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Can fiddler crabs detect underwater predators? A laboratory test with *Leptuca thayeri*

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Fiddler crabs are intertidal organisms well known to be highly adapted to low tide activity, thus a number of researches have studied their physiological, behavioral and sensory adaptations to such a tidal phase. However, recent evidences showed that some fiddler crabs are the main food item of fish, suggesting that they could also be active underwater. Based on these preliminary observations, we designed laboratory trials aimed to investigate the ability to detect underwater predators in *Leptuca thayeri*, across sexes and life stages. We tested a combination of chemical and visual cues, using the predator fish *Sphoeroides greeleyi*, and, as a control, the non-predator fish *Mugil curema*. *Leptuca thayeri* detected the presence of chemical cues coming from the predator fish, although significant differences between adults and juveniles were observed. Adults of *L. thayeri* remained within their burrows and avoided predator exposition, while juveniles were bold and even increased their activity on the sediment surface. We suggest that juvenile crabs' boldness could be explained by a predator inspection behavior, which allows them to gather information about the possible risk of different predatory species, while experienced adults reduce predation risk recognizing the predator itself.

KEY WORDS: predator inspection, chemical cues, *Sphoeroides greeleyi*, underwater activity, aquatic predator.

INTRODUCTION

Predation is an important force of biotic selection pressure on organisms directly affecting their survivorship and breeding success (Koga et al. 1998; Preisser et al. 2005).

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The selective pressure from predators can affect the distribution, foraging locations, activity periods, or even the selection of morphological and behavioral characteristics of prey populations (Hughes & Elnor 1979; Clark et al. 2003; Daleo et al. 2003; Wolff & Horn 2003; Teplitsky et al. 2005; Breviglieri et al. 2013). However, defense mechanisms that mitigate the effects of predation positively influence the selection and survival rate of prey (Boulding 1984; Ens et al. 1993; Mirza & Chivers 2001).

Predator detection reduces the risk of being attacked (Mirza & Chivers 2001; Gazdewich & Chivers 2002). Organisms capable of detecting a predator can survive exhibiting defense responses such as escape (Dalesman et al. 2006), pursuit of shelter (Petranka et al. 1987), agglomeration among individuals (Beauchamp 2007), alarm output (Evans et al. 1993), or reduced activity (Mirza & Chivers 2001). Various signals can be involved in the detection of predators by prey, the most common of which are visual, sound, and chemical cues (Evans et al. 1993; Kiesecker et al. 1996; Durant 2000; Chiussi & Diaz 2002; Breviglieri et al. 2013; Yorzinski & Platt 2014).

However, prey populations are not homogeneous, and certain intrinsic characteristics, such as size or sex, may result in different levels of vulnerability to predation (Bildstein et al. 1989; Tomida et al. 2012). The above characteristics could also affect the response of prey to predator signals.

Fiddler crabs have a pronounced sexual dimorphism, which makes them a good model for investigating intra-specific differences in predatory pressure. While females have two small claws, males have a hypertrophied claw that, in many cases, is bright colored and larger than the crab's body (Crane 1975). This morphological difference between sexes proved to influence predatory pressure in a complex way. In some species, the males were less attacked by predators with respect to females, either because the large claw of males increases the difficulty of manipulation by some predators, or because it can be used as a weapon against them (Bildstein et al. 1989; Levinton & Judge 1993). However, in some other species, bird predation proved to be more efficient on males, since they were easier to target than females, due to their size and color (Koga et al. 2001). Size affects predation risk as well, since large, adult crabs have larger and more powerful claws and stronger carapaces than juvenile, smaller specimens, which are easier to manipulate and crush (Tomida et al. 2012). As a result, in some species the risk of predation by birds influences the spatial distribution and behavioral strategies of juveniles and adults fiddler crabs (Ens et al. 1993).

Fiddler crabs are territorial, central-place foragers that build and defend a burrow, which is of critical importance for their ecology and shapes their behavior (Crane 1975; Koga et al. 1998). They are truly intertidal organisms and most of the species are active on the sediment surface during low tide (Frix et al. 1991; Ens et al. 1993; Weis & Weis 2004). Thus, most studies have investigated the sensory cues underlying predator avoidance only during low tide, when they are exposed to air (Frix et al. 1991; Ens et al. 1993; Koga et al. 2001). However, fiddler crabs were identified as the major food items of the specialized mangrove predator fish *Colomesus psittacus* in the north of Brazil (Krumme et al. 2007) and they were among the most abundant prey found in the stomach of the Gulf Killifish, *Fundulus grandis* (Rozas & LaSalle 1990). These lines of evidence were recently corroborated by a field study showing that the fiddler crab *Leptuca thayeri* is active at high tide, when it leaves the burrows and actively wanders and feeds on sediment surface under water (De Grande et al. 2018).

At low tide, fiddler crabs recognize their predators by visual cues (Layne et al. 1997; Layne 1998). In the aquatic environment, most crustaceans are known to recognize predators through chemical cues (soluble molecules) captured through the chemosensory organs present on their antennae and bristles (Thiel & Breithaupt 2011).

Thus, and although it is well known that fiddler crabs present a highly developed visual definition on land, this sensory cue cannot help *L. thayeri* in detecting predators in estuarine murky waters. In such an environment, chemical cues could potentially be involved, although nothing is known about the predation avoidance strategy these crabs could possibly perform in this environment.

To bridge this gap, we present a laboratory study to investigate whether the fiddler crab *Leptuca thayeri* Rathbun 1900 can detect predators during its underwater activity and which sensory cues could be involved in such antipredatory response. We tested the predator avoidance across two intra-specific levels: sex and age. We tested the following hypotheses: (H1) fiddler crabs recognize aquatic predators by chemical and/or visual signals; (H2) female fiddler crabs (without large claw and potentially more susceptible to predation) are less active than males at high tide; (H3) juvenile crabs (more susceptible to predation) are less active than adults at high tide.

MATERIAL AND METHODS

Study species

Fiddler crabs and fish used in this experiment were collected in the same estuary located in Praia Grande, Southeastern Brazil (23°59'S, 46°24'W). The estuary of Praia Grande has a system of semi-diurnal tides with a range of about 1.5 m. The southeastern edge of this estuary is surrounded by mangrove forests where the fiddler crabs live. The crabs were excavated out of their burrows and then were identified and measured. We collect 160 fiddler crabs *Leptuca thayeri* of which 80 were adults, mean carapace width (CW) \pm SE = 20.18 \pm 0.027 mm, and 80 were juveniles, CW = 11.13 \pm 0.023 mm (Negreiros-Franozo et al. 2003). For each size class we used, respectively, 40 males and 40 females. The crabs were taken to the laboratory and placed directly in terrariums (microcosms which simulated periods of high and low tide) where they remained acclimatizing for 24 hr before the start of the experiment. The terrariums were filled with sediment, 20 cm in depth, collected in the same environment, so that the crabs could build their burrows (Gusmão-Junior et al. 2012) and feed. In each terrarium we placed one specimen for each sex and size class, i.e. a total of four experimental crabs. Although fiddler crabs show complex agonistic behaviors that can range from elaborate displays to intense fights (Crane 1975; Jennions & Backwell 1996), they are not social animals and they do not show true dominance behaviors among each other. Reciprocal interactions could be a confounding effect in our study, since the activity of one crab (i.e. one adult) could potentially inhibit the activity of another (i.e. one juvenile). However, agonistic and territorial behaviors are more frequent among individuals of the same sex and similar size and they rarely restrict the activity on the sediment surface of co-specifics, except for a few seconds (see Jennions & Backwell 1996). In addition, we introduced the experimental crabs in the terrariums at the same time and at low density, a situation that proved to avoid aggressive interactions among residents' neighbors (Backwell & Jennions 2004). Moreover, in the field, juveniles and adults of *L. thayeri* proved to be active at the same time under water during high tide (De Grande et al. 2018). We mainly observe feeding and wandering behaviors (see Results section) and agonistic behaviors were very rare across all our trials. Thus, we assume that activity of a crab does not affect the responsiveness of another crab relative to the predator model.

Twelve pufferfish *Sphoeroides greeleyi* (Gilbert 1900) were used as predators (body length = 112.8 \pm 5.7 mm), and nine planctophagous white mullet *Mugil curema* (Valenciennes 1836) (body length = 114.7 \pm 3.9 mm) were used as non-predator controls. The pufferfish were caught using shrimp bait and the white mullet were caught using a casting net. The lengths of the pufferfish and mullet specimens were compared using a parametric Student's *t*-test to avoid the confounding influence of size, and the results indicated no significant difference ($t = -0.8251$, $P = 0.41$). The fish were acclimatized for 15 days in separate storage tanks (approximately 400 L) equipped with aerators and bacteriological filters. Once a week, the tanks were siphoned and the

water was replaced (approximately 200 L). Twice daily, the pufferfish were fed with fresh shrimps, and the white mullet were fed with a diet for ornamental fish (AlconBasic® – MEP 200 complex). Prior to initiation of the experiments, the diet of both species was suspended for 24 hr.

Experimental design and statistical analysis

We tested whether crabs of different sizes and sexes recognize predator fish by chemical or visual cues, using as response variable the observed rate of underwater activity on the sediment surface during the observation period. The rate of activity was evaluated recording the number of crabs active on the surface sediment, during seven different groups of experimental trials (number of replicates per treatment, $n = 10$), from here on called: chemical predator cues (CP), visual predator cues (VP), interaction between the chemical and visual predator cues (CVP), chemical no predator cues (CC), visual no predator cues (VC), interaction between the chemical and visual no predator cues (CVC) and control (C; Fig. 1). All the treatments, besides the control, were carried out using either *S. greeleyi*, used as predator model, or *M. curema*, used as non-predator model. Each experimental terrarium was observed for a total of 15 min (three replicate observations of 5 min each separated by an interval of 40 min). Data were computed as the percentage of crabs belonging to different sexes and size classes active on the substratum under each experimental condition in the three replicate observations across the 10 independent tests and they were arcsine transformed before the analysis. A preliminary three-way PERMANOVA, using factor sex (fixed and orthogonal), size (fixed and orthogonal), and replicate observation (first, second or third fixed and orthogonal) was performed to test for possible differences in activity observed in the first, second or third replicate across sexes and sizes. Since the factor replicate observation never resulted to significantly affect the observed activity (Pseudo-F = 0.21, $df = 2$, $P = 0.82$; PERMANOVA test) we included in the analysis all the performed observations. A four-way Permutational Analysis of Variance (PERMANOVA, Anderson 2001) was applied to test for differences in crab activity across the factors: sex (fixed and orthogonal), size (fixed and orthogonal), fish presence (fixed and orthogonal, three levels = *S. greeleyi*, *M. curema*, no fish) and presence of sensory cue (fixed and nested in factor 'fish presence', four levels = chemical, visual, chemical + visual, no cue). The analysis was performed on the basis of a Euclidean distance dissimilarity matrix and 9999 permutations interactions. Post-hoc pairwise tests were applied for multiple comparisons among significant factors. A minimum significance level of 5% was adopted in all the cases.

Crab rearing and experimental setting

The experimental terrariums (30 × 70 × 45 cm) had two compartments: one compartment for the crabs (30 × 60 × 45 cm) and the other for the fish (30 × 10 × 45 cm). To divide the terrariums into two compartments we used a glass plate (30 × 45 cm) with or without perforations of 5 mm in diameter. In tests involving an opaque partition, this was provided by covering the glass plate with a black plastic sheet, which was perforated as well in the trials requiring water exchange between compartments. Different experimental setups were used (Fig. 1): (a) Terrariums in which the partition plate was covered by the opaque plastic sheet but both plates were perforated to allow for water exchange between the compartments, although avoiding visual contact; (b) Terrariums with transparent partition plates without perforations, to allow for visual detection of fishes but not chemical communications; (c) Terrariums with glass perforated partition only, to allow for both the chemical and visual detection of fish; (d) Finally, as a single control test, we performed the same trials without the presence of any fish in terrariums. Procedural controls, such as trials with opaque or perforated partition and no fish presence, were not performed since they would strongly increase the work effort adding no information on the senses involved in predator detection. The fact that we used sheets of

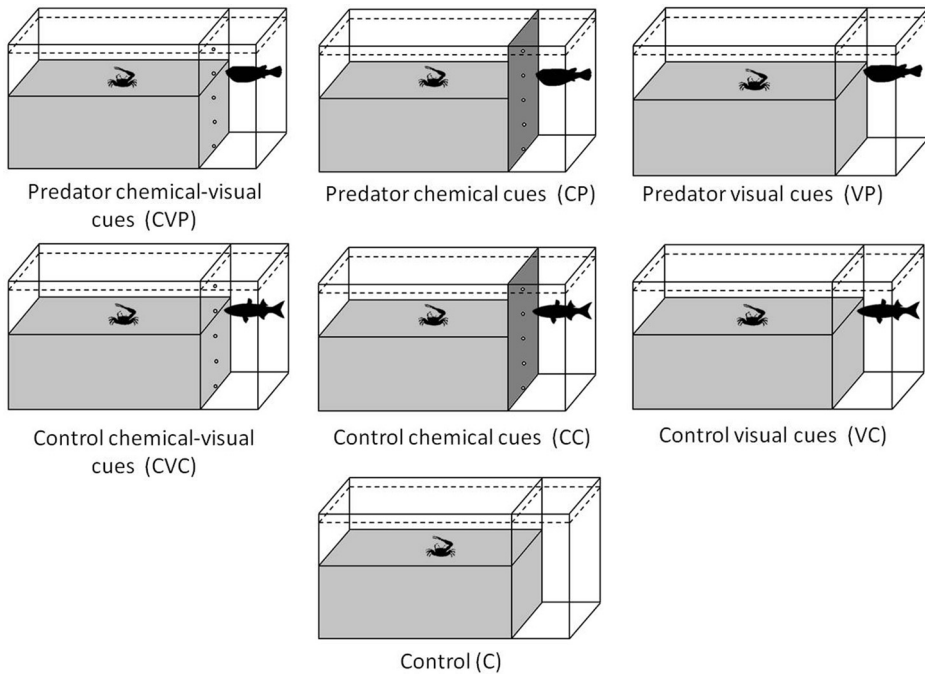


Fig. 1. — Experimental design. Top row, from left to right: terrariums established to test chemical and visual cues of predator fish (CVP), chemical cues of predator fish (CP) and visual cues of predator fish (VP). Middle row, from left to right: terrariums established to test chemical and visual cues of control fish (CVC), chemical cues of control fish (CC) and visual cues of control fish (VC). Bottom row, terrarium established as controls (C). Procedural controls, such as trials with opaque or perforated partition and no fish presence, were not performed since they would strongly increase the work effort adding no information on the senses involved in predator's detection.

inert plastic and no differences were detected among trials involving transparent vs opaque and predator vs non-predator fish strengthened our experimental design choice. For all tests, fish were kept for 4 hr in the experimental terrariums during the simulated high tides. After introduction of the fish in the compartment we waited 30 min to observe the crabs' behavior. In order to simulate the tidal regime to which *L. thayeri* is submitted in southeastern Brazil, we reproduced two 6-hr submersion periods per day (one at day and one at night), using water also coming from Praia Grande estuary. The water flowed into the terrarium through hoses placed in the bottom. In crabs compartments, the pipes entered from the bottom and they ran vertically through the entire sediment column and the hoses were thus on the surface sediment. Thus, the terrariums were gradually filled from the bottom up and emptied from the top down. During the flooded phase, aerators were connected in each terrarium. The physicochemical parameters of each terrarium were measured, including air temperature, salinity, dissolved oxygen saturation and water temperature. The values of the above parameters were as follows (mean \pm SD): air temperature = 28.10 ± 0.8 °C; water temperature = 28.00 ± 0.2 °C; salinity = 32.07 ± 1.8 ; percentage of dissolved oxygen saturation = $67.13 \pm 24.6\%$. Twelve hours of light (white light, 15 W) and 12 hr of dark were provided. After each test the water of each terrarium was discharged and replaced. Terrarium walls were covered (except the side facing the observer) in order to avoid visual contact among different terrariums. We also used black plastic curtains to prevent the interference of the observer on animals.

RESULTS

Leptuca thayeri experimental specimens were recorded inactive in their burrows in 88.40% of the observations. In 8.45% of the observations they were feeding (scooping the sediment and putting it in their mouth) and in 2.73% they were wandering on sediment surface (Table 1).

Leptuca thayeri response to predator fish cues significantly depended on the size of the crabs, the presence of a predator and the nature of the sensory cue (Table 2, Fig. 2). Regardless of sex, the activity of adults was strongly reduced when chemical cues coming from a fish were present (Table 2, Fig. 2A-B). In predator fish tests, the chemical cues were more effective than the visual ones in suppressing surface activity (chemical vs visual cues: $t = 7.94$, $P < 0.001$; chemical vs chemical + visual: $t = 2$, $P = 0.08$; visual vs chemical + visual: $t = 4.23$, $P = 0.003$, pairwise test), while no significant differences in activity were observed in the presence of chemical vs visual cues coming from a non-predator fish. On the other hand, the activity of juveniles was significantly enhanced in presence of chemical stimuli from a fish, especially when a predator fish was present (Fig. 2C-D).

DISCUSSION

Leptuca thayeri proved to be able to detect the presence of a predator fish by means of chemical cues during their underwater activity in the laboratory. However, we recorded different responses between juveniles and adults when chemical cues from the predator were present.

Chemical detection of aquatic predators was also described in the fiddler crab *Leptuca cumulanta*, that avoided the predator fish *Sphoeroides testudineus* and blue crab *Callinectes sapidus* (Chiussi & Diaz 2002), and it is the most commonly utilized sensory cue by crustaceans to recognize predators in aquatic environments (Thiel & Breithaupt 2011). Underwater, sight is disfavored because of limited light propagation, low light intensity and turbidity (Aksnes & Giske 1993; Kiesecker et al. 1996). Moreover, aquatic media are ideal for the diffusion of chemical cues, and predator detection based upon these cues has been described for different groups of animals, including amphibians, fish and crustaceans (Petranka et al. 1987; Kats & Dill 1998; Brown & Godin 1999; Wisenden 2000; Chiussi et al. 2001).

Table 1.

Percentage of behavioral activity in *Leptuca thayeri* of different size and sex classes. Data from total behaviors observed throughout the study excluding the trial effects.

Sex/Size class	Inactive (%)	Feeding (%)	Wandering (%)
Juvenile female	81.77	15.62	3.64
Juvenile male	88.54	9.37	2.08
Adult female	93.22	4.16	0.0
Adult male	90.1	4.68	5.2
Total	88.4075	8.4575	2.73

Table 2.

Results of 4-way PERMANOVA test for differences in surface activity of crabs of different sex and size under different situations of presence/absence of chemical/visual stimuli of predator/non predator fish. Data were arcsine transformed. The degrees of freedom, df, mean square values, MS, Pseudo-F values, F and probability levels are shown, together with the results of relevant post hoc tests for the significant interaction sex \times size \times cue (fish).

Source	df	MS	F	P
Size = sz	1	0.264	54.03	< 0.001
Sex = sx	1	0.007	1.48	0.230
fish presence = fish	2	0.089	18.17	< 0.001
cue (fish)	4	0.247	50.64	< 0.001
sz \times sx	1	0.055	11.35	0.002
sz \times fish	2	0.128	26.16	< 0.001
sx \times fish	2	0.002	0.48	0.628
sz \times cue (fish)	4	0.339	69.46	< 0.001
sx \times cue (fish)	4	0.017	3.41	0.013
sz \times sx \times fish	2	0.006	1.26	0.298
sz \times sx \times cue (fish)	4	0.015	3.04	0.026
Res	56	0.005		
Total	83			
Pairwise post hoc tests adults vs juveniles			<i>t</i>	<i>P</i>
Within level 'predator fish' and within the level 'chemical cue'			23.072	< 0.001
Within level 'predator fish' and within the level 'chemical + visual cue'			1.414	0.192
Within level 'non predator fish' and within the level 'chemical cue'			2.443	0.039
Within level 'non predator fish' and within the level 'chemical + visual cue'			2.828	0.023
Within level 'no fish' and within level 'no cues'			0.581	0.573

We cannot exclude the importance of other sensory cues for the response of our test species. For instance, vibrations and waves caused by the movements of the fish and propagated to the crabs could also play a role. However, they seem to have a limited importance for our fiddler crabs, since we showed that crabs' response to cues coming from the predator was distinct from non-predator fish and control.

In our tests, the presence of chemical cues from a predator fish was related to different activity patterns of adults and juveniles, respectively. While a significantly higher proportion of adult crabs sheltered in their burrows during the experimental tests where the odor of the predator fish was present, the juveniles were significantly

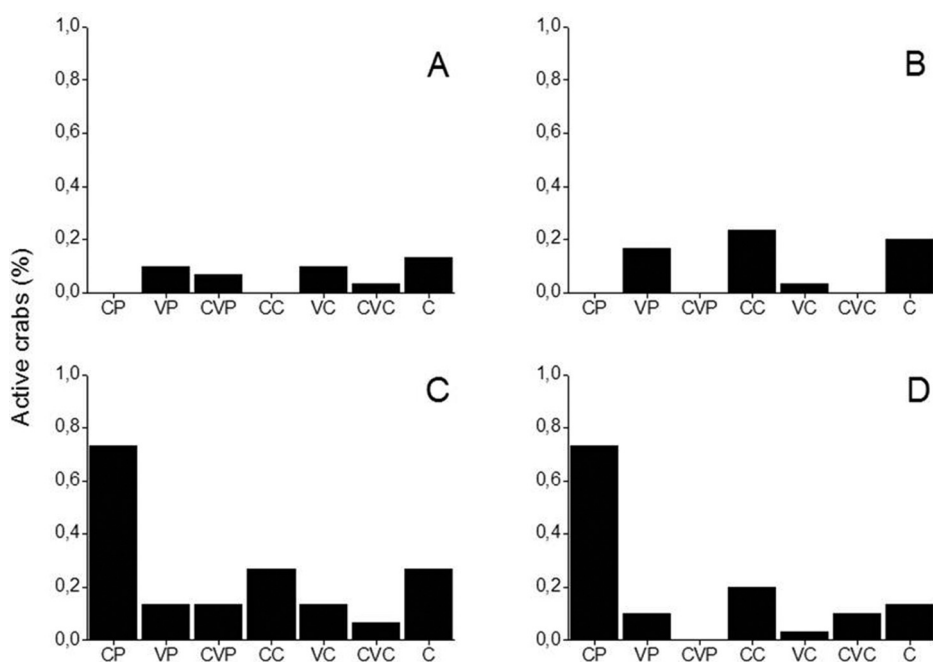


Fig. 2. — Percentage of *Leptuca thayeri* active on sediment surface among the treatments: chemical cues of predator fish (CP), visual cues of predator fish (VP) and chemical and visual cues of predator fish (CVP), chemical cues of control fish (CC), visual cues of control fish (VC) and chemical and visual cues of control fish (CVC). Results for: adult female (A), adult male (B), juvenile female (C), juvenile male (D).

more active during these treatments than in the control ones. The detection of the odor of predators also caused different behavioral responses in juvenile and adult lobster *Homarus americanus* (Wahle 1992). In this case, however, the juveniles remained in shelters longer than the adults in the presence of stimulus. A more pronounced avoidance response to predators in juveniles was also observed in other groups, such as the fish *Pimephales promelas* (Mirza & Chivers 2003) and the snail *Lymnaea stagnalis* (Rundle & Brönmark 2001). Differences in intraspecific anti-predator response are usually associated with efficient morphological adaptations (Rundle & Brönmark 2001). For instance, larger individuals, often adults, are less vulnerable to predation because their size imposes greater capture or manipulation costs for the predators and they do not show avoidance response to predator cues (Werner et al. 1983; Christensen 1996). Adult fiddler crabs are less vulnerable to predators than juveniles, especially the males (Bildstein et al. 1989; Mace & Curran 2011), but, paradoxically to this, in this study the juveniles *L. thayeri* increased their activity in the presence of predator cues.

The increase of prey activity as a response of predator cues was reported for hermit crab *Clibanarius vittatus* (Hazlett 1996), nymphs of the stoneflies *Paragnetina media* (Williams 1986) and the paradise fish *Macropodus opercularis* (Gerlai 1993). In the case of hermit crab and stonefly, it was suggested that the detected increase was an escape behavior (Williams 1986; Hazlett 1996). However, in the case of paradise fish, the increase of activity was described as a predator inspection behavior (Gerlai 1993). Since, in our tests, the juveniles were mostly actively feeding near their burrow entrances, i.e. in a

relatively safe position, we suggest that the increased activity we observed in juvenile *L. thayeri* could be explained as a case of chemical predator inspection.

The main benefit of predator inspection is that the prey can get information about the real threat of the predator (Pitcher 1992; Brown & Godin 1999; Fishman 1999). Inspection behavior, for example, can provide the prey with information about satiety of predator (Licht 1989), its motivation to attack (Murphy & Pitcher 1997) and types of prey that the predator ate (Brown & Godin 1999). Chemical inspection is critical when visual information is limited and some aquatic organisms, like the tetra fish *Hemigrammus erythrozonus*, can get information about the threat of predation by chemical cues (Brown & Godin 1999). Fiddler crabs have a horizontal/vertical visual system (How et al. 2012) well adapted for detecting predators during their activity in an aerial environment (Layne et al. 1997; Zeil & Hemmi 2006). However, they have a null point of discrimination in their vision which is not observed in aquatic crustaceans, like mantis shrimps (How et al. 2014). In our tests, we noted no responses by *L. thayeri* to visual cues represented by the fish *S. greeleyi* or *M. curema*. We suggest that fiddler crabs do not rely on vision during their underwater activity. Therefore, the best way for fiddler crabs to obtain information on predation risk at high tide could be through chemical cues, which could explain a higher activity of juvenile *L. thayeri* in tests with predator odor.

Inspection of the predator is particularly important during juvenile stages (Brown & Smith 1998; Brown & Braithwaite 2004). The juveniles can learn predator characteristics and exhibit more efficient defense behaviors when adult (Berejikian 1995; Brown & Smith 1998; Mirza & Chivers 2000). Juveniles exposed to predators have a higher chance of survival in subsequent encounters (Berejikian 1995; Mirza & Chivers 2000; McCormick & Holmes 2006) and the tendency to boldness trend in juvenile phases could favor individuals to obtain information on the risk of predation. Boldness traits in the juvenile phase have been reported in the poeciliid fish *Brachyraphis episcopa* (Brown & Braithwaite 2004; Brown et al. 2005) and of the cricket *Gryllus integer* (Hedrick & Kortet 2012).

In conclusion, this study shows that the presence of chemical signals coming from a predator fish affects the underwater activity of *L. thayeri*. Adults avoid surface activity when those stimuli are present, regardless of sex, while juveniles significantly increase their activity. We suggest that the activity of juveniles in the presence of predators could be linked to a predator inspection behavior, a behavioral trait observed during the juvenile phases of other aquatic animals, but never observed in fiddler crabs.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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ETHICAL STANDARD

The Authorization and Information System on biodiversity (SISBIO) of the Ministry of Environment approved this study (protocol number 38711-1), as well as the Technical Scientific Committee of the Forestry Institute, Ministry of Environment (COTEC; protocol number 205/2013 D151/2012 GH). At the conclusion of the experiments, the crabs and fish were released back into their respective natural habitats.

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