COMPETITIVE INTERACTIONS BETWEEN *DIADEMA ANTILLARUM* AND *TRIPNEUSTES VENTRICOSUS*

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Abstract: Both *Diadema antillarum* and *Tripneustes ventricosus* use coral and other hard substrate at the top of coral promontories at night, which may create a potential conflict for space. The purpose of this study was to first examine the potential for competition between *T. ventricosus* and *D. antillarum* for substrate at night. I tested this by establishing twenty transects and documenting the abundance and distribution of *D. antillarum* and *T. tripnesutes* day and night. *D. antillarum* and *T. ventricosus* were spatially segregated during the day; *D. antillarum* was found on reefs and *T. ventricosus* was found on sand and grass habitats. At night, *T. ventricosus* densities on top of reef promontories were highest when *D. antillarum* populations were lowest, and *T. ventricosus* densities on top of coral promontories were lowest when *D. antillarum* populations were highest. This suggested competition for hard substrate at night. Then, I determined whether *D. antillarum* competitively excluded *T. ventricosus* from these habitats. I hypothesized that *T. ventricosus* would behaviorally respond to manipulated densities of resident *D. antillarum*. After removing *D. antillarum*, the number of *T. ventricosus* migrating to the top of promontories increased significantly. My findings suggest that competition exists between *D. antillarum* and *T. ventricosus* for reef substrate at night, and that *D. antillarum* may potentially be excluding *T. ventricosus* from these habitats.

Key Words: aggression, competition, exclusion, lottery hypothesis, sea urchins

INTRODUCTION

The spiny sea urchin, *Diadema antillarum*, and the West Indian sea egg, *Tripneustes ventricosus*, are abundant tropical sea urchins that potentially compete with each other for space. In Discovery Bay, Jamaica, both species are found in a heterogeneous environment of discrete patches of coral heads and turtlegrass beds. Reef patches are a combination of live coral and coral rock eroded by *D. antillarum*.

These two species are spatially segregated during the day with *D. antillarum* occupying coral reefs and *T. ventricosus* occupying turtlegrass beds; however, both *D. antillarum* and *T. ventricosus* inhabit patches of hard substrate at night when *T. ventricosus* migrates into these habitats. Williams (1981) suggests that *D. antillarum* migrates to the tops of reefs at night to graze on damselfish algal lawns while these fishes are inactive. Tertschnig (1988) documented that *T. ventricosus* in the West Indies migrates to coral patches at night to escape predation from fish and night-active helmet conchs. However, both of these potential predators are rare in Discovery Bay. Regardless, *T. ventricosus* at Discovery Bay still migrates to rocky outcrops at night (personal observation), which presents a potential conflict between *D. antillarum* and *T. ventricosus*.

The purpose of this study was to (1) examine the potential for competition between *T. ventricosus* and *D. antillarum* for

surfaces at night, and (2) determine whether *D. antillarum* competitively excludes *T. ventricosus* from these habitats. If competition exists between *D. antillarum* and *T. ventricosus,* then the abundances of these two species should exhibit an inverse relationship. If competition can be demonstrated, we can also address a secondary corollary question: is the nature of this conflict consistent with competitive exclusion of *T. ventricosus* by *D. antillarum* at night? I assumed that *D. antillarum* is a better competitor than *T. ventricosus* because it is actively aggressive via pushing, biting, and waving its spines (Ferrie et al. 2003). Therefore, I predicted that the densities of *T. ventricosus* would increase when *D. antillarum* was completely removed.

METHODS

All observations and experiments were conducted in the back reef at Discovery Bay, Jamaica on 4 - 9 March, 2005. The study site covered an area of approximately 3000 m^2 and was located northwest of the marine laboratory (Fig. 1).

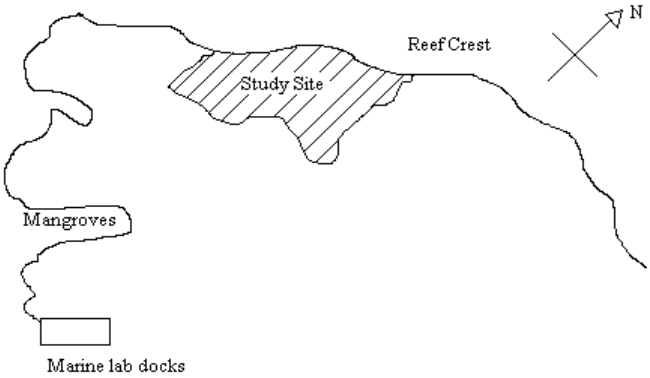

Figure. 1. Western end of Discovery Bay, Jamaica. All observational studies and experimental manipulations were conducted at the study site.

I. *Competition*

To test whether *D. antillarum* and *T. ventricosus* are spatially segregated during the day and use the same substrate at night, I established twenty 10 x 2 m belt transects in which all *D. antillarum* and *T. ventricosus* were counted both day and night. All transects were east-west, parallel to the reef crest, approximately 10 m from the reef crest at 1 - 2 m depth.

In each transect, I counted the total number of *D. antillarum* and *T. ventricuosus*, and the number of *T. ventricosus* up on coral and reef rock. At every 1 m interval, the substrate was categorized according to three habitat classes: 1) reef habitat: hard substrate with adequate hiding refuges for *D. antillarum*, 2) habitat dominated by *Thalassia testudinum* with little or no refuges, or 3) sand and rubble.

II: *Competitive Exclusion*

To determine whether the presence of *D. antillarum* competitively excludes *T. ventricosus* from reef substrate at night, I performed a removal experiment. Patches of coral and coral rock in the backreef provided discrete areas for removals of resident *D. antillarum*. From a total of 39 patches surveyed in day-night transects, 20 coral patches (3 x 3 m) were chosen randomly for this experiment. The size of each patch was standardized in both control and treatment groups. Each patch consisted of live coral and reef rock nested in a bed of turtlegrass or sand. Ten patches were randomly assigned as controls, and ten patches were manipulated. Control patches were areas with naturally occur-

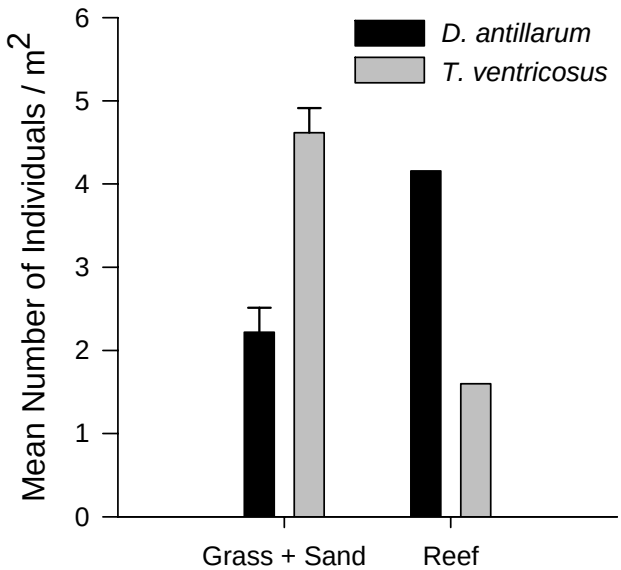

Figure 2. Day comparison of substrate preference in *Tripneustes ventricosus* and *Diadema antillarum*.

ring resident *D. antillarum* which I did not remove. Treatments were patches in which all *D. antillarum* were removed and placed at least 10 m away. I also monitored treatment patches daily and removed any *D. antillarum* there. I counted separately the total number of *T. ventricosus* surrounding the coral and coral rock, the number of *T. ventricosus* on top of the coral and coral rock, and the total number of *D. antillarum* in the patches for three consecutive nights.

RESULTS

I: *Competition*

The two-way ANOVA revealed that sea urchin abundances during the day were a function of the interaction between substrate type and species (2-way ANOVA, $F = 24.8$, df = 3, 36, $P < 0.0001$; Fig. 2). Total sea urchins (species were combined) were marginally more abundant on grass and sand substrate than on reef patches (2-way ANOVA, $F = 3.35$, df = 1, 36, $P = 0.0754$). There was no effect of species on abundance (2-way ANOVA, $F = 0.08$, df = 1, 36, $P = 0.78$).

At night, the number of *T. ventricosus* on the top of reef patches decreased proportionally with increasing numbers of *D. antillarum* ($r^2 = 0.57$, df = 1, 39, $P < 0.0001$; Fig. 3).

II: *Competitive Exclusion*

To determine the effects of *D. antillarum* removal on *T. ventricosus* usage on reef patches, I performed a one-way ANOVA comparing number of *T. ventricosus* on treatment v. control reefs. The number of *T. ventricosus* increased in patches when *D. antillarum* was removed compared to control groups ($F = 12.19$, df = 1, 18, $P = 0.00026$; Fig. 4).

DISCUSSION

Under natural conditions, high densities of *D. antillarum* were associated with low *T. ventricosus* densities. Experimental removals of *D. antillarum* from reefs of coral and coral rock at night resulted in significant increases in *T. ventricosus* on this space within 24 h. This provides strong evidence of competition for reef substrate between these two species of sea urchins at night, and suggests that this habitat type may be a limiting resource at night.

It is possible that urchin distributions may be influenced by priority effects.

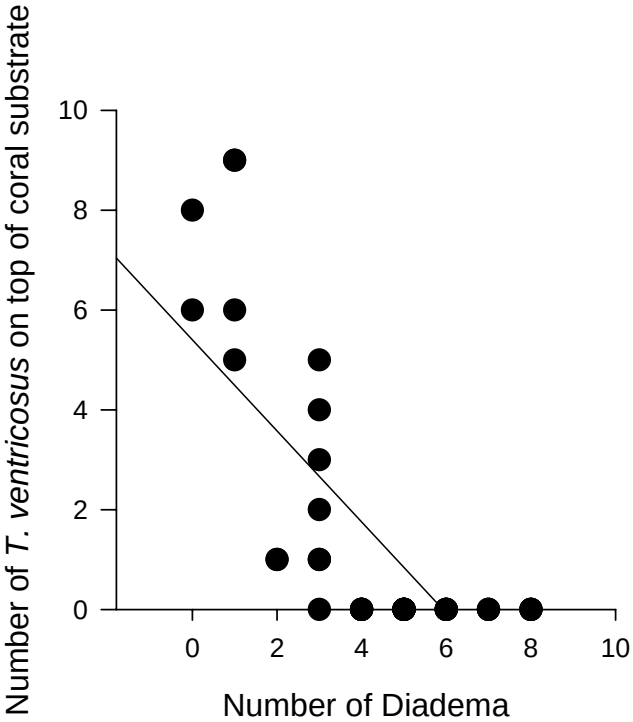

Figure 3. *Diadema antillarum* and *Tripneustes ventricosus* abundances on top of reef patches are inversely related (y = 5.40 – 0.91x).

One of the main assumptions of the lottery hypothesis is that vacant space is randomly colonized by organisms and randomly renewed as organisms die (Sale 1977, 1978). Since *D. antillarum* is found in reef patches during the day, *D. antillarum* may have an advantage simply because it is present on reef patches before *T. ventricosus*. This may explain why areas with high densities of *D. antillarum* have low densities of *T. ventricosus.* Recently, strong evidence of priority effects has been shown in similarly-sized gobies of different species on the Great Barrier Reef (Munday 2004). Munday attributed the coexistence of these coral-dwelling fishes to the priority effects of the lottery hypothesis. Therefore, it is possible that *D. antillarum* simply is able to secure and retain space on rocky outcrops excluding *T. ventricosus* which migrates away from the reef each day to forage in turtle-grass.

An alternative explanation is that *D. antillarum* may be physically superior to *T. ventricosus* in some way, thereby making it a superior competitor. *D. antillarum* may be competitively better because of its heavily armored body, its aggressive nature, and numerous long, thin, sharp spines. Though *T. ventricosus* bodies are larger than those of *D. antillarum* (approximately five centimeters greater), *D. antillarum* spines are double the length of *T. ventricosus* spines (Humann et al. 1997). The long spines of *D. antillarum* may deter *T. ventricosus* from venturing to outcrops when there are high densities of *D. antillarum*. In addition, Shulman (1990) found that *D. antillarum* exhibited biting and pushing behavior when placed next to an intruder. Studies between *T. ventricosus* and *D. antil-*

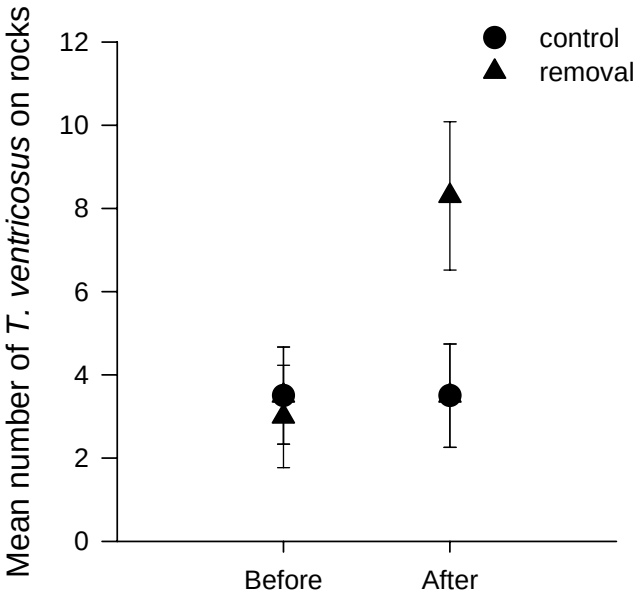

Figure 4. Comparison of *Tripneustes ventricosus* mean abundances on reef patches before removal experiment and after *Diadema* removal

larum have shown that *D. antillarum* is the more aggressive species (Ferrie et al. 2003). Therefore, *D. antillarum* most likely exhibits agnostic interactions with *T. ventricosus*. The attacks by *D. antillarum* may restrict *T. ventricosus* from the top of reefs at night.

Although my results provide strong evidence of competition between these two sea urchins, I did not measure active competition between *D. antillarum* and *T. ventricosus*. An additional study could examine the nature of direct interactions between *T. ventricosus* and *D. antillarum*, and could determine if the habitat use patterns observed in this study are the result of priority effects.

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