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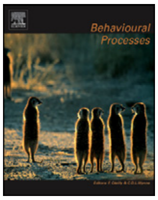

Prior residence and body size influence interactions between black sea urchins

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ABSTRACT

Body size and prior residence can modulate agonistic interaction in several animal species, but scientists know little about these relationships in echinoderms. In this study, we tested the effects of these traits on interactions in the black sea urchin (*Echinometra lucunter*). After a sea urchin was isolated for 24-h in a glass tank to establish prior residence, we introduced an intruder animal adjacent to the resident in the tank and observed interactions for 30 min. The intruder animal was larger, smaller, or size-matched to the resident. We found body size and prior residence concomitantly modulated interactions among black sea urchins, with prior residence as the major determinant. Black sea urchins mainly exhibited opponent inspection and fleeing responses during interaction to avoid fights, especially when a fight could be seriously disadvantageous (small intruder *vs.* large resident).

1. Introduction

Prior residence and body size commonly modulate aggressive encounters amongst individuals of the same species. Prior residence modulates aggressive encounters when the time an individual spends in a residence increases its odds of winning an aggressive encounter (Beaugrand and Zayan, 1985; Huntingford and Turner, 1987; Krasne et al., 1997; Barreto and Volpato, 2006a,b; Lopuch and Matula, 2008). The degree to which prior residence affects aggressive encounter success is positively related to factors such as an animal's familiarity with the area and fighting location (Beaugrand and Zayan, 1985). The resident advantage can also be due to a simple mechanical advantage of using the burrow during fights (Fayed et al., 2008). Resident animals tend to value a disputed area more than an intruder and, hence, may defend it more strongly (Smith and Riechert, 1984). Alternatively, an animal in search of a territory may inspect several resident animals and choose to fight with a weaker resident so as to conquer the territory (Grafen, 1987). Animal size influences the outcome of an aggressive dispute: the larger individual will generally dominate (Noble and Curtis, 1939; Turner and Huntingford, 1986; Frafjord, 1993; Berdoy et al., 1995; Chellappa et al., 1999; Jonart et al., 2007).

When territorial ownership and body size are concomitantly asymmetrical, the outcome of an aggressive dispute can differ from that of a dispute with one asymmetric trait. Turner (1994) shows that when small Mozambique tilapia (*Oreochromis mossambicus*) are intruders, they lose all aggressive paired encounters with larger resident tilapia; and when small tilapia are residents, they only lose half the aggressive encounters with larger intruders. In this example, prior residence overrides the effect of body size.

Although few studies address aggressive behaviour in echinoids, some identify residence effects in starfish (Woober, 1975) and sea urchins (Tsuchiya and Nishihira, 1985), including field observations of *Echinometra lucunter* (Grünbaum et al., 1978; Shulman, 1990) where resident animals were often the aggressors and usually succeeded in retaining their patch. The present study expands the paradigm of agonistic interactions in echinoids by addressing how body size and prior residence interact to determine the outcome of territorial disputes using controlled laboratory conditions in *E. lucunter*.

2. Materials and methods

2.1. Sea urchin holding and experimental tank conditions

We kept stock populations of the black sea urchin, *E. lucunter* (Linnaeus, 1758), for a maximum of three consecutive days inside an 80-L indoor plastic tank (56 cm × 35 cm × 41 cm) at approximately one animal per six liters of sea water, and nine animals per tank.

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Table 1
Mean (±S.D.) shell diameter of black sea urchins *Echinometra lucunter*.

Intruder size	Shell diameter (cm)		Difference (intr – res)
	Resident	Intruder	
Small	5.9 ± 0.15	4.9 ± 0.15	-0.98 ± 0.01^{a}
Size-matched	5.9 ± 0.17	5.9 ± 0.19	0.04 ± 0.04^{b}
Large	5.7 ± 0.31	6.8 ± 0.33	1.15 ± 0.06^{c}

Mean of differences between intruder and resident shell diameter that do not share a same letter is statistically different (ANOVA; $F_{(2,30)} = 104.3$; $P < 0.000001$).

We maintained water temperature at 24 °C, provided continuous aeration, and maintained 12 h of daylight.

At the start of the experiment, we placed each animal into its own glass aquarium (70 cm × 30 cm × 45 cm) within a 10 cm water column. We provided continuous aeration with an air stone that was connected to an air pump via plastic tubing, and maintained water temperature at approximately 24 °C.

2.2. *Experimental protocol*

To begin the experiment, we randomly selected sea urchins from the stock tank and isolated them inside their experimental aquaria for 24 h in order to establish prior residence. Next, we placed one intruder sea urchin into each experimental aquarium so that its spines were in contact with the spines of the resident. Finally, we registered the interaction and animal position in the tank for 30 min. We used three size classes based on differences in shell diameter between intruder and resident animals: intruder ≈1 cm smaller than resident, intruder ≈1 cm larger than resident, or intruder size-matched to resident ($n = 10$ each size class). We found "actual" differences between intruder and resident shell diameters within a size class to be statistically different among classes (Table 1), therefore verifying distinct differences among the animal size classes.

2.3. *Behaviour recording method*

To identify sea urchin position, we drew a 70 cm × 30 cm grid divided into 10 cm squares onto the bottom of each experimental aquarium. To evaluate a change in position, we registered the position of the animal in the grid every minute for a total of 30 min. Based on the methods of Thines and Vandenbussche (1966) and Jordão and Volpato (2000), we plotted sea urchin position on an *X*–*Y* axis. Mathematical analysis considered a set of 10 points per each resident and intruder sea urchin each 10 min. Thus, for each animal of the pairs of sea urchins, we collected 30 points in 30 min. The mean of the position on *X*-axis and the mean on *Y*-axis were the barycentric coordinates (calculated to each 10-min period along 30 min). From these data we evaluated (1) the distance between the intruder and the resident animals and (2) the dispersion of animals inside the aquaria. Dispersion is the mean distance between each position in the grid and its respective barycentre (the point at the centre of a system). As dispersion values increased, the movement of an animal throughout the aquarium became broader.

To measure sea urchin social interaction, we based on the ethogram of the aggressive behaviour of *E. lucunter* which we previously obtained from underwater observations of pairs in the field (Morishita, 2007). Aggressive behaviour in the ethogram mainly involved inspection responses between opponents, where agonistic interactions resulted in intruder removal and lack of agonistic interactions resulted in co-habitation. Agonistic encounters from the above study included pushing (most common) and biting, which have also been reported from underwater observations by Grünbaum et al. (1978) and Shulman (1990). Inspection responses were movement of spines and position of tube feet in relation to an opponent (retracted or extended in radial position, opposite to or directed to the opponent).

2.4. *Statistical analyses*

We used Shapiro–Wilk's test to assess data normality. Based on those results, we determined that data could be square-root transformed to improve homogeneity of variance needed for parametric analyses. We used a repeated measure one-way ANOVA to analyze the distances between intruder and resident (dependent variable) among size classes (independent variable) over time. We also used a repeated measures one-way ANOVA to analyze the dispersions (dependent variable) of intruder and resident (class factor) within each size classes over time. In both cases, we conducted post hoc comparisons with a Tukey's HSD test. We used Friedman ANOVA and post hoc Dunnett's multiple comparison tests to analyze temporal spine movement data, within each size class, and territorial ownership condition. We used a Wilcoxon test to analyze data of both spine movement and tube foot position between resident and intruder within each time interval and size class. We set statistical significance at $\alpha = 0.05$.

3. Results

The distance between intruder and resident significantly increased over time (Fig. 1; $F_{(2,54)} = 5.915$; $P = 0.0048$), but ANOVA showed neither a size class effect ($F_{(1,27)} = 0.080$; $P = 0.9232$), nor an interaction between time and size class ($F_{(2,54)} = 0.301$; $P = 0.8758$).

Dispersion within the small intruder size class was significantly higher for intruder, rather than resident, sea urchins, in all time intervals (Fig. 2; $F_{(2,36)} = 3.919$; $P = 0.0289$). Dispersion between intruder and resident did not differ in the size-matched class ($F_{(1,18)} = 1.456$; $P = 0.2431$) and the large intruder class ($F_{(1,18)} = 2.993$; $P = 0.1008$). Furthermore, we found no interaction between time and residence for size-matched intruders ($F_{(2,36)} = 1.227$; $P = 0.3052$) and larger intruders ($F_{(2,36)} = 1.120$; $P = 0.3375$). Dispersion values of intruders and residents, however, varied over time. They were lower in the 10–20 min time interval than in all other time intervals, for size-matched intruders ($F_{(2,36)} = 5.367$; $P = 0.0091$) and larger intruders ($F_{(2,36)} = 3.344$; $P = 0.0466$).

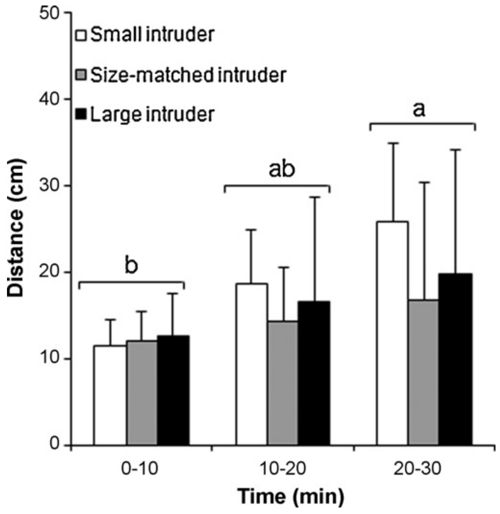

Fig. 1. Distance (mean ± S.D.) between intruder and resident of *Echinometra lucunter* over time. Different letters indicate statistically significant differences at $P < 0.05$ (repeated measures one-way ANOVA and post hoc comparisons with a Tukey's HSD test).