BRILL Crustaceana 00 (0) 1-16
CRUSTACEANA

AGONISTIC INTERACTION IN THE MALE FIDDLER CRAB *UCA LEPTODACTYLA* RATHBUN, 1898 AT VARYING DENSITIES

BY

L. C. SANTOS[1]), C. E. R. D. ALENCAR[2]), F. A. M. FREIRE[2]) and A. C. LUCHIARI[1,3])

[1]) Departamento de Fisiologia, Centro de Biociências, Universidade Federal
do Rio Grande do Norte, Natal, RN, Brazil

[2]) Departamento de Botânica, Ecologia e Zoologia, Centro de Biociências,
Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil

ABSTRACT

In this study we tested the effect of population density on agonistic interactions in male *Uca leptodactyla* Rathbun, 1898. We recorded the crab behaviour in pairs or in 5 animal groups, composed of conspecific and heterospecific living in the same area (sympatric) and distinct areas (allopatric) of the mangrove forest. Allopatric conspecific crabs showed higher approaching and signalling than the other conditions. The higher the crab density, the lower the interaction intensity between animals. Low-level agonistic signals were mainly displayed in high density (groups), while claw touch mainly occurs in pairs. Allopatric conspecifics showed the more intense agonistic interactions. Therefore, *Uca* seems to decrease energy investment in unnecessary fights against sympatric and conspecific crabs. Population density is a major factor driving agonistic behaviour mainly when conspecific animals are kept together. This may occur due to the increased competition for the same resources.

Key words. — Fiddler crab, agonistic interactions, density, energy investment, *Uca leptodactyla*

RESUMO

Testamos o efeito da densidade populacional nas interações agonísticas de *Uca leptodactyla* Rathbun, 1898 macho. Registramos o comportamento do caranguejo quando em pares ou em grupos de cinco animais, composto por heteroespecíficos e coespecíficos que habitam a mesma área (simpátricos) e áreas distintas (alopátricos) do mangue. Os caranguejos coespecíficos alopátricos mostraram maior aproximação e sinalização do que qualquer das outras condições. Quanto mais elevada a densidade de caranguejos, menor é a intensidade das interações entre os animais. Sinais agonísticas de baixo nível foram exibidos principalmente em alta densidade (grupos), enquanto o toque entre quelas ocorre principalmente em pares. Os coespecíficos alopátricos mostraram interações agonísticas mais intensas. Assim, concluímos que o caranguejo *Uca* parece diminuir o investimento energético em lutas desnecessárias contra coespecíficos simpátricos. A densidade é um fator determinante da relação agonística, principalmente quando animais coespecíficos são mantidos juntos, o que parece ser devido à competição pelos mesmos recursos.

---

[3]) Corresponding author; e-mail: analuchiari@yahoo.com.br

DOI 10.1163/15685403-00003443

INTRODUCTION

It is common for animals to engage in agonistic interactions in order to obtain or defend resources that allow their survival and reproduction, such as food, shelter or mates. The fiddler crab often displays the major claw (chelae) to defend territory and burrows, and to control other crabs' access to its resource (Mautz et al., 2011). They also use the claw wave to court potential mates and to inform its own agonistic potential to other males (Murai & Backwell, 2006).

The burrows constructed by these animals are valuable resources, not only due to the energy consumed for building, but also because it is used against predation, desiccation/inundation and mating (Booksmythe et al., 2010). Hence, ownership of the burrow/territory increases an animal's motivation to hold and defend the resource (Fayed et al., 2008). For territorial defence, agonistic interactions occur in signalling escalation, which is initiated by simple claw movements and culminate in intense physical contacts, sometimes leading to the chelae loss or to death. The fiddler crab can identify conspecifics by the cheliped display (Booksmythe et al., 2010), which is a species-specific signal (Araujo et al., 2013), and increases defensive signals if the intruder gets closer (Zucker, 1974).

The major claw movements can symbolize many conditions: species recognition, opponent size estimation, reproductive status identification or aggressive power detection (Bradbury & Vehrencamp, 1998). The signals for a threat are distinct from other signals; the crab may only fight those that highly threaten its territoriality (Booksmythe et al., 2010). However, many factors influence the fight reaction; for instance, the signaling strategy of males can be modified by information sent by other crabs occupying the same area (Peake, 2005), while the wave rate decreases when competitors are present (Burford et al., 1998).

Therefore, any factor that interferes with the number of fiddler crab sharing the same area may contribute to behavioural changes. Some authors have studied population density effects in several animals; for instance, the isopod *Asellus aquaticus* (cf. Linnaeus, 1758) (Bertin & Cézilly, 2005) and the earwig *Forficula auricularia* Linnaeus, 1758 (Tomkins & Brown, 2004) intensify aggressive behaviour when the number of individuals increase, while the seed bug *Neacoryphus bicrucis* (cf. Say, 1825) (Mclain, 1992) and many Fig wasps (28 species; Reinhold, 2003) decrease agonistic displays when population enlarge. While all these results are still inconclusive to propose a general effect of population density, some positive and negative effects can be seen both in high and low densities; for example, predation risk is increased when in areas with few animals, but each individual increases its access to environmental resources (food, territory and mates) (Viscido & Wethey, 2002). Therefore, high densities may affect the number and type of signals released by males in order to maintain territorial stability, since it increases the chance of losing the territory and other resources. According to Knell

(2009), who reviewed aggressive tactics in many animals, it seems that in some cases reproductive strategies are favoured at low densities, while aggressive ones are more common at high densities. However, Knell only used cases in which aggression was related to mating success, and showed that both responses (increase and decrease in aggression due to increased population density) are possible.

Only a few studies approach population density effects on crabs' behavioural repertory. For example, Ribeiro et al. (2010) showed that the population density of *Uca uruguayensis* Nobili, 1901 affects males' mating strategy: at high density it copulates in the burrow (underground mating) while at low densities the crab copulates outside (surface mating). Meanwhile, Mansfield (2009) observed that *Uca crassipes* (White, 1847) fight more in high- than in low-density populations in the field, but not in the laboratory. While population density is an important ecological factor with selective effects for species evolution, information about species interaction upon their abundance is still scarce.

The fiddler crab *Uca leptodactyla* Rathbun, 1898 inhabits mangrove forests of the West Atlantic coast, from southern U.S.A. to southeast Brazil (Crane, 1975; Melo, 1996). On the northeast coast of Brazil, *U. leptodactyla* is a very abundant species (Bezerra & Matthews-Cascon, 2006) and some inhabited areas of the mangroves are shared with other *Uca* species (Masunari, 2006). In the mangrove forest of the Cerará-Mirim River (northeast coast of Brazil) both *U. leptodactyla* and *U. rapax* (Smith, 1870) can be found in sympatry (fig. 1D), but only few aspects of their social behaviour have been addressed in the literature. It is known that crab population density interferes with the mangroves ecology and the species interaction evolution. Thus, the aim of this study was: (1) to test the effect of population density on male *U. leptodactyla* agonistic behaviour and (2) to analyse how a male interacts with conspecifics and heterospecifics that inhabits either the same area (immediate neighbour) or distinct areas of the mangroves. Therefore, as an ultimate goal, this study may contribute to increasing knowledge about the relation between population density and aggression, in terms of diversity of behaviour evolution.

MATERIALS AND METHODS

The study was conducted in the estuary of the Ceará-Mirim River, located in the city of Extremoz, east of Rio Grande do Norte State (5°40′32.25″S 35°14′19.61″W) (fig. 1). The mangroves of the Ceará-Mirim River comprise 17 000 m^2, the average temperature is 26.1°C and the annual relative humidity is 77% (IDEMA, 2008). The mangrove forest belongs to Centro Tecnológico de Aquicultura (CTA) of Universidade Federal do Rio Grande do Norte (UFRN). In

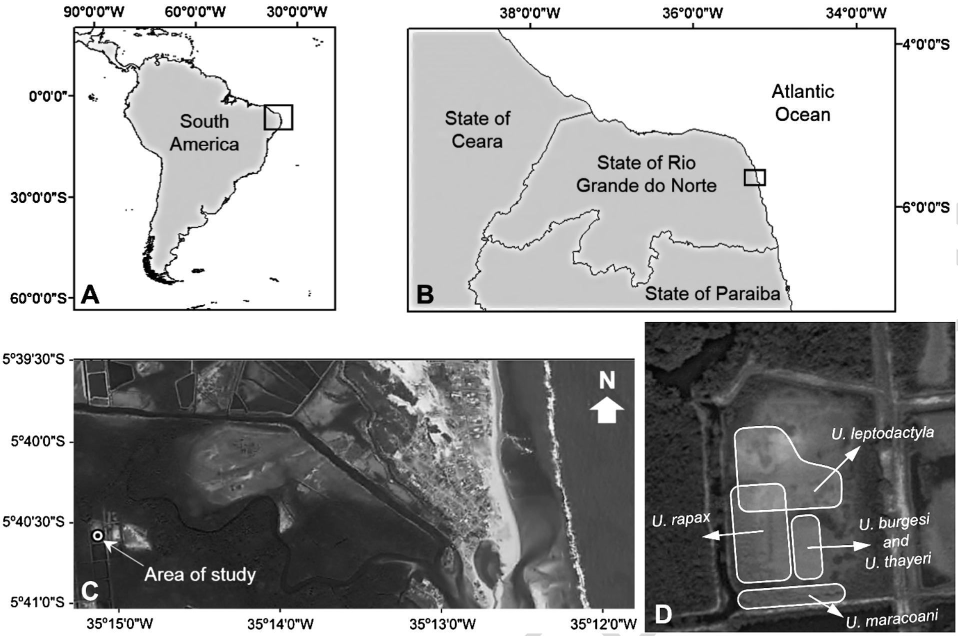

Fig. 1. Geographic location of the Ceará-Mirim River estuary (A), the city of Extremoz, Rio Grande do Norte State (B), Brazil (C) (05°40′32.25″S 35°14′19.61″W), and *Uca* species distribution in the mangrove forest (D).

this mangrove forest, five *Uca* species can be found: *U. maracoani* (Latreille, 1802-1803), *U. thayeri* Rathbun, 1900, *U. burgersi* Holthuis, 1967, *U. rapax* (Smith, 1870) and *U. leptodactyla* (fig. 1D). Not all of these species occupy the same areas due to differences in flooding and substrate composition. The most exposed area of the mangrove forest (far from the river and presenting low vegetation density) is mainly shared by two *Uca* species: *U. leptodactyla* and *U. rapax*. However, some abiotic factors, such as lunar phase and tide amplitude, affect the number of animals in the area (personal observation; Macia et al., 2001). Therefore, the two most abundant species, *U. leptodactyla* and *U. rapax*, were chosen as our experimental groups.

U. leptodactyla and *U. rapax* behaviour at varied population densities was recorded and compared at two levels of recognition: (1) neighbourhood: male crabs inhabiting the same area (within 50 cm from the focal crab burrow), which were called “sympatric” animals (immediate neighbours) and male crabs inhabiting distant areas (at least 3 m away from the focal crab burrow), which were called “allopatric” animals; and (2) species: male crabs used for the behaviour analysis were conspecific animals (*U. leptodactyla*) and heterospecific animals (*U. leptodactyla* and *U. rapax*). In all groups, one *U. leptodactyla* crab was kept as the focal animal.

Two levels of population density were tested: two animals including the focal (2), and five animals including the focal animal (5). Therefore, the experimental treatments with varied density, neighborhood and species were divided into eight treatments named: Sympatric Conspecific Pair (SC2), Allopatric Conspecific Pair (AC2), Sympatric Heterospecific Pair (SH2), Allopatric Heterospecific Pair (AH2), Sympatric Conspecific Group (SC5), Allopatric Conspecific Group (AC5), Sympatric Heterospecific Group (SH5) and Allopatric Heterospecific Group (AH5). For the heterospecific groups (SH5 and AH5), the focal crab was *U. leptodactyla* and the other 4 crabs were *U. rapax*. The number of animals vs. species used reflects observed densities at the studied area throughout seasons and lunar phases during the past years; periods of increased ratio *U. rapax*/*U. leptodactyla* and others with increased ratio *U. leptodactyla*/*U. rapax*. Therefore, we selected two densities considered extreme: on the 1 : 1 condition we could evaluate whether there is any interaction between species, while on the condition 1 : 4 we evaluated whether the density interferes on interspecific interaction. According to Knell (2005), it may represent extreme levels of experimental treatments to find a specific pattern. The sample sizes (n) used in each treatment equal 7.

The experiment was carried out during the daylight period (from 9 am to 3 pm) of full and new moon days at low-tide time because the animals are more active at this period. Data were collected from August to September 2012, in order to minimize the influence of temperature, relative humidity and luminosity fluctuation.

Fifty-six quadrats (30 × 30 cm) were distributed in the site of study and buried in the soil in order to prevent animals from escaping (walls were 15 cm high after quadrats were buried). Each quadrat was precisely located around one burrow of *U. leptodactyla*, where there was a resident animal (focal animal). For the sympatric treatments, other animals in the quadrat were removed by hand (taking care to not damage the focal-animal's burrow) and their burrows closed with natural substrate (mud). The same animals removed from a quadrat were after reintroduced as the neighbors (sympatric crabs). For the allopatric treatments, all animals inhabiting the quadrat area were carefully removed from the quadrat and extra burrows were closed. Animals from a distant area were collected by hand and introduced in the quadrat to comprise the treatment group. The crabs were always similar in size (*U. leptodactyla*: CW 8.39 ± 2.03 mm and CL 7.01 ± 1.67 mm; *U. rapax*: CW 9.04 ± 1.87 mm and CL 8.20 ± 2.35 mm) and selected by the species to compose the conspecific and heterospecific groups, and by the living area to compose the sympatric and allopatric groups. Animals were allowed to explore the quadrat for 5 min for acclimation and then their behaviour was recorded for 5 min (consistent with Booksmythe et al., 2010 and Detto et al., 2010). For video records, a camcorder (Sony Digital Video Camera Recorder; DCR-SX45, 14 MP, 720 × 480 pixels) was fixed vertically on a tripod approximately 1.5 m above the quadrat centre.

For videotape analysis, the 30 × 30 quadrat was divided into 3 cm squares, drawn on the front side of the computer screen so that the position of the crabs could be registered every 10 s and then plotted on a x-y axis. Six points were collected for each minute. The mean position of the focal *U. leptodactyla* on x and y axis produced the barycentric coordinate for each 1-min period. For each crab the distance from the focal *U. leptodactyla* was measured every 10 s and then mean distance was calculated. The crabs belonging to the five animal groups were classified as a, b, c and d categories, in accordance to their proximity to the focal animal at the first recorded minute. Thus, animal a was the closest and animal d was the farthest crab to the focal *U. leptodactyla*.

For each animal, we registered the number of agonistic signals and interactions displayed during the five min recording. The scale of signal/interaction was divided into four levels, as modified from Mansfield (2009) and Ayres-Peres et al. (2011): type 1, threat wave (signalization); type 2, major claw touch; type 3, major claw interlace; type 4, hold, suspend and push the other animal (2, 3 and 4: agonistic interactions).

Data were analysed for normality (univariate Shapiro-Wilk test, Shapiro & Wilk, 1965; multivariate Omnibus test, Doornik & Hansen, 2008) and homoscedasticity (univariate Brown-Forsythe test, Brown & Forsythe, 1974; multivariate Box's M test, Anderson, 2003). Parametric tests were used in cases of normal and homoscedastic data; otherwise we used nonparametric equivalent tests. To compare the mean distance of the focal crab to the other animals, we used a one-way ANOVA test for pairs and RM ANOVA (Repeated Measures Analysis of Variance) for 5-animal groups. After that, the Student Newman Keuls (SNK) post hoc ANOVA test was applied to compare the 5-animal groups. The multinomial proportion Goodman test (Goodman, 1964) was used to compare the total number of agonistic interactions displayed. The levels of agonistic interactions were analysed by linear discriminant function (LDA) and nonparametric MANOVA (Permutational Multivariate Analysis of Variance — PERMANOVA), since the LDA may suggest the type of agonistic interaction that best discriminates each condition and, hence, the species relationship by scale of agonistic interaction. For LDA data interpretation, each treatment centroid was inserted in the graph. After that, PERMANOVA test was used to find differences between agonistic interactions in each treatment (Bray-Curtis similarity index).

Univariate analysis (ANOVA and RM ANOVA) was performed using SigmaStat 3.5 while multivariate analysis (LDA and PERMANOVA) was performed using the R software (R Development Core Team, 2012) by the packages "MASS" (Venables & Ripley, 2002) and "ca" (Greenacre & Nenadic, 2010). For all analyses the level of significance was 5% (Zar, 2010).

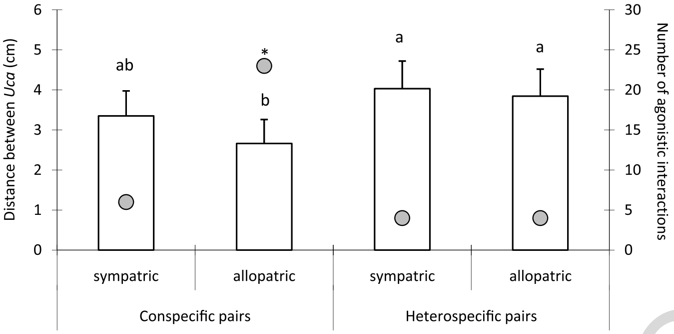

Fig. 2. Distance and agonistic interactions between pairs of the fiddler crab. Four paired *Uca* conditions were tested: pairs of *Uca leptodactyla* Rathbun, 1898 immediate neighbours (sympatric conspecifics) and from different areas (allopatric conspecifics) and pairs of *Uca leptodactyla* and *Uca rapax* (Smith, 1870) immediate neighbours (sympatric heterospecifics) and from different areas (allopatric heterospecifics). Bars are the mean distance ± SD between animals. The same letter means no significance and different letters mean significance value (ANOVA, $p<0.05$). Circles are the total number of agonistic interactions showed by the pairs. An asterisk indicates statistical difference in the agonistic interactions between pairs (Goodman test, $p<0.05$).

RESULTS

The average distances between crabs was shorter in allopatric conspecific *Uca* pairs than in heterospecific pairs (ANOVA: $F_{24,3} = 4.43$, $n = 28$, $p = 0.005$) and also expressed higher number of agonistic interactions (Goodman test: $\alpha = 0.05$ and A $= 7.43$, lower and upper limit of -0.6375 and 0.2897) (fig. 2).

In the groups of five crabs, only conspecifics maintained closer distances between the focus and crab a, while crabs b, c and d were more distant (RM ANOVA: SC5 $F_{34,3,102} = 8.38$, $n = 28$, $p<0.01$; AC5 $F_{34,3,102} = 9.073$, $n = 28$, $p<0.001$; fig. 3a). For the heterospecific groups, there were no difference between animals (RM ANOVA: SH5 $F_{34,3,102} = 0.559$, $n = 28$, $p = 0.643$ and AH5 $F_{34,3,102} = 0.543$, $n = 28$, $p = 0.643$; fig. 3a). Higher agonistic interactions were observed in the allopatric conspecific group (AC5), in which crabs interact the most with the focal crab (Goodman test: $\alpha = 0.05$ and $A = 7.43$, lower and upper limit of -0.1776 and 0.2858; fig. 3b), while the sympatric heterospecific group (SH5) showed less agonistic interaction (fig. 3b).

To verify the agonistic interaction relation with group formation, the linear discriminant analysis (LDA) used the first two axes: LDA1 (78.66%) and LDA2 (13.51%) (fig. 4). According to stepwise forward procedure, the agonistic interaction type 2 was the only significant discriminating variable in all treatments analyzed (Wilks' Lambda (λ) $= 0.77$; $F = 5.83$; $p<0.00$; Tolerance $= 0.98$). However, interaction type 1 was marginally significant (Wilks' Lambda (λ) $= 0.54$; $F = 2.15$; $p<0.056$; Tolerance $= 0.98$), implying a strong discriminatory trend.

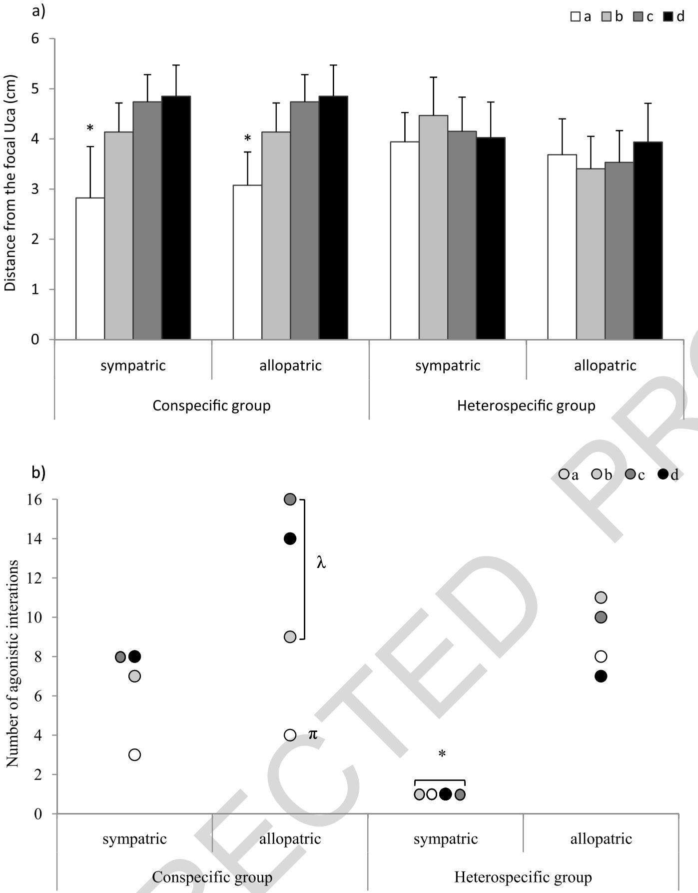

Fig. 3. (a) Distance and (b) agonistic interactions between the focal *Uca leptodactyla* Rathbun, 1998 and the other fiddler crabs in groups of 5 animals. Four conditions were tested: groups of five *Uca leptodactyla* that were immediate neighbour (sympatric conspecifics) or inhabited different areas (allopatric conspecifics) and groups of three *Uca leptodactyla* and two *Uca rapax* (Smith, 1870) that were immediate neighbours (allopatric heterospecifics) or residents of distant areas (allopatric heterospecifics). The crabs were classified as a, b, c and d according to their distance from the focal *Uca leptodactyla* in the first minute of observation; a represents the closer animal to the focal *Uca leptodactyla* and d the farthest crab. (a) Bars show the mean distance ± SD between animals; an asterisk indicates statistical difference between animal a and the others in the same condition (ANOVA, $p<0.05$). (b) Circles show the total number of agonistic interactions initiated by each animal in the group; different Greek letters indicates statistical differences between the crabs in the same condition (allopatric conspecifics) and an asterisk indicates statistical difference between crabs from different conditions (Goodman test, $p<0.05$).

We observed the discriminating power of agonistic interaction type 2 in treatments AC2 and AC5, while interaction type 1 was more frequent in treatment AC5 (fig. 4).

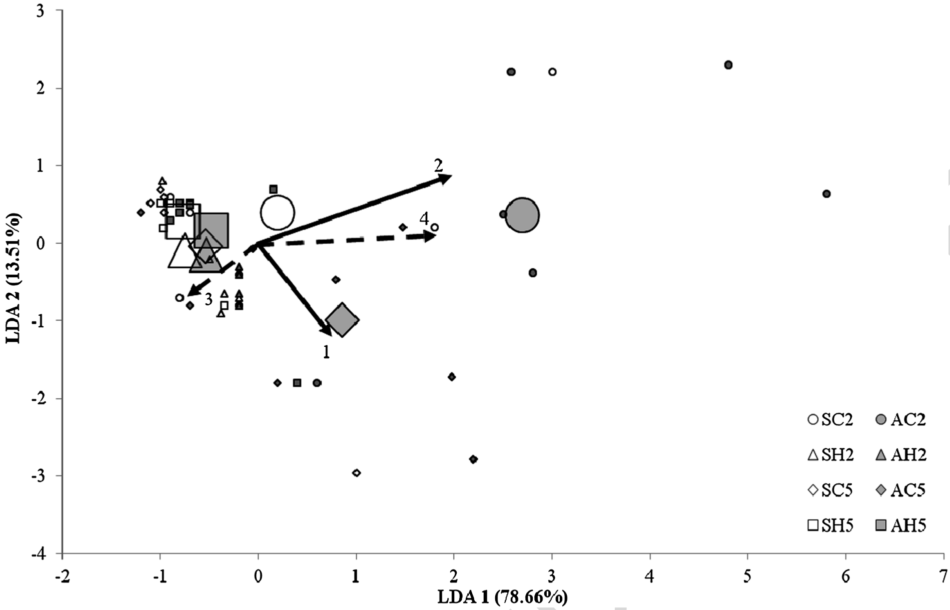

Fig. 4. Relationship between agonistic interactions (type 1, 2, 3 and 4) and conditions tested: SC2, sympatric conspecific pair; AC2, allopatric conspecific pair; SH2, sympatric heterospecific pair; AH2, allopatric heterospecific pair; SC5, sympatric conspecific group; AC5, allopatric conspecific group; SH5, sympatric heterospecific group; AH5, allopatric heterospecific group. Small symbols are the eigenvectors of the LDA and big symbols are the corresponding centroid. Agonistic interactions 1 and 2 are marginally significant and highly significant, respectively (solid arrows). Agonistic interactions 3 and 4 do not show statistical significance (dashed arrows).

According to the LDA results, the PERMANOVA comparison between treatments found only interactions type 1 and 2 to be statistically different between interactions and treatments ($F = 3.127$; $p = 0.002$; permutations = 9999). AC2 is statistically similar to AC5, indicating the absence of density effect when animals are allopatric conspecifics. Heterospecific groups (SH2, SH5, AH2 and AH5) were always similar, indicating they do not interact even when density is varied or grouped with either sympatric or allopatric crabs. On the other hand, AC2 differed from SC2, suggesting the neighbourhood effect on agonist interactions, but AC5 was similar to SC5, implying that increased density decreases the neighbourhood effect (table I).

DISCUSSION

We found that our experimental crab *Uca leptodactyla* reacts with different patterns and intensities depending on the species, neighbourhood and density of other crabs. Heterospecific groups (~~3~~ *U. leptodactyla* + ~~2~~ *U. rapax*) show a low

TABLE I
PERMANOVA statistics for *Uca leptodactyla* Rathbun, 1898

	SC2	AC2	SH2	AH2	SC5	AC5	SH5	AH5
SC2	–	0.0461*	0.3144	0.2942	0.7103	0.0604	0.2623	0.6169
AC2	3.32	–	0.0122*	0.013*	0.0117*	0.0818	0.0007*	0.0061*
SH2	1.2	6.242	–	1	0.8786	0.0335*	0.2606	0.7059
AH2	1.2	6.242	0.00	–	0.7138	0.03*	0.2604	0.4727
SC5	0.6346	4.112	0.2308	0.2308	–	0.0778	0.5064	0.9761
AC5	3.057	2.433	3.75	3.75	2.642	–	0.0036*	0.0242*
SH5	1.773	7.627	3	3	0.5	7.703	–	0.9891
AH5	0.4365	4.662	0.75	0.75	0.1765	4.038	0.4286	–

Above the diagonal are p-values; below the diagonal are F statistics. Studied conditions related to agonistic interactions are presented: SC2, sympatric conspecific pair; AC2, allopatric conspecific pair; SH2, sympatric heterospecific pair; AH2, allopatric heterospecific pair; SC5, sympatric conspecific group; AC5, allopatric conspecific group; SH5, sympatric heterospecific group; AH5, allopatric heterospecific group.
* Significant value.

interactive rate, while conspecifics exhibit more approaches and confrontation (fig. 3). Our study indicates that the higher the density of crabs, the less intense animals interact. Among the agonistic interactions, the major claw touch (type 2) is the most commonly used (fig. 4), since it allows the evaluation of the opponent's ability (Lailvaux et al., 2009).

Evaluation of the opponent

The close proximity between *U. leptodactyla* conspecifics shows that crabs may evaluate each other's agonistic potential before engaging in territorial disputes. Crabs have high-energy loss during the agonistic behaviour interaction, which may decrease fitness due to reduced metabolic storage for reproduction (Sneddon et al., 1998). Vertebrates such as fishes and lizards also decrease energy reserves and accumulate lactic acid in their muscles after intense agonistic interactions (Neat et al., 1998; Ancona et al., 2010). This condition affects the animal's performance in territory defence, foraging and reproduction. In fact, Sneddon et al. (1998) showed an increase in haemolymph glucose in crabs immediately after fights, indicating how stressful these interactions could be. Thus, individual assessments are crucial helping the crab to avoid unnecessary energy expenditure.

Crabs approached allopatric conspecifics more than sympatric ones, indicating a need for closer evaluation of intruders. Free walking animals generally do not have a defined territory and engage in combats with residents to drive them out of their burrows in order to occupy it (Backwell & Jennions, 2004). This behaviour seems to be a greater threat when the opponent is a stranger (allopatric), since sympatric crabs share the territory and were probably well previously evaluated for the agonistic potential. In this regard, Booksmythe et al. (2010) observed that *U. mjoebergi* presents shorter fights between neighbours than with strangers. Our study supports their finding; when *U. leptodactyla* were paired with conspecifics from distant areas (allopatric to them), they increase signalling and aggressive behaviour (fig. 2).

Sharing space with others

The relationship maintained between sympatric conspecifics has its advantages, especially in situations of territorial defence against intruders. The cooperative territorial defence has already been shown in other *Uca* species, as *U. mjoebergi* (Backwell & Jennions, 2004) and *U. annulipes* (Detto et al., 2010; Milner et al., 2010). While sympatric conspecific groups greatly differ from allopatric conspecific groups in terms of aggression (fig. 4), we found that the interactions between heterospecifics were rather weak or absent (fig. 4 and table I). In areas occupied by more than one crab species, heterospecific interactions are reduced due to low competition and low interference between species (Pope & Hayne, 2008). Although *U. leptodactyla* and *U. rapax* share the same mangrove areas, according to Genoni (1991), Sayão-Aguiar et al. (2012) and Machado et al. (2013), they have morphological specializations for the micro-habitats they occupy (their chaela diverge), and their burrows shape and structure differ and, thus, they hardly fight for the same area. The low level of interaction between *U. leptodactyla* and *U. rapax* observed in this study may have arisen from these differences to decrease competition between them.

In fact, the main barriers for *Uca* distribution seem to be associated with the granulometry of the substrate in which they live and feed (Costa & Negreiros-Fransozo, 2001). Many authors have suggested that species are adapted to the sediment characteristics (Aspey, 1978; Icely & Jones, 1978; Macintosh, 1988). The features that allow species to inhabit and feed at different areas of the mangroves include, for example, the presence of specialized setae in the feeding appendages (Miller, 1961; Maitland, 1990; O'Connor, 1990; Wolcott & O'Connor, 1992; Mounton & Felder, 1996). Accordingly, Costa & Negreiros-Fransozo (2001) showed that *U. leptodactyla* have plumose setae at the second maxilliped while *U. rapax* does not. This adaptation is considered to influence the resource usage of the *Uca* species, since the plumose setae is probably more efficient to sort and remove organic matter associated with the finest sediments (Icely & Jones, 1978).

Population density and aggression

The population density increase in a given area appears to be inversely related to agonistic interactions between conspecifics in *U. leptodactyla* (figs. 3 and 4).

This relationship has also been observed in other species of invertebrates (Mclain, 1992; Reinhold, 2003) and vertebrates (Craig et al., 1969; Luchiari & Freire, 2009), in which increasing the group size decreases aggressive interactions (for revision, see Knell, 2009). On the other hand, our results fully disagree those from Mansfield (2009), using other species of *Uca*. This author studied *U. crassipes* agonistic interactions in two areas with different population densities and found that interactions increased with increased density in the field, but not in the laboratory. The author explained that in the laboratory, crabs did not have burrows and thus, she did not observe the same patterns as in the field. Although increased competition was evident in the field, Mansfield (2009) was unable to identify the resource for which the crabs were competing. It seems territory is the prime resource over which the crabs fight (Mautz et al., 2011).

The behavioural response we observed in fiddler crabs is evident in other species. Knell (2009) suggests that population density influences evolutionary selection for aggression. The author proposes that any response to variation in population density emanates from the species habitat, ecology and biology. The fiddler crab *U. leptodactyla* is highly territorial, and spends much of its time defending a burrow/territory and other resources. Thus, recognition of the neighbour is highly relevant for deciding whether to fight or keep vigilance. The increased density of unfamiliar animals must be a factor determining the increased aggression to hold their resource. However, studies addressing the impact of sympatric versus allopatric relationships are still novel and warrant additional investigation.

In another crab group, *Carcinus mediterraneus* Czerniavsky, 1884, Vannini (1981) observed that increased density did not affect aggressive behaviour but lead to a greater excretion of nitrogen products. While our study seems to indicate a decrease in aggression upon increased density, both ours and Vannini's results suggest an adaptation to crowding: the decrease in resources and compulsory coexistence of naturally aggressive species lead to a more evaluating/threatening type of behaviour than physically dangerous agonistic interactions.

Conclusions

Our study only addresses the behaviour of pairs and 5-individual groups. A more extensive study including other densities and abiotic factors that may affect the number of animals present in a particular area (seasonality, tide, moon phase) could contribute to better comprehending the effects of density on the fiddler crab behaviour. Our study provides an initial understanding of the relationship between *Uca* species density and agonistic behaviour. Studies on other *Uca* species in sympatry may bring new insights into the relationship maintained by these animals.

~~In~~ this study confirms that the genus *Uca* can distinguish conspecifics and heterospecifics and show different agonistic interactions among sympatric and allopatric conspecifics. Thus, the fiddler crab can reduce the energy spent in unnecessary battles and invest in territory and neighbour inspection, which maintains better energetic harmony among neighbouring groups in the community.

ACKNOWLEDGEMENTS

We thank anonymous reviewers for helpful comments and constructive criticism. We also thank Ms. Diana Salajan for the English review. This work was supported by the Sociedade Brasileira de Carcinologia, SBC (Brazil) under Grant number 01/2012.

REFERENCES

ANCONA, S., H. DRUMMOND & J. ZALDÍVAR-RAE, 2010. Male whiptail lizards adjust energetically costly mate guarding to male-male competition and female reproductive value. Animal Behaviour, **79**: 75-82.

ANDERSON, T. W., 2003. Introduction to multivariate statistical analysis (3^{rd} ed.): 280-370. (Wiley-Interscience, New York, NY).

ARAUJO, S. B. L., A. C. RORATO, D. M. PEREZ & M. R. PIE, 2013. A spatially explicit model of synchronization in fiddler crab waving displays. PLoS ONE, **8**: e57362.

ASPEY, W. P., 1978. Fiddler crab behavioural ecology: burrow density in *Uca pugnax* (Smith) and *Uca pulitator* (Box) (Decapoda, Brachyura). Crustaceana, **34**: 235-244.

AYRES-PERES, L., P. B. ARAÚJO & S. SANTOS, 2011. Description of the agonistic behaviour of *Aegla longirostri* (Decapoda: Aeglidae). Journal of Crustacean Biology, **31**: 379-388.

BACKWELL, P. R. Y. & M. D. JENNIONS, 2004. Coalition among male fiddler crabs. Nature, **430**: 417.

BERTIN, A. & F. CÉZILLY, 2005. Density-dependent influence of male characters on mate-locating efficiency and pairing success in the waterlouse *Asellus aquaticus*: an experimental study. Journal of Zoology, **265**: 333-338.

BEZERRA, L. E. A. & H. MATTHEWS-CASCON, 2006. Population structure of the fiddler crab *Uca leptodactyla* Rathbun, 1898 (Brachyura: Ocypodidae) in a tropical mangrove of northeast Brazil. Thalassas, **22**: 65-74.

BOOKSMYTHE, I., M. D. JENNIONS & P. R. Y. BACKWELL, 2010. Investigating the "dear enemy" phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. Animal Behaviour, **79**: 419-423.

BRADBURY, J. W. & S. L. VEHRENCAMP, 1998. Principles of animal communication. (Sinauer Associates, Sunderland, MA).

BROWN, M. B. & A. B. FORSYTHE, 1974. Robust tests for the equality of variances. J. American Statistical Association, **69**: 364-367.

BURFORD, F. R. L., P. K. MCGREGOR & R. F. OLIVEIRA, 1998. Chorusing by male European fiddler crabs, *Uca tangeri*: a study of visual communication networks. Acta Ethologica, **1**: 33-41.

COSTA, T. M. & M. L. NEGREIROS-FRANSOZO, 2001. Morphological adaptations of the second maxilliped in semiterrestrial crabs of the genus *Uca* Leach, 1814 (Decapoda, Ocypodidae) from a subtropical Brazilian mangrove. Nauplius, **9**: 123-131.

CRAIG, J. V., D. K. BISWAS & A. M. GUHL, 1969. Agonistic behaviour influenced by strangeness, crowding and heredity in female domestic fowl (*Gallus gallus*). Animal Behaviour, **17**: 498-506.

CRANE, J., 1975. Fiddler crabs of the world. In: Ocypodidae: genus *Uca*: 547-944. (Princeton University Press, Princeton, NJ).

DETTO, T., M. D. JENNIONS & P. R. Y. BACKWELL, 2010. When and why do territorial coalitions occur? Experimental evidence for factors that promote territorial coalitions in fiddler crabs. The American Naturalist, **175**: E119-E125.

DOORNIK, J. A. & H. HANSEN, 2008. An omnibus test for univariate and multivariate normality. Oxford Bulletin of Economics and Statistics, **70**: 927-939.

FAYED, S. A., M. D. JENNIONS & P. R. Y. BACKWELL, 2008. What factors contribute to an ownership advantage? Biology Letters, **4**: 143-145.

GENONI, G. P., 1991. Increased burrowing by fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae) in response to low food supply. Journal of Experimental Marine Biology and Ecology, **147**: 267-285.

GOODMAN, L. A., 1964. Simultaneous confidence intervals for contrast among multinomial populations. The Annals of Mathematical Statistics, **35**: 716-725.

GREENACRE, M. & O. NENADIC, 2010. Simple, multiple and joint correspondence analysis. R package version 0.33, available online at http://CRAN.R-project.org/package=ca. (R Foundation for Statistical Computing, Vienna).

ICELY, J. D. & D. A. JONES, 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African Shore. Estuarine and Costal Marine Science, **6**: 315-325.

IDEMA, 2008. Instituto de desenvolvimento sustentável e meio ambiente do Rio Grande do Norte. Perfil do seu município: Extremoz, V.10: 1-23. (IDEMA, Lagoa Nova).

KNELL, R. J., 2009. Population density and the evolution of male aggression. Journal of Zoology, **278**: 83-90.

LAILVAUX, S. P., L. T. REANEY & P. R. Y. BACKWELL, 2009. Dishonest signaling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. Functional Ecology, **23**: 359-366.

LUCHIARI, A. C. & F. A. M. FREIRE, 2009. Effects of environmental colour on growth of Nile tilapia, *Oreochromis niloticus* (Linnaeus, 1758) housed individually or in groups. Journal of Applied Ichthyology, **25**: 162-167.

MACHADO, G. B. O., J. B. L. GUSMÃO-JUNIOR & T. M. COSTA, 2013. Burrow morphology of *Uca uruguayensis* and *Uca leptodactylus* (Decapoda: Ocypodidae) from a subtropical mangrove forest in the western Atlantic. Integrative Zoology, **8**: 307-314.

MACIA, A., I. QUINCARDETE & J. PAULA, 2001. A comparison of alternative methods for estimating population density of the fiddler crab *Uca annulipes* at Saco Mangrove, Inhaca Island (Mozambique). Hydrobiologia, **449**: 213-219.

MACINTOSH, D. J., 1988. The ecology and physiology of decapods of mangrove swamps. Zoological Symposium, **59**: 315-341.

MAITLAND, D. P., 1990. Feeding and mouthpart morphology in the semaphore crab *Heloecius cordiformis* (Decapoda: Brachyura: Ocypodidae). Marine Biology, **105**: 287-296.

MANSFIELD, C., 2009. The effects of density on intraspecific aggression in the fiddler crab, *Uca crassipes*, on Mo'orea, French Polynesia. UCB Moorea class: biology and geomorphology of Tropical Islands, available online at http://escholarship.org/uc/item/2jz4s7z8.

MASUNARI, S., 2006. Distribution and abundance of fiddler crabs *Uca* Leach (Crustacea Decapoda Ocypodidae) in Guaratuba Bay, Parana State, southern Brazil. Revista Brasileira de Zoologia, **23**: 901-914.

Mautz, B., T. Detto, B. B. M. Wong, H. Kokko, M. D. Jennions & P. R. Y. Backwell, 2011. Male fiddler crabs defend multiple burrows to attract additional females. Behavioural Ecology, **22**: 261-267.

Mclain, D. K., 1992. Population density and the intensity of sexual selection on body length in spatially or temporally restricted natural populations of a seed bug. Behavoral Ecology and Sociobiology, **30**: 347-356.

Melo, G. A. S., 1996. Manual de identificação dos Brachyura (Caranguejos e siris) do litoral Brasileiro. (Plêiade FAPESP, São Paulo).

Miller, D. C., 1961. The feeding mechanisms of the fiddler crab, with ecological considerations of feeding adaptations. Zoological: New York Zoological Society, **46**: 89-101.

Milner, R. N. C., M. D. Jennions & P. R. Y. Backwell, 2010. Safe sex: male-female coalitions and pre-copulatory mate-guarding in a fiddler crab. Biology Letters, **6**: 180-182.

Mounton, E. C. & D. L. Felder, 1996. Burrow distribution and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. Estuaries, **19**: 51-61.

Murai, M. & P. R. Y. Backwell, 2006. A conspicuous courtship signal in the fiddler crab *Uca perplexa*: female choice based on display structure. Behavioural Ecology and Sociobiology, **60**: 736-741.

Neat, F. C., A. C. Taylor & F. A. Huntingford, 1998. Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. Animal Behaviour, **55**: 875-882.

O'Connor, N. J., 1990. Morphological differentiation and molting of juvenile fiddler crab (*Uca pulginator* and *Uca pugnax*). Journal of Crustacean Biology, **10**: 608-612.

Peake, T. M., 2005. Eavesdropping in communication networks. In: P. K. McGregor (ed.), Animal communication networks: 13-37. (Cambridge University Press, New York, NY).

Pope, D. S. & B. R. Haney, 2008. Interspecific signaling competition between two hood-building fiddler crab species, *Uca latimanus* and *U. musica musica*. Animal Behaviour, **76**: 2037-2048.

R Development Core Team, 2012. R: a language and environment for statistical computing, available online at http://www.R-project.org/. (R Foundation for Statistical Computing, Vienna).

Reinhold, K., 2003. Influence of male relatedness on lethal combat in fig wasps: a theoretical analysis. Proceedings of the Royal Society of London B: Biological Sciences, **270**: 117101175.

Ribeiro, P. D., P. Daleo & O. O. Iribarne, 2010. Density affects mating mode and large male mating advantage in a fiddler crab. Oecologia, **164**: 931-941.

Sayão-Aguiar, B., M. A. A. Pinheiro & K. D. Colpo, 2012. Sediment bioturbation potential of *Uca rapax* and *Uca uruguayensis* as a result of their feeding activity. Journal of Crustacean Biology, **32**: 223-229.

Shapiro, S. S. & M. B. Wilk, 1965. An analysis of variance test for normality (complete samples). Biometrika, **52**: 591-611.

Sneddon, L. U., F. A. Huntingford & A. C. Taylor, 1998. Impact of an ecological factor on the costs of resource acquisition: fighting and metabolic physiology of crabs. Functional Ecology, **12**: 808-815.

Tomkins, J. L. & G. S. Brown, 2004. Population density drives the local evolution of a threshold dimorphism. Nature, **431**: 1099-1103.

Vannini, M., 1981. Notes on some factors affecting aggressive behaviour in *Carcinus mediterraneus*. Marine Biology, **61**: 235-241.

Venables, W. N. & B. D. Ripley, 2002. Modern applied statistics with S (4th ed.). (Springer, New York, NY).

Viscido, S. V. & D. S. Wethey, 2002. Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. Animal Behaviour, **63**: 735-741.

Wolcott, D. L. & N. J. O'Connor, 1992. Herbivory in crabs: adaptations and ecological considerations. American Society of Zoologists, **32**: 370-381.

ZAR, J. H., 2010. Biostatistical analysis (5th ed.): 547-944. (Prentice-Hall, Englewood Cliffs, NJ).

ZUCKER, N., 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). American Midland Naturalist, **91**: 224-236.

First received 20 January 2014.
Final version accepted 12 May 2015.