THE EFFECT OF SCHOOL SIZE AND COMPOSITION ON AGGRESSIVE BEHAVIOR IN THE TERRITORIAL THREESPOT DAMSELFISH, *STEGASTES PLANIFRONS*

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Abstract: Threespot damselfish exhibit territoriality to protect algal resources and brooding space. The resources within a damselfish territory are also used by other fish on the reef. Fish invading the territory use schooling as a method of overwhelming the ability of the damselfish to defend its territory. We predict that as school size increases, the likelihood that a damselfish will chase the school will increase, the likelihood that a school will return to the territory will increase, and the time from territory invasion to damselfish attack will decrease. Additionally, there is some debate on whether damselfish show more aggression towards ecologically similar species (i.e., those with greater overlap in resource use). We tested these ideas by observing interactions of intruding fish with territorial *Stegastes planifrons* (threespot damselfish) on the back reef of Discovery Bay, Jamaica. The probability of being chased and probability of returning both increased with school size, but time spent in territory was unaffected by school size. Type of fish did not affect any of these response variables. It appears that school size is an important determinant of damselfish aggressive behavior toward other fish.

Key words: algae gardens, interspecific interactions, schooling, territoriality

INTRODUCTION

Damselfish (Pomacentridae) in tropical coral reefs maintain territories to protect food resources and as a substrate on which their eggs mature. These fish maintain gardens of their favored algal species and aggressively chase off fish that may enter the territory to consume the algae or damselfish eggs (Deloach 1999). Intruding fish use schooling as a technique to overwhelm the damselfish and thereby decrease its ability to defend its territory. Foster (1985) found that the feeding rate of A*canthurus coeruleus* (blue tang) individuals in damselfish territories was positively correlated with the size of the school of *A. coeruleus*. Robertson et al. (1976) found that solitary individuals had both a high probability of being attacked and a low feeding rate, whereas schooling fish suffered few attacks and had a higher feeding rate; they suggested that this pattern resulted from the inability of the damselfish to attack all fish simultaneously. Both studies suggest that schooling confers a benefit to fish attempting to invade a damselfish territory.

Though these studies have elucidated the adaptive benefits of schooling for the individuals in the group, the effects of intruding schools on damselfish behavioral response have not been examined. Because larger schools have been shown to be more successful in exploiting territorial resources and thus represent an increased threat to the damselfish, we predicted that *Stegastes planifrons* (threespot damselfish) is more likely to show an aggressive response to schools of increasing size. Additionally, the likelihood of a fish in a school being chased multiple times should decrease with school size because higher numbers of intruding fish will overwhelm the damselfish. Therefore, we predicted that fish in larger schools would be more likely to return after being chased. Finally, damselfish should respond more quickly to the greater threat of the larger school, so we predicted that the time a school spends in a territory before being attacked would decrease with school size.

Additionally, it has been shown that damselfish are more aggressive towards fish which exhibit greater niche overlap with them

(Ebersole 1977). Manson (1978) found that *Acanthurus bohianus* (ocean surgeon) was attacked at a much higher rate than *Holocentrus* spp. (squirrelfish), reflecting the greater dietary overlap of *A. behainus* with dusky damselfish (*Stegastes fuscus*). However, Cressler (1981) found no difference between attacks on parrotfish (*Scarus* spp.) and *Acanthurus* spp., despite parrotfish having a higher degree of dietary overlap. Our study aimed to examine effects of both species and school size on the aggressive behavior of *S. planifrons*.

METHODS

We examined *S. planifrons* territorial behavior on 4 - 8 March 2004 at Discovery Bay, Jamaica, at three sites (East Back Reef, the West Back Reef and Columbus Park). We haphazardly selected damselfish territories and observed the focal fish until we could determine the boundaries of its territory. We then observed all fish entering this territory during a 10 min period. For every territory invasion, we recorded the number and species of intruding fish, the size (relative to the focal damselfish) of the intruder(s), and the time that intruding fish spent in the territory before being chased off or leaving. We also recorded whether the focal damselfish chased away the intruding fish, the number of fish that were chased, and whether the intruding fish immediately returned to the territory after being chased.

To evaluate effects of fish type on damselfish response, we grouped all species into families. Only three families (parrotfish, surgeonfish or wrasse) had a large enough sample size to test for differences among families in whether at least one fish was chased, whether they returned (chi-square tests), and how much time they spent in the territory (Kruskal-Wallis test). We also tested for effects of intruding group size (range one to twelve fish) on whether the fish were chased, whether they returned (logistic regressions), and time spent in territory (linear regression). For groups of two to twelve fish, we also tested the effects of school size on the proportion of schooling individuals chased. All species were included for these analyses, except schools of hardhead silversides and bar jacks that were clearly transients in the territory. Aggressive interactions with neighboring damselfish were not included in any of the analyses.

RESULTS

We observed 42 focal damselfish for a total of 420 min and recorded 248 territorial intrusions by other fishes (Table 1). Fish type (parrotfish, surgeonfish or wrasse) did not affect how much time each individual or group spent in a damselfish territory (Kruskal-Wallis, χ^2 = 0.39, df = 2, P = 0.82; Fig. 1), whether at least one fish was chased (χ^2 = 3.609 df = 2, P = 0.17;

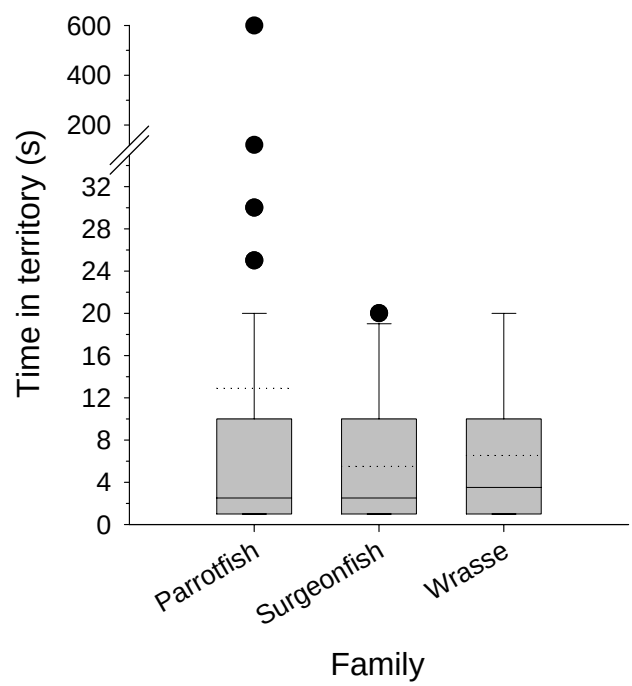

Figure 1. Time spent in damselfish territory before being chased or leaving compared among the three most commonly encountered fish families. Box plots show median and interquartile range. Whiskers show 10th/90th percentiles. Dotted lines are means. Points are outliers.

Table 1), or whether the fish immediately returned to the territory after being chased (χ^2 = 2.42, df = 2, P = 0.30; Table 1).

There was no relationship between school size and time spent in a territory before initiation of damselfish aggression (r^2 = 0.00002, P = 0.95, n = 250), but larger schools showed a marginally significant trend toward a higher probability of being chased (logistic regression: χ^2 = 3.31, df = 1, P = 0.068; Fig. 2). As school size increased, the probability of returning after being chased by a territorial damselfish increased (logistic regression: χ^2 = 14.7, df = 1, P < 0.0001; Fig. 3). There was a significant negative linear relationship between the size of the group and the proportion that were chased (r^2 = 0.15, P < 0.0016, n = 65; Fig. 4).

Discussion

S. planifrons did not respond differently to intruding parrotfish, surgeonfish or wrasse, indicating that either damselfish response is consistent regardless of the nature of the threat or that these three groups present a similar level of threat. Additionally, we found that fish in these three groups were equally likely to return after being chased, which suggests that response to damselfish aggression is similar across groups. However, less frequently encountered fish groups may have a different relationship with damselfish. For example, damselfish at-

Table 1. Total number of observations of fish entering damselfish territories, the number of times at least one fish was chased by the focal damselfish, the number of schools (more than one individual) observed, and the number of immediate returns after a chase.

Group	# observations	# chases	# schools	# returns
Balloonfish	1	0	0	0
Blennies	9	5	1	4
Butterflyfish	3	3	0	1
Croaker	2	2	0	0
Damselfish	33	27	1	5
Eel	1	1	0	0
Goatfish	1	0	1	0
Gobies	3	3	0	1
Grunt	7	6	0	2
Hamlet	2	1	0	0
Parrotfish	112	88	57	26
Jacks	1	0	1	0
Silversides	2	0	2	0
Squirrelfish	8	1	0	1
Surgeonfish	20	14	1	3
Wrasse	44	39	16	16

tacked squirrelfish only one out of eight times, despite squirrelfish often being present in the territory for the entire 10 min observation period.

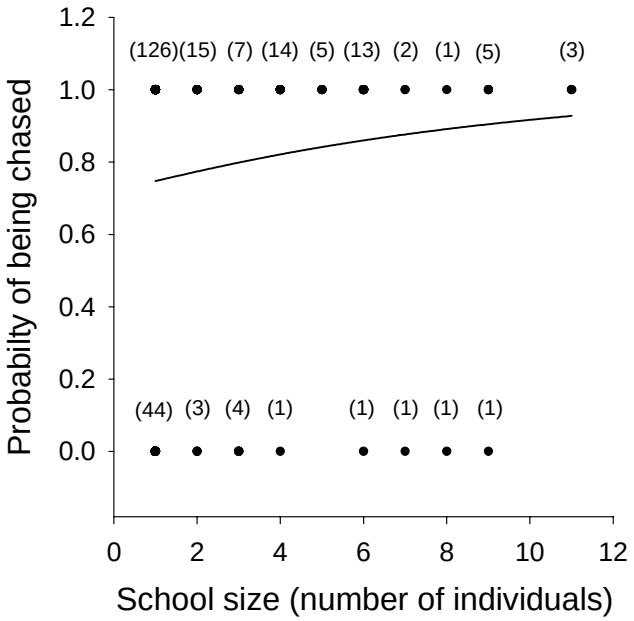

Figure 2. School size versus probability of being chased by focal damselfish. Points show observations and numbers indicate number of overlapping points. Line shows best fit logisitic function.

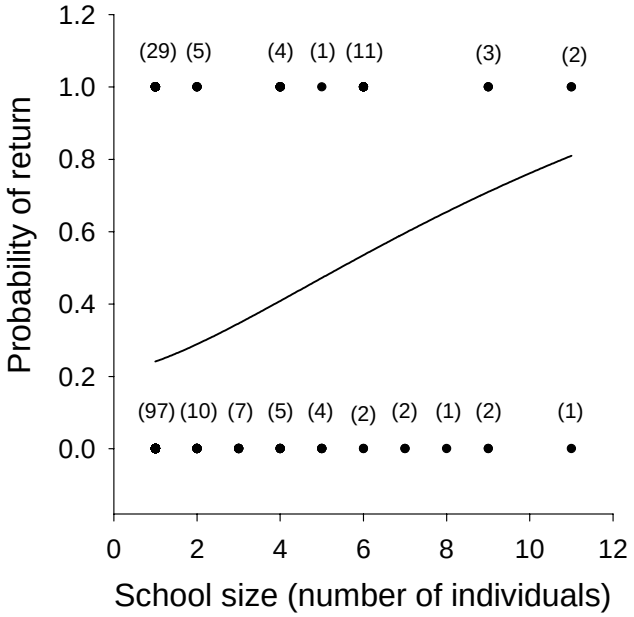

Figure 3. School size versus probability of returning after being chased by focal damselfish. Points show observations and numbers indicate number of overlapping points. Line shows best fit logisitic function.

School size appeared to be a much more important factor than fish type, with increased school size leading to a greater probability of at least one fish being chased. Two potential reasons for this pattern are that damselfish perceive larger schools as a greater threat to their territories and/or that larger schools tend to be more visible (Shannon et al. 2000). However, we found no effect of school size on the time it took a damselfish to initiate an attack after territory invasion. Such a pattern would be expected if visibility of school were important.

Our finding that the proportion of individuals attacked decreased with school size supports the interpretation of Robertson (1976) and Foster (1985) that schooling enhances the ability of individual fish to invade damselfish territories. Furthermore, return rate of invading fish after an attack increased with school size. This finding suggests that individuals in larger schools have a lower probability of being chased multiple times, and therefore are more likely to risk an immediate return.

Though damselfish encountered individ-

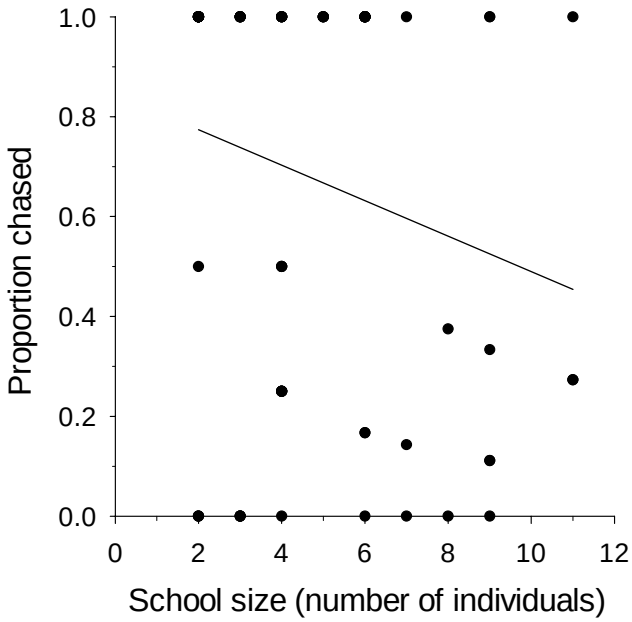

Figure 4. School size versus proportion of individuals reacted to by focal damselfish. Individuals in larger schools have a lower probability of being chased.

ual intruders more often than schools (170 versus 77, respectively), the total number of intruding schooling fish was greater than the total number of intruding individual fish (362 versus 170, respectively). This suggests that the impact of schools on damselfish may be greater than their encounter rate indicates, especially if individuals within schools have a higher feeding rate. Thus, selection pressure on damselfish behavior should be driven in part by interactions with schooling fish.

LITERATURE CITED

Cressler, W. 1981. Territorial responses of damselfishes (family Pomacentridae) against schooling competitors (*Scarus croicensis* & *Acanthurus* spp.). Dartmouth Studies in Tropical Ecology.

DeLoach, N. 1997. Reef Fish Behavior: Florida, Caribbean, Bahamas. New World Publications Inc: Jacksonville Fl, p. 180 - 207.

Ebersole, J.P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. Ecology 58: 914 - 20.

Foster, S. A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. Animal Behavior 33: 782 - 92.

Manson, M. 1978. The adaptive significance of interspecific territoriality in the reef fish *Eupemocantrus fuscus* (Pomacentridae). Dartmouth Studies in Tropical Ecology.

Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher and M. G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. Ecology 57: 1208 - 20.

Shannon, C. B., A. K. Frank, E. M. Mahar and M. S. Calvi. 2000. Effects of damselfish territorial defense on species composition and spatial structure and mixed species schools. Dartmouth Studies in Tropical Ecology, p. 186 - 92.