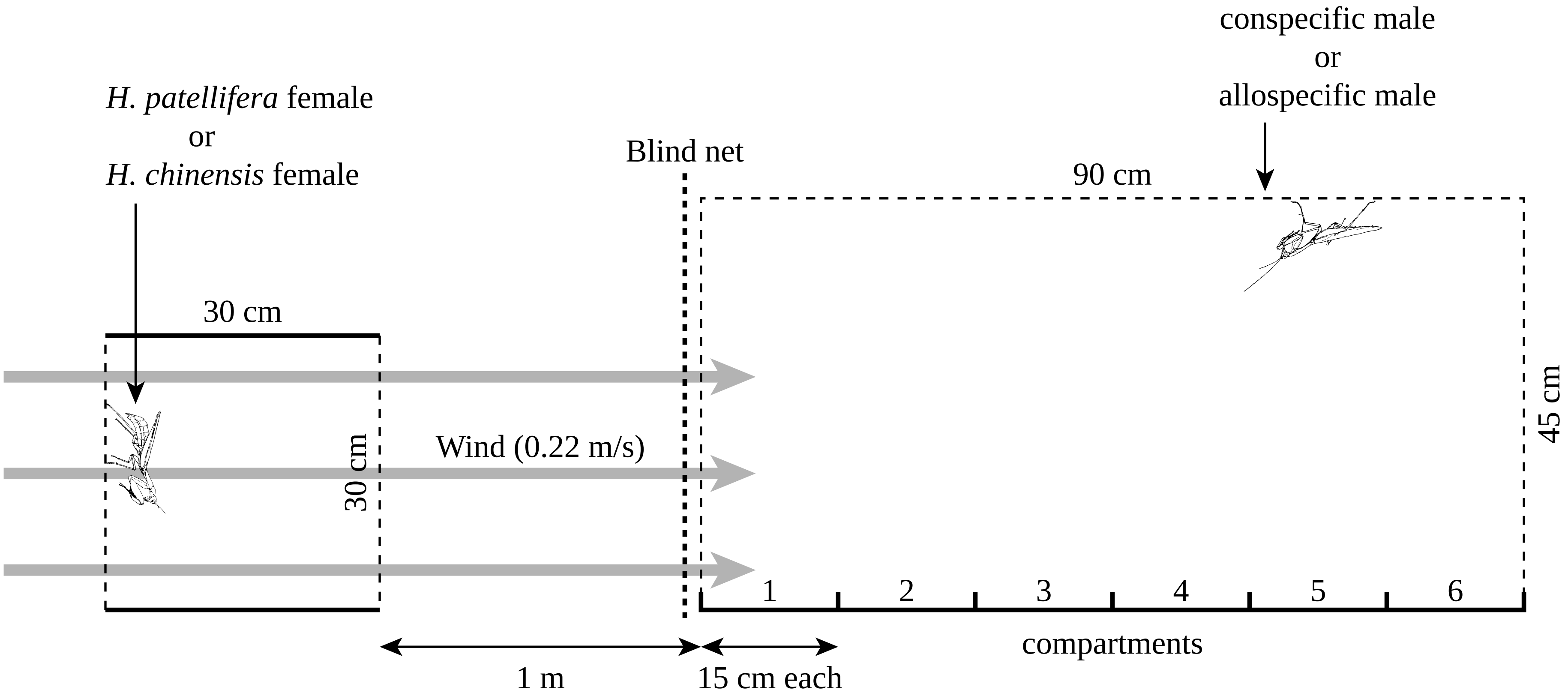
Figure 1. Schematic of an apparatus for observing the response of male praying mantises to virgin females. A single male of *H. patellifera* or *H. chinensis* was placed in a 90 cm x 45 cm x 45 cm net chamber, and a 30 cm cubic net chamber containing a conspecific or allospecific female was placed 1 m away. A fan was used to blow air that the female should be upwind of the fan, and then observation was continued for 15 minutes after the female showed a calling posture. A blind net was placed between the net cages of the female and male to prevent the male from seeing the female.

Figure 2. The response of *H. patellifera* males to a female of *H. patellifera* or *H. chinensis* shows a calling posture, respectively. The horizontal axis shows the number of compartments where males moved from the starting point, and the vertical axis shows the individuals under the experiment. *H. patellifera* males significantly approached toward conspecific females more than allospecific females (Mann-Whitney $U$ test, $U = 2{,}660.0$, $p < 0.001$).

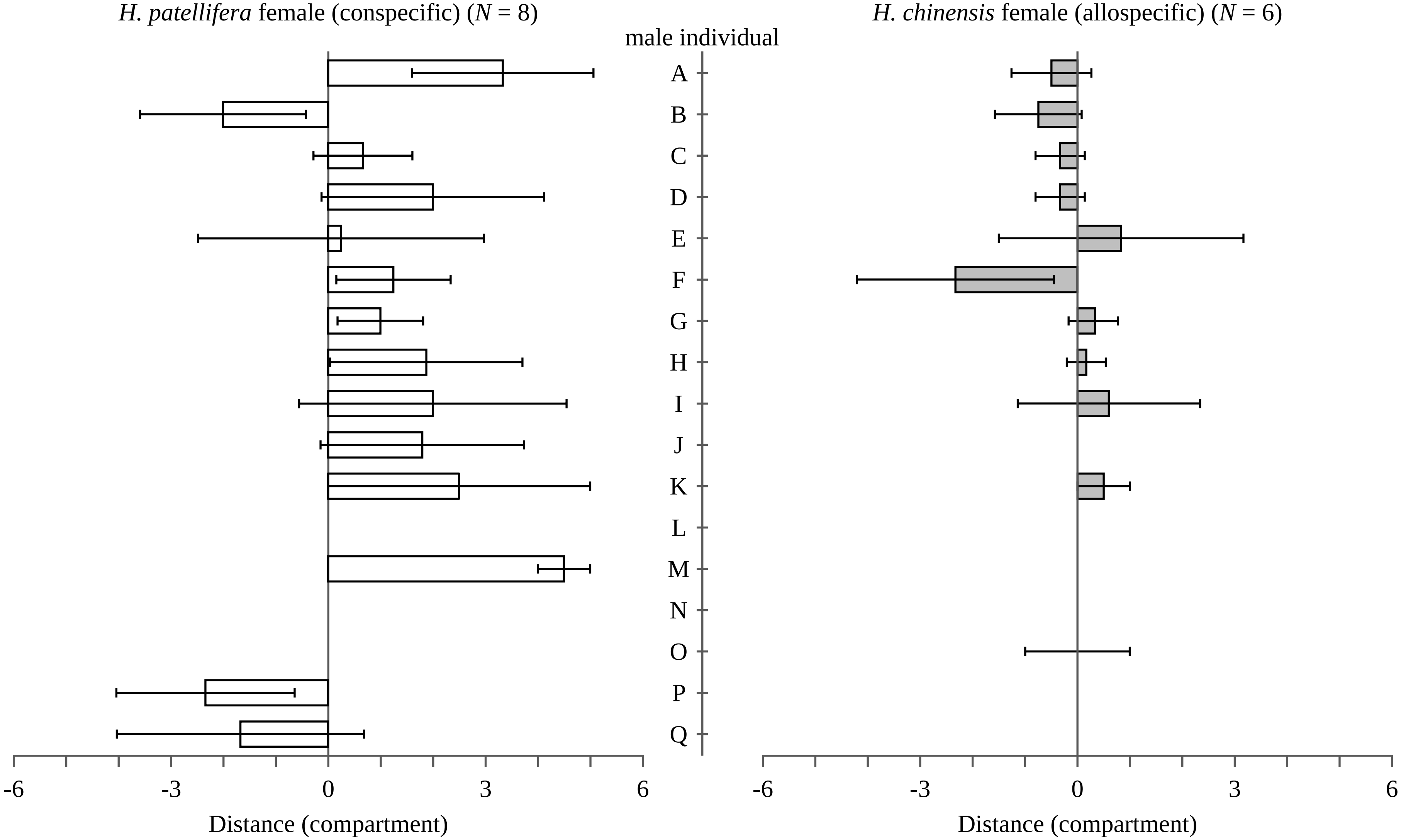
Figure 3. The response of *H. chinensis* males to a female of *H. patellifera* or *H. chinensis* shows a calling posture, respectively. The horizontal axis shows the number of compartments where males moved from the starting point, and the vertical axis shows the individuals under the experiment. *H. chinensis* males significantly approached toward conspecific females more than allospecific females (Mann-Whitney $U$ test, $U = 1{,}012.5$, $p < 0.001$). 0

Figure 4. The approached distance by males of *H. patellifera* and *H. chinensis* to crude headspace extracts from females showed a calling behavior (3.0 FEh) of both species, respectively. Only males that were full and stationary were used in the experiment. Males of both species responded only to crude headspace extracts obtained from conspecific females, respectively.

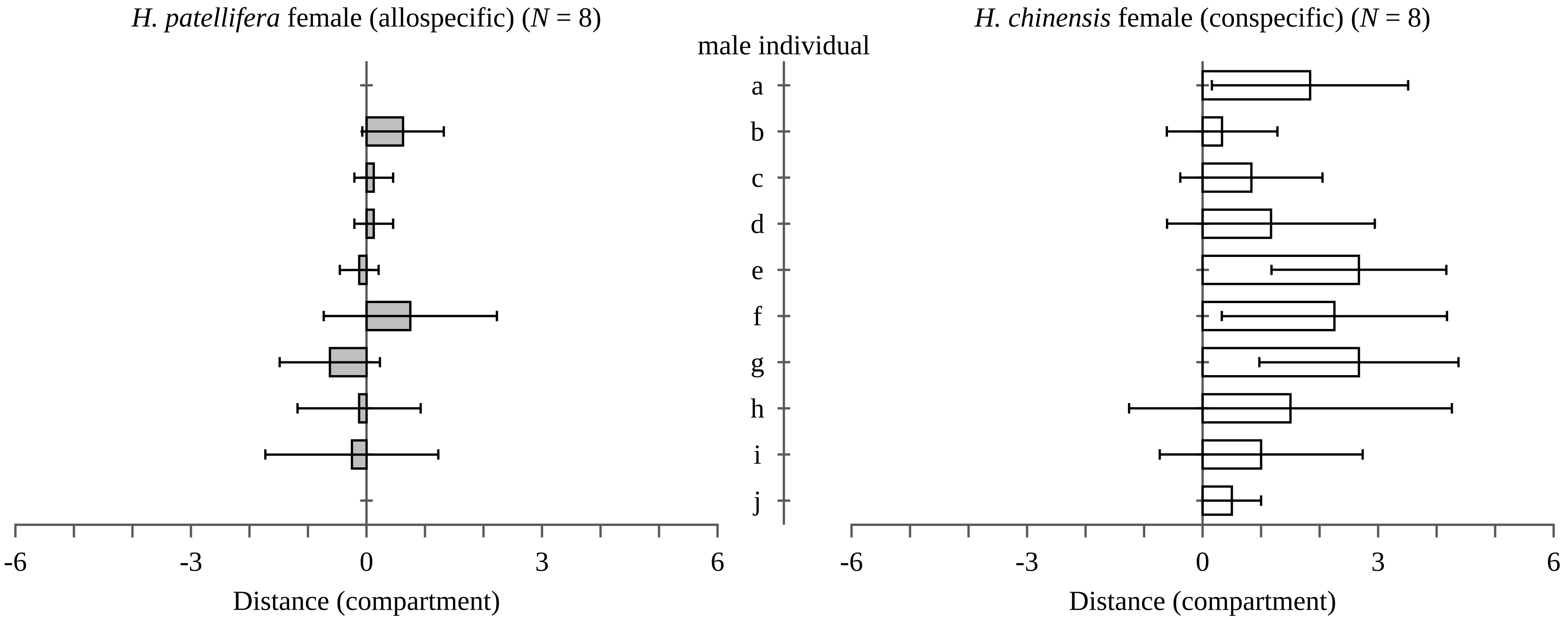
Saji et al. Figure 1



Saji et al. Figure 2



Saji et al.  Figure 3



Saji et al.  Figure 4