Behavioural Processes 162 (2019) 90–96

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Testing the dear enemy relationship in fiddler crabs: Is there a difference between fighting conspecific and heterospecific opponents?

Bruno R. Fogo[a,b], Fábio H.C. Sanches[a,c,*], Tânia M. Costa[b]

[a] Postgraduate Program in Biological Sciences (Zoology), São Paulo State University (Unesp), Institute of Biosciences, Botucatu, São Paulo, Brazil
[b] Laboratory of Ecology and Animal Behavior, São Paulo State University (Unesp), Institute of Biosciences, Coastal Campus, São Vicente, São Paulo, Brazil
[c] Institute of Marine Science, Federal University of São Paulo (IMar/Unifesp), Santos, São Paulo, Brazil

ARTICLE INFO

Keywords:
Aggressiveness
Interspecific competition
Intraspecific competition
Opponent recognition
Territoriality

ABSTRACT

Reduction of aggressiveness toward familiar neighbors, when compared to aggressiveness toward unfamiliar strangers, can decrease the costs of territory defense. This phenomenon is known as the “dear enemy effect”. Individuals may shift their aggressiveness toward neighbors or strangers from the same or different species, depending on the relative threat associated with different opponents. Therefore, a reduced level of aggressiveness between heterospecific neighbors is expected in relation to conspecific intruders, since the latter compete not only for territory, but also for mates. Herein we investigated the occurrence of the dear enemy effect in territorial fights between conspecific pairs of *Leptuca leptodactyla* and heterospecific pairs of *L. leptodactyla* versus *Leptuca uruguayensis*. Across both conspecific and heterospecific fights, medium- and high-intensity fight components were more used in resident–stranger than in resident–neighbor fights. Thus, residents showed a dear enemy response, regardless of opponent species. Moreover, conspecific fights induced a greater number of low- and medium-intensity fight components than did fights between heterospecifics, both neighbors and strangers. Finally, conspecific resident–stranger fights took longer than heterospecific resident–stranger fights. Our results indicate that fiddler crabs adjust their territorial response according to the species and resident status of intruders, consistent with the risks posed by different intruder types.

1. Introduction

Evolution has often favored behavioral mechanisms that minimize energy expenditure in social interactions, especially among animals that share resources. In this sense, a range of studies has demonstrated that territorial animals may be less aggressive to their established known neighbors than to strangers (Temeles, 1994). This pattern of apparent social behavior has been observed in mammals (Palphramand and White, 2007), birds (Briefer et al., 2008), reptiles (Husak and Fox, 2003), amphibians (Jaeger, 1981), fishes (Leiser, 2003), and invertebrates (Booksmythe et al., 2010a; Tanner and Adler, 2009), and is known as the “dear enemy effect” (Temeles, 1994).

Fight intensity should be measured by time and energy expenditure, which will further penalize animal choice (Jaeger, 1981). Selection, in turn, should favor individuals that adjust aggressiveness depending on the perceived threat, i.e. caused by neighbors or strangers. Usually, strangers are unfamiliar intruders that offer a greater threat to residents because they lack both territories and mates, and are searching for new ones to usurp (Temeles, 1994). Neighbors, in contrast, are familiar animals whose intrusions do not represent a great threat because they already have their own territory and therefore may only be seeking to take the resident's mates (Temeles, 1994). Thus, territorial animals often respond less aggressively to neighbor intrusions and such responses provide time and energy budgets that may be used for essential activities instead of unnecessary territorial defense (Briefer et al., 2008; Husak and Fox, 2003). Interestingly, experimental evidence has also shown that appropriate neighbor-stranger responses are likely to vary when neighbors threaten residents as equally as strangers (e.g. Briefer et al., 2008; Leiser, 2003). Therefore, responses to familiar or unfamiliar intruders should be weighed by the threat to resident fitness by each intruder category in different social and spatial cases.

Residents are often faced by other types of intrusion besides those of their own species. This may happen in cases where territories are home to mixed-species populations, where both conspecific and heterospecific opponents surround residents (Booksmythe et al., 2010b; Clark and Backwell, 2017; Tynkkynen et al., 2004). Even if they possess distinct life strategies, different species may exploit the same food resources (Li et al., 2014) and oviposition patches (Mohamad et al.,

---

[*] Corresponding author at: Institute of Marine Science, Federal University of São Paulo (IMar/Unifesp), Santos, São Paulo, Brazil.
E-mail address: fabiohcsanches@yahoo.com.br (F.H.C. Sanches).

https://doi.org/10.1016/j.beproc.2019.02.001
Received 13 September 2018; Received in revised form 5 February 2019; Accepted 5 February 2019

2015), or share limited territorial boundaries (Tynkkynen et al., 2006, 2004). Alternatively, heterospecifics do not compete for mates (Booksmythe et al., 2010b; Lehtonen and Wong, 2017), which could represent a lower threat than that associated with mate competition between conspecifics. However, males from some species may pay a cost for courting heterospecific females they will not mate (Sanches et al., 2018). On the other hand, heterospecific pressures may lead to reduction of the resident's territory (Clark and Backwell, 2017), trigger submissive behavior between species (Roux et al., 2013; Tanner and Adler, 2009) or cause species-preferred habitat exclusion (Martin and Martin, 2001). As a consequence, subordinate species may be forced to live in low-quality territories or forage for sub-optimal resources, which could further affect individual reproductive success (Mohamad et al., 2015; Tynkkynen et al., 2006). Therefore, according to the niche overlap between species, heterospecifics may arise as dominant species and impose the same pressures as conspecifics, and should not be neglected as inferior competitors.

Studies investigating reduction of aggressiveness in neighbor-stranger recognition tend to focus almost exclusively on conspecific animals, most of them using playback signals or chemical scents as stimuli (Lehtonen and Wong, 2017; Temeles, 1994). Fewer studies have investigated interaction between species. Heterospecific dear enemy relationships have been demonstrated in social species, such as ants (Grangier et al., 2007; Heinze et al., 1996; Langen et al., 2000; Roux et al., 2013; Tanner and Adler, 2009) and cichlid fishes (Lehtonen et al., 2010; Lehtonen and Wong, 2017; Ochi et al., 2012), while studies with other taxa are scarce. Nevertheless, it is important to know how neighbor-stranger recognition affects species with different contexts of territoriality and to use other sensory modes rather than what has already been demonstrated (Lehtonen and Wong, 2017). These approaches are necessary to test contexts mediated by aggressiveness toward conspecific or heterospecific opponents in the natural environment.

Based on the statements above, fiddler crabs are good models in studies addressing aggressive responses to opponents as they live in mixed-species populations and overlap territories in limited spaces (Clark and Backwell, 2017; Sanches et al., 2018). In these species, residents defend a small area around a central burrow on the sediment surface (Crane, 1975). Males have one major claw used to attract females in waving displays or to defend their territory (Crane, 1975). Strangers are former residents that either abandoned or were evicted from their burrow by another male (Booksmythe et al., 2010a). Residents retaliate with aggressiveness toward neighbors and strangers that break into the territorial boundaries or that try to steal their burrows (Crane, 1975). In this context, we aimed to investigate the occurrence of the dear enemy effect in territorial fights between conspecific and heterospecific fiddler crabs. We wanted to test whether there were differences in fight intensity and duration between conspecifics of *Leptuca leptodactyla* and between this species and *Leptuca uruguayensis*, a sympatric species that cohabits in mixed-species muddy-sand banks. We expected that the dear enemy effect would occur in both cases, but aggressiveness would be more intense among conspecifics, since heterospecifics might not compete for potential mates.

2. Methods

2.1. Study site and species

We studied *L. leptodactyla* and *L. uruguayensis* populations from August, September and November 2014 and January to March 2015 in a muddy-sand bank (24°26′18.11″S, 47°04′20.41″W) at the Una do Prelado river, Estação Ecológica Juréia-Itatins, southern coast of São Paulo, Brazil. This site is home to a 450 m^2 area where fiddler crab species partly overlap, forming several mixed aggregates. Species densities were measured during spring low tide by using three randomly cast quadrat replicates (25 cm-side quadrat plots). Each burrow within the quadrat was excavated and all males were collected, identified according to their species and had their carapace width (CW) and major claw length (MCL) measured in millimeters (mm). Mean density estimates showed that *L. leptodactyla* and *L. uruguayensis* occur in mixed populations, with *L. leptodactyla* (80.6 ± 21.8 individuals/m^2; mean ± standard deviation) living in higher density than *L. uruguayensis* (14.6 ± 4.3 individuals/m^2; Student's *T*-test $T10 = 8.93$, $P = 0.0001$). CW and MCL differed between males of each species; *L. leptodactyla* ($N = 161$) CW (8.09 mm ± 1.11 mm) and MCL (14.83 mm ± 3.44 mm) were larger than *L. uruguayensis* (N = 161) CW (7.34 mm ± 1.07 mm; Student's *T*-test: $T320 = 8.435$, $P = 0.0001$) and MCL (11.78 mm ± 2.91 mm; Student's *T*-test: $T320 = 6.169$, $P = 0.0001$).

2.2. Dear enemy effect

To test fight intensity and duration between familiar resident–neighbor and unfamiliar resident–stranger opponents, we evaluated naturally occurring fights. We observed male-male encounters between conspecific and heterospecific intrusions of neighbors and strangers in resident territory. Fights were categorized according to combat type (resident–neighbor/resident–stranger) and opponent type (same species fights; “conspecific”/between-species fights, “heterospecific”). Thus, resident–neighbor fight types were: (1) *L. leptodactyla* × *L. leptodactyla* ($N = 22$); (2) *L. leptodactyla* × *L. uruguayensis* ($N = 22$). The experimental design for resident–stranger fights was set in the same way: (3) *L. leptodactyla* × *L. leptodactyla* ($N = 22$); and (4) *L. leptodactyla* × *L. uruguayensis* ($N = 22$). Although the study was entirely observational, we removed outlying data of claw size difference (CSD) between opponents to control for the size effect in each fight type category. See Table 1 for male MCL in each fight type category.

Fight components used in this study were based on Booksmythe et al. (2010a). We only used physical components, namely: 1 – touch/

Table 1
Mean ± standard deviation of opponent’s major claw length (MCL) within each fight type category. The results of the comparison between opponents are showed in the same line.

Experimental group	Opponent type	Major claw length (mm)		Student's *T*-test	
		Resident	Neighbor	*T* statistic	*P* value
Resident–neighbor	Conspecific	15.52 ± 2.60	16.75 ± 1.92	T42 = −1.757	0.08
Resident–neighbor	Heterospecific	15.42 ± 3.37	14.00 ± 2.57	T42 = 1.572	0.12

Experimental group	Opponent type	Major claw length (mm)		Student's *T*-test	
		Resident	Stranger	*t* statistic	*P* value
Resident–stranger	Conspecific	13.80 ± 3.38	15.62 ± 2.86	T42 = −1.922	0.06
Resident–stranger	Heterospecific	12.71 ± 2.63	12.54 ± 2.44	T42 = 0.225	0.82

push: a crab used the major claw to hit an opponent; 2 – grapple: crabs interlocked their claws pushing or pulling each other; 3 – flick: a crab turned or tossed the opponent through interlocking or grabbing the external part of the claw or; 4–dig out: when a resident moved back into the burrow followed by the opponent trying to widen the burrow entrance. Movements like touching/pushing are common and may not necessarily inflict any kind of damage to opponents; these were considered low-intensity components. Grappling is a transitioning movement associated with fight persistence, and may inflict injuries or claw loss; this was considered a medium-intensity component (Callander et al., 2012). On the other hand, flicking and digging out were classified as high-intensity components. Flicking is a finalization movement, because males which are flicked a few centimeters away usually give up the fight, whereas digging out is an aggressive attempt to evict a crab from the burrow (Booksmythe et al., 2010a; Jennions and Backwell, 1996).

Fights were observed during semi-diurnal low tides throughout the entire cycle until the high tide reached the observation area. We searched for active resident–neighbor pairs on the sediment surface or strangers moving through the population until they fought a resident. Encounters were observed from approximately 1.5 m away so to not disrupt focal pair behavioral responses. We observed fights from the initial moment the first component was used, and we finished observing when the focal pair stopped fighting and distanced themselves (± 5 cm). To avoid any motivation effect (mating cycle, early or late tidal exposure period and circadian rhythm), fight types were randomly observed without repetition of the same category.

After each encounter ceased, fight duration was obtained. Normally, in resident–stranger fights, combat only ended when the stranger stole the burrow or abandoned the fight. Then, we considered as winners males that owned the burrow at the end of the fight. In resident–neighbor fights, these judgments were not possible since each crab generally returned to its own burrow. We collected both males to identify their species and to take MCL measurements using calipers. There was no manipulation during fight observations to avoid detrimental effects.

2.3. Statistical analysis

In our four fight pairs (one per fight type category), outliers were removed to control the size effect between opponents. We used the CSD between opponents and removed individuals data when CSD values were outside of the mean range of values for which two standard deviations were added or subtracted and the residual values were higher or lower than 2.5% of the distribution (Wilkinson et al., 1996). Additionally, Student's T-tests were used to compare the opponents MCL within each fight type category (see Table 1 for more details).

We analyzed the effects of combat type and opponent type on fight intensity and duration using generalized linear mixed models (GLMMs); R packages *glmmADMB* (Skaug et al., 2013) and *lme4* (Bates et al., 2015). As for the dependent variable, we used the count data of low-intensity (touch/push), medium-intensity (grapple), and binary responses of the high-intensity components (flick/dig out) and analyzed them separately in a different set of models. Combat type (two levels: resident–neighbor and resident–stranger fights) and opponent type (orthogonal to combat type, two levels: conspecific and heterospecific fights) were fitted as fixed effects. To account for aggressiveness and motivation variation biases, we used the Fight ID as a random effect. Low- and medium-intensity count data were fitted to a Poisson distribution with a log link function, and the overdispersion parameter was checked in the final models. High-intensity components were fitted to the binary part of the data set (presence/absence) to a binomial distribution with a logit link function to identify which factors affected their occurrence in the fight. Fight duration models were fitted to a gamma distribution with a log link function. We used the same random and fixed factors that were set in the models above. Size is an important determinant of fight intensity and duration for fiddler crabs (Jennions and Backwell, 1996; Morrell et al., 2005), so we tested whether opponents CSD as a covariate could have any effects on the response variables. We used five potential candidate models that included as fixed factors; (1) the two main effects (combat type, opponent type); (2) the three main effects (combat type, opponent type, CSD); and models with (3) two main; or (4) the three main effects and their all multiple combinations; and (5) another model structure with the combat type and opponent type main effects and their interactions versus CSD (See Supplementary material Appendix 1 Table A1 for more details). We compared these models using Akaike information criterion (AIC) and selected the model with the lowest ΔAIC difference. We provide results from the model with the lowest AIC, where was pretended to be a best estimated model (Burnham and Anderson, 1998). Where relevant, post-hocs for all comparisons at different levels between factors were performed via the *multcomp* package (Hothorn et al., 2008) with Tukey contrasts and false discovery rate (FDR) adjustment for multiple comparisons.

Pearson correlations were used between MCL of residents and their opponents to test size-assortative fighting. Regarding resident–stranger fights, we used Fisher's exact test to compare proportions of winners because of the small sample sizes. All statistical tests were two-tailed and considered significant when $P < 0.05$.

2.4. Ethical note

All procedures were conducted in agreement with the Brazilian legislation and under a license to conduct studies in conservation units from the Comissão Técnico-Científica, Instituto Florestal (COTEC; protocol number 260108–002.036/2014).

3. Results

We tested whether CSD or their interaction term between fixed factors was important in the final models. As they were not relevant to explain low-, medium-intensity components and the fight duration across fight type categories, we did not use them. The best-fit model for low-intensity components based on ΔAIC comparison included: combat type factor + opponent type factor + Fight ID as random effect (AIC = 468.3, Supplementary material Appendix 1 Table A1). There was no difference in touch/push movements employed between resident–neighbor (low-intensity: 241 occurrences in 44 fights) and resident–stranger fights (low-intensity: 207/44) (combat type effect; $Z = 0.90$, $P = 0.36$, Fig. 1a). On the other hand, conspecific fights employed more touching and pushing (low-intensity: 277/44) than heterospecific fights (low-intensity: 171/44) (opponent type effect; $Z = -2.44$, $P = 0.01$, Fig. 1b).

The model that best fitted medium-intensity component included: combat type factor + opponent type factor + Fight ID as random effect (AIC = 252.6, Supplementary material Appendix 1 Table A1). Males were more likely to grapple each other in resident–stranger (medium-intensity: 80/44) than resident–neighbor fights (medium-intensity: 27/44) (combat type effect; $Z = -3.77$, $P = 0.0001$, Fig. 2a), with conspecific opponents (medium-intensity: 76/44) grappling more than heterospecific opponents (medium-intensity: 31/44) (opponent type effect; $Z = -3.08$, $P = 0.002$, Fig. 2b).

The best model of high-intensity components included: combat type factor + opponent type factor + CSD + combat type factor × CSD + opponent type factor × CSD + Fight ID as random effect (AIC = 76.7, Supplementary material Appendix 1 Table A1). Males were more likely to flick or dig out their opponents in resident–stranger (high-intensity: 53/44) than resident–neighbor fights (high-intensity: 1/44) (combat type effect; $Z = -2.15$, $P = 0.03$, Fig. 3a). Furthermore, there was no difference between number of flick/dig out movements employed between conspecific (high-intensity: 27/44) and heterospecific (high-intensity: 27/44) opponents (opponent type effect;

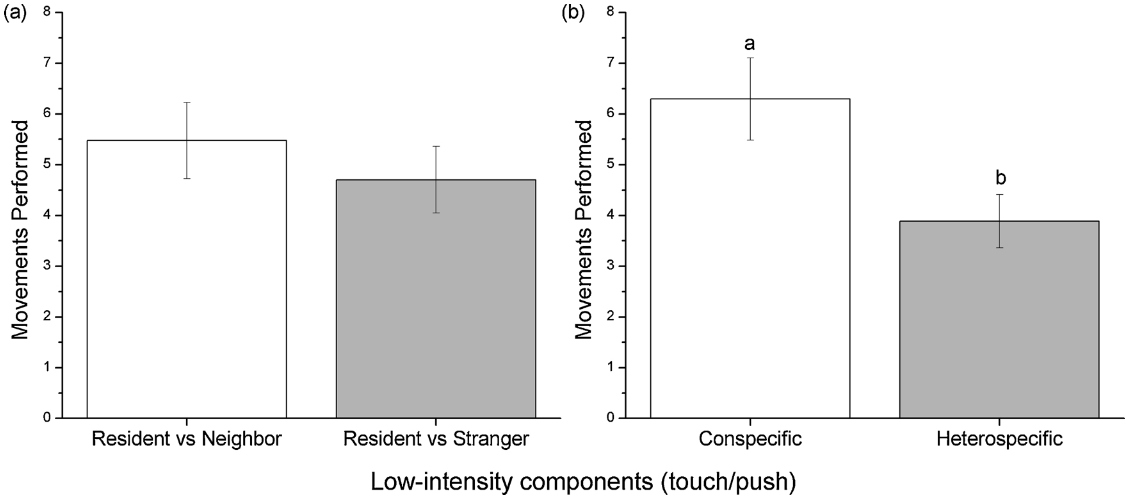

Fig. 1. Mean ± standard error (SE) of low-intensity components (touch and push movements) employed in; (a) resident-neighbor (N = 44) and resident-stranger fights (N = 44), and (b) between conspecific (N = 44) and heterospecific fights (N = 44). Statistical differences are represented by different lowercase letters. Note: The figure vertical axis is scaled from 0 to 8.

$Z = 1.73$, $P = 0.08$, Fig. 3b). The CSD effect ($Z = -0.08$, $P = 0.93$) their interaction with combat type ($Z = 1.29$, $P = 0.19$), nor opponent type ($Z = -1.81$, $P = 0.06$) explained the occurrence of high-intensity components.

In the fight duration, the model that fit better included: combat type factor + opponent type factor + combat type factor × opponent type factor + Fight ID as random effect (AIC = 856, Supplementary material Appendix 1 Table A1). Interaction between combat type × opponent type was statistically significant (combat type × opponent type effect; $Z = 2.19$, $P = 0.02$). Conspecific resident–stranger fights took longer (119.99 ± 26.79 s) than heterospecific resident–stranger fights (32.04 ± 4.98 s; $Z = -2.69$, $P = 0.04$, adjusted P value, FDR method, Fig. 4). There was no difference in duration between conspecific resident–stranger (119.99 ± 26.79 s) and conspecific resident–neighbor fights (32.53 ± 4.64 s; $Z = -2.31$, $P = 0.06$), nor between heterospecific resident–neighbor fights (40.85 ± 6.33 s; $Z = -1.90$, $P = 0.11$). There was no difference in duration between conspecific resident–neighbor (32.53 ± 4.64 s) and heterospecific resident–neighbor fights (40.85 ± 6.33 s; $Z = 0.28$, $P = 0.78$), nor between heterospecific resident–stranger fights (32.04 ± 4.98 s; $Z = -0.27$, $P = 0.78$). There was no difference in fight duration between heterospecific resident–neighbor (40.85 ± 6.33 s) and heterospecific resident–stranger fights (32.04 ± 4.98 s; $Z = 0.55$, $P = 0.78$).

Fighting was size assortative. Opponents MCL was correlated with both conspecific (Pearson correlation r20 = 0.44, $P = 0.03$) and heterospecific (Pearson correlation r20 = 0.59, $P = 0.003$) resident–neighbor fights, and between conspecific (Pearson correlation r20 = 0.42, $P = 0.04$) and heterospecific (Pearson correlation r20 = 0.57, $P = 0.005$) resident–stranger fights. To assess how fights affected the chance of a resident win (which contributes to overall fitness), we compared resident winning proportion between resident–stranger fight type categories. Overall, residents showed no difference in winning ratio when fighting against conspecific (13 victories in 22 fights) or heterospecific strangers (16/22) (Fisher's exact test: $P = 0.52$).

4. Discussion

We found that the dear enemy effect occured in both conspecific and heterospecific fights in fiddler crabs. In resident–stranger fights, medium and high-intensity movements were more likely to be used

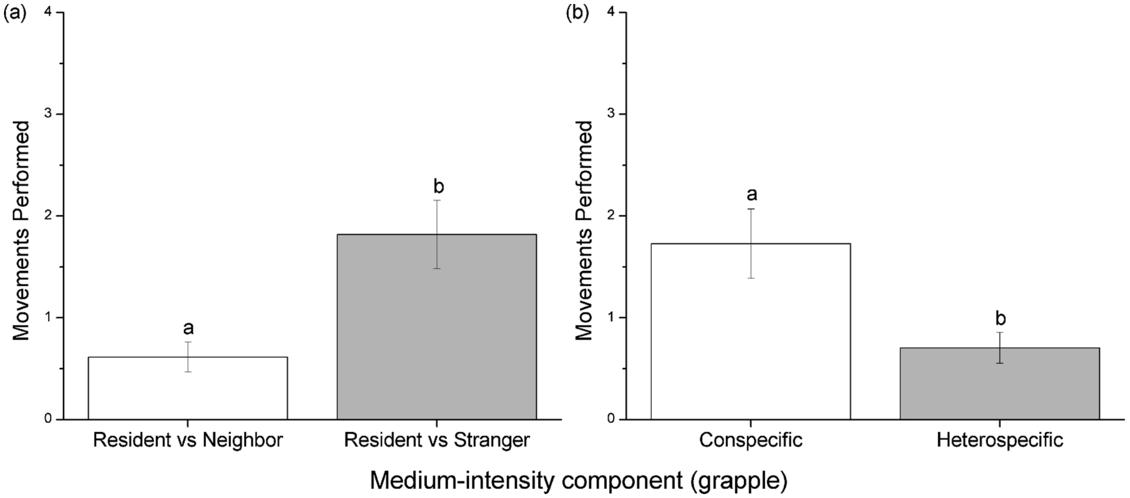

Fig. 2. Mean ± SE of medium-intensity component (grapple movement) employed in; (a) resident-neighbor (N = 44) and resident-stranger fights (N = 44), and (b) between conspecific (N = 44) and heterospecific fights (N = 44). Statistical differences are represented by different lowercase letters. Note: The figure vertical axis is scaled from 0 to 4.

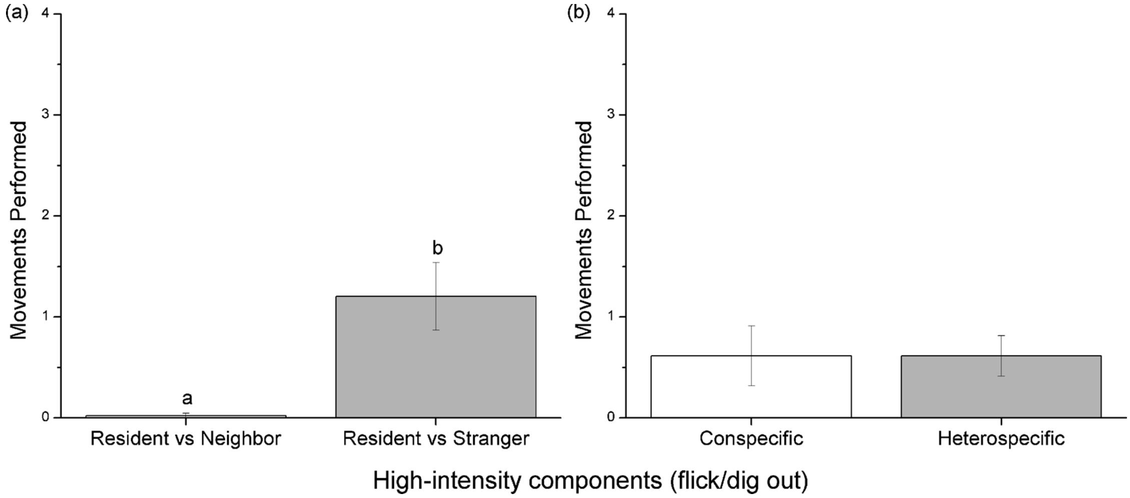

Fig. 3. Mean ± SE of high-intensity components (flick and dig out movements) employed in; (a) resident-neighbor (N = 44) and resident-stranger fights (N = 44), and (b) between conspecific (N = 44) and heterospecific fights (N = 44). Statistical differences are represented by different lowercase letters. Note: The figure vertical axis is scaled from 0 to 4.

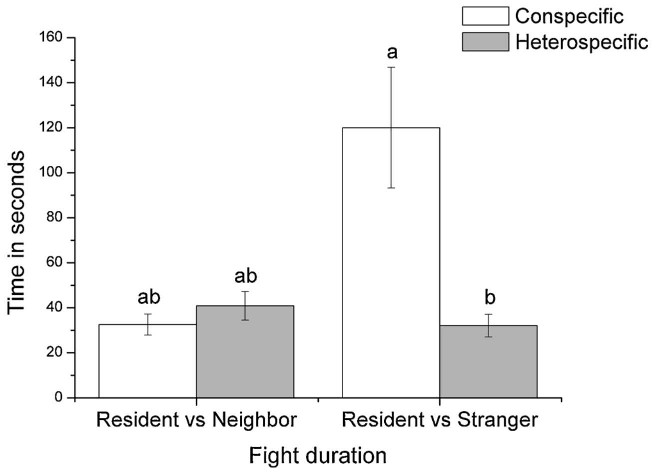

Fig. 4. Mean ± SE of fight duration between conspecifics and heterospecifics resident-neighbor and resident-stranger fight type categories (N = 22). Statistical differences are represented by different lowercase letters.

than in resident–neighbor fights, regardless of stranger species. Fights between conspecifics included a greater number of low- and medium-intensity movements than with heterospecific opponents, irrespective of combat type. Additionally, conspecific resident–stranger fights took longer than heterospecific resident–stranger fights, indicating a higher risk to the resident. These results give us a broader view of this issue (see also: Booksmythe et al., 2010a; Pratt and McLain, 2006) and provide support to established coexistence between fiddler crab species in mixed colonies.

Resident–stranger pairs escalated more medium- and high-intensity components than resident–neighbor pairs. Additionally, by controlling the CSD effect across our experiment, we showed that differences in combat type were not biased by size difference between opponents, but by the threat each one represents across fight type categories. These responses may be an indicative of burrow value to residents. The burrow involves “multipurpose” functions (as predicted by Temeles, 1994), such as; refuge during high tide (Jennions and Backwell, 1996), protection against bird predation and desiccation (Allen et al., 2012; Koga et al., 1998), as well as mating grounds (Ribeiro et al., 2010). After negotiating and establishing territorial borders around the burrow, resident–neighbor fights may occur by expansion of feeding areas or to disrupt neighbor efforts (e.g. waving displays) to attract females (Pratt and McLain, 2006). Therefore, escalation to more intense aggressive movements is unnecessary in resident–neighbor fights, as losing the fight to a neighbor will cause fewer negative effects. Contrary to that, movements like grappling and flicking are likely to inflict injuries, such as propodus damage or major claw loss if the fight persists (Booksmythe et al., 2010a; Callander et al., 2012) whereas digging out involves time and energy expenditure (Booksmythe et al., 2010a). Thus, escalation to aggressive components in resident–stranger fights may occur because the burrow is of crucial importance, and strangers are motivated to fight and persists to access the resident's territory (Booksmythe et al., 2010a). Interestingly, residents defended their territories vigorously regardless of stranger species, elucidating that threats imposed by strangers are the same across conspecific and heterospecific intrusions.

Conspecifics used more low- and medium-intensity components than heterospecifics, regardless whether fights were against a neighbor or a stranger. In this context, studies have shown that fiddler crabs may use their carapace, major claw coloration (Detto, 2007; Detto et al., 2006) or ritualized species-specific waving displays (Perez and Backwell, 2017) as cues to differ between conspecific or heterospecific mates. We believe it is possible that these cues could be used by residents to assess conspecific-heterospecific identity, and evaluate threats to their fitness over territorial competition. Males may invest more in conspecific aggression avoiding wasting time and energy repelling heterospecifics as they pose no threat for mates (Booksmythe et al., 2010b). Therefore, avoiding any conspecific opponent type closer to the territorial borders may turn residents more conspicuous to females and increase their mating opportunities. Alternatively, fight intensity could be context-dependent of the competitor's relative abilities and strategies. For instance, both the sequence and quantitative contribution of movements employed in *Minuca pugnax* and *L. pugilator* conspecific fights differ in resident–stranger combat and between species (Hyatt and Salmon, 1978). This suggests the number of movements employed in conspecific or heterospecific fights could be shaped by the nature of the fight style of each opponent species when fighting for resources.

Fights were size-assortative across all combat types, similar to previous studies on fiddler crabs (Booksmythe et al., 2010a; Morrell et al., 2005). This suggest that residents may judge size-matched neighbors as a higher threat, since much smaller or larger neighbors may not interfere with their activities when compared to an equal ability neighbor. Similarly, strangers may look for size-matched residents to get a new territory. Fighting much smaller residents means that strangers would spend time suiting the burrow (e.g. enlarging or excavating) to their own size (Fayed et al., 2008). Furthermore, in previous studies, fight duration increased between two size-matched opponents and decreased as CSD between opponents increased, e.g. fights between a larger versus smaller opponent (Morrell et al., 2005). Following our results, conspecific resident–stranger fights took longer than heterospecific resident–stranger fights. We showed that the MCL size did not have any effect on fight duration, since we controlled the CSD between opponents. This result shows that time spent by residents in repelling size-matched conspecific strangers is consistent with a higher threat posed by this category in the dear enemy context. However, despite the greater difference in time expenditure, there were no clear advantages to resident fitness in fighting against conspecific or heterospecific strangers once the chances of residents winning against conspecific or heterospecific strangers were the same. Therefore, both conspecific and heterospecific strangers should not be neglected as inferior competitors when the resident's territory is at stake.

Resident–stranger fights were more intense irrespective of opponent type. In this context, it has been suggested that residents may assess neighbor/stranger status through behavioral cues (Pratt and McLain, 2006). Given the course of opponent actions, residents must retaliate according to opponent threat level or persistence (Booksmythe et al., 2010a). For instance, in *L. pugilator*, it was observed that resident–stranger fights were usually initiated by strangers employing grappling movements and quickly changed to more intense movements, whereas resident–neighbor fights began with major claw displays and transitioned to less intense movements, such as touching (Pratt and McLain, 2006). Based on this evidence, it is possible that resident defensive responses were consistent according to combat type. Although such patterns require careful conclusions, our observations bring valuable results on the threat posed by intrusions of different competitors to fiddler crab residents.

In summary, we showed evidence of dear enemy relationship between conspecific and heterospecific fiddler crab species living in mixed populations. Competition against conspecifics was more intense, since we predicted that heterospecifics did not compete for females, but this possibility needs further investigation. Our work, however, did not discriminate whether movements were employed by resident or opponent male. Low interference between heterospecifics was previously shown in other studies with birds (Matyjasiak, 2005), fishes (Lehtonen et al., 2010) and ants (Tanner and Adler, 2009). Nonetheless, this is the first study demonstrating comparative differences in fight intensity and duration within and between size-matched fiddler crab species in a dear enemy context. Residents appeared to balance the costs of territorial defense with opponent motivation, fight strategies and self-fitness risks represented by conspecifics and heterospecifics. Living in mixed-colonies may provide differences in intensity, number of movements and time for residents to repel conspecific and heterospecific intrusions into their territories.

Acknowledgments

We are grateful to A.L. Arvigo, F.R. DeGrande, L.F. Natálio, M. Citadin, R. de Carvalho, R. de O. Rodrigues, P.J. Jimenez, P. Granado and J.C.F. Pardo for their assistance during fieldwork. This work was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), with financial support granted to T.M. Costa (2010/09763-9) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – PIBIC/Unesp to B.R. Fogo (30930).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.02.001.

References

Allen, B.J., Rodgers, B., Tuan, Y., Levinton, J.S., 2012. Size-dependent temperature and desiccation constraints on performance capacity: implications for sexual selection in a fiddler crab. J. Exp. Mar. Biol. Ecol. 438, 93–99. https://doi.org/10.1016/j.jembe.2012.09.009.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 361–373. https://doi.org/10.18637/jss.v067.i01.

Booksmythe, I., Jennions, M.D., Backwell, P.R.Y., 2010a. Investigating the “dear enemy” phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. Anim. Behav. 79, 419–423. https://doi.org/10.1016/j.anbehav.2009.11.020.

Booksmythe, I., Jennions, M.D., Backwell, P.R.Y., 2010b. Interspecific assistance: fiddler crabs help heterospecific neighbours in territory defence. Biol. Lett. 6, 748–750. https://doi.org/10.1098/rsbl.2010.0454.

Briefer, E., Rybak, F., Aubin, T., 2008. When to be a dear enemy: flexible acoustic relationships of neighbouring skylarks, *Alauda arvensis*. Anim. Behav. 76, 1319–1325. https://doi.org/10.1016/j.anbehav.2008.06.017.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Callander, S., Bolton, J., Jennions, M.D., Backwell, P.R.Y., 2012. A farewell to arms: Males with regenerated claws fight harder over resources. Anim. Behav. 84, 619–622. https://doi.org/10.1016/j.anbehav.2012.06.017.

Clark, H.L., Backwell, P.R.Y., 2017. Territorial battles between fiddler crab species. R. Soc. Open Sci. 4, 160621. https://doi.org/10.1098/rsos.160621.

Crane, J., 1975. Fiddler crabs of the world. Ocypodidae: Genus *Uca*. Princeton University Press, Princeton, NJ, USA.

Detto, T., 2007. The fiddler crab *Uca mjoebergi* uses colour vision in mate choice. Proc. R. Soc. B Biol. Sci. 274, 2785–2790. https://doi.org/10.1098/rspb.2007.1059.

Detto, T., Backwell, P.R.Y., Hemmi, J.M., Zeil, J., 2006. Visually mediated species and neighbour recognition in fiddler crabs (*Uca mjoebergi* and *Uca capricornis*). Proc. R. Soc. B 273, 1661–1666. https://doi.org/10.1098/rspb.2006.3503.

Fayed, S.A., Jennions, M.D., Backwell, P.R.Y., 2008. What factors contribute to an ownership advantage? Biol. Lett. 4, 143–145. https://doi.org/10.1098/rsbl.2007.0534.

Grangier, J., Le Breton, J., Dejean, A., Orivel, J., 2007. Coexistence between *Cyphomyrmex* ants and dominant populations of *Wasmannia auropunctata*. Behav. Processes 74, 93–96. https://doi.org/10.1016/j.beproc.2006.10.009.

Heinze, J., Foitzik, S., Hippert, A., Hölldobler, B., 1996. Apparent dear-enemy phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi*. Ethology 102, 510–522. https://doi.org/10.1111/j.1439-0310.1996.tb01143.x.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometric. J. 50, 346–363. https://doi.org/10.1002/bimj.200810425.

Husak, J.F., Fox, S.F., 2003. Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. Anim. Behav. 65, 391–396. https://doi.org/10.1006/anbe.2003.2058.

Hyatt, G.W., Salmon, M., 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: a quantitative analysis. Behaviour 65, 182–211. https://doi.org/10.1163/156853978X00602.

Jaeger, R.G., 1981. Dear enemy recognition and the costs of aggression between salamanders. Am. Nat. 117, 962–974. https://doi.org/10.1086/283780.

Jennions, M.D., Backwell, P.R.Y.Y., 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. Biol. J. Linn. Soc. 57, 293–306. https://doi.org/10.1111/j.1095-8312.1996.tb01851.x.

Koga, T., Backwell, P.R.Y., Jennions, M.D., Christy, J.H., 1998. Elevated behaviour predation risk and courtship changes in a fiddler mating crab. R. Soc. 265, 1385–1390. https://doi.org/10.1098/rspb.1998.0446.

Langen, T.A., Tripet, F., Nonacs, P., 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. Behav. Ecol. Sociobiol. 48, 285–292. https://doi.org/10.1007/s002650000223.

Lehtonen, T.K., McCrary, J.K., Meyer, A., 2010. Territorial aggression can be sensitive to the status of heterospecific intruders. Behav. Processes 84, 598–601. https://doi.org/10.1016/j.beproc.2010.02.021.

Lehtonen, T.K., Wong, B.B.M., 2017. Males are quicker to adjust aggression towards heterospecific intruders in a cichlid fish. Anim. Behav. 124, 145–151. https://doi.org/10.1016/j.anbehav.2016.12.013.

Leiser, J.K., 2003. When are neighbours ‘dear enemies’ and when are they not? The responses of territorial male variegated pupfish, *Cyprinodon variegatus*, to neighbours, strangers and heterospecifics. Anim. Behav. 65, 453–462. https://doi.org/10.1006/anbe.2003.2087.

Li, Y., Wang, J., Metzner, W., Luo, B., Jiang, T., Yang, S., Shi, L., Huang, X., Yue, X., Feng, J., 2014. Behavioral responses to echolocation calls from sympatric heterospecific bats: Implications for interspecific competition. Behav. Ecol. Sociobiol. 68, 657–667. https://doi.org/10.1007/s00265-013-1680-9.

Martin, P.R., Martin, T.E., 2001. Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology 82, 189. https://doi.org/10.1890/0012-9658(2001)082[0189:EAFCOS]2.0.CO;2.

Matyjasiak, P., 2005. Birds associate species-specific acoustic and visual cues: recognition of heterospecific rivals by male blackcaps. Behav. Ecol. 16, 467–471. https://doi.org/10.1093/beheco/ari012.

Mohamad, R., Wajnberg, E., Monge, J.P., Goubault, M., 2015. The effect of direct interspecific competition on patch exploitation strategies in parasitoid wasps. Oecologia 177, 305–315. https://doi.org/10.1007/s00442-014-3124-2.

Morrell, L.J., Backwell, P.R.Y., Metcalfe, N.B., 2005. Fighting in fiddler crabs *Uca mjoebergi*: what determines duration? Anim. Behav. 70, 653–662. https://doi.org/10.1016/j.anbehav.2004.11.014.

Ochi, H., Awata, S., Kohda, M., 2012. Differential attack by a cichlid fish on resident and non-resident fish of another cichlid species. Behaviour 149, 99–109. https://doi.org/10.1163/156853912X629139.

Palphramand, K.L., White, P.C.L., 2007. Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. Anim. Behav. 74, 429–436. https://doi.org/10.1016/j.anbehav.2006.10.026.

Perez, D.M., Backwell, P.R.Y., 2017. Female preferences for conspecific and heterospecific wave patterns in a fiddler crab. J. Exp. Mar. Biol. Ecol. 486, 155–159. https://doi.org/10.1016/j.jembe.2016.09.018.

Pratt, A., McLain, D.K., 2006. How dear is my enemy: intruder–resident and resident–resident encounters in male sand fiddler crabs (*Uca pugilator*). Behaviour 143, 597–617. https://doi.org/10.1163/156853906776759501.

Ribeiro, P.D., Daleo, P., Iribarne, O.O., 2010. Density affects mating mode and large male mating advantage in a fiddler crab. Oecologia 164, 931–941. https://doi.org/10.1007/s00442-010-1801-3.

Roux, O., Rossi, V., Céréghino, R., Compin, A., Martin, J.M., Dejean, A., 2013. How to coexist with fire ants: the roles of behaviour and cuticular compounds. Behav. Processes 98, 51–57. https://doi.org/10.1016/j.beproc.2013.04.014.

Sanches, F.H.C., Costa, T.M., Barreto, R.E., Backwell, P.R.Y., 2018. The cost of living in mixed species populations: a fiddler crab example. J. Exp. Mar. Biol. Ecol. 500, 30–33. https://doi.org/10.1016/j.jembe.2017.12.010.

Skaug, H.J., Fournier, D.A., Nielsen, A., Magnusson, A., Bolker, B.M., 2013. Generalized Linear Mixed Models Using AD Model Builder. R Package Version 0.7.7.

Tanner, C.J., Adler, F.R., 2009. To fight or not to fight: context-dependent interspecific aggression in competing ants. Anim. Behav. 77, 297–305. https://doi.org/10.1016/j.anbehav.2008.10.016.

Temeles, E.J., 1994. The role of neighbours in territorial systems: when are they “dear enemies”? Anim. Behav. 47, 339–350. https://doi.org/10.1006/anbe.1994.1047.

Tynkkynen, K., Kotiaho, J.S., Luojumäki, M., Suhonen, J., 2006. Interspecific territoriality in *Calopteryx* damselflies: the role of secondary sexual characters. Anim. Behav. 71, 299–306. https://doi.org/10.1016/j.anbehav.2005.03.042.

Tynkkynen, K., Rantala, M.J., Suhonen, J., 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. J. Evol. Biol. 17, 759–767. https://doi.org/10.1111/j.1420-9101.2004.00733.x.

Wilkinson, L., Blank, G., Gruber, C., 1996. Desktop Data Analysis SYSTAT. Prentice Hall PTR, Upper Saddle River, NJ, USA.