

# Resource attractiveness of the male beaugregory damselfish and his decision to court or defend

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We examined the decisions territorial male beaugregory damselfish (*Stegastes leucostictus*) make when presented with mating and aggressive situations simultaneously. Specifically, we tested how males responded to simultaneous and consecutive presentations of conspecific males and females in bottles. We hypothesized that (1) territorial males would show lower levels of courtship toward females when a competing male is also present compared to when only the female is present and (2) territorial males would show higher levels of aggression toward intruding males when a female is also present on their territories than when only the intruder is present. We predicted that males with high-quality breeding sites would court females and attack competitors more vigorously than males with low-quality breeding sites. Males on low-quality breeding sites exhibited fewer conspicuous courtship displays toward bottled females and a lower bite rate toward bottled males than did the males on high-quality breeding sites. We concluded that poor breeding-site quality was responsible for the decline in the most conspicuous aspects of both courtship and aggression. When presented simultaneously with a bottled male and a bottled female, defenders of both breeding-site types drastically reduced the number of courtship displays and the amount of time they spent near the female. Thus, all aspects of courtship were reduced in the presence of a male intruder. Time spent near the bottled male also decreased in these simultaneous presentations; however, this decrease was less dramatic than the reduction in time spent near bottled females. Habitat quality did not affect these trade-off decisions, but the bite rate exhibited toward the bottled male increased in the simultaneous presentations compared to the single presentations. Due to this increase in a territorial male's defensive behavior when a female is present, we conclude that the presence of a female temporarily increased the value of a territory. We suggest that the possible loss of a territory to an intruding male takes priority over the potential benefits of successfully courting a single female and that it is a male's future reproduction, as well as his current reproduction, by which he assesses his benefits. *Key words*: aggression, beaugregory damselfish, Caribbean, coral reefs, courtship, mate choice, *Stegastes leucostictus*, territoriality. [*Behav Ecol* 13:676–681 (2002)]

Discussions of both aggression and mate choice have focused on the trade-offs involved in making decisions. That is, aggression and mate choice are analyzed with respect to the costs and benefits individuals accrue from performing those behaviors. For example, during aggressive encounters, individuals selecting an appropriate aggressive response might base that decision on the quality of the resources at stake and on their own relative abilities (Enquist and Lemiar, 1987; Lemiar and Enquist, 1984; Parker, 1974). Benefits gained from winning a fight must be at least equivalent to the costs of the fight tactic used. Empirical studies on multiple species have supported this cost–benefit relationship when animals engage in aggression, especially when in defense of resources of different qualities (e.g., fish; Itzkowitz, 1979; Johnsson et al., 2000; Nijmon and Heuts, 2000; birds; Ewald and Orians, 1983; spiders; Riechert, 1979; see also review by Riechert, 1998). Similarly, mate choice has been viewed as a process of assessing the relative qualities among prospective mates (e.g., Halliday, 1983; Janetos, 1980; Johnstone et al., 1996; Moore and Moore, 1988; Real, 1990; Sullivan, 1994; Wittenberger, 1983). Here also, the cost of the behavioral tactic used to secure a mate is expected to be balanced or exceeded by the

benefits gained from that mating. Empirical work has found that mate searching varies in response to certain risks, such as predation (fish; Candolin and Voigt, 1998; Endler, 1987; Forsgren, 1992; Forsgren and Magnhagen, 1993; water striders; Sih et al., 1990; fiddler crabs; Koga et al., 1998; see also review by Magnhagen, 1991), revealing that mate choice decisions also involve trade-offs.

Animals may often be faced with multiple trade-off decisions simultaneously. For example, individuals may be confronted with both mates and competitors, thereby forcing aggression and mate choice decisions to overlap. In the variegated pupfish (*Cyprinodon variegatus*), the entrance of a female into a male's territory will stimulate neighbors to intrude and disrupt the courtship of the territorial male (Itzkowitz, 1974). Kodric-Brown and Brown (1984) observed that territorial males of various species seem to court a female while simultaneously defending against an intruder. Also, the mate-guarding behavior of some birds might decrease their opportunity for extrapair fertilizations (Westneat et al., 1990). Although territorial individuals have been observed to deal with these competing options, few studies have empirically determined the choices made when these competing options are presented simultaneously. In a laboratory study, Candolin (1997) showed that male three-spined sticklebacks (*Gasterosteus aculeatus*) significantly reduced their courtship and time spent with females when competitors were present. However, her study did not include male–male interactions, making it unclear what the decisions would be regarding a trade-off between courtship and aggression.

When a territorial male is presented with a potential mate

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and a competing male, the optimal behavior may depend on subtle fitness consequences introduced by this situation. For example, if the cost of losing a mating is higher than the cost of losing a territory, then courtship should take precedence over aggression. Furthermore, if the competitor threatens to attract the female away from the territorial male, the presence of the competitor might cause the territorial male to increase his courtship relative to a situation with no competitor. Alternatively, if the cost of losing a territory is higher than the cost of losing a mating, then territorial defense should take priority over that of courting a female. The cost of losing a territory would depend on the reproductive benefit territorial owners have over nonterritorial owners, the general availability of territories, and the quality of an individual's territory (reviewed by Maher and Lott, 2000). Territory quality might, in fact, alter how males deal with these trade-off decisions. For example, Real (1991) and Reynolds (1993) suggest that some males might court less because they hold more attractive resources; therefore, it might benefit males with high-quality territories to put more emphasis on defense while males with low-quality resources emphasize courtship. The presence of a female on a territory may in fact cause the territory to momentarily become more valuable, and consequently, territory owners might then be more aggressive toward competitors than when no female is present (*sensu* Enquist and Lemiar, 1987; Lemiar and Enquist, 1984; Parker, 1974). Related findings have been shown in brown-headed skinks (*Eumeces laiceps*) where males incurred more risk when guarding a female than isolated males (Cooper, 1999). Overall, if mating behavior and territorial defense are in conflict, the time devoted to a male intruder or to a female should be less when they are presented simultaneously than when they are presented individually.

In the present study, we examined how the simultaneous presence of male competitors and potential mates affects the fighting and mating decisions of natural populations of the beaugregory damselfish (*Stegastes leucostictus*). Males of this species defend small, permanent territories where competing males often court the same females that pass near their territories (Santangelo and Itzkowitz, personal observations). Natural aggressive interactions between established territorial neighbors are uncommon (Itzkowitz et al., 1995), but intrusions with fights do occur when a receptive female is present (Itzkowitz, personal observation). Therefore, *S. leucostictus* provides a good social system in which to test the trade-off decisions territorial males make when simultaneously presented with competitors and potential mates. We also examined the effects of territory quality on the resident's choice of engaging in courtship and/or defense. Previous studies have shown that our artificial breeding sites (see Methods for description) quickly improve the reproductive success of beaugregory damselfish males in comparison to their natural rubble breeding sites (Itzkowitz, 1991; Itzkowitz and Makie, 1986; Itzkowitz et al., 1995). Itzkowitz and Haley (1999) showed that males on artificial breeding sites increase their courtship intensity toward females and suggested that courtship is an honest indicator of breeding-site quality. This also suggests that males assess breeding-site quality, and therefore breeding-site quality could influence how males deal with mating and aggression decisions. An increase in territory quality has been shown to increase the aggressive intensity of *S. planifrons*, a damselfish closely related to the beaugregory damselfish (Itzkowitz, 1979). We therefore predicted that males with high-quality artificial breeding sites would show higher levels of aggression to both the single and the simultaneous male and female presentations compared to the males with lower quality breeding sites. Although beaugregory damselfish males have been shown to court more when they hold more attrac-

tive resources (Itzkowitz and Haley, 1999), the presence of an intruding male competitor could interact with territory quality such that males defending high quality territories court less than those defending lower quality territories.

A beaugregory damselfish male's decision to court or defend may depend on his current reproduction (i.e., number of eggs within his breeding site) or both his previous and current reproductive success (i.e., the number of eggs he has secured overall in his territory). Because males will eat the eggs of their neighbors (Itzkowitz, personal observation), we predicted that the more eggs a territorial male guards, the more aggressive will be his defense. If males base their assessment of breeding-site quality on the number of eggs they obtained within that territory, then, regardless of their current reproduction, territorial males may be more aggressive toward competitors if their previous reproductive success is high. Although a previous study (Itzkowitz and Haley, 1999) found no relationship between a male's courtship and his current or previous reproductive success, these factors may influence the courtship of territorial males when they are presented with a female and a male competitor together.

## METHODS

### Locality and social system

This study was performed in the sand and rubble habitat found in the backreef environment in Discovery Bay, Jamaica. The study was carried out during July 1998.

Male beaugregory damselfish establish permanent, all-purpose territories in quiet, shallow backreef habitats. Within their small territories (1–2 m diameter), there is typically a breeding site consisting of a piece of rubble that has a smoothed-walled crevice. When mating, a female enters the male's territory and deposits her adhesive eggs on smooth walls within the crevice of the breeding site and then leaves. The male provides no direct parental care except to protect the eggs against diurnal fish predators (Itzkowitz and Makie, 1986). Within 6 days the eggs hatch, and the larvae float away as plankton. Successful males often have multiple clutches from several females, and these males will remain on the same territory for long periods of time, whereas unsuccessful males move often until they find a territory of suitable quality (Itzkowitz et al., 1995). The relative size differences between males does not significantly correlate to their differences in reproductive success (Itzkowitz and Makie, 1986). Nonterritorial males do not reproduce. We have never observed, nor has it ever been reported, that males will sneak into another male's territory to spawn. Therefore, the purpose of all intrusions appears to be the acquisition of the territorial male's resources (i.e., food, breeding site, females, etc.). Females have not been studied as thoroughly as males. They hold territories in the vicinity of males but often travel considerable distances, bypassing closer males, before choosing a mate and spawning (Horne and Itzkowitz, 1995; Renshaw, 1994).

### Natural and artificial breeding sites

Natural breeding sites within the territories of reproductively successful males are highly variable but typically have a piece of rubble that is usually less than 0.5 m in height or diameter and contains a protected smooth-walled crevice (see previous section). In an effort to compare males defending similar breeding sites, artificial sites were devised (see Itzkowitz, 1991; Itzkowitz and Makie, 1986; Itzkowitz and Haley, 1999). These breeding sites were placed onto or next to males already defending natural sites. Males began defending these artificial sites almost immediately. The sites consist of four 15-cm

length of 10-cm diam PVC pipe bolted in an “+” pattern on a 30-cm square plastic base (see photograph in Itzkowitz and Haley, 1999). Eggs were often deposited within the plastic tubes within 48 h. Eggs were too small to count in the field, and therefore estimates of reproductive success were based on length  $\times$  width ( $\text{cm}^2$ ) measurements of the oval egg clusters. In this study we used only eggs that were deposited within the past 24 h, as indicated by their bright yellow color. After 24 h, the eggs darken and become black on the day of hatching (approximately 6 days after being deposited).

### Experimental design

We provided each of 28 males defending natural breeding sites with a new artificial site. In a similar area, approximately 6 m away from the artificial sites, we tagged the natural breeding sites of 28 other males. We separated the artificial sites from the natural sites into two distinct areas because it allowed us to shorten the time to both find and swim to specific males while carrying a specific combination of stimulus bottles. Given our experience in this backreef habitat (e.g., Itzkowitz, 1990, 1991; Itzkowitz and Haley, 1999; Itzkowitz and Mackie, 1986; Itzkowitz et al., 1995, 2000), we were confident that our selection of two separate localities for the different habitat qualities would yield groups of males that were highly similar. The results presented here are consistent with these past studies, indicating that the differences between groups of males was based on the quality of their sites and not on their general location.

Over a 21-day period, we monitored the reproductive success of males defending only the artificial breeding sites. Accurate measurements of the number of eggs found within natural sites are extremely difficult, and previous studies have found that most males on natural sites rarely reproduce (Itzkowitz, 1991).

On each of 7 consecutive days, we randomly selected 10 males using artificial breeding sites (out of 28) and another 10 using natural rubble (out of 28). Random selection was performed by picking numbers out of a hat that corresponded to particular males. The decision to use only 10 males a day from each breeding site quality type was based on time limitations, as the daily presentations took between 4 and 5 h. On each day of testing, each male tested was presented with (1) a bottled female and an empty bottle (the “single female” condition), (2) a bottled male and an empty bottle (the “single male” condition), and (3) a bottled male and a bottled female (the “paired male” and “paired female” conditions). The order of the presentations was alternated between days. At the end of the testing period, all males had been tested at least twice. Three males (one from the artificial sites and two from the natural sites) were dropped from the analysis due to missing data. The final sample sizes were 27 for the artificial sites and 26 for the natural sites.

The males and females were presented in 1-l Nalgene bottles with holes drilled into the covers to allow for the passage of any possible olfaction or auditory stimuli between individuals. This is a common method of presenting both heterospecifics and conspecifics to damselfish males (Itzkowitz and Haley, 1999; Itzkowitz and Mackie, 1986; Itzkowitz et al., 1995; Myrberg and Thresher, 1974). Also, within our experiment, test subjects appeared to behave normally toward bottled individuals and recognized them as conspecifics (i.e., presented males were attacked, whereas presented females were courted). Therefore, it is unlikely that the results presented are an artifact of presenting the stimuli fish in bottles.

To control for the effect of bottle numbers, an empty bottle accompanied the single presentations of the female and the male. In both the paired and single presentations, the two 1-l

Nalgene bottles were placed on opposite sides of the male’s territory at about 30 cm from the breeding site (therefore the bottles were approximately 90 cm from each other). We observed the defender’s behavior for 180 s. The bottled males and females were collected on each day of testing and thus there were daily changes in the males and females. On each day, the male and female used for the paired presentations were different from individuals used for the single male and single female presentations. Once a day’s testing was completed, all four fish were released immediately.

After placing the two bottles near a male, we took the following records for 180 s: (1) the time the defender was within 10 cm of a bottle, (2) the number of times the defender made biting movements at the jar of the male, and (3) the number of courtship dips performed at any distance from the female’s bottle. The dip display is a rapid downward movement of several centimeters and then a fast upward movement of about 10 cm. During a succession of dips, the dorsum of the male becomes bright yellow.

### Analysis

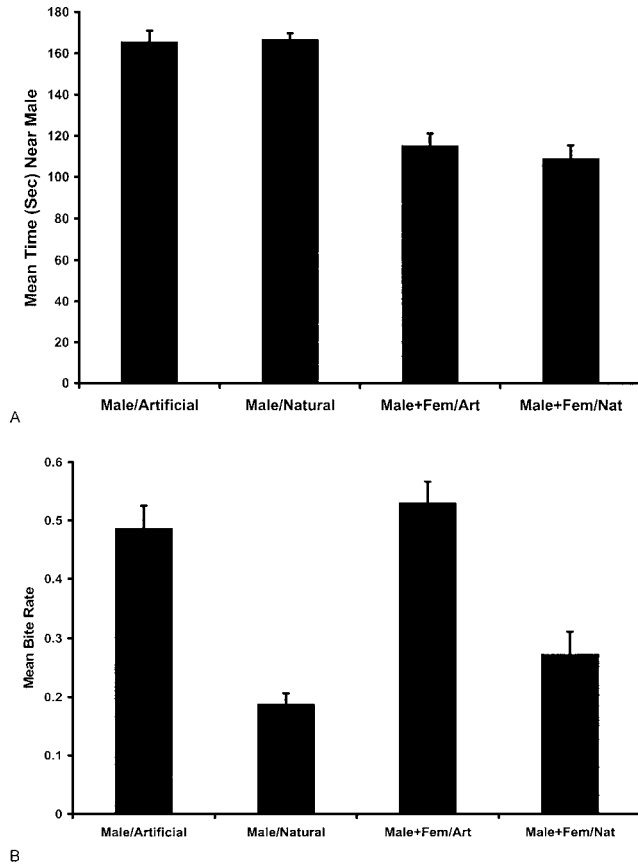
During the course of the study, each of the 53 males received at least two replicates of each stimulus (i.e., a single female presentation, a single male presentation, and a paired presentation of a male and female). From these replicates, means were generated for each behavior engaged in by the territorial male for each type of presentation (i.e., time near male, time near female, number of bites, bite rate, and number of dips). We analyzed behavior toward the bottled male and toward the bottled female separately. Each of the dependent measures was subjected to a 2 (single presentation vs. paired presentation)  $\times$  2 (artificial breeding site vs. natural breeding site) mixed within-subject factorial analysis of variance (ANOVA), with single versus paired presentations a within subject (i.e., repeated-measures factor) and artificial versus natural breeding sites a between subject (i.e., independent groups factor). To account for any heterogeneity of variances between groups, we set our significance level at 0.025. Variance heterogeneity causes an increase in the probability of making a Type I error, therefore adopting a lower significance level is an appropriate correction (Keppel, 1991). Furthermore, non-parametric statistics yielded the same results reported below. However, we used the ANOVA because of the ease it lends to testing, presenting, and discussing data.

## RESULTS

### Behavior toward the bottled male

Means (and standard errors) for time the defending fish spent near the bottled male are presented in Figure 1A. Less time was spent near the bottled male when the bottled female was also present compared to when she was not present (63% vs. 92% of session time;  $F_{1,51} = 106.79$ ,  $p < .0001$ ). There was no significant main effect of breeding-site quality (artificial vs. natural;  $F_{1,51} = 0.04$ ,  $p > .80$ ), nor was the interaction significant ( $F_{1,51} = 0.27$ ,  $p > .60$ ). In summary, breeding-site quality did not influence the amount of time a defender spent near a bottled male, and the presence of a female uniformly reduced the time near the bottled male.

To remove the confounding influence of the time spent near the bottled male, we calculated bite rate (i.e., number of bites per second of time near the bottled male) to measure the level of the territorial male’s aggression. Both main effects were significant for bite rate (Figure 1B). Defenders of artificial breeding sites had a higher mean bite rate (0.51) than defenders of natural breeding sites (0.24) ( $F_{1,51} = 12.50$ ,  $p =$



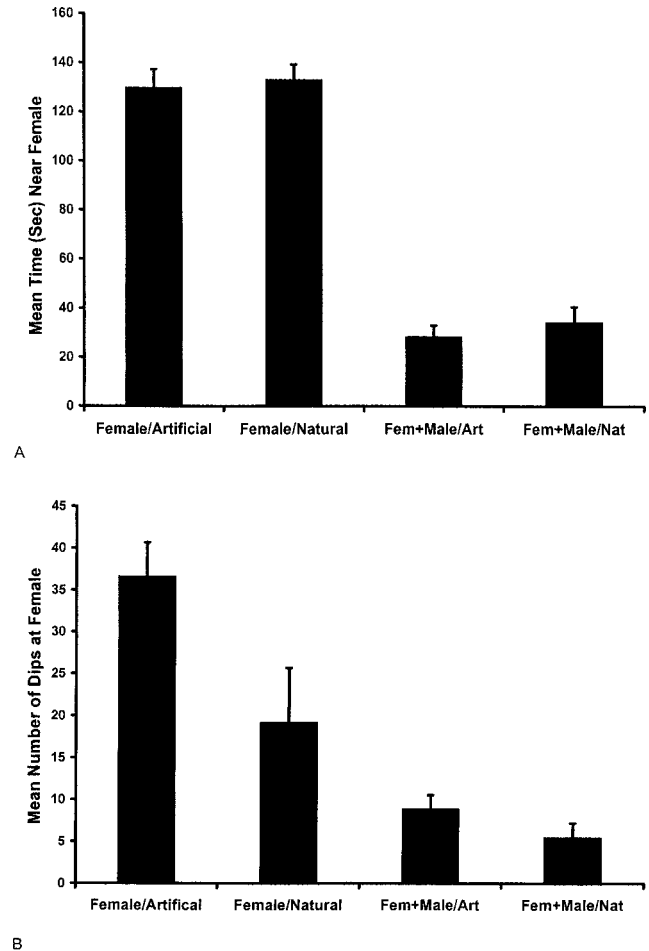
**Figure 1**  
The behavior of territorial males toward male competitors in both single and double bottle presentations and both natural breeding sites and artificial breeding sites. Male/Artificial = single male and an empty bottle presented to defenders using artificial breeding sites; Male/Natural = single male and an empty bottle presented to defenders using natural breeding sites; Male+Fem/Art = a male and a female presented to defenders using artificial sites; Male+Fem/Nat = a male and a female presented to defenders using natural sites. (A) The mean and SE of the amount of time defenders spent within 10 cm of the bottled male. (B) The mean and SE of the defenders' bite rates (i.e., number of bites toward the bottled male/s spent near the bottled male) directed at the bottled male.

.0009). Also, the bite rate was higher for the paired condition (0.41) than for the single condition (0.33;  $F_{1,51} = 37.12$ ,  $p < .0001$ ). However, the interaction between the two breeding site types and the two types of presentation was not significant ( $F_{1,51} = 1.59$ ,  $p = .21$ ), indicating that the presence or absence of the bottled female had an additive effect on bite rate across breeding-site qualities.

In summary, a comparison of territorial males' bite rate revealed that males defending artificial breeding sites had a higher biting intensity toward the male intruder than those defending natural breeding sites and that the presence of a female uniformly increased biting intensity toward the male intruder across breeding-site qualities.

#### Behavior toward the bottled female

Defending males spent much more time near the bottled female in the single condition (73% of session time) than in the paired condition (17% of session time; Figure 2A;  $F_{1,51} = 365.51$ ,  $p < .0001$ ). The main effect of breeding-site quality



**Figure 2**  
The behavior of territorial males toward females in both single and double bottle presentations and both natural breeding sites and artificial breeding sites. Female/Artificial = single female and an empty bottle presented to defenders using artificial breeding sites; Female/Natural = single female and an empty bottle presented to defenders using natural breeding sites; Fem+Male/Art = a female and a male presented to defenders using artificial sites; Fem+Male/Nat = a female and a male presented to defenders using natural sites. (A) The mean and SE of the amount of time defenders spent within 10 cm of the bottled female. (B) The mean and SE of the number of dips defenders performed toward the bottled female.

( $F_{1,51} = 0.50$ ,  $p = .49$ ) and the interaction ( $F_{1,51} = 0.00$ ,  $p = .99$ ) were not significant.

Males performed more dips in the single condition than in the paired condition (Figure 2B;  $F_{1,51} = 29.78$ ,  $p < .0001$ ) and performed more dips on artificial breeding sites than on natural breeding sites ( $F_{1,51} = 5.89$ ,  $p = .0188$ ). The interaction, however, was not significant ( $F_{1,51} = 4.12$ ,  $p = 0.05$ ;  $\alpha = 0.025$ ; see Methods), indicating that the effect of breeding-site quality and the effect of the presence or absence of a bottled male on the number of dips performed were additive.

In summary, although the time the defender spent near the bottled female was influenced only by the presence or absence of the male and not by breeding-site quality, the defender's courtship was influenced by both factors. That is, defenders of artificial breeding sites dipped more than defenders of natural breeding sites. Furthermore, the presence of a bottled male reduced the number of dips performed by territorial males, and the amount of this reduction was about equal for

each breeding-site quality (i.e., there is no significant interaction between breeding-site type and presentation type).

### Reproductive success, courtship, and aggression

Similar to previous studies that used these types of artificial sites, reproductive success among males was highly variable (e.g., Itzkowitz, 1991; Itzkowitz and Makie, 1986). To assess the influence of daily reproductive success on the defender's courtship and aggressiveness, we compared the number of eggs within a male's breeding site with number of dips elicited toward the single bottled female and the number of bites directed against the single bottled male on each day of testing. We tested these relationships with the 10 males tested on each day of the study. Neither the number of dips nor the number of bites was significantly correlated with the number of eggs on any of the 7 test days (Pearson correlation test;  $p > .05$  for each day). (Note that for  $N = 10$ , the power to detect a medium effect size of  $r = .30$  is 0.13.)

To test if overall reproductive success influenced the aggression or courtship of a defender, we also compared the total number of eggs a male acquired during the study with his mean number of dips toward a single bottled female and his mean bite rate toward a single bottled male. As 10 males out of 28 were randomly selected on each day of testing, mean values were based on a variable number of tests. Neither the mean bite rate nor the mean dip number was significantly correlated with the total number of eggs a male received (bite rate vs. total eggs,  $N = 27$ ,  $r = .23$ ,  $p > .05$ ; dips vs. total eggs,  $N = 27$ ,  $r = -0.08$ ,  $p > .05$ ). (Note that for  $N = 27$ , the power to detect a medium effect size of  $r = .30$  is 0.34.)

In the double bottle experiment, the paucity of courtship dips and the time spent near the bottled female precluded any analysis comparing reproduction to courtship behavior. However, similar to the single bottled male, there was no significant correlation between the bite rate directed at the male in the paired condition with the number of new eggs for any of the 7 test days (Pearson correlation test;  $p > .05$  for each day).

In summary, the presence or absence of eggs, as well as the quantity of eggs, were not significantly correlated to aggression against bottled males nor to courtship directed at the bottled females. Furthermore, the mean bite rate and the mean dip number (for single presentations only) were not significantly correlated for males on artificial sites ( $N = 28$ ,  $r = .19$ ,  $p > .05$ ) nor for males on natural sites ( $N = 28$ ,  $r = .35$ ,  $p > .05$ ), indicating that there was no significant relation between aggression behavior and courtship behavior.

### DISCUSSION

Territorial males on both habitat quality types spent less time with the bottled male and the bottled female when we presented them together compared to when we presented a male and a female singly. This indicates that mating behavior and territorial defense are in conflict in the beaugregory damselfish and that territorial males must engage in a trade-off when both situations occur. Although we predicted that defenders would reduce their courtship to a bottled female by spending time attacking the bottled male, we did not anticipate such a large decrease in courtship behavior. Clearly, our results support the hypothesis that the male values his territory, regardless of its quality, more than he does a potentially receptive female. For instance, defenders reduced their time near the female by about 75% when presented with an intruder and a female simultaneously compared to single-female presentations. Furthermore, defenders also substantially reduced their conspicuous courtship dips. Aggressive behavior toward the bottled male was less affected by the presence of the bottled

female. That is, territorial males reduced their time near a bottled male by approximately 30% but exhibited a significantly higher bite rate when presented with a male competitor and a female simultaneously compared to single-male competitor presentations. This indicates that, aside from the territory itself, females also hold a value for the male and supports our contention that the presence of a female momentarily increases the value of a territory. This is similar to the findings of Cooper (1999), where the presence of a female skink increased the risk a male incurred because of the potential reproduction she represented.

Within the present study, the overall emphasis on defense instead of courtship by defenders on both high- and low-quality sites indicates that the cost of losing a territory is greater than the cost of losing a mating. In a previous study, Itzkowitz et al. (1995) monitored the intense competition that exists among males for breeding sites and observed that males rarely defeat territory holders and that they acquire new territories only when sites are created by storms that erratically rearrange the habitat. Thus, the difficulty of replacing a breeding site (even of poor quality) lost to a competitor may have long-term reproductive implications that overshadow the loss of any single female. These results imply that the more males intrude on a territory, the more females a territorial owner will ignore, and eventually this strategy will have a negative effect on the male's reproductive success (i.e., with many intrusions, defenders ignore all females). It is at this point that the cost of being territorial will outweigh its benefit, and we can predict that males would abandon territorial behavior.

As expected, males on low-quality sites showed lower aggression toward the male intruder presentations than males on high-quality sites. Similarly, and in support of previous results (Itzkowitz and Haley, 1999), dip displays toward female presentations were also significantly lower for males on low-quality sites than for males on high-quality sites. The fewer number of dips and lower bite rate exhibited by males on poor sites may reflect the costs associated with such behavior. For example, we have observed males performing the gaudy dip display to be especially vulnerable to predation by the common sand diver predator (*Synodus intermedius*). Itzkowitz and Haley (1999) suggested that males are honest signalers of the quality of their breeding sites because females eventually inspect, and perhaps reject, these breeding sites if the quality is insufficient. This predation cost may be what causes males to be honest signalers; otherwise, even males on low-quality breeding sites should court females at high levels.

In the case of aggression, Itzkowitz (1979) suggested that damselfish appear to reduce the risks of aggression based on a decrease in the potential reproductive payoffs of the territory. This indicates that males are attempting to increase their survival and thus their chances of acquiring a better quality habitat in the future. However, males on high-quality habitats would not gain by restraining themselves and so exhibit elevated aggression to protect their current territory. Alternatively, high-quality habitats may provide males with more food and safety than low-quality habitats and thus allow these males to exhibit more aggression and courtship. However, this appears unlikely because food seems unlimited within the backreef habitat (i.e., damselfish feed on algae), and the relatively open surroundings of the artificial sites appear to provide these males with less safety than males using natural sites crowded by rubble. In fact, all the predatory attempts we observed against beaugregory damselfish were to males on high-quality habitats.

The lack of a significant interaction between habitat quality and bottle presentation (i.e., single vs. simultaneous presentations) for aggression, courtship, and time spent at the bottles indicates that habitat quality had no effect on the male's trade-off decisions. This is surprising because, although territory

quality influenced how territory owners treated intruding males and females, territory quality did not affect how males dealt with the decision to court or defend when they were presented simultaneously with an intruding male and a female.

The presence or absence of eggs did not change the defender's aggressive behavior or courtship behavior in either the single or simultaneous bottle tests. This confirms previous findings where the number of eggs present did not affect the courtship intensity of territorial males (Itzkowitz and Haley, 1999). The fact that courtship and aggression were not related to individual reproductive success but were affected by territory quality, as well as the presence of a male and a female, suggests that territorial males assess the quality of their breeding sites based on their future reproductive potential.

Our inability to accurately predict the trade-off decisions when territorial beaugregory males were confronted with both a female and a male regardless of territory quality was unanticipated because the male's behavior with either single stimulus (i.e., single bottled males or single bottled females) was highly predictable for each of the territory types. Our results clearly indicate that both the territory and the female are important to the male. However, the precise benefit that accrues over time for securing either a territory or a female is not known. We suspect that the complexity behind these trade-off decisions was caused by having males decide between a stake that has a long-term payoff (i.e., the territory) and a short-term payoff (i.e., the female). This kind of mixed-stake cost-benefit model has been effectively used to explain the schedules of reproduction individuals used over their lifetime (Rogers and Sargent, 2001). To better understand the trade-off decisions depicted in this study for the beaugregory damselfish, we believe a starting point is to develop accurate measures for the lifetime reproductive success of identified males defending specific territories (*sensu* Clutton-Brock, 1988).

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