

Interspecific Aggression of the Threespot Damselfish
(Eupomacentrus planifrons) Toward Two Urchin
Species: Diadema antillarum Philippi and
Tripneustes ventricosus

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Abstract

The interspecific aggressions of the territorial Three-spot damselfish Eupomacentrus planifrons toward two species of urchins, Diadema antillarum and Triprionaster ventricosus were examined in situ at the West Bank Reef, Discovery Bay, Jamaica. A diel census showed that both species of urchins are distributed outside of damselfish territories by day, but migrate into the territories at night. This pattern is probably due to diurnal exclusion of the urchins by the damselfish. D. antillarum was found to elicit a significantly greater aggressive response than T. ventricosus. Using various models, experiments were constructed to determine the effects of movement, color, and spine length on the release of territorial aggression. Movement of the urchin was found to be the critical stimulus.

Introduction

Damselfish are one of the few groups of animals that maintain territories both intra- and interspecifically. The Three-spot damselfish, Eupomacentrus planifrons, is one of the most common and widely studied species of the Damselfish. The territories of the adult males are precisely defined, usually one to three meters in diameter, and are centered on an algal lawn growing on dead coral substrate. At least one resource that the damselfish is protecting is food. E. planifrons actively defend their territories by exhibiting aggressive behaviour which includes chasing, fin

erection, pasturing, and biting. E. planifrons not only 2
excludes other herbivorous fish, but is also documented
to exclude such widely divergent taxa as sea urchins.
Ann Williams has shown that the distributions of the
dominant herbivorous sea urchins, Diadema antillarum and
Echinometra viridis, in the East back reef of Discovery
Bay, Jamaica are directly affected by the interference
behaviour of the territorial Three-spot damselfish
(Williams, 1979).

Two of the most common herbivores found on
the West back reef of Discovery Bay are the urchins
D. antillarum and Tipneustes ventricosus. Both species are
known to feed on many of the same algal species as
E. planifrons. D. antillarum is known to be a generalist
species, and feeds on algal mats on the reef surface,
primarily on small algae (Ogden, 1973; Ogden, Brown and
Salesky, 1973). T. ventricosus is shown to feed on algae-
encrusted Thalassia testudinum during the day, and
algae-covered coral by night. (Todd and Kilmarx, 1983).
Preliminary observations have shown both species of urchins
to be actively excluded from territories of E. planifrons,
and hence the algal resources within them, during the
day. The damselfish are, however, inactive at night, and
both species of urchins are known to migrate at this
time. Approximately ~~to~~ 10% of D. antillarum migrate
away from the reef at night to feed on Thalassia
testudinum beds, while the rest remain to feed on
algal mats on the reef surface (Ogden, Brown and Salesky,
1973). T. ventricosus is known to migrate from T. testudinum
beds in the day to rocky outcroppings at night (Todd

This may vary
from one
location to
the next.

and Kilmarx, 1983).

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Although Williams found D. antillarum to be actively excluded from damselfish territories during the day, she suggests that D. antillarum may be able to exist within the system through migration (Williams, 1981).

The effect of Three-spot damselfish interference on the daytime distribution of urchins has been shown, but the diel migration of urchins in and out of damselfish territories has not been examined for these two species. If the urchins and damselfish are competing for the same algal resource, one would predict that both species will be distributed outside of the damselfish territories during the day as a result of active exclusion, but will encroach on the territories at night when the fish are inactive.

Williams (1979) has shown that D. antillarum elicits a more aggressive response from the E. planifrons than the E. viridis, when both are placed simultaneously within a damselfish territory, and aggressiveness is quantified as the number of bites/minute. We conducted a similar experiment to discover the relationships between D. antillarum and T. ventriosus. We also studied the response of E. planifrons to a T. ventriosus individual placed alone in the territory to ensure that the presence of D. antillarum did not alter the fish's response to T. ventriosus.

We also noted the aggressive response of the damselfish to T. ventriosus over a period of time to discover if the fish would habituate to the

relatively slow-moving urchin.

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Recognition of competing reef fish species by E. planifrons has been found to be the result of discriminations based on the form and color of the intruding individual (Thresher, 1976 via Williams, 1979).

Ann Williams (1979) also suggests that movement might stimulate aggressive behaviour on the part of the damselfish. We designed experiments to discover whether movement, color, or spine length of the urchin were used as cues to the recognition of intruding individuals, and whether these factors had an effect on the degree of aggressive behaviour the damselfish displayed.

Study Site

This study was conducted in Discovery Bay, Jamaica between February 27 and March 3, 1984. Diel census data were collected from a $10 \times 15 \text{ m}^2$ plot located 10 meters south of the reef crest in the west back reef (depth = 1-1.5 meters).

This particular plot was chosen for its heterogeneity of substrates. It included *Thalassia testudinum* patches, bare sand, algal lawns on low rocky substrate, and live corals and coral rock formations with numerous damselfish territories. All experimental trials were executed within a group of coral rock formations which were colonized by *Eupomacentrus planifrons*, and divided into approximately 15 distinct territories. Any lab work necessary was accomplished in the wet lab of the Discovery Bay Marine Laboratory.

Methods

The diel census was taken between 1400 and 1500 on February 27, 1984 and 2130 and 2230 on February 28, 1984. This was accomplished by systematically swimming the width of the plot in strips approximately 4 meters wide. In this manner we were able to

visually observe and note the position and number of D. antillarum and T. ventriosus throughout the area. We formulated four categories to describe the location of the urchins: exposed (on rock promontories inside damselfish territories); in crevices (of rocks in damselfish territories); in patches of Thalassia testudinum, and on bare sand. A Chi-squared test was used to compare differences in night and day distributions for T. ventriosus.

We executed a series of experiments which consisted of placing a pair of urchins of comparable test diameter on the algae laws of a territory of E. planifrons. We quantified the aggressive behavior of the fish in terms of bites inflicted per minute for each test individual. We also noted which individual of the pair was attacked first. The first experiment was a D. antillarum vs. T. ventriosus combination. Each of the nine trials was terminated approximately two minutes after D. antillarum had exited the territory. In addition we calculated the mean time D. antillarum spent inside an E. planifrons territory from data taken during the two experiments involving live D. antillarum.

The subsequent experiments involved the following pairs: a black long spine model vs. a live D. antillarum; a black long spine model vs. a black short spine model, and a black long spine model vs. a white long spine model. The three models were constructed using half of a potato as the urchin test. Spines were removed from three live D. antillarum with scissors, and were inserted into the potato halves. One long spine and one short spine model were coated with black paint, while one long spine model was coated with white paint. Two lead weights were attached to the bottom of each model via "staples" made of paper clips.

The time of the live D. antillarum vs. black long spine model was determined by the time it took D. antillarum to exit the territory. This experiment involved six trials. The two experiments involving models only had eight trials apiece and a duration of 1.5 minutes per trial. In addition to these standard methods, an experiment which consisted of placing a T. ventricosus individual alone into a domselfish territory was also performed. The number of bites received per minute was recorded for a period of five minutes, and plotted as a function of time.

Mann-Whitney U tests were used to compare the bites per minute received by each individual within each of the following experimental pairs: D. anillarum vs. T. ventricosus; T. ventricosus alone vs. T. ventricosus in the presence of D. anillarum; D. anillarum vs a black long spine model; black long spine vs black short spine model; and black long spine model vs. white long spine model.

Results.

The diel census shows that there is a significant difference between the night and day distributions of T. ventricosus. (Table 1, $\chi^2 = 216.2$, $p < .001$). During the day, T. ventricosus is typically found outside of damselfish territories, in patches of T. testudinum or on sand. Although few D. antillarum individuals were seen in the study areas, they were found to inhabit coral rock crevices during the day and to migrate to more exposed areas with damselfish territories at night.

Table 2 presents the mean number of bites received per individual for each pair in the experimental series. E. planifrons showed significantly more aggressive behavior toward D. antillarum than T. ventricosus. (Mann-Whitney U test, $U = 81$, $U' = 0$, $p < .01$). When T. ventricosus was placed in the territory alone, it did not elicit significantly more aggression than when it was placed in the territory with D. antillarum. (Mann-Whitney U test, $U = 25.5$, $U' = 55.5$, $p > .05$) Fig. 1 shows the average number of bites received by T. ventricosus when it was placed alone in the damselfish territory, as a function of time. There appears to be a trend for decreasing agonistic behavior with time

spent in the territory.

D. antillarum also elicited significantly more aggressive behavior than an immobile black long spine model. (Mann-Whitney U test, $U=7, U'=31, p<.05$) The mean length of time D. antillarum spent inside damselfish territories for both experiments involving live urchins was 1.00 min, with a standard error of 0.21. Significant differences were not found within each pair for the final two experiments. These experiments involved a black long spine model vs. a white long spine model, and a black long spine model vs. a black short spine model. (Mann-Whitney U tests; $U=17, U'=47, p>.05$; $U=23, U'=41, p>.05$ respectively.)

Figure 2 represents which individual was attacked first in each experimental pair. D. antillarum was attacked before T. ventriosus in all trials. In the remaining experiments there was not such a clear cut distinction. Yet within each pair, the individual which most closely resembled D. antillarum provoked the higher percentage of first attacks.

Table 1. Results of diel census.

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	Exposed in damselfish territories		In crevices in damselfish territories		In <i>Thalassia testudinum</i> patches		On Bare Sand	
	DAY	NIGHT	DAY	NIGHT	DAY	NIGHT	DAY	NIGHT
<i>T. ventriosus</i>	35	191	11	0	161	34	81	38
<i>D. antillarum</i>	0	12	12	0	0	0	1	0

Table 2. Average number of bites per minute received by individuals in each experimental combination.

Experimental Pair	<i>D. antillarum</i> vs. <i>T. ventriosus</i>		<i>T. ventriosus</i> alone	<i>D. antillarum</i> vs. Black Long Spine Mollusks		Black Model vs. White Model	Black long spine vs. Short Spine		
Number of Trials	9		9	6		8	8		
Average bites/minute (\pm STD. ERROR)	13.13 \pm 2.89	1.33 \pm 0.39	2.8 \pm 0.82	16.52 \pm 3.16	5.36 \pm 2.25	9.55 \pm 3.00	2.82 \pm 1.73	5.22 \pm 2.35	5.82 \pm 1.91

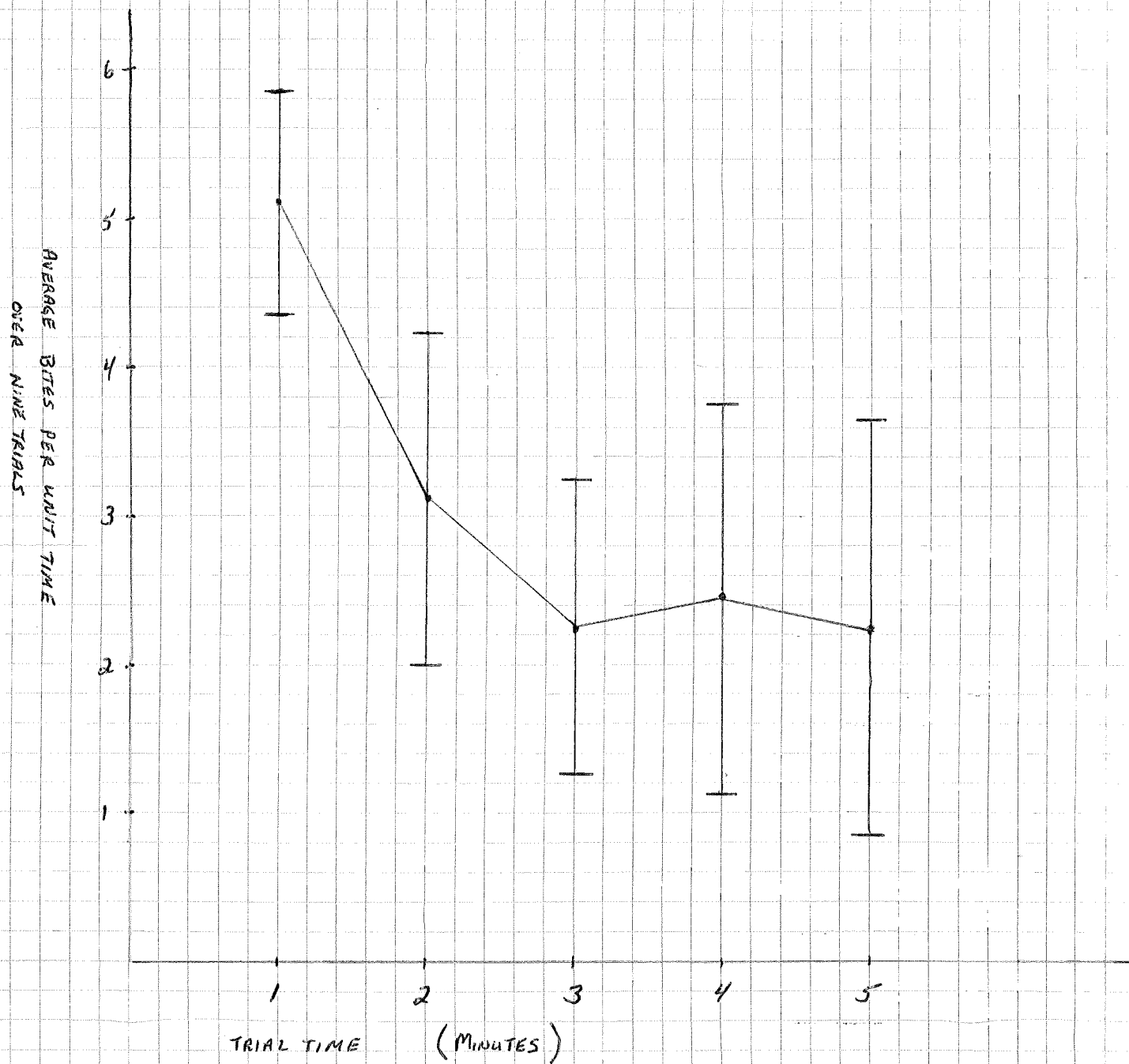


FIG. 1 Average bites received by *T. ventriosus* as a function of time.

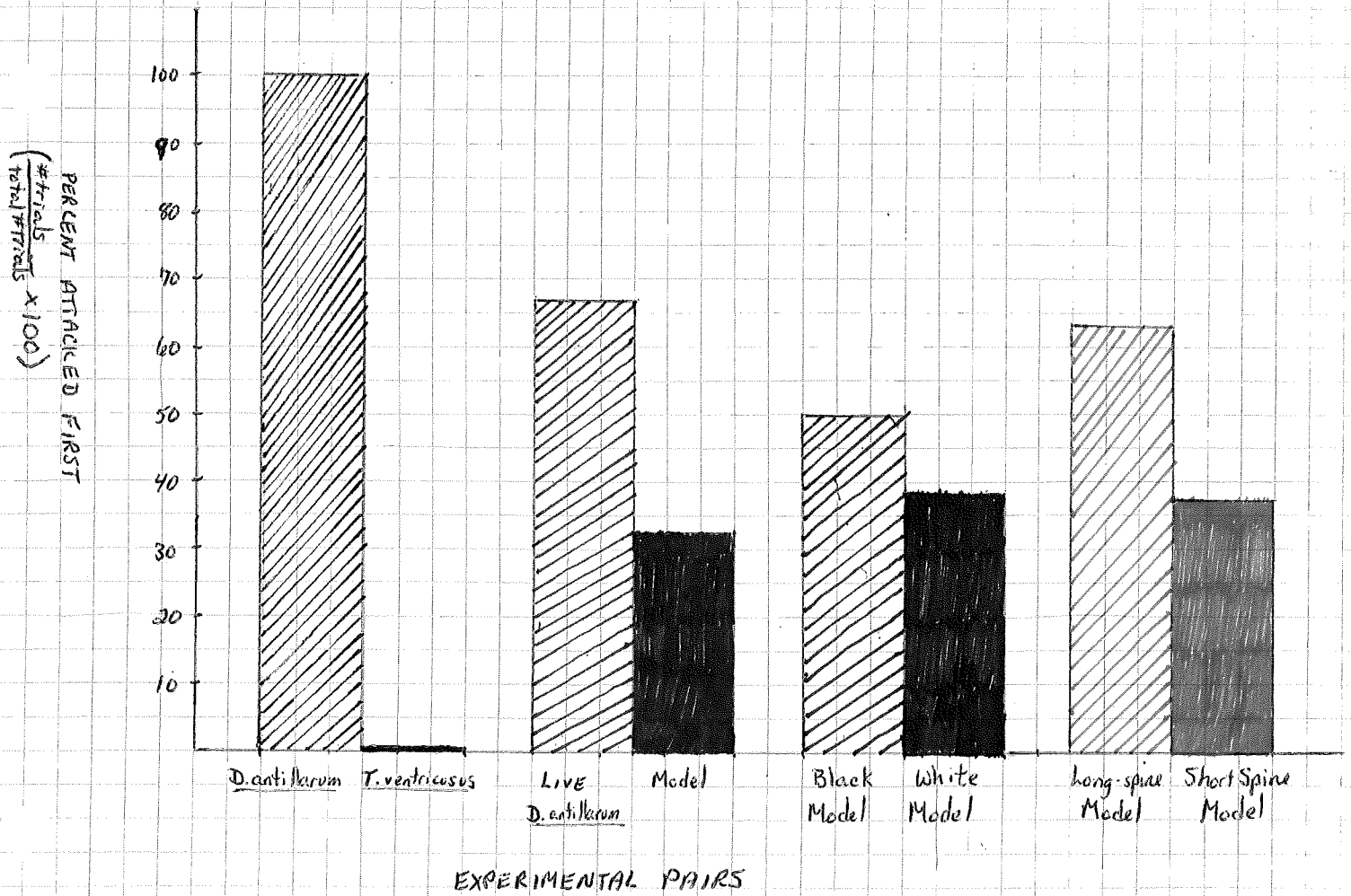


FIG. 2. Number of first attacks exerted by *E. planifrons* on experimentally presented pairs of urchins.

The diel census data showed that both D. antillarum and T. ventriosus are exposed and inside damselfish territories at night. T. ventriosus migrates into the territories from surrounding Thalassia testudinum beds and sand. D. antillarum, typically found in crevices and in the lower and outermost sections of damselfish territories in the day, simply migrates to more exposed positions within the territories. Both species enter the territories to feed on algal mats. We believe that this migration occurs at night due to the active exclusion of the urchins by E. planifrons during the day.

We found that E. planifrons was more aggressive toward D. antillarum, and always chase to attack it first (FIG. 2). Out of all experiments performed, D. antillarum elicited the most aggressive response in terms of bites/minute. In the T. ventriosus vs D. antillarum trial, D. antillarum received 13.13 bites/min., and in the D. antillarum vs Black long spine model, it received 16.52 bites/min. (Table 2). The damselfish was extremely persistent in its attempts to evict D. antillarum. The fish broke off spines and would later carry each broken spine to the edge of its territory and drop it outside of the boundary.

T. ventriosus elicited the lowest level of aggression as compared to other urchins in our experiments, including all models. We showed that this low level was not an artifact of being adjacent to D. antillarum in the first experiment by conducting an experiment with T. ventriosus alone (Table 2).

When attacked, T. ventricosus clamps firmly onto the substrate rather than engaging in a hasty retreat as in the case of D. antillarum. Due to this behaviour, E. planifrons was unsuccessful in evicting T. ventricosus. In all trials performed, only once was the damselfish able to flip the T. ventricosus out of its territory. In the case of D. antillarum, E. planifrons continually attacks the urchin until it exits the territory. In the case of T. ventricosus, attack frequency decreased over time (Fig. 1). The urchin did appear irritated when attacked and in some cases began to move slowly away from the point of attack. To clarify the habituation trend, the experiment should be continued for periods longer than 5 minutes to determine if T. ventricosus eventually exits the territory.

If the aggressive response of the damselfish does decline to the point of ineffectiveness, the fish may habituate to the T. ventricosus. This may explain why some T. ventricosus are found within E. planifrons territories during the day.

Aggressive interactions are highly indicative of active competition among species (Case and Gilpin, 1974 via Williams 1981). The level of aggression exhibited by the damselfish toward the urchins can be used as an indicator of the amount of competition between the fish and urchin species. Therefore the data suggest that there is a greater level of competition between E. planifrons and D. antillarum than T. ventricosus due to the much greater attack frequency on D. antillarum. D. antillarum is known to be a rapid and effective grazer, and

overgrazing by this species has been documented in many marine systems (Carol Stacum, pers. communication).

Thus, D. antillarum may present more of a threat to E. planifrons than T. ventriosus. Low (1971) showed that damselfish are able to distinguish between intruding species of fish. Because territorial maintenance is energetically costly to the damselfish, they more aggressively exclude those species with the greatest similarities in diet (from McEvoy, 1982).

Nyberg and Thresher (1974) determined the maximum distance of attack for several fish species and found the highest maximum attack distances for those species with the most similar diets (from McEvoy, 1982). It would be interesting to determine the maximum attack distances for both D. antillarum and T. ventriosus. One would predict a higher maximum attack distance value for D. antillarum if it actually has a greater overlap in food resources than T. ventriosus.

The actual overlap indices should be calculated for the three species in order to correlate aggressiveness levels with diet similarities. Ebersole (1977) created, through calculations, the Potential Competitive Impact of a species, which includes the degree of overlap in diet between damselfish and urchins, ~~and~~ a value such as this can be used to predict which species of urchins would elicit the most aggressive response.

Having shown that D. antillarum elicits a higher level of aggression, we examined which physical factors might stimulate the aggressive response. D. antillarum is a very mobile urchin, and shows

increased spine agitation and mobility when disturbed. T. ventricosus, on the other hand, is relatively slow-moving and tends to firmly grasp its substrate when disturbed. We found movement to be a very important factor in eliciting damselfish aggression. In the experiment of D. antillacum vs. the Black long spine model, the moving D. antillacum received over three times as many bites/minute than the T. ventricosus immobile model (Table 2). We cannot, however, completely rule out the possibility that E. planifrons is responding to a chemical stimulus. If this is the case, it could explain why the fish frequently removes broken spines from its territory. If D. antillacum exudes a chemical compound, the broken spines would possibly attract ~~the urchin's~~ predators. It is widely known that cutting open an urchin will attract fish, especially the blue-headed wrasse, which we observed to elicit high levels of aggressive behaviour from E. planifrons as well. We do believe, however, that movement is a more important stimulus than any possible chemical compound. During trials involving T. ventricosus, we observed that when it began to move as a result of the damselfish's advances, the slight movement seemed to provoke a more vigorous attack. Also, during an experimental trial, one of the models received only two bites, but these bites were directed toward a flake of paint that was moving. We observed that when the models rocked back and forth with the surge, the movement provoked a more vigorous attack as well. Our data agrees with Thresher's work on intruding fish species. He found that movement proved to be a critical factor

in releasing territorial aggression toward other species. Thresher also theorized that a slow moving intruder would be able to encroach further than a fast moving intruder. (Thresher, 1976 v. Williams 1979). This could help to explain why the slow moving T. ventriosus is sometimes found exposed in damselfish territories during the day, and why D. aculeatum is rare.

We found that color did not have a significant effect on the amount of aggressive behavior elicited by two long-spine models. These results are logical when examined from an evolutionary standpoint. While D. aculeatum are known to exist in the population, although infrequently. If white coloration decreases the attack frequency, one would expect to see a higher proportion of white individuals in the population, due to high selective pressures. We also found that spine length was not a determining factor of attack frequency. The mean bites received per minute for both the black long spine model and the black short spine model were very similar, 5.22 ± 2.35 and 5.8 ± 1.91 , respectively. (Table 2).

Therefore we conclude that movement is the major factor involved in the release of territorial aggression toward these urchins.

The characteristics observed throughout this study suggest a history of coevolution

swimming
no effect
of spine length
on attack frequency
white models

between D. anillorum, E. planifrons and T. ventriosus. These three species share food resources as well as habitat, and their specific interactions suggest precise niche partitioning. E. planifrons defends the algal lawns on coral rock promontories, and it is selectively more aggressive to the more mobile D. anillorum. This allows the slower T. ventriosus to encroach on the territories during the day. The mobility of D. anillorum stimulates an increase in aggressive behaviour, thereby preventing it from attaining its desired food source during the day. Yet it is this factor which allows the species to exist in the system, solely through nightly migrations. These interactions have produced an ecological balance which revolves around diel migrations as the major factor allowing coexistence of three competing species.

good

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Low 1971?

Excellent study and very well-written report! Excellent discussion.