

Sand-bubbler crabs distinguish fiddler crab signals to predict intruders

Daisuke Muramatsu ^{1,2}

¹ Center for Natural Environment Education, Nara University of Education

² Wildlife Research Center of Kyoto University

The Version of Record of this article is published in Behavioral Ecology and Sociobiology, and is available online at <https://doi.org/10.1007/s00265-021-03066-5>".

Abstract

There is growing evidence that animals gain information from heterospecifics, but utilising other species' signals has rarely been reported in invertebrates. Herein, I conducted field experiments in a mixed colony of two crab species, *Scopimera globosa* and *Austruca lactea*, to test whether *S. globosa* discriminate several different displays of neighbouring male *A. lactea*. Three types of 'intruder' (male or female *A. lactea*, or a predatory crab, *Helicana japonica*) were exhibited to the 'performer' (male *A. lactea*) to elicit four different actions (courtship, aggressive, or defensive displays, or evasive behaviours). The actions of the performer, but not the presence of the intruder, were exhibited to the 'audience' (male *A. lactea* or *S. globosa*); the behaviours of the audience were recorded to analyse whether the audience could take advantage of the actions of neighbours. The evasive behaviour of performers elicited similar rates of evasive behaviours from conspecific and heterospecific audiences. Furthermore, courtship and aggressive displays of performers elicited significantly different rates of evasive behaviours from heterospecifics. The courtship displays of male *A. lactea* are more intensive than its aggressive displays; therefore, the reactions of *S. globosa* did not simply increase with the intensity of the performers' displays. Presumably, *S. globosa* recognizes that courtship displays by *A. lactea* do not indicate undesirable circumstances. Altogether, *S. globosa* were able to distinguish two types of display as well as evasive behaviours of male *A. lactea*, an ability that may contribute to their estimation of the risk level of approaching intruders.

Significance Statement

By using field experiments, I demonstrated that sand-bubbler crabs distinguished the courtship and aggressive displays of fiddler crabs and showed evasive behaviours more frequently when they see the aggressive displays. The courtship displays of the fiddler crabs are more intensive than its aggressive displays; therefore, the reactions of the sand-bubbler crabs did not simply increase with the intensity of the performers' displays. The displays of fiddler crabs were performed to other crabs (male or female fiddler crab, or a predatory crab) but not to the sand-bubbler crab; therefore, the sand bubbler crabs may have eavesdropped on heterospecific signals and utilised the heterospecific signals to predict the risk level of approaching intruders. To the best of my knowledge, distinguishing several signals of other species has been found only in some species of mammals, birds, or reptiles.

Keywords

signal eavesdropping; heterospecific cue; claw-waving display; *Scopimera globosa*; *Austruca lactea*

Introduction

Animals living in the same habitat often share the same needs (e.g. food, sunlight, or nest sites) and problems (e.g. predators, parasites or abiological hazards) with other individuals (Coolen et al. 2003; Avarguès-Weber et al. 2013). Any

individual would thus have a chance to gather information from other individuals, including those from heterospecific species (summarised in Table 1). Because heterospecific animals may differ in their vigilance levels, perceptual capacities, and information-gathering methods (Raine et al. 2006; Goodale et al. 2010), they may provide information which cannot be obtained from conspecifics. Thus, gathering information from heterospecifics may be adaptive (Leadbeater and Chittka 2007).

To take advantage of the signals of heterospecifics, audiences need to extract the relevant information from heterospecific signals. For example, black- and yellow-casqued hornbills respond to the Diana monkey's 'eagle' alarm call but not its 'leopard' alarm call, because hornbills are vulnerable to eagles but not leopards (Rainey et al. 2004a, b). Such threat assessment is crucially important because animals have to deal with a trade-off between time spent being vigilant versus time spent on other activities such as foraging or mating (Ings and Chittka 2008).

On intertidal mudflats, there are several species of crabs which use similar resources or are eaten by similar predators. For instance, the sand bubbler crab *Scopimera globosa* and the fiddler crab *Austruca lactea* often live in a mixed-species colony on upper intertidal mudflat. The body colour of *S. globosa* is cryptic, but males of *A. lactea* has an enlarged bright white claw and are more conspicuous than *S. globosa* (Fig. 1a, b). Both *S. globosa* and *A. lactea* carry compound eyes on long eye stalks to which they ensure a panoramic visual field in a flat environment (Zeil & Hemmi, 2006). Fiddler crabs can detect other crabs up to 2 m away (Zeil et al., 2006), and *S. globosa* may have somewhat similar visual ability. Each individual of both species defends a burrow and small area around it, and feeds on detritus in the topsoil. Males of *A. lactea* can be a threat for *S. globosa* since they have an enlarged claw and sometimes usurp the burrows from *S. globosa* (D. Muramatsu, pers. obs.). Both species were occasionally preyed on by a predaceous crab, *Helicana japonica* (Fig. 1d). Therefore, these species share the same resource (food and shelter) and predators, and it may be adaptive to gather information from heterospecifics.

Males of *S. globosa* and *A. lactea* are known to use claw-waving display for intraspecific communication. Males of *S. globosa* perform simple up-and-down waving that function as courtship behaviour (Moriito and Wada 2000; Ohata et al. 2005). By contrast, males of *A. lactea* perform four distinctive claw-waving displays: lateral-circular, circular, lateral-flick, and rapid-vertical waving in different context (Muramatsu, 2011a, b; summarised in Table 2). It has been predicted that lateral-circular waving is used to attract females into the male's burrow, circular waving is performed toward unspecified distant females to advertise the signaller's general quality, lateral-flick waving is used to an offensive territorial display relating border disputes, and rapid-vertical waving is a defensive territorial display used for burrow guarding (Muramatsu, 2011a, b). For sake of simplicity, I categorised these displays into three groups: courtship, aggressive or defensive displays (Table 3). These three types of display can be used as cues of incoming intruders because courtship displays (lateral-circular or circular waving) tend to be performed in the presence of burrowless females, aggressive display (lateral-flick waving) is mostly performed toward resident males in the breeding season, and defensive display (rapid-vertical waving) is performed toward burrowless males (Muramatsu, 2011a, b). Crabs around male *A. lactea* can thus roughly predict the incoming intruders by utilising the displays; the information may be useful for both conspecific and heterospecific audiences. In addition to the waving displays, evasive behaviours (Escape into the burrow, move back to the burrow, or freeze) of nearby crabs may also be a good indicator of approaching shared predators (Table 3).

In the present study, field experiments were conducted to test whether the displays and evasive behaviours of male *A. lactea* are utilised by conspecific *A. lactea* and heterospecific *S. globosa* audiences as cues of incoming intruders. The waving displays of *A. lactea* are more informative than that of *S. globosa*, and it might be beneficial for *S. globosa* to use the heterospecific signal as an information resource. If males of *A. lactea* perform different displays or evasive behaviour when they perceived different types of intruders, both conspecific and heterospecific neighbours can estimate the risk level of intruders. The most hazardous intruder for both *S. globosa* and *A. lactea* must be their shared predator, *H. japonica*. Males of *A. lactea* may also be the threats for both species because they have a large weapon (Fig. 1b) and sometimes usurp burrows from *A. lactea* and *S.*

globosa. Females of *A. lactea* are less risky for both species as they have only small claws (Fig. 1c), and can also be a potential mate for male *A. lactea*. If nearby crabs can utilise information from *A. lactea* males, they could acquire information about approaching predators or less hazardous intruders and decide whether to escape or how long to hide. Deciding whether to hide would be important for these crabs because once crabs hide inside a burrow, they temporarily lose their sight and face a threat of ambushing predators waiting at the entrance to the burrow for the sight-impaired crabs to emerge (see Hugie, 2004). By using *A. lactea* as a sentinel, nearby crabs may be able to stay at the mudflat surface and continue feeding and other activities unless and until an actual threat arises.

Herein, I randomly exhibit an ‘intruder’ (male or female *A. lactea*, or *H. japonica*) to a ‘performer’ (male *A. lactea*) to elicit four different actions (courtship display, aggressive display, defensive display, or evasive behaviour), and investigate whether the ‘audience’ (male *A. lactea* or male *S. globosa*) can utilise the behaviour of the performer to predict the risk level of approaching intruders without seeing them. First, I confirmed if the performers react differently in response to the three types of intruder. Second, I checked if the conspecific audiences distinguish the several displays or evasive behaviour. Finally, I checked if the heterospecific audience can distinguish the behaviours of the performer and behave accordingly. If *A. lactea* and/or *S. globosa* audiences can distinguish the displays of performer (male *A. lactea*), they may be able to use them as cues for predicting the risk level of approaching intruders.

Methods

Experimental set-up

The study site was located in a mixed colony of three crab species, *S. globosa*, *A. lactea*, and *H. japonica*, centred on an intertidal mudflat in the estuary of the Yabusa River, Kagoshima, Japan (31.697N, 130.287E). There were no distinct avian predators in the study site (Muramatsu, 2017). Crabs were active on the mudflat surface during diurnal low tides, except on days with heavy rain (Muramatsu and Koga, 2016). The densities of *S. globosa* and *A. lactea* at this study site were 0.1 ± 0.2 individual/m² (range: 0.0–1.2) and 13.1 ± 2.9 individual/m² (mean $\pm$ SD, range: 4.6–21.0), respectively (calculated from the raw data of Muramatsu 2010a; observed from 11 May to 6 Sep. 2002, except neap tides and rainy days).

For a series of field experiments, a wooden enclosure that forms a passage with two blind corners was placed on the mudflat each day to fence in a pair of neighbouring crabs and their burrows: one crab serving as performer (male *A. lactea*) and another as audience (male *A. lactea* or male *S. globosa*) (Fig. 2). The burrow of the performer was placed at one corner of the passage, and the performer is visible from the audience. The burrows were natural and intact, and the two crabs were familiar with each other. The enclosure was high enough so that the crabs were visually and physically isolated from the rest of the population. Crabs other than the performer and audience were captured and removed from the enclosure, and their burrows were covered with soil to obliterate the entrances. Crabs were captured by blocking their return to their burrows with a wooden stick (for details, see Muramatsu, 2010b), or by live traps (Muramatsu, 2018). I then captured a burrowless crab (*H. japonica*, male *A. lactea*, or female *A. lactea*) to be used as an ‘intruder’. It generally takes 5 to 20 minutes to capture the intruder in the field. In the experiments, the intruder was released to the passage at the opposite side of the audience by hand (Fig. 2). By this treatment, the performer and audience escaped into their burrow and the intruder stayed motionless at around the wall of the enclosure. I stayed motionless and waited until crabs resumed normal activities such as feeding or grooming (it generally takes 5 to 20 minutes), then started videotaping. Released intruder generally started moving first and walked through the passage to the performer. The pocket (a wider area of the passage) just before the blind corner often trapped the intruder for a while, making it possible to gain time until the performer and audience resume normal activities. The videotaping was treated as successful when the intruder walked through the blind corner of the passage and became visible to the performer after the performer and audience resumed normal activities

(example of the video clip: SI 1). It was not possible to record data blind because my study involved focal animals in the field.

The appearance of the intruder elicited four different actions from the performer: courtship, aggressive, or defensive displays, or evasive behaviour (Table 3). The actions of the performer, but not the presence of the intruder, were visible to the audience. The audience's behaviours observed before the intruder became visible to the audience (i.e. before the intruder cross the line of sight from the audience) were videotaped to analyse whether they behaved differently after seeing four types of performer actions. The actions of the performer will be 'no reaction' if the intruder move quickly (often occurred in *H. japonica*) and become visible to the audience before the performer shows any special behaviours. The same set of the quadrat (i.e., the same performer and audience) was used for three different types of intruders in a random order. In some cases, however, I could not complete recording three intruders since the performer or the audience closed the burrow entrance and stopped their surface activity. After the experiments, crabs were captured and marked by painting on the carapace to avoid duplication; the paint was coated with cyanoacrylate adhesive to prevent abrasion (see Muramatsu & Koga, 2016). After retaining the crabs for 10 min in a glass jar to allow the adhesive to solidify, resident crabs were released into their own burrows, and burrowless crabs were released on the mudflat surface. It typically takes 40 minutes to set-up the enclosure and 20 minutes to replace the intruders.

Statistical analyses

The reactions of performers in relation to intruder type were compared using the two-tailed *G* test with Williams' correction by using the script made by Hurd (2001).

To test whether audience behaviour varied with the performer's action, multinomial log-linear models (the multinom function of the nnet package; Ripley and Venables, 2016) were applied, implemented in the R statistical package (R Core Team 2020). The audience's behaviour (courtship, aggressive, or defensive display, evasive behaviour, or no reaction) was analysed as a categorical response variable, and the type of intruder (*H. japonica*, male *A. lactea*, or female *A. lactea*), performer's action (courtship, aggressive, or defensive display, or evasive behaviour) and type of audience (male *A. lactea* or male *S. globosa*) were fitted as explanatory variables. I calculated Akaike information criterion (AIC; Akaike, 1974) values for all combinations of explanatory variables, and the model that yielded the smallest AIC value was selected as the best model to predict audience behaviour.

Fisher's exact test was used to investigate whether the performer's actions affected the behaviour of male *A. lactea*. Fisher's exact test with sequential Bonferroni adjustments (Rice 1989) were used for post-hoc pairwise comparisons. I also tested whether a performer's actions affect the behaviour of male *S. globosa* by using Fisher's exact test. Ryan's multiple comparison tests of proportions (Ryan 1960) were used as post-hoc tests by using the script made by Aoki (2004) since the reactions of the *S. globosa* were binary (evasive behaviour or no reaction). Unless otherwise stated, all tests were two-tailed and the level of significance set at 5% ($\alpha = 0.05$).

Results

A total of 259 records (89 intruding *H. japonica*, 87 male *A. lactea*, and 83 female *A. lactea*) from 105 enclosures were successfully obtained.

Reactions of the performer to the intruder

The reactions of the performer (male *A. lactea*) differed significantly depending on the type of intruder (*G* test: $G = 113.03$, $df = 6$, $p < 0.001$). *Helicana japonica* elicited evasive behaviour, male *A. lactea* elicited defensive display, and female *A. lactea* elicited courtship display most frequently from the performer (Fig. 3).

Factors affecting the behaviours of the audience

Although both performer action and type of intruder contributed to predicting audience behaviour, the results of multinomial log-linear analysis showed that performer actions associated most strongly with audience behaviour, as all models contained performer actions ranked higher than the other models (Table 4). The best model contained performer action and type of audience as the explanatory variables, suggesting that the behaviours of audiences were determined mainly by performer actions, and that males of *S. globosa* and *A. lactea* responded differently to performer actions.

Audience behaviour

Male *A. lactea* audiences behaved differently in response to the actions of performer (Fisher's exact test: $p < 0.001$). Courtship display of performers elicited courtship, aggressive, and defensive displays, along with evasive behaviour, though 70.4% of audience reactions actually fell into the no reaction category (Fig. 4). Aggressive display by performers did not elicit any claw-waving displays from audiences but elicited evasive behaviours from 36.4% of the audiences. A similar frequency of evasive behaviour was elicited by performers' defensive displays, though some courtship and defensive displays were also observed. Evasive behaviour by performers elicited evasive behaviours from 65.0% of the audiences, and 5.0% of the audiences performed defensive displays in response to the evasive behaviour of performers. After the sequential Bonferroni adjustment was applied (Rice 1989), the audience's reactions to courtship display and evasive behaviours and the reactions to courtship and defensive displays differed significantly (Fig. 4).

Male *S. globosa* audiences also behaved differently in response to the actions of performer (Fisher's exact test: $p < 0.001$). No waving display of *S. globosa* was observed in response to performer actions; therefore, the responses of *S. globosa* were either evasive behaviours or no reaction (Fig. 5). Courtship display by performers rarely (12.9%) elicited evasive behaviours in audiences. Aggressive and defensive displays of performers elicited evasive behaviours from audiences in 47.4% and 32.1% of cases, respectively. Evasive behaviours by performers elicited evasive behaviours from 70.4% of the audiences. After Ryan's multiple comparison tests of proportions were applied (Ryan 1960), the audience's reactions to courtship and aggressive displays, to courtship display and evasive behaviours, and to defensive display and evasive behaviours differed significantly (Fig. 5).

Courtship, aggressive, and defensive displays, and evasive behaviour by performers elicited evasive behaviours from *A. lactea* and *S. globosa* at roughly similar rates (7.4%, 36.4%, 43.3%, and 65.0% from *A. lactea*, and 12.9%, 47.4%, 32.1%, and 70.4% from *S. globosa*, respectively). Evasive behaviours by *S. globosa* tended to occur slightly more frequently than with *A. lactea*, but the reaction of *S. globosa* was less frequent when the performer showed defensive displays.

Discussion

The results of the present study showed that the actions of the performer (male *A. lactea*) roughly reflect the type of intruder; evasive behaviours were mostly elicited by intruding *H. japonica*, aggressive and defensive displays were most frequently elicited by intruding male *A. lactea*, and courtship displays were most frequently elicited by intruding female *A. lactea* (Fig. 3). Therefore, crabs around the performers were able to predict the approaching intruder by the displays or evasive behaviours of the performer. The types of approaching intruder may be an important information for both conspecific *A. lactea* and heterospecific *S. globosa* because these species beware of the three types of intruder in different alert levels. Although the study site (an intertidal mudflat) was basically a flat environment, there were some dimples and obstacles like shells, stones or driftweeds. Therefore, approaching intruders may not always be visible, and gathering information from nearby crabs may be beneficial for the crabs living on mudflats.

For conspecific *A. lactea* audiences, deciphering the actions of the performer may not be difficult because their waving displays are regularly used for intraspecific communication (Lin and Liu Severinghaus 1990; Muramatsu 2011a, b). In the present study, however, the actions of the performers were elicited by the intruder, not by the audiences. Therefore, the actions of the performers were not signals for the audience, but were cues of something that elicit the waving displays or evasive behaviours from performers. Although we cannot know whether the audiences were able to predict the type of the intruder by using the actions of the performer, at least they seemed to perceive different levels of threat from the cues. Indeed, the frequency of the evasive behaviours caused by the performer actions were related with the expected risk level: evasive behaviours of the audiences were most frequently elicited by the evasive behaviours of the performer, followed by the defensive and aggressive displays, but courtship displays of the performer rarely elicited the evasive behaviours from the audiences (Fig. 4). These reactions of the audience were correct because most of the evasive behaviours of performers were elicited by approaching *H. japonica*, and the defensive and aggressive displays of the performer most strongly related with approaching male *A. lactea* (Fig. 3).

Although I expected that audience *A. lactea* males may copy the courtship displays of performers, audience males did not frequently perform courtship displays when seeing the courtship displays of performers. While 43.4% of the performers showed courtship displays when female *A. lactea* approached (Fig. 3), only 3.7% of the audiences performed courtship displays after watching the courtship displays of performers (Fig. 4). In *A. mjoebergi*, by contrast, males without watching a female eavesdrop on the waving displays of nearby males and perform courtship displays to some extent: the median wave rate is 12 waves/min when a female is not visible, while it was 20 waves/min when a female is visible (Milner et al. 2010). The difference between *A. lactea* and *A. mjoebergi* may be caused by signal reliability. Milner et al. (2010) presented three or more courting males to the focal male for over three minutes; therefore, it is highly likely that there are a burrowless female nearby. In the present study, however, the cue of a female was just one waving male (performer) showing courtship display for a limited period of time (the time before the intruder cross the line of sight from the audience; generally less than 30 seconds). The lower reliability and/or weaker stimuli of waving performers might not be enough to elicit the courtship display from audience males.

The several distinct waving displays and evasive behaviours of *A. lactea* males may also be a good information resource for heterospecifics; however, the detection and discrimination of these waving displays would not be easy for heterospecifics because heterospecific individuals do not share the same evolutionary history and perceptual adaptations to detect signals (Magrath et al. 2015). In the present study, however, the courtship and aggressive displays of male *A. lactea* elicited evasive behaviours of neighbouring *S. globosa* at significantly different rates (12.9% and 47.4%, respectively), suggesting that *S. globosa* were able to distinguish the two types of heterospecific display. The courtship displays of male *A. lactea* are much more intensive and conspicuous than aggressive displays (Muramatsu, 2011a); therefore, the reactions of *S. globosa* did not simply increase with the intensity of performer displays. Courtship displays can be highly intensive and threaten other individuals if they do not decipher the message correctly (Borgia and Presgraves 1998; Patricelli et al. 2002; Coleman et al. 2004; How et al. 2008). *Scopimera globosa* may have learned that *A. lactea* courtship displays do not indicate undesirable circumstances for them; alternatively, their behavioural rules may be innate. By contrast, less conspicuous aggressive displays by male *A. lactea* frequently elicited evasive behaviours in *S. globosa*. Evasive behaviours of *S. globosa* do not seem to be elicited by threats to performers because the performers' aggressive displays were directed towards the intruder, not the audience. Therefore, *S. globosa* may have reacted based on their prediction that something that elicit the aggressive displays from male *A. lactea* was approaching.

The results of the present study showed that the proportions of evasive behaviours elicited by the four different performer actions were quite similar in the two types of audience (*A. lactea* and *S. globosa*). Thus, the behaviours of *A. lactea* elicited similar levels of evasive reaction from conspecific and heterospecific crabs. Because performer actions (i.e., the actions of neighbours) roughly reflect the type of intruder, audiences may have learned or evolved to predict the risk level of an approaching intruder by the use of performer's action. However, the reaction of *S. globosa* was imperfect because they did not show evasive

behaviours as frequently as *A. lactea* when the performer showed defensive displays. The inconspicuous nature of the defensive display motion (Muramatsu, 2011a, b) may not have evoked the reaction or learning processes of *S. globosa*. Alternatively, approaching intruders that elicit defensive displays from *A. lactea* males may not be a serious threat for *S. globosa*. The latter seems less plausible because *A. lactea* males are relatively large and occasionally usurp burrows from *S. globosa*.

Within the two species investigated in the present study, *A. lactea* would be a better information source, as their density is much higher than *S. globosa* (approximately 100 times higher in the study area) and they have conspicuous and distinctive claw-waving displays that represent the information of approaching intruders. However, whether the communication between *S. globosa* and *A. lactea* is one-way or bidirectional remains unknown because I did not conduct experiments using *S. globosa* as performers, due to the lower density of *S. globosa* in the study area. Further investigation into the reactions of *A. lactea* to the behaviours of *S. globosa* would be valuable.

Summary

Evasive behaviours by performers elicited evasive behaviours from both types of audience (*A. lactea* and *S. globosa*) at similar rates (65.0% and 70.4%, respectively). This suggests that evasive behaviours of male *A. lactea* elicit conspecific and heterospecific responses at similar rates. Moreover, courtship and aggressive displays by performers elicited evasive behaviours of heterospecific *S. globosa* at significantly different rates (12.9% and 47.4%, respectively). The courtship displays of male *A. lactea* are much more intensive and conspicuous than aggressive displays; therefore, the reactions of *S. globosa* did not simply increase with the intensity of the performers' displays. Presumably, *S. globosa* can recognize that courtship displays by *A. lactea* do not indicate undesirable circumstances. Altogether, *S. globosa* were able to discriminate two types of display and evasive behaviours by male *A. lactea*, and that ability may contribute to reducing the risk of approaching intruders.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-021-03066-5>

Acknowledgements I thank the members of Wildlife Research Center of Kyoto University for the constructive discussion about this study. This work was supported in part by the Sasakawa Scientific Research Grant (Grant number 26-447).

Funding This work was supported in part by the Sasakawa Scientific Research Grant (Grant number 26-447).

Conflicts of interest/Competing interests I declare that I have no competing interests related to this study.

Data availability The data used in the present study are available at: https://docs.google.com/spreadsheets/d/1NNs17KkfhG-feezoBevbYuS_fEvUxjwg6gMwqOny-eg/edit?usp=sharing.

Code availability The codes used in the present study are available at: https://docs.google.com/spreadsheets/d/1NNs17KkfhG-feezoBevbYuS_fEvUxjwg6gMwqOny-eg/edit?usp=sharing.

Ethics approval All procedures performed in this study involving animals were executed in accordance with the ethical standards of the guidelines for animal studies in the wild issued by the Wildlife Research Center of Kyoto University (1; 22

February 2017). This article does not contain any study with human participants.

Consent to participate Not applicable

Consent for publication Not applicable

References

- Akaike H (1974) A new look at the statistical model identification. *IEEE Trans Automat Contr* 19:716–723.
<https://doi.org/10.1109/TAC.1974.1100705>
- Aoki S (2004) http://aoki2.si.gunma-u.ac.jp/R/src/p_multi_comp.R (accessed 31 Jul. 2021).
- Avarguès-Weber A, Dawson EH, Chittka L (2013) Mechanisms of social learning across species boundaries. *J Zool* 290:1–11.
<https://doi.org/10.1111/jzo.12015>
- Borgia G, Presgraves DC (1998) Coevolution of elaborated male display traits in the spotted bowerbird: an experimental test of the threat reduction hypothesis. *Anim Behav* 56:1121–1128. <https://doi.org/10.1006/anbe.1998.0908>
- Carrasco MF, Blumstein DT (2012) Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls. *Ethology* 118:243–250. <https://doi.org/10.1111/j.1439-0310.2011.02002.x>
- Coleman SW, Patricelli GL, Borgia G (2004) Variable female preferences drive complex male displays. *Nature* 428:742–745.
<https://doi.org/10.1038/nature02419>
- Coolen I, Bergen Y V., Day RL, Laland KN (2003) Species difference in adaptive use of public information in sticklebacks. *Proc R Soc London Ser B Biol Sci* 270:2413–2419. <https://doi.org/10.1098/rspb.2003.2525>
- Fallow PM, Magrath RD (2010) Eavesdropping on other species: mutual interspecific understanding of urgency information in avian alarm calls. *Anim Behav* 79:411–417. <https://doi.org/10.1016/j.anbehav.2009.11.018>
- Fichtel C (2004) Reciprocal recognition of sifaka (*Propithecus verreauxi verreauxi*) and redfronted lemur (*Eulemur fulvus rufus*) alarm calls. *Anim Cogn* 7:45–52. <https://doi.org/10.1007/s10071-003-0180-0>
- Goodale E, Kotagama SW (2008) Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behav Ecol* 19:887–894. <https://doi.org/10.1093/beheco/arn045>
- Goodale E, Beauchamp G, Magrath RD, et al (2010) Interspecific information transfer influences animal community structure. *Trends Ecol Evol* 25:354–361. <https://doi.org/10.1016/j.tree.2010.01.002>
- Hetrick SA, Sieving KE (2012) Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behav Ecol* 23:83–92. <https://doi.org/10.1093/beheco/arr160>
- How MJ, Hemmi JM, Zeil J, Peters R (2008) Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. *Anim Behav* 75:1015–1022. <https://doi.org/10.1016/j.anbehav.2007.09.004>
- Hugie DM (2004) A waiting game between the black-bellied plover and its fiddler crab prey. *Anim Behav* 67:823–831.
<https://doi.org/10.1016/j.anbehav.2003.03.023>
- Hurd P (2001) Log-likelihood tests of independence & goodness of fit.
<https://websites.pmc.ucsc.edu/~mclapham/Rtips/G%20test.txt> (accessed 31 Jul. 2021).
- Ings TC, Chittka L (2008) Speed-Accuracy Tradeoffs and False Alarms in Bee Responses to Cryptic Predators. *Curr Biol* 18:1520–1524. <https://doi.org/10.1016/j.cub.2008.07.074>
- Lea AJ, Barrera JP, Tom LM, Blumstein DT (2008) Heterospecific eavesdropping in a nonsocial species. *Behav Ecol* 19:1041–1046. <https://doi.org/10.1093/beheco/arn064>

- Leadbeater E, Chittka L (2007) Social Learning in Insects – From Miniature Brains to Consensus Building. *Curr Biol* 17:703–713. <https://doi.org/10.1016/j.cub.2007.06.012>
- Lin H-C, Liu Severinghaus L (1990) The reproductive behaviour and mate choice of the fiddler crab (*Uca lactea lactea*) in Mid-Taiwan. *Behaviour* 113:292–307. <https://doi.org/10.1163/156853990X00536>
- Magrath RD, Haff TM, Fallow PM, Radford AN (2015) Eavesdropping on heterospecific alarm calls: from mechanisms to consequences. *Biol Rev* 90:560–586. <https://doi.org/10.1111/brev.12122>
- Magrath RD, Pitcher BJ, Gardner JL (2007) A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behav Ecol* 18:944–951. <https://doi.org/10.1093/beheco/arm063>
- Milner RNC, Jennions MD, Backwell PRY (2010) Eavesdropping in crabs: an agency for lady detection. *Biol Lett* 6:755–757. <https://doi.org/10.1098/rsbl.2010.0384>
- Moriito M, Wada K (2000) The presence of neighbors affects waving display frequency by *Scopimera globosa* (Decapoda, Ocypodidae). *J Ethol* 18:43–45. <https://doi.org/10.1007/s101640070023>
- Muramatsu D (2010a) Sand structure construction in *Uca lactea* (De Haan, 1835) is related to tidal cycle but not to male or female densities. *Crustaceana* 83:29–37. <https://doi.org/10.1163/001121609X12487811051624>
- Muramatsu D (2010b) Temporary loss of a sexual signal (claw loss) affects the frequency of sand structure construction in the fiddler crab, *Uca lactea*. *Ethol Ecol Evol* 22:87–93. <https://doi.org/10.1080/03949370903516040>
- Muramatsu D (2011a) For whom the male waves: four types of claw-waving display and their audiences in the fiddler crab, *Uca lactea*. *J Ethol* 29:3–8. <https://doi.org/10.1007/s10164-010-0216-2>
- Muramatsu D (2011b) The function of the four types of waving display in *Uca lactea*: Effects of audience, sand structure, and body size. *Ethology* 117:408–415. <https://doi.org/10.1111/j.1439-0310.2011.01884.x>
- Muramatsu D (2017) Sand ornaments used to attract females are avoided by rival males in the fiddler crab *Uca lactea*. *Ethol Ecol Evol* 29:501–510. <https://doi.org/10.1080/03949370.2016.1243156>
- Muramatsu D (2018) A fiddler crab caught in a live trap. In: *Movie Arch. Anim. Behav. Data No.* momo180623ul01b. <http://www.momo-p.com/showdetail-e.php?movieid=momo180623ul01b>
- Muramatsu D, Koga T (2016) Fighting with an unreliable weapon: opponent choice and risk avoidance in fiddler crab contests. *Behav Ecol Sociobiol* 70:713–724. <https://doi.org/10.1007/s00265-016-2094-2>
- Nieh JC, Barreto LS, Contrera FAL, Imperatriz-Fonseca VL (2004) Olfactory eavesdropping by a competitively foraging stingless bee, *Trigona spinipes*. *Proc R Soc B Biol Sci* 271:1633–1640. <https://doi.org/10.1098/rspb.2004.2717>
- Oda R, Masataka N (1998) The responses of Verreaux's sifakas to anti-predator alarm calls given by sympatric ring-tailed lemurs. *Folia Primatol* 69:357–360. <https://doi.org/10.1159/000021651>
- Ohata M, Wada K, Koga T (2005) Waving display by male *Scopimera globosa* (Brachyura: Ocypodoidea) as courtship behavior. *J Crustac Biol* 25:637–639. <https://doi.org/10.1651/c-2604.1>
- Patricelli GL, Uy JAC, Walsh G, Borgia G (2002) Male displays adjusted to female's response. *Nature* 415:279–280. <https://doi.org/10.1038/415279a>
- R Core Team (2020) R: a language and environment for statistical computing. <https://www.r-project.org/> (accessed 11 May 2020)
- Raine NE, Ings TC, Dornhaus A, et al (2006) Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behavior.. In: *Advances in the Study of Behavior*. pp 305–354
- Rainey HJ, Zuberbühler K, Slater PJB (2004a) The responses of black-casqued hornbills to predator vocalisations and primate alarm calls. *Behaviour* 141:1263–1277. <https://doi.org/10.1163/1568539042729658>
- Rainey HJ, Zuberbühler K, Slater PJB (2004b) Hornbills can distinguish between primate alarm calls. *Proc R Soc London Ser B Biol Sci* 271:755–759. <https://doi.org/10.1098/rspb.2003.2619>

- Reznikova JI (1982) Interspecific Communication Between Ants. Behaviour 80:84–95. <https://doi.org/10.1163/156853982X00454>
- Rice WR (1989) Analyzing tables of statistical tests. Evolution (N Y) 43:223–225. <https://doi.org/10.2307/2409177>
- Ripley B, Venables W (2016) Package ‘nnet.’ <https://cran.microsoft.com/snapshot/2016-08-05/web/packages/nnet/nnet.pdf> (accessed 11 May 2020)
- Ryan TH (1960) Significance tests for multiple comparison of proportions, variances, and other statistics. Psychol Bull 57:318–328. <https://doi.org/10.1037/h0044320>
- Seiler M, Schwitzer C, Gamba M, Holderied MW (2013) Interspecific semantic alarm call recognition in the solitary Sahamalaza sportive lemur, *Lepilemur sahamalazensis*. PLoS One 8:e67397. <https://doi.org/10.1371/journal.pone.0067397>
- Shriner WM (1998) Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. Anim Behav 55:529–536. <https://doi.org/10.1006/anbe.1997.0623>
- Templeton CN, Greene E (2007) Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. Proc Natl Acad Sci U S A 104:5479–5482. <https://doi.org/10.1073/pnas.0605183104>
- Vitousek MN, Adelman JS, Gregory NC, Clair JJHS (2007) Heterospecific alarm call recognition in a non-vocal reptile. Biol Lett 3:632–634. <https://doi.org/10.1098/rsbl.2007.0443>
- Windfelder TL (2001) Interspecific communication in mixed-species groups of tamarins: Evidence from playback experiments. Anim Behav 61:1193–1201. <https://doi.org/10.1006/anbe.2000.1701>
- Zeil J, Hemmi JM (2006) The visual ecology of fiddler crabs. J Comp Physiol A 192:1–25. <https://doi.org/10.1007/s00359-005-0048-7>
- Zeil J, Hemmi JM, Backwell PRY (2006) Fiddler crabs. Curr Biol 16:R40–R41. <https://doi.org/10.1016/j.cub.2006.01.012>
- Zuberbühler K (2000) Interspecies semantic communication in two forest primates. Proc R Soc London Ser B Biol Sci 267:713–718. <https://doi.org/10.1098/rspb.2000.1061>

Table 1 Case examples of information gathering from heterospecific signals

Performer	Audience	Description	Distinguish multiple signals	Reference
Lemur and sifaka (bidirectional)		Redfronted lemur <i>Eulemur fulvus rufus</i> and Verreaux's sifaka <i>Propithecus verreauxi verreauxi</i> distinguish each other's "aerial" and "general" alarm calls and behave accordingly.	Yes	Fichtel, 2004
Tamarin and tamarin (bidirectional)		Saddle-back tamarin <i>Saguinus fuscicollis</i> and emperor tamarin <i>S. imperator</i> respond to each other's long calls and approach to the sound source (speaker).	No	Windfelder, 2001
Marmot and ground squirrel (bidirectional)		Yellow-bellied marmot <i>Marmota flaviventris</i> and golden-mantled ground squirrel <i>Spermophilus lateralis</i> similarly respond to each other's anti-predator calls.	No	Shriner, 1998
Monkey	Monkey	Diana monkeys <i>Cercopithecus diana</i> distinguish the "eagle" and "leopard" alarm calls of Campbell's monkeys <i>C. campbelli</i> , and behave appropriately.	Yes	Zuberbühler, 2000
Lemur	Lemur	Sahamalaza sportive lemurs <i>Lepilemur sahamalazensis</i> increase vigilance after listening alarm calls of blue-eyed black lemur <i>Eulemur flavifrons</i> , but decrease vigilance after listening contact calls of the black lemur.	Yes	Seiler et al. 2013
Sifaka	Lemur	Ringtailed lemurs <i>Lemur catta</i> distinguish "aerial" and "terrestrial" alarm calls of Verreaux's sifaka <i>Propithecus verreauxi verreauxi</i> .	Yes	Oda & Masataka, 1998
Marmot	Mule deer	Mule deer <i>Odocoileus hemionus</i> increase vigilance after hearing the broadcast alarm calls of yellow-bellied marmot <i>Marmota flaviventris</i> .	No	Carrasco & Blumstein, 2012
Coua and magpie-robin	Lemur	Sahamalaza sportive lemurs <i>Lepilemur sahamalazensis</i> increase vigilance after listening alarm calls of crested coua <i>Coua cristata</i> or Madagascar magpie-robin <i>Copsychus albospectularis</i> , but decrease vigilance after listening songs of these two bird species.	Yes	Seiler et al. 2013
Monkey	Hornbill	Yellow-casqued hornbills <i>Ceratogymna elata</i> distinguish the "eagle" and "leopard" alarm calls of Diana monkeys <i>Cercopithecus diana</i> , and behave accordingly.	Yes	Rainey et al. 2004a, b

Go-away bird	Dik-dik	On hearing the alarm call of white-bellied go-away bird <i>Corythaixoides leucogaster</i> , Gunther's dik-dik <i>Madoqua guentheri</i> increase vigilance and evasive behaviour, and decrease foraging activity compared with a nonthreatening bird song.	Yes	Lea et al., 2008
Scrubwren and fairy-wren (bidirectional)		White-browed scrubwren <i>Sericornis frontalis</i> and superb fairy-wren <i>Malurus cyaneus</i> flee to cover in response to the each other's alarm calls. Both species are more likely to flee in response to conspecific and heterospecific alarm calls that included more elements (graded signals).	Yes	Magrath et al., 2007; Fallow & Magrath, 2010
Chickadee	Nuthatche	Red-breasted nuthatches <i>Sitta canadensis</i> distinguish two types of alarm call of black-capped chickadees <i>Poecile atricapillus</i> and respond differently.	Yes	Templeton & Greene, 2007
Titmouse	Chickadee	Carolina chickadees <i>Poecile carolinensis</i> distinguish three different levels of the calls of tufted titmice <i>Baeolophus bicolor</i> and respond differently.	Yes	Hetrick & Sieving, 2012
Drongo	Babbler	Orange-billed babblers <i>Turdoides rufescens</i> move quickly away from the playback speaker after hearing either conspecifics alarm calls or that of greater racket-tailed drongo <i>Dicrurus paradiseus</i> .	No	Goodale & Kotagama, 2008
Mockingbird	Marine iguana	Galapagos marine iguanas <i>Amblyrhynchus cristatus</i> exhibit anti-predator behaviour (alert or escape) during playback of the alarm call than during the song of Galapagos mockingbird <i>Nesomimus parvulus</i> .	Yes	Vitousek et al. 2007
Flycatcher	Day gecko	Madagascan giant day geckos <i>Phelsuma kochi</i> change their body colour quicker, darker and longer duration in response to the alarm calls than songs of Madagascar paradise flycatcher <i>Terpsiphone mutata</i> .	Yes	Ito et al., 2013
Ant	Ant	The amount of prey of <i>Formica pratensis</i> increases on the presence of subdominant ant <i>F. cunicularia</i> (perhaps because <i>F. pratensis</i> detect the chemical trails of <i>F. cunicularia</i>).	No	Reznikova, 1982
Stingless bee	Stingless bee	Stingless bee <i>Trigona spinipes</i> utilise odour marks of <i>Melipona rufiventris</i> to detect and take over the food source.	No	Nieh et al., 2004
Fiddler crab	Sand-bubbler	Sand-bubbler crab <i>Scopimera globosa</i> distinguish two types of display in	Yes	Present study

crab

fiddler crabs *Austruca lactea* and respond accordingly.

“bidirectional” in the first and second columns indicates that the roles (performer and audience) can be reversed. “No” in the fourth column indicates there is no apparent evidence in the reference, and it does not assertively deny the possibility of “Yes”. Note that signals listed here may or may not be performed toward heterospecifics, i.e., the audiences may use the heterospecific signals as cues.

Table 2 Descriptions of the four types of claw-waving display by male *A. lactea*

Type of waving	Description
Lateral-circular waving	Combination of slow extension, fast dorsal flexion, and circumduction of a large claw, performed with vigorous body elevation and back-and-forth side-steps. Often seen in the breeding season and mostly performed to female audiences. Observed more frequently in the enclosure with female audiences than with male audiences. Categorised as a courtship display in this study.
Circular waving	Simple circumduction of a large claw, frequently performed just before the breeding season and during the breeding season. Most conspicuous waving from a distance. The audience is not clear in most cases, but performed more frequently in the enclosure with female audiences than with male audiences. Categorised as a courtship display in this study since this waving may act as a long-distance courtship signal to attract females from afar.
Lateral-flick waving	Simple lateral extensions of a large claw toward a nearby audience. Larger males performed more frequently than smaller males. Rarely performed to females in the breeding season. Categorised as an aggressive display in this study.
Rapid-vertical waving	Rapid dorso-ventral protraction and retraction of a large claw, performed mainly toward intruding burrowless males. The stroke is compact and not conspicuous from a distance. Categorised as a defensive display in this study.

Definitions, behavioural descriptions, and video clips of the four types of claw-waving display are presented in (Muramatsu 2011a), and the function of each display is discussed in (Muramatsu 2011b).

Table 3 Behaviours shown by performer (*A. lactea*) and audience (*A. lactea*, *S. globosa*) males in experimental trials

Behavioural category	Description
Courtship display*	Performs lateral-circular waving or circular waving.
Aggressive display*	Turns the major claw towards the intruder or perform lateral-flick waving.
Defensive display*	Performs rapid-vertical waving.
Evasive behaviour	Escapes into the burrow, moves back to the burrow, or freezes (suddenly stops moving and remains motionless).
No reaction	Shows no clear reaction and maintains normal behaviour (largely feeding or grooming).

*Note that the courtship, aggressive, defensive displays were performed only by male *A. lactea*.

Table 4 Values of Akaike information criterion (AIC), ranked in increasing order, for multinomial log-linear models via neural networks

Rank	Model term(s)	AIC	Δ AIC
1	Performer's action, type of audience	355.4	0.0
2	Performer's action	365.1	9.7
3	Performer's action, type of audience, type of intruder	365.7	10.3
4	Performer's action, type of intruder	375.3	19.9
5	Type of audience, type of intruder	379.5	24.1
6	Type of audience	384.3	28.9
7	Type of intruder	389.7	34.3
8	(none)	394.6	39.2

Figure Legends

Fig. 1 Four types of crab used in the experiments

(a) male *Scopimera globosa*, (b) male *Austruca lactea*, (c) female *A. lactea*, and (d) female *Helicana japonica*. I did not discriminate the sex of *H. japonica* in the experiments.

Fig. 2 Top view of the experimental enclosure

Grey circles indicate the location of the intruder (I), performer (P), and audience (A). The boundaries are 10 cm high, which prevents the crabs from climbing up. The average distance of the burrows of performer and audience was 12.8 ± 2.4 (mean $\pm$ SD) cm.

Fig. 3 Reactions of the performer to the intruder

Performers' reactions to three types of intruders are shown separately.

Fig. 4 Behaviours of male *A. lactea* in response to performer actions

Individual comparisons marked with an asterisk indicate statistically significant differences after applying the sequential Bonferroni adjustment. Note that the significance levels were set to $\alpha = 0.008$ for comparing courtship display and evasive behaviour, and $\alpha = 0.01$ for courtship and defensive displays.

Fig. 5 Behaviours of male *S. globosa* in response to performer actions

Individual comparisons marked with an asterisk indicate statistically significant differences after applying Ryan's multiple comparison tests of proportions. Note that the significance levels were set to $\alpha = 0.008$ for comparing courtship display and evasive behaviour, $\alpha = 0.013$ for courtship and aggressive displays, and $\alpha = 0.013$ for defensive display and evasive behaviour.

SI 1 Example of video clip

The intruder (male *A. lactea* at the left) walked to the performer (male *A. lactea* at the upper right). The performer showed defensive display (rapid-vertical waving: see Muramatsu 2011a, b). The audience (male *S. globosa* at the lower right) escaped into his burrow just after watching the display of the performer. The intruder was not visible from the audience when the audience started escaping.



Fig. 1

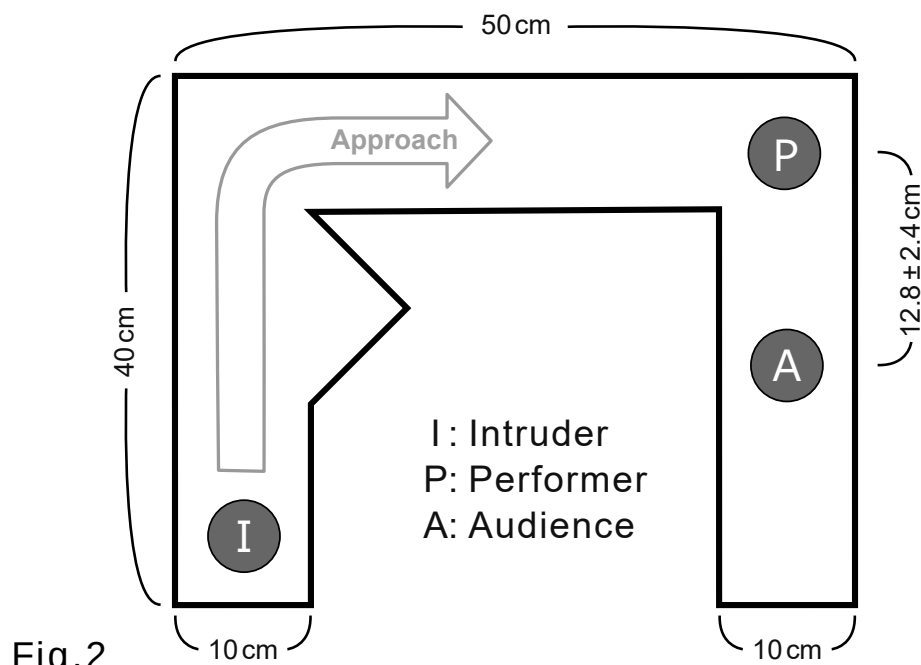


Fig.2

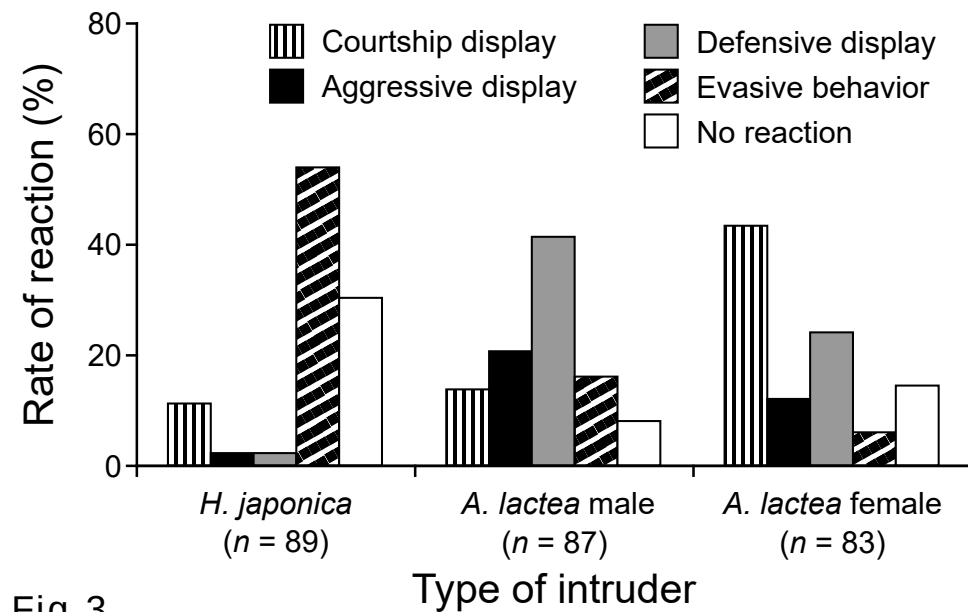


Fig.3

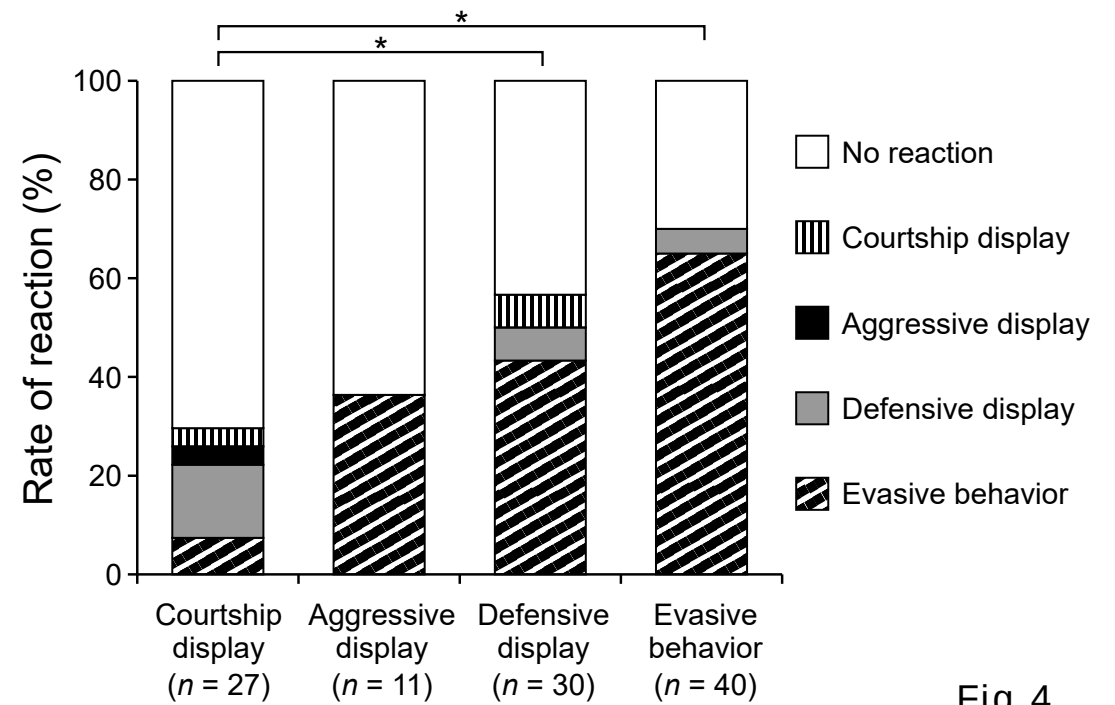


Fig.4

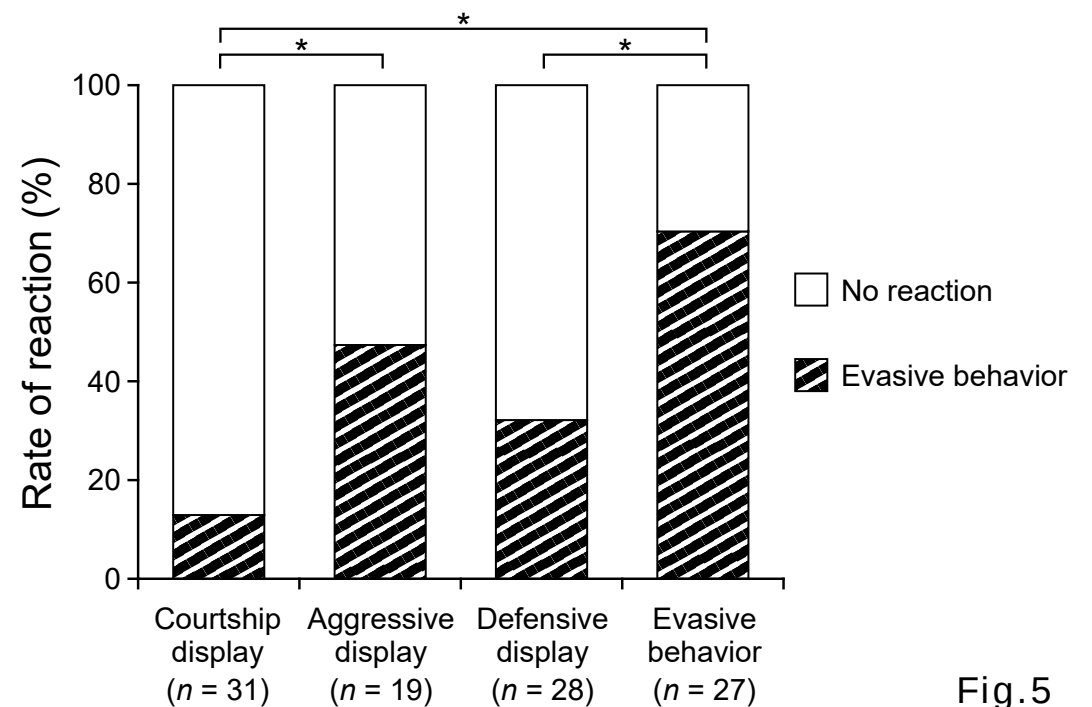


Fig.5