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Fighting off the intruder: context-dependent territory defence in the damselfish *Stegastes fuscus*

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Abstract Dusky damselfish (*Stegastes fuscus*) behaviour was investigated under natural and controlled conditions to evaluate how territory and familiarity affect aggressive behaviour. In the natural environment, fish occupies territories of 2.74 ± 1.3 m^2 and the most frequent behaviours exhibited were monitoring swimming, feeding, shelter occupation and agonistic interactions. Larger-territory individuals spend more time in monitoring swimming than smaller-territory ones, which results in a reduction of food intake. Agonistic interactions were more frequent with heterospecifics than conspecifics. Whenever agonistic interaction occurred, confrontations were not frequent. Territorial behaviour in the lab was evaluated considering two variables: prior residence and familiarity between conspecific opponents. Resident fish invested more against intruders irrespective of the intruder's identity (familiar or unfamiliar). When no previous territory was established, *S. fuscus* showed lower aggressive behaviour, and it was even lower when a familiar fish was the opponent. Data from the field and the lab suggest that *S. fuscus* territoriality and aggression are related to the size of the defended area and the competitor's identity. Thus, reduced reef areas may result in increased interindividual aggression, while the intruders' recognition may be a key trait controlling agonistic behaviour in the reef community where *S. fuscus* is inserted.

Keywords Territory · Social behaviour · Recognition · Aggression · Dusky damselfish

Introduction

Territorial behaviour is characterized by the establishment and defence of a specific area against possible intruders and competitors, a significant determinant of social organization in several fish groups (Noble 1939; Maher and Lott 1995; Grant 1997; Myrberg and Thresher 1974; Alwany et al. 2005). The adaptive value of territoriality derives from the exclusive use of available food resources and land areas, including refuge and breeding sites (Grant 1997). Whatever the main reason for territorial defence, resource availability adds value to the defended area (Robertson 1996). The owner of the territory spends a lot of time and energy patrolling the area (Eurich et al. 2018; Robles et al. 2018). When encounters with invading individuals occur, animals use many strategies, which vary according to the defended site and competitor's potential assessment (Steger and Caldwell 1983; Marden and Waage 1990; Eshel and Sansone 1995).

Damselfish are a diverse group that a great major occurs in tropical shores, especially in reef environments (Frederich and Parmentier 2016, Pratchett et al.

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2016). Many damselfish species establish territories around rock or coral shelters where they maintain filamentous algal turfs (Hixon and Brostoff 1983; Hata and Ceccarelli 2016). Their farming behaviour affects other herbivorous-fish diet patterns (Jones 1992), and the structure of the benthic (Gibson et al. 2001; Hata and Kato 2006; Ceccarelli 2007) and coralline communities (Wellington 1982). These areas (algae and small invertebrates associated) are their primary food source but are also used to attract mates and hold eggs. The size of the territory seems to vary between owners, usually following a compromise between time and energy invested in maintaining and defending the area and benefits obtained from it (hiding spots, dietary needs, and spawning sites) (Jan et al. 2003; Silva et al. 2009). Due to the high investment in farming the territories, damselfish actively defend it from intruders, mainly from herbivorous fish and invertebrates (Hattori and Shibuno 2013; Irving 2019).

The intruder identity is a crucial feature driving agonistic behaviour, as those that present similarities in diet and territorial requirements represent more significant threat (Eurich et al. 2018; Robles et al. 2018). Low-cost strategies are used when intruders pose little threat, but signs and agonistic displays escalate as the threat increases (Smith and Parker 1976; Enquist et al. 1990). However, in subsequent encounters, identifying the individuals whom one has interacted before may lessen the intensity of aggression (Hsu et al. 2006). For instance, territorial species have been shown to react more aggressively toward unfamiliar conspecific than neighbours, (Stoddard et al. 1991; Fox and Baird 1992; Bee and Gerhardt 2001; Frostman and Sherman 2004; Briefer et al. 2008; Saeki et al. 2018). One explanation relies on the invaders' recognition, which leads to a dear enemy effect (Temeles 1994; Itzkowitz and Leiser 1999; Leiser 2003; Briefer et al. 2008; Carazo et al. 2008). In this case, territorial fish can recognize neighbours and reduce aggression toward them when territory borders are established, but it is still aggressive to strangers (Sogawa and Kohda 2018). However, territory owners may assume an opposite strategy and behave aggressively towards familiar neighbours to reduce chances of territory invasion and resource taking, a phenomenon called nasty neighbour effect and the opposite of the dear enemy effect (Christensen and Radford 2018). Although there is evidence that damselfish discriminate against the level of the threat imposed by invaders of its territory (Irving 2019), the hypothesis that territory size and intruder's recognition affect aggressive outcomes was not tested.

Here we used a species of damselfish, the dusky damselfish *S. fuscus, to approach how familiarity influences territory defence. S. fuscus* (Cuvier, 1830) is an endemic Brazilian species found in shallow, coral, or rocky bottoms and near the shore in most reef ecosystems (Ferreira et al. 2004; Pugh 2005). Individuals exhibit marked territoriality and highly aggressive behaviour to protect food sources and shelters (Robertson 1996; Ferreira et al. 1998; Menegatti et al. 2003). Adult *S. fuscus* are monomorphic solitary individuals, males and females display territorial behaviour and dominance, spending time to protect its territory from other fish (Menegatti et al. 2003; Pugh 2005). When young, *S. fuscus* show bright blue spots on a grey body, while adults are dark brown and may show purple dots on the head during the breeding season (Souza et al. 2007). Males guard and aerate the eggs adhered to the substrate after breeding (Breder and Rosen 1966). Although they are ubiquitous to the Brazilian coast, there are only a few studies regarding territoriality (Osorio et al. 2006; Aued 2012) and agonistic interrelationships in *S. fuscus* (Menegatti et al. 2003). Given its importance to the reef community, and the lack of information on the factors that modulate this animal's behavioural responses, here we investigate the aggressive response of *S. fuscus* related to territory size and intruders identity (conspecifics vs. heterospecifics) in its natural environment, and tested the effects of territoriality and familiarity on aggressive behaviour in the laboratory. Due to vast areas occupied by these animals in the reefs, it is common to observe them monitoring the territories and displaying aggressive behaviour. Thus, we hypothesized that the bigger the territory the higher the aggressive behaviour against unknown individuals, and expected this response is decreased by the fish's ability to recognize individuals whom it has previously met.

Materials and methods

Natural environment sampling

Studied area

The study was performed at Buzios beach (Fig. 1), located on the southern coast of Rio Grande do Norte State, at Nísia Floresta, Brazil. The beach is formed by

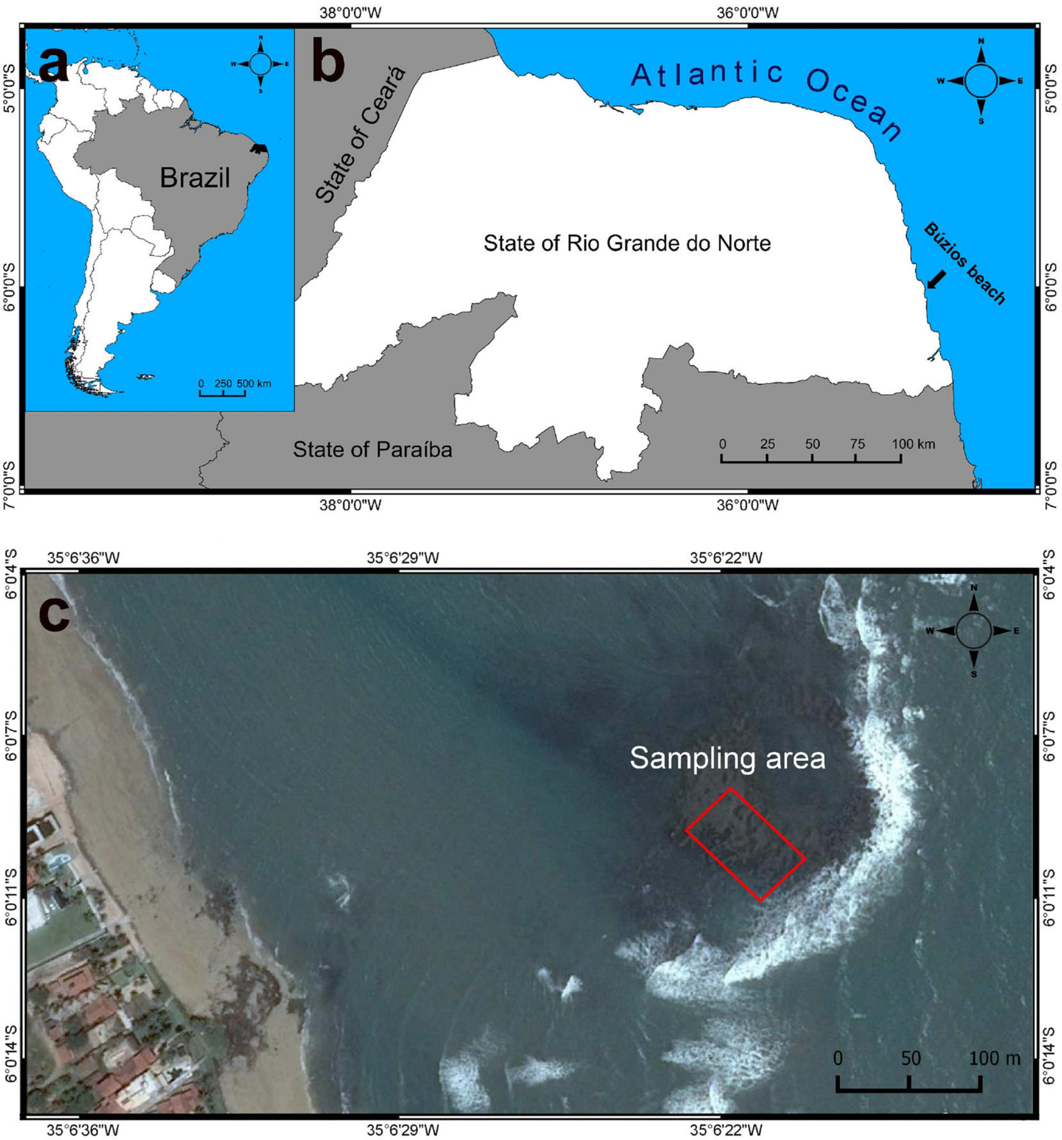

Fig. 1 **a** Map of the study location (Latitude: 6°0′10.17"S; Longitude: 35°6'20.81"W), South America, Brazil, Rio Grande do Norte, **b** Rio Grande do Norte, Buzios Beach, **c** Satellite image of the observation sampling area (georeferenced image)

sandstone reefs, composed mainly of quartz sand, organic fragments, and iron oxide (Manso 2003). The reefs are found in parallel to the coast and mostly covered by macroalgae, zoanthid (*Palythoa sp*. and *Zoanthus sp*.), and stony coral species *Siderastrea stallata* (Canan 2007).

Behavioural recordings

Adult *S. fuscus* ($n = 17$) were observed by free diving (snorkelling) in areas up to 170 cm depth. Fish activities were recorded using an underwater video camera (GoPro Hero3 Silver Digital). The observations/ video recordings were made from 07:00 to 12:00 only at low tide amplitude (between 0.0 m and 0.3 m). The subjects were randomly selected and after habituation to the observer (usually 5 min, 1.5 m from the animal shelter), each fish's behaviour was video recorded for 30 min. The camera was mounted on a PVC tripod, with the observer positioned behind the camera. *S. fuscus* were not classified according to sex because they are monomorphic even in the breeding season (Souza et al. 2007).

The study area was divided into sectors sampled daily in order to avoid resampling individuals. The video recordings were observed to identify behavioural repertoire and the most frequent behaviours exhibited (Table 1).

Territory size estimation

The distance travelled by fish was used to evaluate territory size. The four most distant points of the area used by each animal were marked with a coloured iron weight and the distances formed by every 2 distal points were measured with a measuring tape (modified from Aued 2012). The average value was used to calculate the circular area (area = $\pi.r^2$, according to Crosby and Reese 1996).

Controlled condition sampling

General procedures

One hundred and fifty-two *S. fuscus* were collected with a cast net (3 m diameter; 10 mm mesh size) from tide pools at Búzios beach (6°03′25"S and 35°05′53"W), Nísia Floresta, Rio Grande do Norte State, Brazil, as authorised by the Brazilian Institute of Environment and Natural Resources (IBAMA Licence Number 41869/2013; SISBIO number 5462480). The fish were immediately stored in 30-L tanks containing seawater and air stones to maintain a high oxygen level.

The fish were transferred to holding tanks (100 × 30 × 30 cm; 90 L) at the Fish Laboratory, Department of Physiology and Behavior, Federal University of Rio

Table 1 Behavioural inventory of damselfish (*Stegastes fuscus*) observed in its natural environment ($n = 17$)

Behaviour	Description
Feeding/food intake	Food intake (bite and swallow), excluding the search for food.
Threaten	Next to the intruder, the fish bristles the dorsal fin and expands the pelvic anal fins. During this display, the colour of the body may also change.
Bilateral attack	The fish bites the lateral part of the intruder's body and passes above or below them, attacking again on the other side of the body. The movement is fast and can occur several times in succession.
Side attack	The fish opens its mouth and bites the intruder's body, closing it upon contact. These attacks are focused on the medial side of the body, the belly, back, fins or the head of the intruder. The attacker positions its mouth perpendicular to the intruder 's body, pushing it.
Medial attack	The fish bites the mediolateral part of the intruder's body, describing a semi-circular path along the horizontal axis of its body.
Brief frontal confrontation	Two fish juxtapose their jaws and one of them pushes the other, or both mutually push in quick movements, one towards the other.
Long frontal confrontation	Similar to the brief frontal confrontation, but the interaction is maintained for more than 3 s.
Side by side confrontation	Two fish orient side by side with their heads in the same direction or, more often, in opposite directions, curling the body vigorously. While one moves its body, the other can attack the distal portion of the opponent's anal or dorsal fin.
Shelter occupation	The fish remains in the shelter.
Front display	Two fish position their mouths frontally, maintaining it open or closed, without contact. Then they undulate their bodies. This usually precedes the frontal confrontation.
Lateral display	The fish approaches an intruder laterally and opens its mouth without touching them. This behaviour may result in an attack.
Monitoring swimming	The fish randomly swims through the territory without any specific focus.
Keeping guard over the intruder	The fish closely observes another animal that is swimming and feeding in its territory. There are no signs of threatening or agonistic interactions between them. Usually observed between different tropic classes.
Tail bite	The fish bites the intruder's tail, usually approaching from behind.
Wave	The fish curls its body in the anterior to posterior direction while positioned next to the intruder.
Threatening wave	The intruder exhibits rapid and intense body curling that leads to the aggressor being repelled.
Resting	The fish stays in one place while maintaining some fin movement.
Chasing	The fish follows the intruder as it swims away. This behaviour may culminate in attacks on the intruder.
Territory theft	After a series of agonistic interactions, the original owner of the territory is expelled and another fish takes possession of the shelter and foraging area.
"Tourbillion"	A rapid circular movement(s) around the intruder in order to generate an intense disturbance around the fish, without touching it. The intruder (at the centre of the disturbance) loses its position in the water column and becomes disoriented.

Grande do Norte (UFRN). Each tank was divided into 10 small compartments and received 10 fish, each in a closed space. Glass walls between individuals prevented aggressive behaviour and deaths, however, the tanks system allowed visual, acoustic, and olfactory contact between them. Every four tanks formed a closed recirculating water system, in which water was kept aerated and filtered (mechanical, chemical, biological, and UV light filters), maintained at 28 ± 1 °C. Saltwater was previously prepared (Red Sea Salt, Red Sea, Houston, USA) and salinity was maintained at 36 ppt. The room light cycle was set at 12/12-light/dark, with lights on at 07:00. Fish were kept under the above-described conditions for 1 month before behavioural tests.

Fish were fed twice a day ad libitum with frozen *Artemia salina*, shrimp paste and dried food pellets (algae-based tetra marine salt granules). All animal procedures complied with the Ethics Committee for Animal Use of the Federal University of Rio Grande do Norte (CEUA 056/2014).

Five days before testing, individual weight and length were measured. The experimental tanks (40 × 30 × 25 cm) were filled with water under the same conditions as the stocking system and maintained with constant aeration via air stone. These tanks were wrapped with white paper to prevent fish visual contact with external stimuli from the laboratory, keeping only the front wall uncovered for behavioural recording. A camera was attached to a tripod placed 1.5 m away and in front of the tank. Fish were allowed to acclimate to the experimental tanks, and behaviour was then recorded. After the experimental tests, all animals were returned to the natural environment (Búzios beach) from where they were collected.

Experimental design

To evaluate the effects of established territory and conspecific recognition on agonistic interactions in *S. fuscus*, four experimental conditions were designed, and all experimental phases were recorded for subsequent behavioural analysis. Briefly, some fish were allowed to be residents in the experimental tank to establish territory, and then resident and non-resident fish were paired to a conspecific for the first interaction. Fish were separated and re-paired after 24 h with the same fish they faced (known conspecific) or with a different fish (unknown conspecific). Each experimental group is described below:

(a) Territoriality and familiarity (T-F; n = 14 pairs) In order to allow fish to establish residence, 14 animals were isolated in the experimental tanks for 48 h. During this period, fish were able to explore the tank and use a clay tile placed in one of the tank's corners as a refuge. Animals were fed as per the stock system. After this period, the experimental tank was divided into two compartments by an opaque glass partition and the resident animal was restricted to the refuge side. A conspecific intruder was then introduced into the other half of the tank (similar size and weight: Length Coefficient of Variation (LCV) = 0.03 ± 0.02 cm and Weight Coefficient of Variation (WCV) = 0.12 ± 0.12 g). Neither the resident nor the intruder had previously confronted each other. The animals were separated for two minutes, and then the partition was gently removed to allow contact between them. Their behaviour was recorded for 10 min and the intruder fish was moved to its compartment in the stock system. On the following day (after 24 h), the same procedure was repeated and the conflict occurred again between the same pair of fish (known animals), which was recorded for 10 min.

(b) Non-territoriality and familiarity (NT-F; n = 14 pairs) In this experimental group, the animals were not allowed to establish residence in the experimental tank. On the first day, one fish was placed in each half of the tank (previously separated by an opaque partition) and acclimated for 2 min. Next, the partition was removed and the interaction between the animals was recorded for 10 min. The encounter was observed by the experimenter who made notes regarding which fish was displaying aggressive behaviour and assuming a more dominant position, and which fish was avoiding the fight and assuming a more submissive posture. It was also observed fish body colour (winners become darker while losers become paler) and the position of the fish in the tank (winners occupy the bottom area while losers stay close to the water surface) at the end of the encounter. After that, a blind experimenter observed the videos searching for the same characteristics and determined the winner and loser again. In all cases, the blind observations matched the first observations. Animals were then transferred from the tank to their compartments in the stock system to prevent territory establishment. On the following day, the same procedure was repeated, and the conflict occurred with the same individuals (known animal). The fish exhibited similar size and weight (LCV = 0.01 ± 0.02 cm and WCV = 0.18 ±

0.14 g). The interactions were recorded for 10 min. There was no refuge in the tank.

(c) Territoriality and unfamiliarity (T-UF; n = 16 pairs) This group's experimental procedure was similar to the one above (*T-F*), differing only on the second day. Twenty-four hours after the first confrontation, a second match occurred between the resident animal and an unknown conspecific (two different intruders, one for the first confrontation and another for the second). The fish were of similar size and weight (1st confrontation: LCV = 0.03 ± 0.02 cm and WCV = 0.11 ± 0.10 g; 2nd confrontation: LCV = 0.02 ± 0.02 cm and WCV = 0.12 ± 0.11 g). Once again, the behaviour was recorded for 10 min each day.

(d) Non-territoriality and unfamiliarity (NT-UF; n = 16 pairs) The experimental protocol for this group was similar to that of the NT-F group, however, at the end of the first encounter, fish were transferred to their compartments in the stock system and the behavioural recordings were analysed to determine the winner based on the number and type of agonistic displays, position in the tank and body colour. Behaviours were checked two times to determine the winner and loser, as described above. After 24 h of the first confrontation, a second encounter took place, in which the winner of the previous encounter faced an unknown conspecific (an animal not previously paired with any other). The fish used for each confrontation were similar in size and weight (1st confrontation: LCV = 0.02 ± 0.02 cm and WCV = 0.14 ± 0.12 g; 2nd confrontation: LCV = 0.02 ± 0.01 cm and WCV = 0.10 ± 0.09 g). Interactions were recorded for 10 min each day. There was no refuge in the tank.

Behavioural analysis

Video files were transferred and analysed using ZebTrack video tracking software (Pinheiro-da-Silva et al. 2016). The following parameters were quantified: frequency of agonistic displays, type and the total number of agonistic displays. Based on these data, the winner and loser of each encounter were determined. The most frequent agonistic displays were then individually evaluated for each animal in each group and the sum of all aggressive behaviours were considered for statistical analysis. The position of each fish was tracked to evaluate tank areas occupation; the tank was divided into four areas: upper-left quarter, lower-left quarter, upper-right quarter and lower-right quarter. For the territoriality groups, the refuge was located in the lower-left quarter.

Statistical analysis

For the field data, the behavioural frequencies showed normal distribution and were analysed by Simple Linear Regression (Pearson's correlation). The most common behaviours (dependent variable: monitoring swimming, food intake, agonistic interaction with heterospecifics) were correlated with territory size (independent variable). The regression between territory size and shelter occupation or number of confrontations with conspecifics was analysed using Spearman's correlation coefficient due to the non-normal data distribution. To evaluate the differences between agonistic interactions with conspecifics and heterospecifics slopes, we used ANCOVA considering as factor the fish identity (conspecific or heterospecific) and as covariate the agonistic interactions observed.

For the laboratory data, the coefficient of variation of weight and the standard length of the fish in each group were compared using the unpaired Student's t test. The behavioural data collected were compared between the individuals of each group using Two-Way RM ANOVA, considering as factors the encounter (1st or 2nd) and the individual identity (resident/winner or intruder/loser). Different types of agonistic interactions were compared between the two fish for every encounter by Student's t test. We also compared the winners' agonistic behaviour on the two encounters when fish had territory established versus without territory. For this comparison, we used Two-Way RM ANOVA considering territory and encounter as factors. The comparison between two fish in an encounter, focusing on single types of agonistic behaviour is shown in Table 2, and the statistical test used was unpaired Student's t test. Two-Way RM ANOVA compared occupation of the four areas of the experimental tank, considering individual identity and encounter as factors. When ANOVA results were significant, the post hoc comparison test of Tukey was performed.

We used SigmaStat 4.0 to run the analysis. In all cases, the statistical significance was set at $\alpha < 0.05$.

Table 2 Total number of the most common agonistic displays observed during *Stegastes fuscus* encounters

			Aggressive behaviour							
		Fish identity	Treats		Chases		Side attacks		Tail bites	
T-F	Day 1	Resident	1.79 ± 1.42	$p < 0.001$	12.50 ± 9.48	$p = 0.001$	12.93 ± 9.42	$p = 0.001$	3.57 ± 2.93	$p = 0.001$
		Intruder	0.07 ± 0.27		1.79 ± 2.78		1.07 ± 1.33		0.29 ± 0.83	
	Day 2	Resident	1.79 ± 2.49	$p = 0.25$	15.4 ± 11.3	$p = 0.01$	13.8 ± 12.31	$p = 0.01$	4.64 ± 6.08	$p = 0.02$
		Intruder	0.64 ± 2.13		4.21 ± 8.58		3.21 ± 8.82		0.57 ± 1.40	
T-UF	Day 1	Resident	4.13 ± 3.40	$p = 0.32$	12.06 ± 8.38	$p = 0.001$	11.7 ± 8.15	$p = 0.001$	3.75 ± 3.97	$p = 0.001$
		Intruder 1	1.25 ± 1.34		3.31 ± 3.63		1.44 ± 2.39		0.63 ± 1.09	
	Day 2	Resident	6.25 ± 3.55	$p = 0.7$	14.06 ± 8.40	$p = 0.007$	13.7 ± 9.41	$p = 0.014$	4.31 ± 2.57	$p = 0.02$
		Intruder 2	0.38 ± 0.89		1.94 ± 4.63		1.19 ± 3.53		0.19 ± 0.54	
NT - F	Day 1	Winner	1.73 ± 1.53	$p < 0.001$	16.1 ± 9.61	$p < 0.001$	9.13 ± 11.09	$p = 0.004$	2.80 ± 2.68	$p < 0.001$
		Loser	0.00 ± 0.00		0.40 ± 0.91		0.20 ± 0.77		0.00 ± 0.00	
	Day 2	Winner	1.87 ± 1.41	$p = 0.003$	11.6 ± 7.00	$p < 0.001$	4.53 ± 4.49	$p < 0.001$	1.60 ± 2.10	$p = 0.01$
		Loser	0.40 ± 1.06		0.27 ± 1.03		0.13 ± 0.35		0.00 ± 0.00	
NT -NF	Day 1	Winner	1.38 ± 1.15	$p = 0.85$	4.50 ± 3.27	$p < 0.001$	4.06 ± 3.23	$p < 0.001$	2.13 ± 2.36	$p = 0.004$
		Loser 1	0.63 ± 0.81		0.13 ± 0.34		0.75 ± 1.24		0.19 ± 0.75	
	Day 2	Winner	1.94 ± 2.72	$p = 0.901$	9.44 ± 10.70	$p = 0.45$	8.06 ± 10.78	$p = 0.63$	2.31 ± 2.75	$p = 0.55$
		Loser 2	1.79 ± 1.42		12.5 ± 9.48		12.9 ± 9.42		3.57 ± 2.93	

Groups of fishes observed: T-F: one fish had established territoriality and the same pair of fish was matched on both contests (familiarity on the second contest); T-UF: one fish had established territoriality and it faced a different conspecific in each contest (unfamiliarity); NT-F: none of the fish owned the territory and the same pair of fish was matched on both contests (familiarity on the second contest); and NT-UF: none of the fish owned the territory and the winner of the first contest was faced with a different conspecific on the second contest. Values are the number of the agonistic display presented by the fish ± SD. Beside each fish pair agonistic behaviour value there is the statistical significance (Student t test; p value) between fish behaviour (resident vs. intruder or winner vs. loser) within the encounter (same day)

Results

Natural environment sampling

The accumulated behaviour of 17 adult *S. fuscus* was recorded for 510 min. The most widely observed behaviours (Table 1) were monitoring for intruders, food intake, shelter occupation and agonistic interactions. The average territory size was $27{,}400 \pm 13{,}300\ \text{cm}^2$.

Territory size and monitoring were statistically significant, showing positive relationship, as demonstrated by the angular coefficient ($y = 66.9 + 0.032x$) and Pearson's correlation coefficient ($r = 0.54$, $p = 0.03$; Fig. 2a). Territory size and food intake were also statistically significant, but showed negative relationship according to the angular coefficient ($y = 27.64–0.05x$) and Pearson's correlation coefficient ($r = -0.68$, $p = 0.003$; Fig. 2b). There was no significant correlation between territory size and shelter occupation (Spearman $r = -0.23$, $p = 0.39$). Although territory size exhibited no correlation with aggressive behaviours against the total number of intruders (Pearson $r = 0.34$, $p = 0.15$; Fig. 2c), it was negatively correlated to conspecifics intruders (Spearman $r = -0.33$, $p = 0.016$; Fig. 2d), and positively correlated to heterospecifics intruders (Pearson $r = 0.47$, $p = 0.04$; Fig. 2d). The ANCOVA results indicate the differences between the two slopes (aggression against conspecifics and aggression against heterospecifics). There is a significant interaction effect between the factor identity (conspecific or heterospecific) and the covariate agonistic interactions ($F = 12.07$, $p = 0.002$). Thus, the comparison of the slopes is considered statistically significant, and the slopes coefficients are different.

Controlled condition sampling

Data analysis identified thirteen different agonistic displays during the encounters, differing in presence and frequency between the groups analysed. The most representative agonistic displays present in all four groups were threats, chases, side attacks and tail bites. The comparison between fish aggressive behaviours in each group is shown in Table 2.

The total number of agonistic behaviours is presented in Fig. 3. For the T-F group, Two-Way RM ANOVA

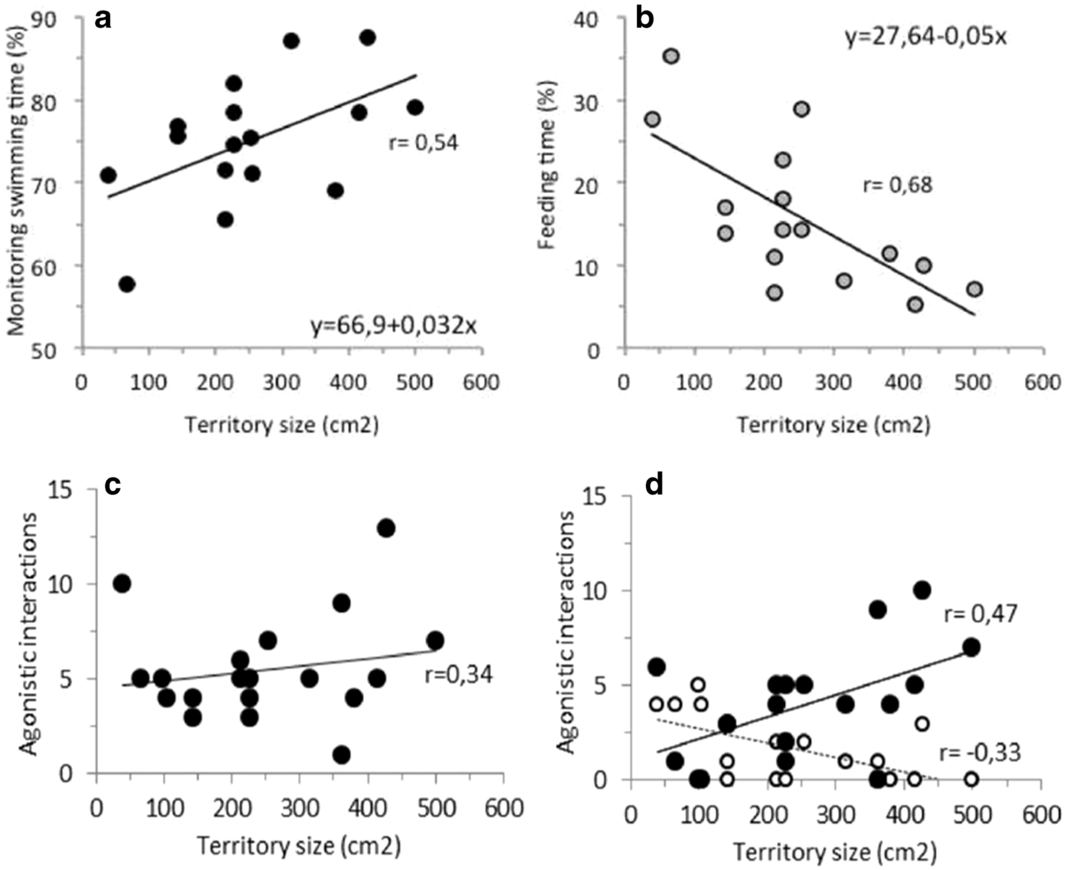

Fig. 2 Correlations between territory size, and **a** monitor swimming time (Pearson, $p < 0.05$), **b** feeding time (Pearson, $p < 0.05$). Correlation between territory size and the number of agonistic interactions by damselfish (*Stegastes fuscus*) in their natural environment based on 30 min in situ observation periods. **a** Total number of agonistic interactions (Pearson, $p > 0.05$) and **b** agonistic interactions against conspecifics, represented by white circles (dashed line; Spearman, $p < 0.05$) and agonistic interactions against heterospecifics, represented by black circles (full line; Pearson, $p < 0.05$)

found the main effect of individual identity (resident/intruder) ($F(1,26) = 18.82$, $p < 0.01$) to be significant, but the main effect of encounter (1st/2nd) ($F(1,26) = 1.23$, $p = 0.27$) was non-significant. The interaction terms identity × encounter ($F(2,26) = 0.08$, $p = 0.77$) was also found non-significant. Tukey test showed there were significantly higher agonistic displays exhibited by the resident during both the first and second encounters ($p < 0.05$; Fig. 3a).

For the NT-F group, in which no prior territory was established and the second match occurred between familiar individuals, Two-Way RM ANOVA revealed a significant effect of identity ($F(1,26) = 36.22$, $p < 0.01$) and encounter ($F(1,26) = 7.72$, $p = 0.01$). ANOVA also revealed a significant interaction term identity × encounter ($F(1,26) = 6.01$, $p = 0.021$). Tukey test showed a significantly higher number of agonistic displays by the winners in both the first and the second encounter and that the winner showed a significantly lower number of agonistic displays on the second encounter compared to the first encounter ($p < 0.05$; Fig. 3b).

For the T-UF group, Two-Way RM ANOVA showed a significant effect of identity ($F(1,30) = 52.17$, $p < 0.01$), but found the main effect of encounter non-significant ($F(1,30) = 0.43$, $p = 0.51$). ANOVA also revealed non-significant interaction term identity × encounter ($F(2,30) = 2.60$, $p = 0.11$). Tukey test showed no significant differences in the number of displays exhibited by the residents between day 1 and day 2, but resident fish showed a significantly higher number of agonistic displays than the intruder ($p < 0.05$; Fig. 3c).

For the NT-UF group, in which there was no resident animal and no familiarity during encounters, Two-Way RM ANOVA showed a significant main effect of the

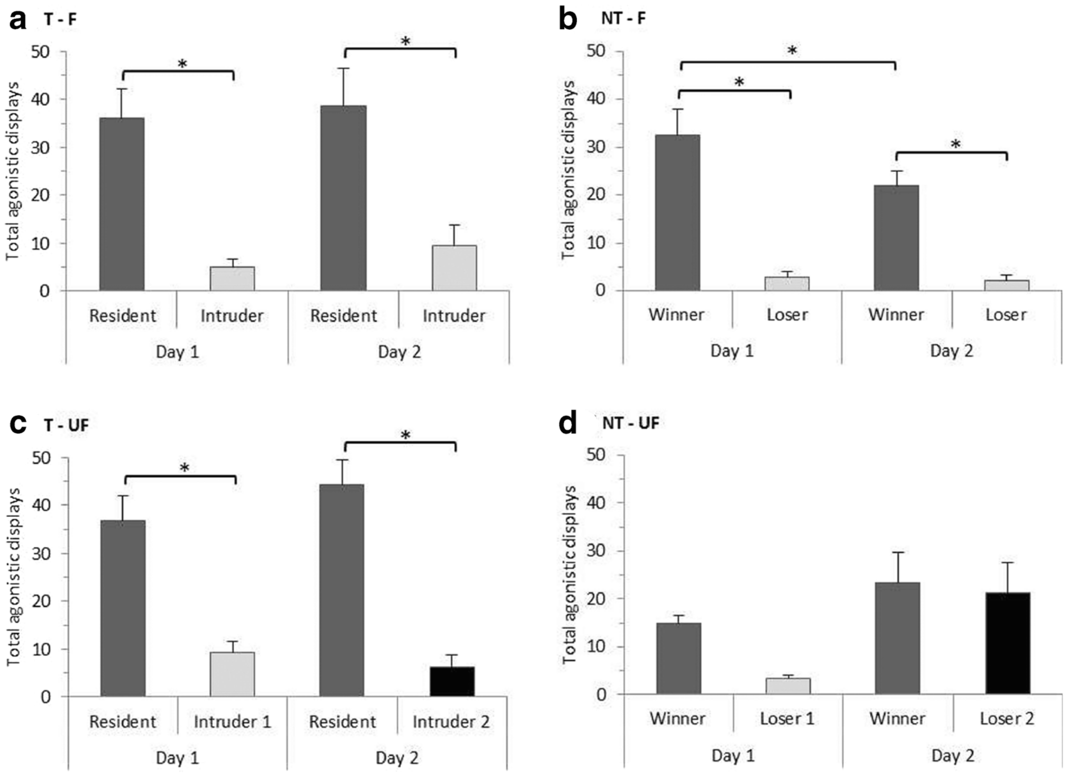

Fig. 3 Total agonistic displays during the first and second contests between pairs of damselfish *Stegastes fuscus*. **a** T-F: one fish had established territoriality and the same pair of fish was matched on both contests (familiarity on the second contest); **b** NT-F: none of the fish owned the territory and the same pair of fish was matched on both contests (familiarity on the second contest); **c** T-UF: one fish had established territoriality and it faced a different conspecific in each contest (unfamiliarity); and **d** NT-UF: none of the fish owned the territory and the winner of the first contest was faced with a different conspecific on the second contest. The asterisk indicates significance value on the comparison between resident vs. intruder or winner vs. loser or between day 1 and day 2 for the same fish (Two-Way ANOVA; p < 0.05)

encounter (F(1,30) = 9.31, $p = 0.005$), but found other main effects non-significant (F(1,30) = 1.94, $p = 0.17$). It also detected non-significant interaction terms identity × encounter interaction (F(2,30) = 1.24, $p = 0.27$). Tukey test confirmed that winner fish showed significant higher number of agonistic displays on day 1 ($p < 0.05$) but number of agonistic displays was non-significant between winner and loser on the second day ($p > 0.05$; Fig. 3d).

Comparison between the number of agonistic displays by the resident fish in the two conditions involving prior territory (T-F and T-UF), and the winning fish in the two conditions without territory (NT-F and NT-UF) showed a significant main effect of the territoriality (F(1,59) = 12.33, $p < 0.001$), but found a non-significant effect of encounter (F(1,59) = 0.61, $p = 0.43$). Two-Way RM ANOVA detected non-significant interaction terms territoriality × encounter interaction (F(1,59) = 1.19, p = 0.27). Tukey test indicates that residents (territorial) exhibited a significantly higher number of agonistic displays than the winners (non-territorial) during both the first and second encounters (p < 0.05; Fig. 4).

Concerning the animal occupation of the tank areas during encounters (appendix Fig. 5), it was found that area 1 was mostly occupied by the intruder than by the resident for the T-F group in the second encounter (Two-Way RM ANOVA: identity F = 4.08, $p = 0.04$; encounter F = 0.01, $P = 0.91$; identity x encounter F = 1.78, $p = 0.19$), while the occupation of area 4 and the lower area containing the refuge was higher for residents (Two-Way RM ANOVA: identity F = 17.68, $p < 0.001$; encounter F = 0.02, $P = 0.86$; identity x encounter F = 1.35, $p = 0.25$)). In the NT-F group, the losing animal remained significantly longer in areas 1 (Two-Way RM ANOVA: identity F = 5.96, $p = 0.02$; encounter F =

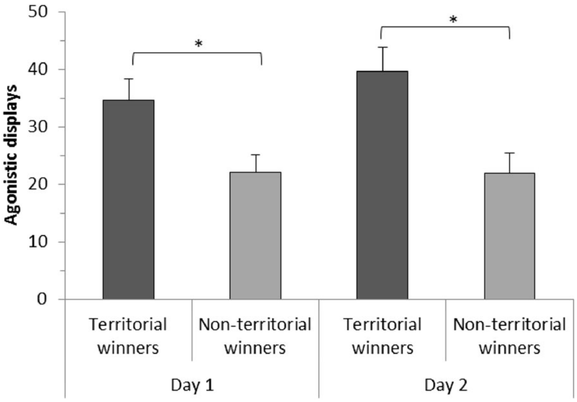

Fig. 4 Total number of agonistic displays emitted by winners that had established territory (T-F and T-UF, $n = 30$) and winners without territory (NT-F and NT-UF, $n = 30$) on the first and second contests. The asterisk indicates significance value (Two-Way ANOVA; $p < 0.05$)

0.55, $P = 0.46$; identity x encounter $F = 0.67$, $p = 0.41$)) and 2 (Two-Way RM ANOVA: identity $F = 15.89$, $p < 0.001$; encounter $F = 0.01$, $P = 0.93$; identity x encounter $F = 0.01$, $p = 0.97$)), which were the upper zones of the tank, compared to the winners of the two encounters. The winners used area 3 only on the first day of confrontation (Two-Way RM ANOVA: identity $F = 32.65$, $p < 0.001$; encounter $F = 0.19$, $P = 0.66$; identity x encounter $F = 0.01$, $p = 0.89$). For the T-UF group, the resident occupied mainly area 4 in the first encounter (Two-Way RM ANOVA: identity $F = 7.12$, $p = 0.01$; encounter $F = 0.14$, $P = 0.70$; identity x encounter $F = 0.05$, $p = 0.81$) and in the second encounter it remained longer in area 2 of the tank (Two-Way RM ANOVA: identity $F = 30.66$, $p = 0.01$; encounter $F = 4.59$, $P = 0.05$; identity x encounter $F = 4.08$, $p = 0.06$). The NT-UF group showed no difference in occupation during the encounters (Two-Way RM ANOVA, $p > 0.05$).

Discussion

S. fuscus establishes territories measuring 2.74 ± 1.3 m^2 on average. The bigger the territory, the higher the monitoring and fighting frequency and lower the feeding frequency in the natural environment. The identity of the intruder seems to influence agonistic behaviour. In nature, *S. fuscus* with vast territories present more aggressive behaviour against heterospecifics than conspecifics. At the same time, laboratory observations indicate territoriality is a significant factor that confers fighting advantages (i.e., to win encounters irrespective of the opponent identity) and that familiarity with the opponent is essential when there is no territory established.

Optimum territory size varies following the fish's body size (Jan et al. 2003), availability and abundance of food, and presence of potential competitors in the same area (Thresher 1976; Grant 1997). In a previous study conducted in the natural environment, *S. fuscus* was shown to occupy territories covering 1.37 m^2 (Aued 2012), an area smaller than that recorded in the present study. This difference may have derived from variations in resource exploitation among the individuals assessed, or from the 30-min observation trial period adopted here, which was significantly longer than the 5 min recorded by other researchers (Menegatti et al. 2003; Aued 2012). Larger territory size was negatively correlated with food intake and positively correlated with monitoring (Fig. 2).

Defending a large territory means more time spent monitoring for and expelling intruders, which may shorten the time devoted to other activities, such as feeding. Territory maintenance costs were also reported in other studies (Puckett and Dill 1985; Grant 1997; Cleveland 1999; Hsu et al. 2006; Silva et al. 2009; Eurich et al. 2018). However, benefits associated with the availability of food resources, the attractiveness of potential mates/substrate for laying eggs, and better shelter(s) seem to outweigh these costs (Grant 1997; Cowlishaw 2014). In this respect, the economic defensibility theory proposed by Brown (1964) reinforces the importance of territorial defence in *S. fuscus*, that is, despite being a costly behaviour, defending a territory guarantees certain benefits for individual success.

The territorial species tent to present intense aggressiveness (McCormick and Meekan 2007). Individuals aggressively defend their territories from species with similar trophic requirements (Cowlishaw 2014). Thus, conspecifics are usually their main competitors (Osorio et al. 2006). In the natural environment, we observed that *S. fuscus* aggressive displays were more frequent towards heterospecifics than conspecifics (Fig. 2d). As other authors have noticed, it indicates a preference for signalling territoriality in order to avoid embattles with potentially high-energy costs (Cleveland 1999; Menegatti et al. 2003), leading to the idea that *S. fuscus* recognize their conspecific neighbours and reduce aggression towards it while continues to defend the area from unknown intruders. This idea is supported by the dear enemy theory and was then tested in the laboratory under more controlled conditions.

Territorial and aggressive behaviour were observed in tanks, where animals that had previously established territory won encounters irrespective of familiarity with the intruders (T-F and T-UF groups; Fig. 3). Whereas *S. fuscus* is considered highly territorial, the previous residence increased the likelihood of victory in a territorial dispute. Similar results were obtained by Poulos and McCormick (2014) for other damselfish species. These data corroborate studies by Chellappa et al. (1999) and Switzer (2004), who suggest that previously established residence is an essential factor for a successful confrontation, what may be related to the resource value effect of each animal (*pay-off*), since the resident is usually more motivated to fight for its territory (Grant 1997; O'Connor et al. 2015). *S. fuscus* showed many high-energy expenditure behaviours, such as direct agonistic confrontations, as well as low to moderate energy expenditure behaviours involving chases (Table 2).

The contrasting results regarding aggressive displays between the natural environment and laboratory could be attributed to two reasons. First, territory size in the laboratory was greatly reduced, and it may have increased its importance to the owner. The resource value and the costs of losing the territory may have reinforced the resident-fish's agonistic investment, which corroborates findings from Svensson et al. (2012). The resident used a few threatening signals but a large number of high-energy strategies (side attacks and backbites), which are more effective in guaranteeing dominance. Hsu et al. (2006) proposed that a set of components may influence the choice of confrontation strategy; one of them is territory size. In this respect, it is worth noting that *S. fuscus* establish large territorial areas in nature (~2.74 m^2), and the occupation of less than 3% in the experimental tank (0.08 m^2) may have been a relevant factor for the most persistent territorial defence and increased aggressive behaviour. The second reason for the differences observed in the laboratory may rely on handling stress. The territorial fish (T-F and T-UF groups) were more aggressive than non-territorial ones, while NT-UF group showed highly reduced aggressive behaviour (Fig. 3). Handling fish between its home tank and the experimental tank may have affected the animal's response in the confrontation. Catching, netting and handling fish were shown to induce stress (Young et al. 2019), increase cortisol release (Barcellos et al. 2011) and decrease locomotion (Sopinka et al. 2016). A recent study from Bolognesi et al. (2019) showed that tactile stimulation reduced aggression in territorial fish, leading to fewer attacks in a confrontation. Thus, in the present study, handling *S. fuscus* may have affected the behavioural response observed during the agonistic encounter, causing a reduction of the intruder's motivation to attack (while resident did not suffer handling) and decreasing interactions when both fish (NT groups) were tested.

Although we cannot exclude handling stress effects, it was imposed for all treatments and variations in aggressive displays between familiar and unfamiliar groups may have derived from some level of opponent recognition. Agonistic levels were significantly lower when the encounter occurred between familiar competitors without previously established territory. The results obtained for NT-F and NT-UF groups show that winners exhibited less aggressive behaviour against a familiar fish (second confrontation), but winners paired with an unknown individual did not show significant differences in aggressiveness. This result corroborates the findings of Keeley and Grant (1993) and Earley et al. (2003), who showed low levels of aggression in confrontations between familiar animals, therefore suggesting animals recognize their partners.

Several studies have indicated that interindividual recognition may reduce combat costs (Miklósi et al. 1995, 1997; Pagel and Dawkins 1997; Saeki et al. 2018; Sogawa and Kohda 2018). Fish seem to form memories of the confrontation and its participants (Doutrelant et al. 2001; Hsu et al. 2006). It was shown that losers exhibit avoidance responses and physiological changes (increased ventilation rate and cortisol levels) when paired with dominant individuals (Miklósi et al. 1995; Morris et al. 1995; Johnsson 1997; Miklósi et al. 1997; O'Connor et al. 2000; Utne-Palm and Hart 2000).

For the NT-UF group, similar levels of aggressiveness were expected in the first and second encounters compared to the other groups. However, there was low agonistic investment by the winner during the first confrontation, and it did not change the pattern on the second confrontation even with the second intruder being more aggressive than the first one. It is known that naïve animals (not exposed to previous agonistic interaction) may face a better match than animals involved in recent combats (Hsu and Wolf 1999; Hsu et al. 2006). Moreover, previous experiences determine future behavioural decisions and, therefore, it seems that the winner of a low-intensity confrontation may act similarly in later confrontations, expecting to obtain the same benefits. However, in order to confirm this hypothesis, more studies that observe combatants signals/interactions, such as body and eye colouring, and chemical signs are needed, in addition to physiological measures that may help understand the status of each animal (cortisol, glucose, and testosterone levels).

In conclusion, the present study shows that territoriality is a determining factor in confrontation outcomes in *S. fuscus*, and that high-cost agonistic investment guarantees territorial conquest and maintenance. However, interindividual familiarity also influences the nature and results of agonistic interactions. This study contributes to a better understanding of the community's ecological and structural dynamics to which *S. fuscus* belongs. Nevertheless, additional studies addressing signalling processes, the effects of territory size and the investment needed to win a confrontation, among others, are also required for a thorough understanding of the social aspects of reef fish behaviour, which may ultimately lead to improved conservation policies for this and other reef fish species.

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Compliance with ethical standards

Ethical compliance All animal procedures complied with the Ethics Committee for Animal Use of the Federal University of Rio Grande do Norte (CEUA 056/2014).

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