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ORIGINAL ARTICLE

Social behaviors elevate predation risk in fiddler crabs: quantitative evidence from field observations

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Abstract

The flight initiation distance model predicts that prey initiates to escape at a point where the cost of staying exceeds its benefits that they acquire from staying, such as the availability of food resources and mates. Social behaviors, such as courtship or territorial behaviors can generally increase reproductive success, although they have the potential to attract predators. Using refuge enhances the probability of survival. Therefore, for prey, social behaviors increase the benefits, and the use of refuge decreases the costs of staying. However, most empirical studies testing these predictions have used human approaches as predator mimics and have not represented natural predation events in the field. We quantified predator–prey interactions between the predator, the varunid crab (*Helicana japonica*), and its prey, the fiddler crab (*Austruca lactea*), based on field observations. We then demonstrated the effects of social behaviors and distance from a refuge on predation risk and the adjustment of distance according to the predator–prey distance. Fiddler crabs adjusted the prey-prey burrow distances according to the predator–prey distance when it was < 45 cm. When > 45 cm, the prey-prey burrow distances did not influence it. The varunid crabs were shown to target prey that were closer in distance. Predators physically reached prey that were further from their burrows. These results show that predation risk caused prey to regulate prey-prey burrow distances according to predator–prey distances. In addition, varunid crabs frequently contacted fiddler crabs that employed social behaviors, suggesting that social behaviors elevated predation risk.

Significance statement

We quantified predator-prey interactions between the predatory varunid crab and the prey fiddler crab from field observations. We demonstrated that fiddler crabs adjusted their distance from their burrows according to the predator-prey distances. Varunid crabs targeted prey that were closer. Prey that were reached by the predator were situated further away from their burrows and frequently employed social behaviors. These results suggest that the social behaviors of prey elevate predation risk, although prey adjust the distance from the burrow according to the predator-prey distance.

Keywords *Austruca lactea* · Courtship · *Helicana japonica* · Predator–prey interaction · Refuge · Territorial fighting

Introduction

Social behaviors, such as courtship and territorial behaviors, can often attract predators (Roberts et al. 2007; Woods et al. 2007). Since these are generally designed to be conspicuous for conveying the information of senders, such as resource holding potential, condition, and/or quality to conspecific receivers, predators can also utilize these displays to localize prey. For example, in *Photinus* fireflies, the flash of LED lights, which mimics bioluminescent courtship signals, can draw predators (Woods et al. 2007). Similarly, in wolf spiders, multimodal courtship signals enhance predator detectability (Roberts et al. 2007). Preys that engage in

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social behaviors might also pay less attention to predators' approaches and thus suffer from predation risk. In addition, some prey may encourage courtship/territorial behaviors, even under predation risks, if they may enhance reproductive success. Therefore, prey must balance the risk of displaying social behaviors with defense behaviors, such as escape, according to their situation.

The costs and benefits of escaping from predators are expressed as functions of the distance between the predator and prey, which is an indicator of predation risk (Ydenberg and Dill 1986; Cooper and Frederick 2007; Cooper 2015, 2016). Ydenberg and Dill (1986) proposed an economic model of escape: flight initiation distance (FID), which is the distance between a predator and prey when the prey initiates escape, is determined at a cross point between each function of the cost and benefit (Ydenberg and Dill 1986).

Optimal FID is predicted to be shorter if the resource (e.g., food, territory, and mates) is largely beneficial, that is, prey chooses to face a relatively higher predation risk (Ydenberg and Dill 1986; Cooper and Frederick 2007). In particular, since territories or mates are valuable for reproductive success, prey often employs social behaviors, even if the predation risk is high. For example, the FID of male lizards engaging in courtship or territorial behaviors is shorter than that of solitary males (Cooper 2009). Therefore, the social context of prey may affect the FID and, consequently, their survival.

In general, the presence of nearby refuges increases the chances of prey survival. Hence, the FID is expected to be shorter when the prey is closer to a refuge (Ydenberg and Dill 1986). Several geometrical models exhibiting the attack of a predator and the escape of prey to a refuge have also predicted that the FID shortens when the distance between the prey and refuge is smaller (Kramer and Bonenfant 1997; Cooper and Frederick 2007). However, few studies have tested these predictions, and most have used human approaches as predator mimics (Rhoades and Blumstein 2007; Cooper 2009; Gotanda et al. 2009; Bateman and Fleming 2014; Mcelroy and Mcbrayer 2021), which do not accurately represent natural predation events in the field. Therefore, quantifying actual predator–prey interactions from field observations will help update the assumptions used by theoretical models to predict more realistic outcomes.

Fiddler crabs are suitable for investigating the relationship between social behavior and predation risk in the field. Their carapace exhibits bright coloration (Hemmi et al. 2006; Takeshita 2019), and males engage in social behavior during the reproductive season. When a mate-searching female approaches, a male waves (Murai and Backwell 2006; Takeshita et al. 2018) and emits vibrations (Takeshita and Murai 2016; Mowles et al. 2017) to attract females from their burrows. Most individuals possess their own burrows, and the residents are active in a territory within several dozen centimeters from the burrow. They defend their territory and burrow from conspecifics (Jennions and Backwell 1996; Pratt et al. 2003; Morrell et al. 2005). In the case of predator attacks, fiddler crabs escape to their burrows, which act as a refuge (Jennions et al. 2003; Hemmi 2005a, b). They visually recognize predators (Hemmi 2005b) and also utilize social information from conspecifics escaping to burrows, to escape to their own burrows (Wong et al. 2005; Muramatsu 2021). The predator of fiddler crabs is known to be birds (Thibault and McNeil 1995; Backwell et al. 1998; Koga et al. 1998, 2001; Iribarne and Martinez 1999) and crabs (Pratt et al. 2002; Kuroda et al. 2005; Moto and Wada 2016).

In this study, we focused on the predator–prey interactions between the predator, the varunid crab (*Helicana japonica*), and its prey, the fiddler crab (*Austruca lactea*). *Austruca lactea* inhabits the intertidal zone of the mudflats and are active when the surface that they live on is exposed. In our study site, the density of active individuals on the surface of *A. lactea* was 15.2 ± 2.0 (mean ± SD) individuals/60 × 60 cm^2 during the reproductive season (Takeshita, *unpublished data*). Resident *A. lactea* males courting females use a large claw to conduct wave display (Murai et al. 1987, 2022; Takeshita et al. 2018). Males also fight with neighbors and non-resident individuals to defend their territory and burrow, threatening and physically attacking each other using their large claws (Muramatsu 2011). These social behaviors may increase predation risk because they are conspicuous to predators. Their main predator is the varunid crab, *H. japonica*, which often occurs in sympatry. The varunid crabs generally dash and attempt to catch fiddler crabs, whereas fiddler crabs try to escape into their burrows (see ESM 1). We aimed to quantify these interactions from field observations and investigate the properties of predatory and escape behaviors using the distances between the prey, predator, and burrow of prey. In particular, we elucidated the criteria for making decisions to escape. We also focused on how social behaviors that contribute to reproductive success (i.e., benefits of stay) affect the probability of predation (i.e., costs of stay) in fiddler crabs. Furthermore, we discussed the similarities and dissimilarities between the predictions of theoretical models and our results.

Materials and methods

Field observations were conducted daily (except on days with heavy rain) from late June to early August 2016, 2017, and 2018 during low tide in daylight hours. Data were collected on a tidal flat on Nagaura Island, Kami-Amakusa, Kumamoto, Japan (32° 32′ N, 130° 24′ E). The study site had little vegetation cover and few rocks. These sampling periods fell within the reproductive seasons of *A. lactea* (Yamaguchi 2001).

We found and marked 10–12 burrows of *H. japonica* with a plastic peg to identify the focal predators before the observational periods. During these periods, we checked the marked burrows to determine whether there were any signatures of varunid crab activity (e.g., sediments that they ejected from burrows). These observations were made daily, immediately after the tidal flat was exposed. We then arbitrarily selected two burrows, wherein the presence of varunid crabs (or their signatures) was confirmed, and recorded videos. If there were no signatures in the marked burrows for 3 days continuously, we stopped marking them and found new varunid crabs to replace the lost crabs.

Video recording

A digital video camera (HC-V360M, Panasonic, Japan), mounted on a tripod (ABLE 300HC, SLIK, Japan), was installed above the burrow entrance of predator crabs (approximately 1.5 m). It recorded the activity of the predator and fiddler crabs inhabiting the area. We first videoed a ruler to calibrate the distances before recording predator attacks on the fiddler crabs. The recording duration ranged from 2 to 5 h during low tide.

Data measurements

The data on attacks on fiddler crabs by predators were extracted from the recorded movie files. A total of 103 predator attacks were documented. These data sometimes included those derived from the same predator. The predator target was marked for each attack. Although such cases were rare, we specified multiple targets (up to two) if there were multiple preys on the trajectory of the attack. Thus, the sample size of the targets was 111 individuals for 103 attacks.

From the extracted videos, we captured images either at the moment of the attack or the target escape, whichever occurred earlier. We then measured the coordinates of the varunid crab, fiddler crabs, and the burrows of fiddler crabs from these images by using ImageJ software (NIH, https://imagej.nih.gov/ij/). All resident fiddler crabs within the image were measured. Small crabs or individuals for which we could not specify the burrow were excluded from the measurements. As the ruler was L-shaped and provided three orthogonal reference points, we applied affine transformation using these reference points on the captured images to match the pixel coordinate system with the real world. We then measured the coordinates of the focal objects and calculated the predator–prey distance and the prey's distance from its burrow. Hereafter, all descriptions as "a distance from the burrow" or "prey-burrow distance" were defined as the distance between the prey and the prey's burrow. We took measurements for a total of 2203 fiddler crabs, but these often included pseudo-replications. Furthermore, we determined whether the fiddler crabs that were targeted by the predator had performed social behaviors within 10 s before being attacked. Social behaviors included courtship displays and territorial behaviors, whereas non-social behaviors included feeding, burrowing, moving, and being motionless.

Statistical analysis

We conducted five statistical analyses as follows: (i) To investigate how fiddler crabs adjusted the distance from their burrow with the changing distance from the predator, we applied a segmented mixed-effect model (SMM) (Muggeo et al. 2014), which is a method of analysis in which multiple linear regressions are fitted to partitioned intervals, considering random effects. The response variable was the distance between the potential prey and burrows of prey. The explanatory variables were predator–prey distance, as a fixed effect, and predator ID as a random intercept. This model was compared to two linear mixed models (LMMs), which is a regression analysis that considers random effects. These LMMs included the response variable of the distance between the prey and burrow, the explanatory variable of the distance between the predator and potential prey, and the random effect (model 1), or had only an intercept and a random effect (model 2). The Akaike information criterion (AIC) was lowest in the SMM (SMM: AIC = 12578.85, model 1: AIC = 12611.64, model 2: AIC = 12655.78), implying that SMM provides a better fit for the relationship between the distance between prey and burrow and predator–prey distance than when linear or intercept models are fitted. (ii) To test how the predator selected a target, two LMMs were applied. As the response variable, one model included the predator–prey distance, and the other included the prey-burrow distance. In both models, the explanatory variables were categorical, whether the fiddler crabs were targeted or not, as a fixed effect. Predator ID was used as a random effect. In the former analysis, we first defined the hunting distance of varunid crabs as the maximum value of the predator–prey distance in which the predator initiated a predatory lunge (101.88 cm). We used only data within this distance. The fixed effect (targeted or non-targeted) was tested using the likelihood ratio test (LRT) in both models. (iii) To compare the behavioral features between prey that the predator physically reached (contact) and not (no contact), we applied the following two LMMs. As the response variable, each model included predator–prey distance or prey-burrow distance. Explanatory variables were determined according to whether the target was contacted or not by the predator, as a fixed effect, and predator ID, as a random effect, in both models. We then tested the fixed effect (contacted/non-contacted) by LRT in both models. (iv) Fisher's exact test was applied to compare the frequency of prey with and without social behaviors between the prey that the predator contacted and did not contact. (v) Finally, to compare the prey-burrow distance between prey with and without social behaviors, LMM and LRT were applied. The response variable was the prey-burrow distance. The explanatory variables were social or nonsocial behaviors, as a fixed effect, and predator ID, as a random effect. All analyses were conducted using the software R 4.1.1 (R Core Team 2021) with package "lme4" and source code of SMM (https://www.researchgate.net/publication/292986444_segmented_mixed_models_in_R_code_and_data) by Muggeo et al. (2014).

Data availability

The datasets generated and/or analyzed during the current study are available as supplementary files (ESM 2; ESM 3).

Results

Predator attacks were observed in 103 individuals. In 17 of these cases (16.50%), *H. japonica* reached the fiddler crab prey. In three cases (2.91%), the predators succeeded in catching them (ESM 1).

Helicana japonica used two predatory tactics. First was the rushing tactic, in which the predator dashed to the fiddler crab that was active on the ground (ESM 1). The second was the sit-and-wait tactic: the predator waited near the burrow of the prey and attacked when the prey emerged from it (ESM 4). The number of cases associated with the former and latter tactics was 99 and 4, respectively. In the following analyses, we did not distinguish between the attacks based on tactics.

Relationship between prey-prey's burrow distance and predator–prey distance

The fiddler crabs adjusted their distance from the burrow as a function of the distance between the predator and the prey. The distance from the burrow increased with the predator–prey distance until it was 45.75 cm ($N=2203$; Fig. 1; Table 1). When the distance exceeded 45.75 cm, the distance from the burrow remained approximately constant (Fig. 1; Table 1).

Target choice by the predator

Predators chose targets that were relatively closer to themselves but did not always select targets that were more distant from the burrow. Predator–prey distances were 33.32 ± 16.89 cm (mean ± SD; $N=111$) and 50.69 ± 21.16 cm ($N=2047$) in target and non-target groups, respectively. There was a significant difference in distance from the predator between target and non-target groups (Fig. 2a, $\chi^2=74.34$, $P<0.001$), and 81.08% (90/111) of the targets were within the threshold of SMM (i.e., 45.75 cm). Prey-burrow distances were 5.89 ± 6.57 cm ($N=111$) and 5.36 ± 4.19 cm ($N=2{,}092$) in the target and non-target groups, respectively. There was no significant difference in the prey-burrow distance between the two groups (Fig. 2b, $\chi^2=1.39$, $P=0.24$).

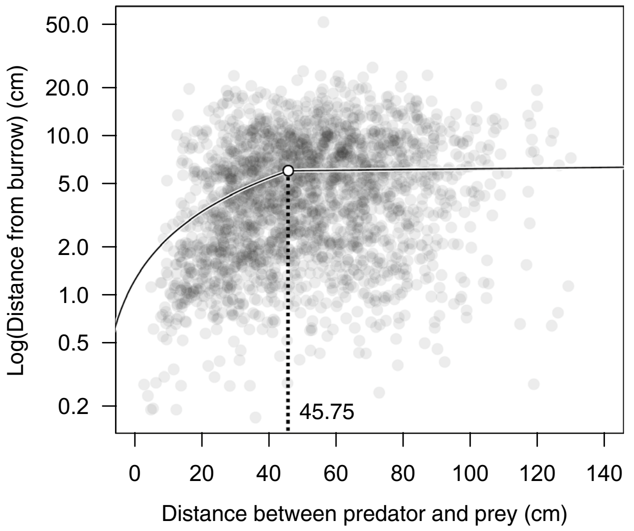

Fig. 1 Relationship between the distance of prey from its burrow and the distance between predator and prey. The solid line shows regression estimated using a segmented mixed-effect model. The dashed vertical line is the threshold of the model. The *Y*-axis is a transformed log scale

Table 1 Results of segmented mixed-effect model for the distance that prey were away from prey's burrows

Predictor	Estimate	Confidence interval (2.5–97.5%)
Intercept	1.23	0.34–2.13
Predator–prey distance	0.10	0.08–0.13
Difference-in-slope	−0.10	−0.13 – −0.07
Breakpoint	45.75	38.01–53.49

Predation success and social behavior of prey

The targets that were contacted by the predator were more distant from the burrow than those that were not in contact, but predator–prey distances did not differ between the two groups. The predator–prey distance was 38.99 ± 20.34 cm ($N=17$) and 32.29 ± 16.11 cm ($N=94$) in contacted and non-contacted targets, respectively. The distance did not significantly affect whether the target was in contact (Fig. 3a, $\chi^2=1.99$, $P=0.16$). The distances at which the target was away from their burrow were 11.20 ± 12.01 cm ($N=17$) and 4.93 ± 4.48 cm ($N=94$)

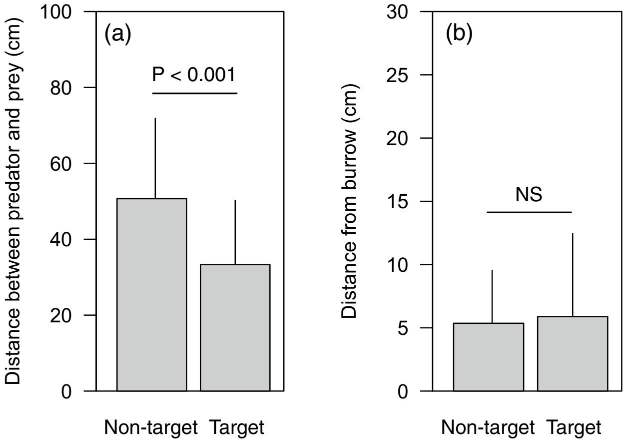

Fig. 2 Comparisons of the **a** distance between predator and prey and **b** the distance of prey from prey's burrow, in target and non-target prey. The bars indicate SD

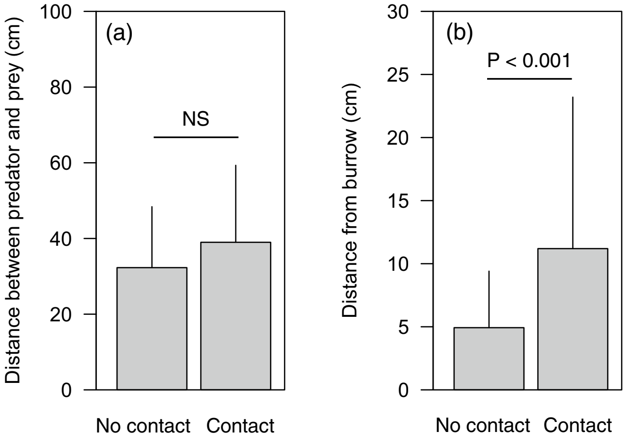

Fig. 3 Comparisons of the **a** distance between predator and prey and **b** the distance of prey from prey's burrow, in contact and non-contact prey. The bars indicate SD

in contacted and non-contacted targets, respectively. This distance differed significantly between contacted and non-contacted targets (Fig. 3b, $\chi^2 = 19.11$, $P < 0.001$).

Predation success was affected by the social behaviors of the prey: the frequency at which prey were contacted by the predators was significantly higher in those who engaged in social behaviors (16/67) than in those who did not (1/44) (Table 2, $P < 0.005$). Focusing on male prey, the frequency at which the targets that showed social behaviors were contacted by predators differed significantly from that of the others (Table 2, $P < 0.05$). The prey-burrow distance was 6.18 ± 7.50 cm and 5.44 ± 4.85 cm for social and non-social prey, respectively. However, there was no significant difference between their distances ($\chi^2 = 0.49$, $P = 0.48$). Social behaviors included courtship (29/67), wave with feeding (17/67), surface mating (3/67), and territorial fighting (18/67), whereas non-social behaviors included feeding (26/44), burrowing (7/44), moving (1/44), and being motionless (10/44).

Table 2 Outcome of contact/no contact and the social/non-social behaviors of fiddler crabs. Parentheses indicate the frequency if data were limited only to male prey

	Social behavior	Non-social behavior	Total
Contact	16 (16)	1 (1)	17 (17)
No contact	51 (49)	43 (27)	94 (76)
Total	67 (65)	44 (28)	111 (93)

Discussion

Fiddler crabs regulated the distance from their burrow by changing the predator–prey distance. The distance from the burrow increased with predator–prey distance up to a threshold of 45.75 cm, indicating that the prey-burrow distance is associated with predation risk for the prey. This result supports the theoretical predictions of Ydenberg and Dill (1986) that refuges decrease the costs of stay. When the predator–prey distance exceeded 45.75 cm, the distance from the burrow remained constant. This could be because the distance from the burrow was determined by their general activities within the range of their territory rather than as a response to predation risk when the predator–prey distance was over 45.75 cm. This threshold may, therefore, be a lower limit of the predator–prey distance where fiddler crabs can be active without regulating the prey-burrow distance due to predator threat. These results also suggest that fiddler crabs generally monitor the position of the varunid crab, at least, within the threshold of 45.75 cm, and that the visual horizon of fiddler crabs would not be broken by the predatory varunid crab beyond this distance (Zeil and Hemmi 2006). However, there is a large variation in the prey-burrow distance, implying that it has been determined not only by predator–prey distance but also by other ecological factors.

Fiddler crabs that engaged in social behaviors such as courtship and territorial behaviors were contacted by the predator more frequently than those that did not. These behaviors are crucial for reproductive success in fiddler crabs; waving displays affect female mate choice (Murai and Backwell 2006; Reaney 2009; Murai et al. 2022). Burrows, which are the resources in territorial fights, also comprise one of the male traits that females assess for mate choice (Christy 1983; Goshima and Murai 1988; Backwell and Passmore 1996; deRivera 2005). Additionally, relationships with neighboring individuals influence the reproductive success (Backwell and Jennions 2004; Takeshita and Murai 2019). However, these behaviors can also attract predators; conspicuous males that generally engage in social behaviors are selectively preyed upon compared to females in *Leptuca beebei* in Panama (Koga et al. 2001), although several migratory shorebird species exclusively forage on females or juveniles of *Leptuca uruguayensis* in Bahia Samborombon, Argentina (Iribarne and Martinez 1999). Social behavior may also cause these crabs to be less aware of predators. Therefore, the increased contact of the predatory crab by social behaviors of the prey crab in our results can be explained by fiddler crabs being willing to risk predator approaches for their reproductive benefit, or they may not be able to detect the approach of the predators.

Varunid crabs employed two predatory tactics: dash-and-capture (rushing) and sit-and-wait, with the former employed more often. The use of the sit-and-wait tactic has been reported in another varunid crab *Helice tridens* that is allied to *H. japonica* and also attacks this prey species (Moto and Wada 2006). Thus, this tactic could be a common predation technique among these carnivorous crabs that prey on *A. lactea*. As our observations were only conducted during the mating season of *A. lactea*, the observational period may have influenced the difference in frequency between these tactics. The rushing tactic may have higher predation efficiency during these periods, because prey that perform social behaviors are on the surface. The frequency of the sit-and-wait tactic may increase in the non-reproductive season of *A. lactea*, because this tactic does not target preys that are active on the surface and the number of such preys that perform entry and exit of the burrows may increase relatively in the non-reproductive season.

Varunid crabs did not target fiddler crabs that were farther from their burrows, despite the probability that such prey could be captured successfully. These results suggest that varunid crabs cannot localize burrows of the targets on the ground. It is possible that varunid crabs do not associate prey burrows with residents. Instead, they may enhance predation efficiency by selecting targets closer than the threshold distance (45.75 cm), where prey safety would be guaranteed. The information that varunid crabs cannot identify refuges may improve the geometrical models of escape behaviors when prey make use of these refuges (Kramer and Bonenfant 1997; Cooper 2016). These models assume that the predator recognizes the position of the prey's refuge, and both the predator and prey run toward the refuge, analogous to a game of musical chairs. However, in the predator–prey system between the varunid crab and the fiddler crab, it seems that the predator simply traces the location of the prey rather than running toward the prey's burrow. Updating this assumption may yield more realistic theoretical predictions.

Predation pressure potentially changes the behavior of the prey. For example, in *L. beebei*, when predation risks are increased experimentally, males wave less and build fewer mud structures that work as sensory traps (Christy 1995), and the number of mate-searching females is reduced relative to the number of surface mating without female mate choice (Koga et al. 1998). However, in our population, such changes did not seem to occur even when fiddler crabs were residents near the burrows of varunid crabs. This may be due to a shorter reproductive season and relatively lower predation risk. Since mating opportunities are limited to a shorter period in this species, courtship behaviors and territorial defense contribute greatly to reproductive success, even if predation risk increases to a certain extent. Comparisons among populations or species would provide more dynamic insights into the ecological and evolutionary consequences of predation pressure, particularly on the social behaviors of prey and the diversity of predation tactics.

In conclusion, based on field observations, we have shown that social behaviors elevate predation risk by quantifying predator–prey and prey-refuge distances. Although fiddler crabs regulated the prey-burrow distance according to the predator–prey distance, the prey-burrow distance was longer in the contacted prey than in those which remained uncontacted. Contacted prey were frequently engaged in social behaviors. These results partly support the predictions of the economic model of Ydenberg and Dill (1986). However, the varunid crab did not seem to localize the burrow of the fiddler crab. This may prompt a need to update certain assumptions of the geometrical model of predator–prey interactions where prey use the refuge (Kramer and Bonenfant 1997; Cooper and Frederick 2007). This predator–prey system may be suitable for testing geometrical models, because *A. lactea* responds to the predation risk of the predatory crabs with the distance to the refuge.

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Declarations

Conflict of interest The authors declare no competing interests.

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