

Caribbean damselfish with varying territory quality: correlated behaviors but not a syndrome

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The behavioral syndrome hypothesis suggests that individual animals within a population behave differently due to specific behavioral types, and these should be consistent across behaviors or in different contexts. In contrast, for animals that live within an environment in which territory quality can change over time, natural selection should have favored behavioral flexibility and modulation of the cost of defense in relation to territory quality. This would require assessment of the territory followed by displays of appropriate types and intensities of behavior. We examined the territorial behavior of male beaugregory damselfish (*Stegastes leucostictus*) by enhancing territory quality using artificial breeding sites and comparing their behavior to males on lower quality natural sites. When male fish were defending high-quality artificial territories, they had higher levels of aggression toward male conspecifics and courtship toward females than when on low-quality natural territories. We also found that aggression and courtship behaviors were correlated on natural sites but not on artificial sites. Behaviors were not correlated within individuals when males switched from natural to artificial territories or from artificial to natural territories. These results indicate that males assess their current territories and adjust behaviors accordingly and that courtship and aggressive behaviors are not linked within a permanent behavioral syndrome. *Key words:* adaptive plasticity, beaugregory damselfish, behavioral syndromes, *Stegastes leucostictus*, territory quality. [*Behav Ecol*]

Personalities, temperaments, or behavioral types have long been the interest of scientists and have been studied in more than 60 species, from ants to zebrafish (reviewed by Gosling 2001). There has been recent interest in empirical studies and theoretical discussions that focus on individual personalities, rather than mean behaviors of a population (see Dall et al. 2004; Sih et al. 2004a, 2004b; Bell 2007; Réale et al. 2007); with interest especially focused on “behavioral syndromes”—when the behaviors of individuals fluctuate consistently across various functional contexts (Sih et al. 2004a; Sih, Bell, Johnson, et al. 2004). The behavioral syndrome hypothesis may provide one explanation: animals behave within their specific behavioral type (or temperament) (Sih et al. 2004a; Sih, Bell, Johnson, et al. 2004; Bell 2007). It is alternatively possible that animals behave differently due to assessments of diverse habitats or situations and exhibit different behavioral responses (Neff and Sherman 2004). Differences in animal behaviors may be due to variation in environmental or life history, not necessarily variation in temperaments.

Explicit behavioral syndromes have been shown in many populations by determining if a rank-order of individuals is maintained across different behaviors or in different situations. For example, male western bluebirds (*Sialia mexicana*) show a significant, positive correlation between aggression toward a heterospecific avian intruder (nest defense) and conspecific male-male aggression, as well as a negative correlation between conspecific male-male aggression and male provisioning rate (parental care) (Duckworth 2006). Female fishing spiders (*Dolomedes triton*) show an adult boldness syndrome across control, foraging, and courtship contexts (Johnson and Sih 2005, 2007). Positive correlations are seen between activity levels in foraging and antipredatory response in the streamside salamander (*Ambystoma barbouri*) (Sih et al. 2003). Three-spined sticklebacks (*Gasterosteus aculeatus*) show

positive correlations of aggression across the contexts of territory defense and antipredatory response (Huntingford 1976a, 1976b), and brook charr (*Salvelinus fontinalis*) exhibit correlations between prey searching (in the field) and activity and space usage (in the laboratory) (Wilson and McLaughlin 2007).

Although many examples of behavioral syndromes exist, the occurrence of these correlated behaviors potentially leads to constraints on behavioral plasticity—animals can only modify their behavior within the limits of their specific behavioral type (or temperament) (Neff and Sherman 2004; Sih et al. 2004a, 2004b; Sih, Bell, Johnson, et al. 2004; Bell 2007). Thus, it would seem that behavioral syndromes would prevent individuals from adaptively altering their behavior. Ideally, individuals should be able to instantaneously change their behavior in accordance with the existing circumstances and display appropriate behaviors (e.g., exhibit adaptive behavioral plasticity) (Neff and Sherman 2004). That is, if there are changes in habitat or threat levels, individuals should respond based on the situation, not due to their personal temperament.

The objective of this study was to determine if male-male aggression and courtship behaviors of male tropical beaugregory damselfish (*Stegastes leucostictus*) are an example of a behavioral syndrome or context-dependent adaptive behavioral plasticity or, perhaps, both. To determine if these behaviors are correlated across various functional situations, we present territorial male beaugregory damselfish with a conspecific stimulus male or female multiple times in 2 different territorial situations: on the natural territory chosen by the fish and on an artificial territory (made of 4 pieces of PVC pipe). The artificial territory is considered to be a superior territory (higher quality breeding site) for male damselfish because fish readily abandon their natural territories for artificial ones and their reproductive success is improved (Itzkowitz and Makie 1986; Itzkowitz 1991).

We hypothesize that male beaugregory damselfish will assess the quality of their territory and adjust their behaviors accordingly (e.g., increase levels of courtship and aggression toward male conspecifics). If aggression and courtship behaviors are

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linked within a behavioral syndrome, then we would expect a positive correlation between the behaviors, regardless of changes in territory quality, though we expect overall behaviors to be higher on high-quality territories (artificial sites) than on low-quality territories (natural sites). If individual behavioral types are maintained, we would expect correlations of behaviors across the population regardless of changes in territory quality. However, if individual beaugregory damselfish are not confined by their behavioral types and are able to change behaviors based on assessment of current territory quality, then we would predict that males would behave at high levels on high-quality territories in order to maximize reproduction, and thus, correlations may not be maintained with changes in territory quality.

MATERIALS AND METHODS

Study species

The beaugregory damselfish (*S. leucostictus*) is a polygynous fish that breeds year round (Itzkowitz 1985). Males defend territories (1–2 m in diameter) in small rubble and sand habitat (Itzkowitz 1985). Within each territory is a smooth surface (usually within a crevice) on which females can deposit their adhesive eggs. While courting females, males perform dip displays (an exaggerated swimming behavior in which the male swims quickly down toward the substrate and then up again), and their dorsal coloration changes from a dull gray color to bright yellow. After the females spawn, they leave the territory, and the male is left to defend the eggs against diurnal predators (Itzkowitz and Makie 1986). Males will also defend their territories from other conspecific males by chasing, biting, and laterally displaying toward offending intruders (Santangelo et al. 2002).

Test subjects

The fish in this study were all located in the shallow back reef of Discovery Bay, Jamaica, and were observed for approximately 3 weeks in June 2007. Eighty-two male damselfish that were defending natural breeding sites were chosen, and a numbered tag was tied to a rock or coral near the center of the territory. In previous studies of the Jamaican beaugregory damselfish, individual territorial males have been uniquely marked using nontoxic acrylic paint and were shown to remain on their territories for at least 60 days (Itzkowitz et al. 1995), thus tagging territories is equivalent to tagging individual fish without any of the possible side effects that marking individual fish may have. Additionally, individual fish can often be identified by specific features (coloration, patterns, fin shape, scars, etc.), and daily efforts were made to identify each fish based on personal observations of such traits.

At the beginning of the study period, artificial breeding sites were placed in the center of the territories of approximately half of the designated males. Artificial breeding sites were constructed from four 10-cm long opaque PVC tubes, each 7.6 cm in diameter. The tubes were bolted to a 30-cm² Plexiglas base in a cross formation. Openings to the tubes occurred in the center of the cross and at each of the 4 ends (for photo see Itzkowitz and Haley 1999). These artificial sites are preferred to natural breeding territories, and when placed within a natural territory, males quickly take residence (Itzkowitz and Makie 1986; Itzkowitz 1991; Itzkowitz et al. 1995). In a previous study, only 5% of males were able to usurp artificial territories from neighbors; males cannot, or do not, oust other males from high-quality sites (Itzkowitz et al. 1995).

The males were arbitrarily assigned into one of 4 experimental groups: males that were observed on their original territory

for the entire study period (natural–natural) ($n = 20$); males that were given an artificial site halfway through the study period (natural–artificial) ($n = 20$); males that were given an artificial site at the beginning of the study period and had it removed halfway through the study period (artificial–natural) ($n = 19$); and males that were observed at an artificial site for the duration of the study (artificial–artificial) ($n = 19$). Within our specific study, each of the 82 fish with tagged territories was observed daily by at least one of the researchers, and in only 4 instances did we remove males from our experimental groups because we questioned the identity of the individual: 1) when artificial sites were removed, one male vacated his territory or was preyed on; 2) when artificial sites were added, one male seemed to share his territory with another male; 3) when artificial sites were added, one male abandoned his site or was preyed on; and (4) one male that remained on an artificial site for the entire 3-week testing period had his territory usurped by a larger heterospecific damselfish.

After the initial placement of the artificial sites for the respective groups, fish were given 48 h to acclimate and establish their new territory. After the initial 7-day study period (Stage 1), artificial sites were removed from one experimental group (artificial–natural) and new artificial sites were introduced to a different experimental group (natural–artificial). Fish were again given a 48-h acclimation period and were tested during a second 7-day study period (Stage 2).

Aggressive Behavior

Additional male beaugregory damselfish to be used as stimuli fish were caught approximately 20 m from the edge of the testing area. These additional males were full-size adults (measured with a caliper; 68.6–89.6 mm total length) and were caught while defending their own territories. The fish were immediately used for testing and released in the same area of capture after testing.

A single stimulus male was placed in a 2-l clear plastic presentation cylinder (165 mm diameter \times 240 mm height) that was covered with a plastic lid with holes that allowed water flow. A 1.5 kg dive weight was placed at the bottom of each presentation cylinder to stabilize movement. The presentation cylinder with fish was placed approximately 10 cm from the edge of the male's breeding site. The resident males' aggressive behaviors were observed during a 3-min testing period. Male aggression was quantified by the amount of time spent within one body length of the presentation cylinder and the number of bites and lateral displays directed toward the stimulus male.

Each resident male was tested with 3 different stimulus males during Stage 1 and an additional 3 males during Stage 2. Each of these 3 tests occurred on a different day during each stage, with no more than 1 day between tests. The same stimulus male was used within each experimental group on any given day, in order to provide direct comparisons between the males within each experimental group. Different stimulus males were often used between experimental groups to control for any possibility of males responding to a particular individual, rather than intruders in general.

Courtship Behavior

Female beaugregory damselfish to be used as stimuli fish were also caught approximately 20 m from the edge of the testing area of the backreef. These females were full size adults (52.4–66.5 mm total length) and were placed near territorial males that were not part of the study to determine if the female elicited a courtship response. Like stimulus males, females

were also immediately used for testing and released in the same area of capture after test completion.

For courtship tests, a single stimulus female was placed in a 2-l clear plastic presentation cylinder (165 mm diameter \times 240 mm height) that was covered with a plastic lid with holes that allowed water flow and a 1.5-kg dive weight to stabilize movement. The presentation cylinder was placed approximately 10 cm from the edge of the male's breeding site. The resident males' courtship behaviors were observed during a 3-min testing period. Courtship was quantified by the amount of time spent within one body length of the presentation cylinder and the number of courtship dips toward the female.

Each resident male was tested with 3 different females during Stage 1 and an additional 3 females during Stage 2. As in the aggression tests, the same stimulus fish was used within each experimental group on any given day, but different females may have been used between experimental groups. Each of the 3 tests occurred on different days, with no more than 1 day between tests. The order in which a courtship test and an aggression test were administered was randomized over each stage and between experimental groups. Aggression and courtship tests could occur on the same day for a given experimental group, with at least 2 h between tests. All observations occurred between 8.30 and 13.00 h.

Statistical Analysis

For both aggression and courtship, the behaviors of the 3 trials were averaged together for each 7-day study stage, and these averages were used to determine if there was a correlation of behaviors between Stage 1 and Stage 2. A 2×4 factorial repeated-measures ANOVA was used to determine effects within and between experimental groups across the 2 experimental stages. Courtship and aggressive behaviors were also analyzed to determine if a correlation between the 2 behaviors existed. Correlations were determined by use of Pearson's r test, and the level of statistical significance was set at $P < 0.025$ (Bonferroni correction) due to multiple comparisons.

RESULTS

A number of significant positive correlations were seen between Stage 1 and Stage 2, but only in the groups in which the territories were unchanged (natural/natural and artificial/artificial). Those individuals that remained on natural sites showed positive correlations in time spent with males ($r = 0.775$, $P < 0.001$), number of bites toward males ($r = 0.854$, $P < 0.001$), number of lateral displays toward males ($r = 0.694$, $P = 0.001$), and number of courtship dips toward females ($r = 0.515$, $P = 0.020$), though not in the amount of time spent with females ($r = -0.049$, $P = 0.839$), between Stage 1 and Stage 2. Individuals in the artificial/artificial group also showed positive correlations between the experimental stages in time spent with males ($r = 0.719$, $P < 0.001$), number of bites toward males ($r = 0.671$, $P = 0.002$), and number of dips toward females ($r = 0.542$, $P = 0.021$), but not lateral displays ($r = 0.149$, $P = 0.544$), or time spent with females ($r = 0.388$, $P = 0.101$). Males in the experimental groups that experienced a switch in territory quality (natural/artificial and artificial/natural) showed no significant correlations between Stage 1 and Stage 2 for any of the aggressive or courtship behaviors (Table 1).

For each of the 5 behaviors analyzed, there was a significant interaction between the experimental stage and the experimental group (Figure 1): time spent with male, $F_{3,54} = 17.643$, $P < 0.001$; bites toward male, $F_{3,54} = 28.592$, $P < 0.001$; lateral displays toward male, $F_{3,54} = 4.900$, $P = 0.004$; time spent with female, $F_{3,54} = 6.038$, $P = 0.001$; and court-

Table 1

Correlations over time (between Stage 1 and Stage 2) of aggressive and courtship behaviors for each of the 4 experimental groups

	Natural/ natural	Natural/ artificial	Artificial/ natural	Artificial/ artificial
Time near male	0.775 <0.001*	0.283 0.227	-0.045 0.854	0.719 0.001*
Bites	0.854 <0.001*	0.413 0.070	0.380 0.108	0.671 0.002*
Lateral Displays	0.694 0.001*	0.022 0.927	0.151 0.537	0.149 0.544
Time near female	-0.049 0.839	0.301 0.198	0.205 0.400	0.388 0.101
Dips	0.515 0.020*	0.166 0.485	0.151 0.536	0.524 0.021*

Top = r value; bottom = P value. Asterisk indicates statistical significance ($P < 0.025$).

ship dips toward female, $F_{3,54} = 4.903$, $P = 0.004$. There were no significant main effects of stage for any of the aggressive or courtship behaviors: time spent with male, $F_{1,18} = 0.064$, $P = 0.803$; bites toward male, $F_{1,18} = 0.046$, $P = 0.833$; lateral displays toward male, $F_{1,18} = 3.681$, $P = 0.071$; time spent with female, $F_{1,18} = 3.605$, $P = 0.074$; and dips toward female, $F_{1,18} = 0.030$, $P = 0.864$. A significant main effect of experimental group is seen for time with male, $F_{3,54} = 9.898$, $P < 0.001$; bites, $F_{3,54} = 17.117$, $P < 0.001$; and lateral displays, $F_{3,54} = 9.694$, $P < 0.001$. No significant main effect of experimental group was seen for time with female, $F_{3,54} = 1.871$, $P = 0.145$; or dips, $F_{3,54} = 2.376$, $P = 0.080$.

Significant correlations were seen among behaviors, but only when male damselfish were on natural sites. Males that remained on natural sites throughout the experiment (natural/natural) showed significant positive correlations among time spent with male, bites toward males, lateral displays toward males and courtship dips toward females, but not time spent with female (see Table 2). Males that were on natural sites during Stage 1 (natural/artificial) showed significant positive correlations among time spent with male, bites, lateral displays, time with female, and dips (though bites and dips were not significantly correlated) but showed no significant correlations among behaviors when they defended artificial sites during Stage 2 (see Table 3). A similar pattern was seen in the experimental group in which males defended artificial sites during Stage 1 and then defended natural sites (artificial/natural): behaviors were not significantly correlated during Stage 1 (artificial sites) but time spent with males, bites, lateral displays, and time spent with females (though not dips) were correlated when males defended natural territories (see Table 4). Males that spent both experimental stages on artificial sites (artificial/artificial) also showed no significant correlations among behaviors (see Table 2).

DISCUSSION

The data support the hypothesis that male beaugregory damselfish assessed the quality of their territory and adjusted their behaviors accordingly. That is, when male fish were defending high-quality territories (artificial sites), they had high levels of aggression toward male conspecifics and courtship toward females. When examining the groups whose territories were changed, this pattern is clear: males that were switched from natural to artificial sites increased aggression and courtship to the levels shown by males that remained on artificial sites

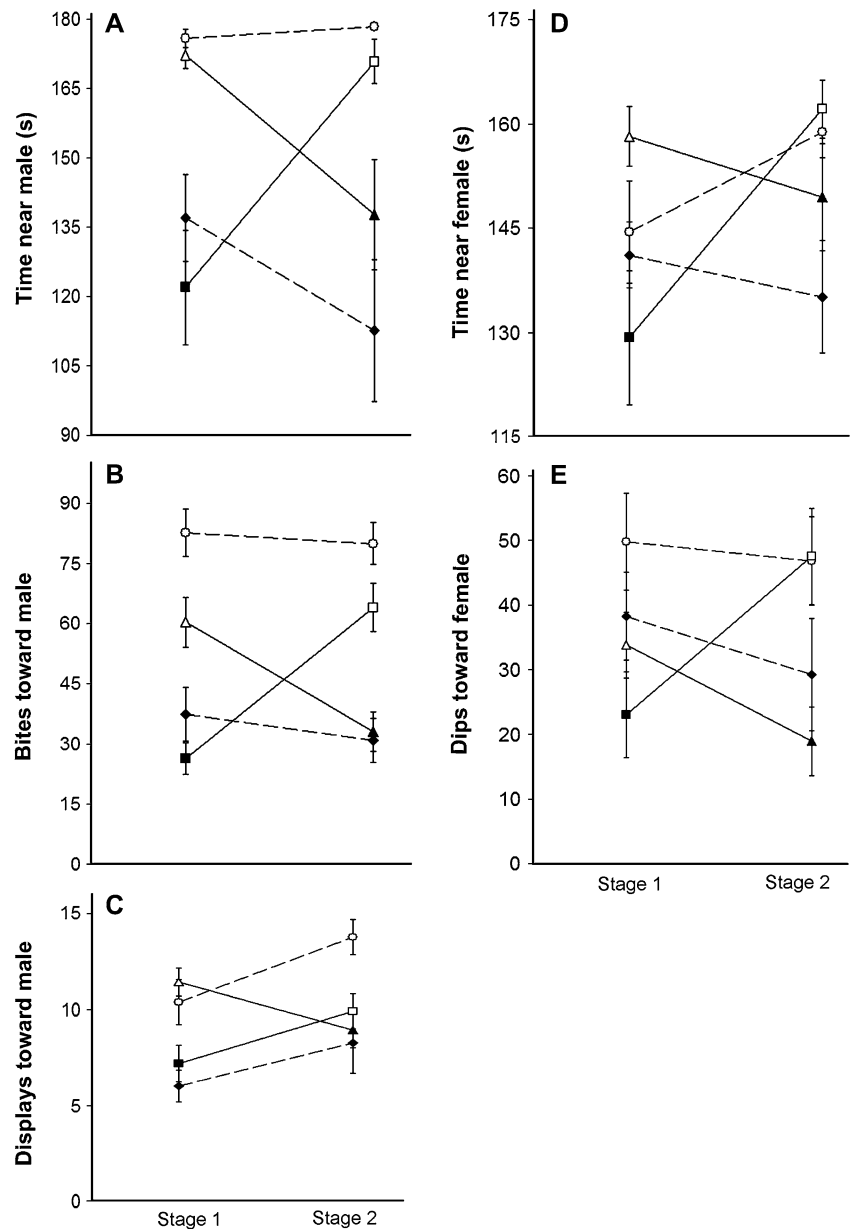


Figure 1

Mean \pm standard error of the mean time or number of aggressive (A, B, C) and courtship (D, E) behaviors during Stage 1 and Stage 2 on natural (filled shapes) and artificial (open shapes). Males that spent both experimental Stages on natural sites (diamond) and artificial sites (circle) did not change behaviors across Stages. Males that switched territories from artificial to natural (triangle) and from natural to artificial (square) adjusted their behaviors in accordance with territory quality.

for the entire observation period, whereas males that began the experiment by defending an artificial site that was then removed showed a decrease in the levels of behaviors to similar levels as males that continually defended natural sites. These changes in behavior were seen within days of territory quality alterations and persisted for the duration of the experiment. It is unlikely that these behavioral changes were due merely to the physical disturbance caused by the switching of sites, or we would have seen similar changes for both experimental groups (i.e., both increase or both decrease) rather than the adjustment of behaviors in accordance with the new territory's quality. The changes in behavior indicate that male beaugregory damselfish are able to assess the quality of the territory that they are defending and adjust their behaviors accordingly.

When comparing Stage 1 with Stage 2 for the experimental groups in which males remained on natural or artificial territories (natural/natural and artificial/artificial), there were significant correlations between stages for most behaviors (Table 1). This is consistent with the behavioral syndromes

hypothesis, which states that individuals behave in a consistent way (or have a reliable behavioral type or temperament) through time (Bell 2007). However, significant correlations across the specific aggression and courtship behaviors are not seen for manipulated experimental groups whose territory quality was switched before Stage 2 (natural/artificial and artificial/natural) (Table 1). This finding contradicts the presence of a behavioral syndrome because the behaviors are not correlated across contexts (Sih et al. 2004a, 2004b; Bell 2007). The lack of significant correlations suggests that the change in the quality of the territory resulted in modifications in behaviors that were not consistent with the behavioral type of the individual. If individual temperaments were maintained, then we would expect correlations of behaviors across the population, regardless of changes in territory quality.

Male damselfish that continually defended natural territories also showed significant positive correlations among different aggressive and courtship behaviors (Table 2), suggesting that the 2 types of behavior may be linked within a behavioral

Table 2

Correlations among various aggressive and courtship behaviors for males on natural sites (natural/natural) and males on artificial sites (artificial/artificial) during the entire observation period (Stage 1 and Stage 2 combined)

	Natural/natural			Artificial/artificial				
	Time near male	Bites	Lateral displays	Time near female	Time near male	Bites	Lateral displays	Time near female
Bites	0.825 <0.001*				0.294 0.222			
Lateral Displays	0.790 <0.001*	0.663 <0.001*			0.299 0.214	0.165 0.501		
Time near female	0.157 0.510	0.159 0.503	-0.013 0.957		0.318 0.185	0.098 0.690	0.058 0.813	
Dips	0.682 0.001*	0.738 <0.001*	0.751 <0.001*	0.117 0.623	0.157 0.520	-0.007 0.976	-0.041 0.867	-0.070 0.777

Top = r value; bottom = P value. Asterisk indicates statistical significance ($P < 0.025$).

syndrome. Time with female was not significantly correlated with the aggression or the courtship dip behaviors, though we suspect that this may be because dips directed at the female do not always occur directly next to the female and males can travel throughout their defended territory performing dips (Snekser JL, Leese J, Ganim A, Itzkowitz M, personal observation). We originally hypothesized that aggression and courtship may be coupled because both types of behaviors may be controlled proximately by androgenic hormones (reviewed by Balthazart 1983), a leading hypothesis for the persistence of behavioral syndromes (Ketterson and Nolan 1999; Bell 2007). Positive correlations among the aggressive and courtship behaviors were also seen when males in each of the manipulated groups were defending natural territories but not when on artificial sites (Tables 3 and 4). Males that remained defending artificial territories (Table 2) also showed no significant correlations among any of the behaviors examined. Although aggression and courtship behaviors appear to be correlated over time on natural territories, they are not correlated when territory quality is increased. This suggests that behavioral syndromes may not be maintained by way of global effects of hormones (Bell 2005; Brydges et al. 2008), at least not courtship and aggression in teleosts.

Taken together, these data suggest that male beaugregory damselfish exhibit adaptive behavioral plasticity by assessing the quality of their territory when changes occur and adaptively adjusting their behaviors in relation to the quality of the territory they are currently defending. However, the significant correlations between behaviors imply that behavioral types can be

maintained over time or within specific contexts, suggesting that, in addition to exhibiting adaptive behavioral plasticity, a behavioral syndrome exists.

Previous discussions of behavioral syndromes have often led to questions of how behavioral syndromes could be evolutionarily stable if they represent a limitation on behavioral plasticity (Neff and Sherman 2004; Sih et al. 2004b). Sih, Bell, and Johnson (2004b) propose that behavioral syndromes and adaptive plasticity are not necessarily mutually exclusive, and an adaptive framework may explain why syndromes are not always stable (Bell and Stamps 2004; Bell 2005; Dingemanse et al. 2007; Johnson and Sih 2007; Brydges et al. 2008). Additionally, selection should favor the decoupling of behaviors across situations if there is a high enough fitness cost to associations (Sherman and Westneat 1988; Reeve and Sherman 1993). It is possible that behavioral syndromes exist for the beaugregory damselfish when they are in their natural habitat, but when territory quality is increased significantly, by way of the availability of an artificial site, the behavioral syndrome is no longer stable due to the opportunity of increased reproductive success. This enhanced mating opportunity may be impetus enough to disintegrate the behavioral syndrome.

An alternative explanation is that the behavioral correlations on natural sites could merely be a byproduct of the diversity of territory quality. Differences in territory quality translate directly to differences in reproductive success for many species (Orians 1961, 1969; Kodric-Brown 1983), including the beaugregory damselfish (Itzkowitz and Makie 1986; Itzkowitz 1991). Central to the theory of the evolution of territoriality

Table 3

Correlations among various aggressive and courtship behaviors for males that spent Stage 1 on natural sites (natural) and then switched to artificial sites (artificial) in Stage 2

	Natural				Artificial			
	Time near male	Bites	Lateral displays	Time near female	Time near male	Bites	Lateral displays	Time near female
Bites	0.846 <0.001*				0.434 0.056			
Lateral Displays	0.840 <0.001*	0.619 0.004*			0.443 0.050	0.336 0.147		
Time near female	0.796 <0.001*	0.688 0.001*	0.731 <0.001*		0.167 0.481	0.130 0.585	0.203 0.392	
Dips	0.514 0.020*	0.398 0.082	0.621 0.003*	0.622 0.003*	-0.002 0.995	0.111 0.640	0.067 0.780	0.462 0.040

Top = r value; bottom = P value. Asterisk indicates statistical significance ($P < 0.025$).

Table 4

Correlations among various aggressive and courtship behaviors for males that spent Stage 1 on artificial sites (artificial) and then had the artificial sites removed (natural) in Stage 2

	Artificial				Natural			
	Time near male	Bites	Lateral displays	Time near female	Time near male	Bites	Lateral displays	Time near female
Bites	0.309				0.735			
	0.197				<0.001*			
Lateral Displays	0.127	0.477			0.877	0.561		
	0.604	0.039			<0.001*	0.012*		
Time near female	0.287	0.149	0.200		0.624	0.587	0.569	
	0.234	0.544	0.412		0.004*	0.008*	0.011*	
Dips	0.196	-0.008	-0.030	-0.101	0.193	0.369	0.205	0.204
	0.420	0.974	0.903	0.681	0.428	0.120	0.399	0.402

Top = r value; bottom = P value. Asterisk indicates statistical significance ($P < 0.025$).

is the concept that individuals are able to assess the costs and benefits associated with a specific territory and choose those that will maximize reproductive success (Brown 1964; Orians 1969). Additionally, we would expect the behavior of the individual territory holder to reflect the quality of the territory (Ewald and Carpenter 1978; Ewald and Bransfield 1987; Camfield 2006). In this study, we see that individual male damselfish on high-quality territories (artificial sites) have higher levels of both courtship and aggression behaviors than those males that defend lower quality, natural sites. It is possible that the significant correlations found across and among behaviors on natural sites have little to do with the intrinsic personalities of individuals and are actually a result of the diversity in territory quality that is found throughout natural sites.

Although we saw correlated behaviors in specific contexts, it does not appear that a behavioral syndrome exists. When trying to determine if behaviors are linked within a syndrome, it is important to be aware of the behavioral ecology of the organism and how they may react to variation within their environment. It is possible that individuals may be prone to certain behavioral types due to intrinsic qualities, such as hormones or pleiotropic genes, but opportunities for increases in reproductive success may override temperaments when individuals are able to assess their environment and respond appropriately.

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