

Attack intensity by two species of territorial damselfish (Pomacentridae) as estimates of competitive overlap with two species of wrasse (Labridae)

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Abstract The intensity of interspecific territorial defense should be based upon the degree of competitive overlap. We tested this relationship in two territorial Caribbean damselfish (dusky, *Stegastes adustus*, and longfin, *S. diencaeous*) with intruders being the bluehead wrasse (*Thalassoma bifasciatum*) and the slippery dick wrasse (*Halichoeres bivittatus*). Based on food habits, the slippery dick and the bluehead wrasse should have the same degree of competitive overlap to the two damselfish species. We also predicted that the larger slippery dick wrasse intruder would receive more aggression than the smaller bluehead wrasse intruder. Neither damselfish species distinguished between the two wrasses suggesting that they were ecologically equivalent. We also tested size differences within both species of wrasse and found that size had no influence on the aggression in the dusky damselfish. The longfin also did not show a size preference for the bluehead but did prefer to attack the larger slippery dick wrasse. In spite of the similarities between the dusky and the longfin damselfish and the similar food habits of the bluehead and the slippery dick wrasse, our results suggest that using intensity of interspecific territorial defense alone may not be an adequate measure of competitive overlap.

Keywords Territory · Interspecific aggression · Caribbean · *Stegastes* · *Thalassoma* · *Halichoeres*

Introduction

The aggression that territorial defenders use against an individual is often considered as a measure of ecological overlap (e.g., Orians and Willson 1964; Moore 1978; Stamps 1977; see also review by Peiman and Robinson 2010). Thus, territorial defenders are expected to ignore non-competitors while vigorously attacking and repelling those species that could take over their territory and/or harvest critical resources (but see Ord and Stamps 2009). Not surprisingly, this has been applied to territorial coral reef damselfish whose attacks against other competing species dramatically influence the amount of resources that accumulate in their territory (Williams 1980; Hixon and Brostoff 1983). Given the vast diversity of species attacked by damselfish (Myrberg and Thresher 1974), defenders appear to reserve their most aggressive intensities toward intruding species that had the greatest competitive overlap. For example, both Ebersole (1977) and Mahoney (1981) conclude that attack intensities against intruding species corresponded to the trophic overlap with the damselfish defender. Ebersole (1977) further clarified competitive overlap in the Caribbean beaugregory damselfish (*Stegastes leucostictus*) as a function of both the resource overlap and the quantity of resource taken by the intruder (see also Moore 1978). Thus, all things being equal, the territorial damselfish should escalate their attacks against larger individuals because they should claim more of the resource.

Here, we more closely examined territorial attack intensity as a function of intruder size using the dusky

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damselfish (*S. adustus*, Troschel, 1865) and the longfin damselfish (*S. diencaeous*, Jordan and Rutter, 1897). We choose these two territorial damselfish species because they are phylogenetically and ecologically closely related (Mullen et al. 2012; Roberston 1995), thus allowing us to judge the generality of our results, at least between closely related species. For intruders, we used the bluehead wrasse (*Thalassoma bifasciatum*, Bloch, 1791) and the slippery dick wrasse (*Halichoeres bivittatus*, Bloch 1769), two of the most common damselfish intruders. Both species continuously hunt for similar types of invertebrates (Randall 1967) and both are also potent egg predators that will devour entire egg clutches found within male damselfish territories (personal observation).

As an estimate of competitive overlap, we measured the aggression directed at each wrasse species when placed inside dusky and longfin territories. We presumed that the larger size of the slippery dick would be more obvious and if size alone influences attack intensity, we predicted that both the dusky and the longfin should preferentially attack the larger slippery dick. Given that size correlates to the amount of food that can be consumed, increasing size for each wrasse species should increase its competitive overlap with the damselfish defender. To examine this prediction, we used two bottles that contained different sized individuals of the same species of wrasse. Each pair had individuals that were either similar or dissimilar in size. If size were an important component to damselfish attack intensity, we predicted that both damselfish species would (1) attack the larger individual of both species more vigorously, and (2) the differences in attack intensities would be a function of the size difference. Similarly, changes in the sizes of the damselfish should also influence competitive overlap and subsequent aggression to wrasses. For this reason, we predicted that larger dusky and longfin damselfish with their increased food requirements should be more aggressive than smaller ones to both wrasse species.

Social differences between the bluehead and the slippery dick may be a confounding influence of the relationship between intruder size and competitive overlap. In particular, bluehead wrasse, much like many other species of coral reef fish (Itzkowitz 1980), often form conspecific swarms. Essentially, in spite of the bluehead wrasse's relatively small size, the bluehead swarm could easily consume as much food as a single large slippery dick. To estimate the influence of swarming on territorial defense, we stimulated swarm formation by placing a bluehead or a slippery dick within a dusky or longfin territory. We initially predicted that the dusky would show a more intense response than the longfin to the bluehead, because our preliminary observations suggested that the bluehead was more common and more likely to swarm in dusky habitat. The slippery dick appeared equally distributed across habitats

of both damselfish species and less likely to swarm, and therefore we predicted that both damselfish species would attack the slippery dick similarly.

Materials and methods

Damselfish species and study site

Dusky and longfin damselfish are common on the shallow Caribbean reefs. Both species are territorial and polygynous, with males maintaining long-term territories that are used for oviposition sites, food, and protection against predators. This field study was conducted in the shallow coral reef located off shore of the Bellairs Research Institute (McGill University), in Holetown, Barbados, West Indies (13°10'N, 59°30'W) during a 3-week period in June 2010 and another in July 2011. During the presentations, no territorial damselfish in this study were defending eggs.

At this study site, there was overlap in their spatial distribution. The dusky were most abundance within 1.5 m of the surface while the adult longfin tend to become more abundant at 1.5 m and deeper. Both species maintain highly stable territories and are rarely usurped by intruders unless a vacancy occurs due to predation (Cheney and Côté 2003; Turgeon et al. 2010; Turgeon, personal communication). At our field site, both species were located approximately 15–20 m from shore. Initial 5-min observation periods were taken of each focal fish to determine the approximate territorial boundaries and nest site location within a territory.

Experimental design

Three experiments were performed with “model bottles” (see Myrberg and Thresher 1974) in which one live wrasse was placed in a 2-l clear plastic (i.e., Nalgene) bottle.

In all experiments, both the bluehead wrasse and the slippery dick wrasse were collected using hand nets from areas adjacent to the study sites. The fish were placed directly into the plastic bottles and held for the duration of the experiment (between 2 and 4 h). Once the trial was completed, the fish were released back to their original sites. During the presentations, we observed no changes in the wrasses' behavior during the trial; for the most part, they swam continuously up and down the sides of the bottles.

The first experiment (“single bottle presentation”) performed in June 2010 consisted of single presentations of a slippery dick or a bluehead to both species of damselfish. The second experiment, also in June 2010, placed a pair of bottles with a single bluehead in one and a slippery dick in the other (“pair presentation”). The single or paired bottles

were placed approximately 30 cm from the male's nest site within his territory. For 3 min, we recorded the time the focal damselfish spent within one body length of a bottle. We chose time as a measure of aggression because it was easy to measure, and it was a response clearly directed at the fish within the bottle. Time had been used as a primary measure of aggression for these damselfish species in previous studies (e.g., Little et al. 2013). Also, in the absence of a wrasse within the bottle, the defending dusky and longfin damselfish rarely approached the empty bottle (Little et al. 2013, and unpublished).

For the single bottle presentations, we also recorded the number of free-swimming bluehead and slippery dick wrasse that entered the focal male's territory during the 3-min test.

For the single bottle tests, the 17 focal dusky males (TL, mean $88.9 \text{ mm} \pm 0.9$) and 17 focal longfin (TL, mean $113.9 \text{ mm} \pm 1.1$) males were tested with 3 different individuals of both wrasse species. Additionally, we tested these same focal damselfish with 3 different paired presentations of bluehead and slippery dick wrasse. The same stimulus or stimulus pair was presented to all 34 focal subjects in a given day to control for individual variation in stimuli fish. Each wrasse was caught in the morning outside the study site and, at the conclusion of each test, each wrasse was released to their captured location.

Slippery dick wrasse grow considerably larger than bluehead wrasse (Böhlke and Chaplin 1968), and this is reflected in the sizes used for this experiment (bluehead wrasse, TL, mean 96.8 mm ; slippery dick wrasse, TL, mean 114.7 mm), an important issue considered in this study. Observations of the dusky were taken while snorkeling, while observations of longfin required the use of SCUBA.

In July 2011, we performed the third model bottle experiment ("paired size presentation"), and we examined the influence of wrasse size on the focal damselfish's response. Although these damselfish were in the same general area as those in July 2010, we used different residents. We tagged the territories of 15 longfin and 20 dusky (i.e., focal dusky, TL, $91.2 \text{ mm} \pm 0.9$; focal longfins, TL, $109.7 \text{ mm} \pm 3.1$). This experiment presented only uni-specific pairs of blueheads and slippery dicks in 2-l clear plastic bottles. Each stimulus pair consisted of two individuals of the same species that were either similar in size (termed symmetrical pairs) or different in size (termed asymmetrical pairs). Each focal damselfish was tested with two different symmetrical and asymmetrical pairs for both wrasse species. The degree of symmetry and asymmetry was dependent on our ability to both recognize the degree of size differences while underwater and our ability to catch the identified fish. As a result of these limitations, the percent mean differences between species for the symmetrical pairs differed slightly (bluehead, 4.7 %; slippery dick, 1.6 %) while there were much greater differences

between species for asymmetrical pairs (i.e., bluehead pairs differed on average about 25 % while slippery dick pairs about 71.2 %). The large difference between asymmetrical pairs of blueheads and slippery dicks reflected natural adult size differences. We anticipated that both species of damselfish would show a more biased response to the asymmetrical pairs of slippery dicks than to blueheads. Each paired presentation lasted 3 min and we measured the amount of time the focal individual spent within one body length of a bottle.

Statistical analysis

Single bottle presentation

The 3 trials examining the time focal damselfish spent within one body length of the bottle were averaged in each treatment and analyzed with a 2×2 repeated measures factorial ANOVA with focal species (dusky/longfin) as a between subjects factor and stimulus species (bluehead/slippery dick) as a within subjects factor.

Pair bottle presentation

The simultaneous presentation of a blue and a slippery dick was analyzed separately from the one bottle presentation because the time near a bottle was no longer an independent measurement. With two levels of each factor, post hoc tests were unnecessary. Results were considered significant at $p \leq 0.05$.

Free swimming intruder abundance

To analyze the number of free-swimming wrasse that were attracted to the single bottles containing the bluehead and the slippery dick wrasse (see above), we counted the number of individuals that arrived during the 180-s presentations. We used the t test to determine if the dusky and the longfin experienced different swarm sizes for each species of wrasse.

Pair size presentation

We used the paired t test to determine if the focal damselfish differentiated the small from larger individual in symmetrical and asymmetrical size presentations.

Size versus aggression

To examine the relationship between body size of damselfish and its level of aggression, we used the Spearman Rank correlation (r) using the total length of the damselfish and the mean time spent near each wrasse species.

Results

Single presentations

The longfin spent more time near the slippery dicks and blueheads than did the dusky (Fig. 1). This difference is reflected in an overall significant main effect ($F_{1,32} = 6.965$, $p = 0.013$). There were no significant effects of wrasse species on the time near a bottle ($F_{1,32} = 3.1$, $p = 0.09$) nor was the interaction significant (focal species \times wrasse species, $F_{1,32} = 0.57$, $p = 0.45$). The size of the damselfish was not significantly correlated ($p > 0.05$) to the total time the dusky or the longfin spent near the slippery dick and the bluehead (dusky: slippery dick, $r = 0.29$; bluehead, $r = -0.32$; longfin: slippery dick, $r = 0.24$; bluehead, $r = 0.18$).

Species pair presentations

When presented with both species of wrasse simultaneously, the dusky and the longfin showed no differences in the overall levels of aggressive behavior performed (Fig. 1). There was no significant effect of focal species

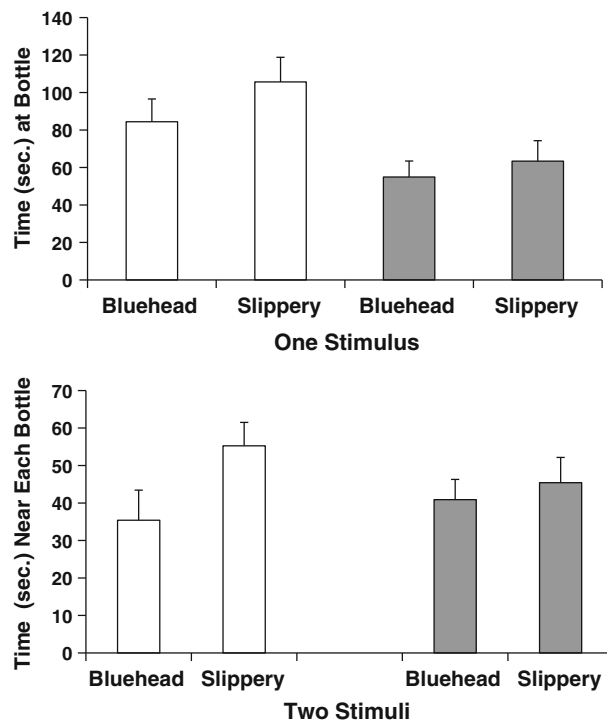


Fig. 1 The *top panel* summarizes the mean (+SE) amount of time the longfin *Stegastes diencaeous* and (white bar) and dusky damselfish *S. adustus* (gray bar) spent near a single bottle bluehead (*Thalassoma bifascatus*) and slippery dick wrasse (*Halichoeres bivittatus*). The *bottom panel* summarizes the paired presentations of a bluehead and a slippery dick to the longfin (white bars) and the dusky (gray bars)

($F_{1,32} = 0.118$, $p = 0.733$) or wrasse species ($F_{1,32} = 3.07$, $p = 0.09$) on time near the paired stimuli. There also was no significant interaction (focal species \times wrasse species, $F_{1,32} = 1.2$, $p = 0.28$).

Estimate of swarm size

More bluehead and slippery dick wrasse were attracted to their own conspecifics in dusky territories than to conspecifics placed with longfin territories (dusky: $t = 3.68$, $p < 0.001$; longfin: $t = 2.24$, $p = 0.03$; Fig. 2). Clearly, slippery dicks were far less likely to join their conspecifics than did blueheads joining their conspecifics.

Pair size presentation

Figure 3 illustrates the mean time that focal damselfish individuals spent near the two bottles that contained either the slippery dick or the bluehead, which represented either symmetrical or asymmetric differences in size. In all cases, except one, the resident focal longfin and the focal dusky did not show a significant difference in the time spent near the larger individual in symmetrical or in asymmetrical pairs of either intruding species. The one exception was that longfins spent significantly more time near the larger slippery dick wrasse in asymmetrical pairs.

We found no significant correlations ($p > 0.05$) between the size of either the longfin or dusky and the mean total time spent near the pairs of slippery dicks or the pairs of bluehead wrasse (longfin: slippery dick, $r = 0.013$; BHW, $r = 0.03$; dusky: slippery dick; $r = 0.23$, bluehead, $r = 0.23$). Although size was not significantly correlated to aggression, the mean total aggression directed against the two species

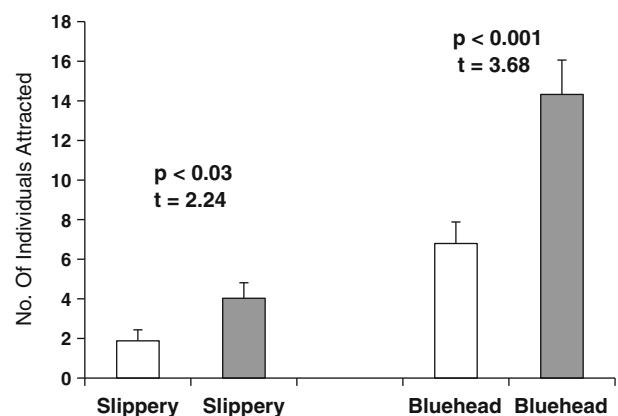
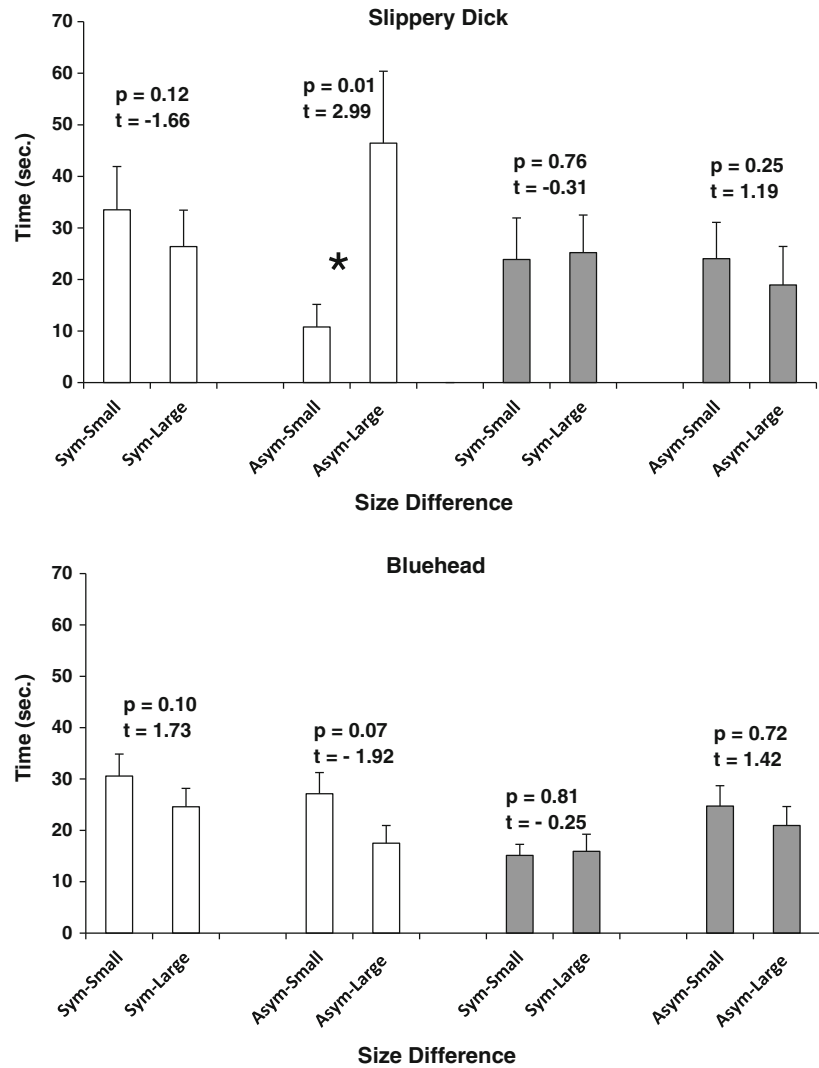


Fig. 2 The number of slippery dicks and blueheads attracted to single presentations of a conspecific individual placed within the territories of the longfin (white bars) and the dusky (gray bars) damselfish. The bars represent the mean number of wrasses (+SE) attracted to the stimulus bottles. The p values and t values test for differences in the amount of each species of wrasse attracted to each damselfish species

Fig. 3 The mean time (+SE) the longfin (white bar) and the dusky (gray bar) spent near the bottle with the smaller and larger wrasse. *Sym* both small and large wrasse were similar in size, *Asym* small and large wrasse were very different in size. *Upper panel* summarizes pairs of slippery dicks and *lower panel* summarizes pairs of blueheads. The *p* values and *t* values test for differences in the time a damselfish species spent near the small and large individual when sizes were symmetric and asymmetric



wrasse was highly correlated for both focal damselfish (longfin: $r = 0.94, p < 0.01$; dusky: $r = 0.80, p < 0.01$).

Discussion

Neither damselfish species showed a preference to attack the larger slippery dick over the dusky in the single or paired presentations. Thus, using attack intensity as a measure of competitive overlap, both damselfish species appeared to compete similarly with both species of wrasse. To further examine the effects of intruder size, we presented longfin and dusky damselfish with uni-specific pairs of wrasses (paired size presentations) that were either similar (symmetrical) or different in size (asymmetrical). The dusky did not respond to larger differences in size for either the bluehead or the slippery dick, again supporting our results from the paired presentations. While the longfin

also did not respond to size differences in asymmetrical pairs of the bluehead, they were more aggressive to the larger slippery dick in the asymmetrical pairs.

Additionally, we found no evidence that the size of the damselfish impacts on its competitive overlap with the two species of wrasses. Interestingly, while damselfish size was a poor predictor of aggressive intensity, the relative aggressiveness of both damselfish species was consistent between both wrasse species. Thus, an individual that exhibits a relatively high aggressive intensity toward the slippery dick was also relatively more aggressive toward the bluehead. We suspect that both species of damselfish are basing their aggressive behavior on the relatively quality of their territories, causing some damselfish to be more aggressive than others. In another Caribbean damselfish, the beaugregory damselfish, territory quality is a consistent predictor of the male’s aggressive intensity (Itzkowitz 1990, 1991).

Our estimate of swarming tendency supported our initial observations that the bluehead wrasse will attract more conspecifics into dusky than longfin territories. Essentially, in terms of swarming, the bluehead wrasse should be a more important competitor to the dusky than the longfin, and, as such, should cause the dusky to attack it with a greater intensity. This was not the case; the single presentations of the bluehead to both dusky and longfin defenders revealed that both damselfish attack the bluehead similarly. The slippery dick was slightly more likely to attract conspecifics into dusky than longfin territories, and but here also they were attacked with similar intensities by both species of damselfish.

We chose the bluehead wrasse and the slippery dick wrasse because they are both common on the shallow Caribbean reefs and appear to have similar food habits (Randall 1967). While food consumed by these two species of wrasse could be a weak measure of their ecological overlap, both damselfish species attacked them with equal intensity (i.e., single and paired hetero-specific experiments), indicating that the magnitude of the overlap with both damselfish species was similar. However, the longfin (and not the dusky) showed a clear preference for the larger individual in asymmetric uni-specific pairs of slippery dick wrasse. Given the presumed relationship between territorial aggression and competitive overlap, this would suggest that size relates to the competitive intensity of the slippery dick wrasse, but only for the longfin damselfish.

At present, we cannot resolve these conflicting results, but they cast doubt as to the generality that a defender's response to an intruder is a straightforward method for understanding ecological overlap and interspecific competition. Ord and Stamps (2009) also pointed out that territorial defenders may attack intruding heterospecifics more intensely than conspecifics, further illustrating that territorial defense may be an unreliable measure of ecological overlap.

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