

8-1-2012

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Recommended Citation

Tootell, Jesse S. and Steele, Mark A. Dr. (2012) "Factors Affecting Courtship Success and Behavior of a Temperate Reef Fish, *Brachyistius frenatus*," *Bulletin of the Southern California Academy of Sciences*: Vol. 111: Iss. 2.

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Cover Page Footnote

This study was made possible by the Marine Biology Semester program of the Ocean Studies Institute. We thank the staff of the Wrigley Marine Science Center for excellent logistical support of this work. This is contribution # 249 from the Wrigley Marine Science Center.

Factors Affecting Courtship Success and Behavior of a Temperate Reef Fish, *Brachyistius frenatus*

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Abstract.—Size can play an important role in determining reproductive success through the establishment of dominance hierarchies and mate selection. We explored the relationship between size of individuals and courtship success in the kelp perch, *Brachyistius frenatus*, off the coast of southern California at Santa Catalina Island. Courtship displays were timed and the length of the interaction was used as a proxy for courtship success. In addition, we observed how much of their time individuals spent performing different activities throughout the day in two adjacent habitats dominated by different macroalgae. We found that body size played a significant role in determining the success of courtship. Large males were slightly more successful than small males, but the male: female size ratio was the best predictor of mating success of male *B. frenatus*, with males that were large relative to the female they were courting being most successful. Time allocated to different activities varied significantly with time of day and habitat. A greater proportion of time was spent on foraging in the morning than in the afternoon, and females spent more of their time foraging than did males. Behaviors other than foraging were only observed in one habitat type (understory algae) and courtship behavior was only observed during the afternoon. Smaller males tended to spend more time searching for receptive females than did larger males.

Introduction

Reproductive success of fish is often a function of size, which can play an important role in determining males' access to females through the mechanisms of mate selection or territoriality (Warner, 1982; Hoffman, 1985). The significance of size also varies depending on the reproductive strategies and morphologies of different fish groups. With only a few unique exceptions in fishes (Bisazza & Pilastro, 1997), larger individuals are generally favored in mate selection for various reasons, but most often because larger females are more fecund and larger males are better able to defend limited resources such as nesting sites or food (Schmale, 1981; Donhower & Brown, 1983; Hughes, 1985; DeMartini, 1988). Body size often has a heritable component and so selection of large mates may produce more fit offspring (Hanson & Smith, 1967).

The family Embiotocidae contains species that are viviparous gonochores and several studies have examined reproductive behavior of members of this family (e.g., Hubbs, 1917; Hubbs, 1921; Shaw & Allen, 1977; Darling, 1980; Hixon, 1981; Baltz, 1984). Only one study (DeMartini, 1988), however, has examined the reproductive behavior of *Brachyistius frenatus*, the subject of this study, in any detail. *Brachyistius frenatus* (kelp perch) is a temperate reef fish that is part of the assemblage of temperate rocky reef fishes

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in southern California (Stephens et al., 2006). As a viviparous species, it has different mating and dispersal patterns than egg-spawning fishes (Hubbs & Hubbs, 1954). Relatively little is known about the courtship behavior of *B. frenatus*. Males can reach sizes equal to those of females, and males are thought to be territorial (Hubbs & Hubbs, 1954; DeMartini, 1988). Females are polyandrous, and agonistic male-male interactions are common, suggesting direct competition for mates or mating territories (DeMartini, 1988). Although it is not clear which resources may be valued, other embiotocids have been shown to establish territories for food and mating sites (Hixon 1981).

The general goals of this study were to explore the courtship behavior of *B. frenatus*, how it is influenced by size, and how allocation of time to courtship influences foraging behavior. Specifically, we (1) evaluated whether body size of males and females influenced courtship success of males; (2) tested how male body size influenced time spent on courtship and time spent searching for mates; (3) tested whether time spent foraging differed between males and females as a consequence of different allocation of time to mating activities by the two sexes; and (4) evaluated whether mating and foraging activities were restricted to particular habitats or times of day.

Methods

Observations of *B. frenatus* were conducted over two weeks in mid November 2010 in Big Fisherman Cove (BFC) on Santa Catalina Island, California. BFC is inside a state marine reserve. Our study was restricted to this single site and time period due to logistical constraints. All evaluations of kelp perch behavior were done on snorkel in water 1.5–5 m deep. The habitat at this site abruptly shifts from *Macrocystis pyrifera* (giant kelp) dominated (deeper) to understory algae dominated rocky reef (shallow) within this depth range. The understory algae include the algae *Eisenia arborea*, *Asparagopsis taxiformis*, *Plocamium cartilagineum*, *Sargassum* spp., and other non-canopy forming species. The observations were divided into two main types: courtship interactions and time budgets.

Courtship Observations

Courtship in *B. frenatus* consists of the male moving into position above the female and performing a display in which his whole body quivers vigorously. The female often stays in motion during his display and the male must then maintain position while continuing to twitch its body. In the most successful courtship interactions, the male will move the ventral side of his body towards that of the female to bring the sexual organs into contact.

During courtship observations ($n=53$), the size of both the male and female participants was estimated visually to the nearest cm, and the interaction was given a numerical score representing the relative success of the mating attempt. The following criteria were used: if the male was rejected by the female immediately upon his display (i.e., she quickly swam away and did not allow the male to move into position above her), then the interaction received a 1. If the interaction lasted for between 2–15 seconds, then it received a 2. If it lasted 15–30 seconds it received a 3, and if it lasted for 30–45 seconds it received a 4. If there was an apparent copulation (regardless of duration), or if the mating display lasted for more than 45 seconds, then it received a 5.

Time Budgets

Time budgets were constructed for 63 fish to establish a basic understanding of how kelp perch allocate time amongst different activities. The observations were done in both

habitat types (*Macrocystis* and understory algae) during two time periods: morning (07:00–11:30) or afternoon (13:00–16:00). Individuals were observed for between 5 and 10 minutes. The activities recorded were courtship, foraging, roaming, agonistic display/chase, and the number of mating attempts. Agonistic displays consisted of two males aligning themselves head to tail with their mouths open, fins erect and the body slightly flexed toward the opponent. Courtship was defined as the act of performing courtship displays, foraging as slow movement with active feeding as evidenced by protrusion of the jaws, and roaming as fast movement with no feeding. Roaming appeared to be done only by males searching for mates and it was often followed by a courtship attempt. Therefore, courtship and roaming were combined into a single response variable for some analyses. All activities were analyzed as percent of the total time observed.

Because of the morphological similarities between male and female *B. frenatus*, the only ways to determine the sex of an individual were to observe the gonopodium on the anterior portion of the anal fin, which was often difficult to see due to light conditions or viewing angle, or to observe the fish in a mating or agonistic interaction. In the closely related shiner perch (*Cymatogaster aggregata*) and other embiotocids (Hubbs, 1917; Shaw & Allen, 1977; Hixon, 1981), only males are involved in agonistic chasing and displays and only males engage in the aforementioned quivering during courtship, so these behaviors were used to identify males when the gonopodium could not be seen. Data from those individuals that were observed but that could not be sexed were excluded from analyses of behavior related to courtship or agonism.

Statistical Analysis

To evaluate the relationship between body size and courtship success, three separate logistic regressions were used. These regressions tested whether courtship success (categorical courtship score) was a function of either male size, female size, or the male:female size ratio.

To explore how behavior patterns were related to size, sex, habitat, and time of day, time budget data were analyzed in different ways to address different questions. Response variables included % time foraging (both sexes), % time engaged in roaming + courtship (males only), and % time roaming (males only). The percent of time spent on courtship and agonism was so low that these behaviors were not statistically analyzed. To test whether time spent searching for mates was related to male body size, we used linear regression to test the relationship between percent of time spent roaming and male body size. To test whether the % of time males spent on mating activities (roaming + courtship) was influenced by time of day, we used a two-sample *t*-test to compare data from males in the morning versus afternoon in the understory habitat (the only habitat in which mating activities occurred). A two-way analysis of variance (ANOVA) with Time and Habitat as fixed factors was used to test whether the % of time spent foraging differed between time periods or habitats. This analysis included the entire time budget observations, including those in which sex of the individual could not be ascertained. A subset of the time budget data set, those observations in which gender had been determined, were evaluated with analysis of covariance (ANCOVA) to test whether % time spent foraging differed between sexes (a fixed, categorical factor) or varied with body size (a covariate). Analyses involving gender as a factor, and those restricted to a single gender, used only data collected in the understory habitat, because this habitat was the only one in which fish could be reliably sexed. Time budget data did not meet the assumption of normality, and transformation did not improve their distribution. We proceeded with parametric

analyses on untransformed data, nevertheless, because ANCOVA and ANOVA are generally robust to violations of normality (Gotelli and Ellison 2004).

Results

Mating Interactions

Males were more successful at courtship when females were small relative to them, as indicated by a significant positive relationship between courtship success score and the male: female size ratio (Fig. 1A; $df=4$, $\chi^2=40.29$, $p<0.001$). Although courtship score tended to increase with male size and decrease with female size (Figs. 1B and 1C), neither relationship was statistically significant ($df=4$; $\chi^2=7.48$, $p=0.112$; $\chi^2=7.67$, $p=0.105$, respectively), emphasizing the importance of the ratio of male to female size. Only two copulations were observed, and these occurred between pairs with male: female ratios of 12:10 cm and 14:14 cm.

Time Budgets

Courtship, agonistic interactions, and roaming were only observed in the understory algae habitat (Fig. 2). Here, courtship + roaming accounted for a higher proportion of total activity in the afternoon than in the morning ($t=3.6$, $df=18$, $p=0.002$). The % time spent foraging also differed significantly between times of day, as well as between habitats (Table 1, $p<0.05$). The increased time spent on mating activities in the afternoon resulted in a lower % of time spent foraging in the afternoon than in the morning. A greater % of time was spent foraging in the *Macrocystis* habitat than in the understory algae habitat where mating behavior occurred. For % time foraging, there was a significant interaction between habitat and time of day because foraging was the only behavior that occurred in the *Macrocystis* habitat, whereas changes between time periods in the percent time spent on various behaviors did occur in the understory habitat. Foraging accounted for 100% of activity of *B. frenatus* when observed in the *Macrocystis* habitat, but in the understory algae habitat it accounted for only 68% of time in the afternoon and 90% in the morning.

Agonistic interactions occurred even in the absence of courtship during the morning, but accounted for about half as much of the time budget during this time as they did in the afternoon (~4.2% and 8.5% respectively). Several times during courtship, males were interrupted by agonistic males. The interruption was always performed by a male of equal or larger size and the interrupting male sometimes courted the female in the broken pairing. Agonistic displays were also never performed by two disproportionately sized males. When chasing occurred, larger males always chased smaller males.

Foraging behavior differed between the genders. Females spent more of their time foraging than males (means \pm SEM of 93% \pm 5.9 vs. 73% \pm 4.8 for females and males, respectively; $F_{1,30}=6.8$, $p=0.01$). Females did not engage in agonistic displays or roam, and thus spent all of their time foraging when not being courted. There was no detectable relationship between size and time spent foraging ($F_{1,30}=0.0$, $p=0.86$).

There was some evidence that male size affected roaming behavior. Small males tended to spend more time roaming than larger males (Fig. 3)($r^2=0.15$, $F_{1,18}=3.2$, $p=0.08$).

Discussion

This study reveals a clear relationship between courtship success and the size of males relative to females in *Brachyistius frenatus*. Females spent significantly more time being courted by males of equal or larger size than themselves than by smaller males, indicating that the relative size of male and female partners was likely a good predictor of

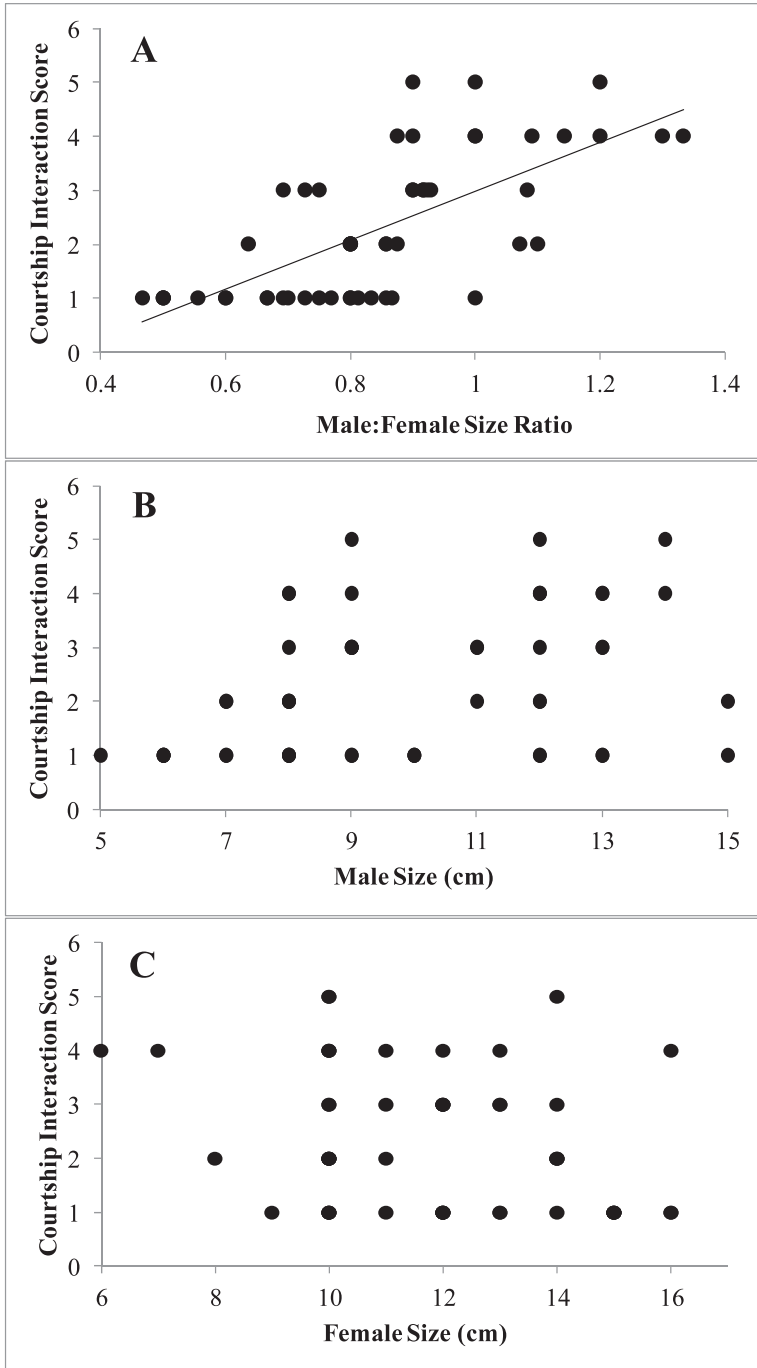


Fig. 1. Relationships between courtship score and A) male:female size ratio, B) male size, and C) female size and for $n=53$ total interactions.

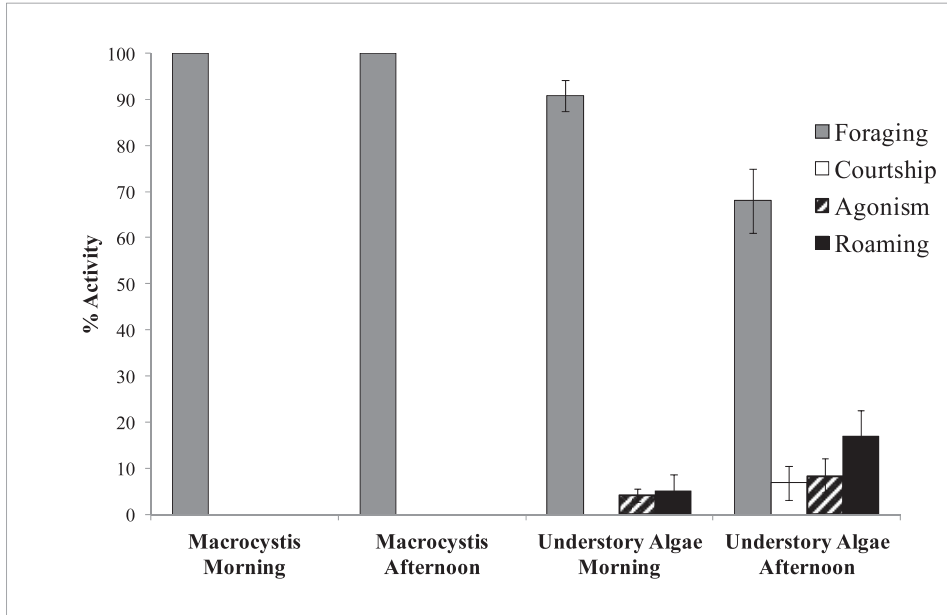


Fig. 2. Percent of time allotted to each activity by *Brachyistius frenatus* in two habitats at two times of day. Bars represent \pm 1 SEM. For *Macrocystis* during afternoon $n=15$, *Macrocystis* during morning $n=15$, understory algae during afternoon $n=17$, and for understory during morning $n=16$.

probability of mating. Somewhat unexpectedly, absolute size of males was not a particularly good predictor of courtship success, with larger males being only slightly more successful than smaller males. However, it should be noted that some of the large males that had poor courtship success were also courting very large females. DeMartini (1988) found that all males preferentially courted large females, but the present study reveals that an apparent preference by females for males larger than themselves renders courting efforts of relatively smaller males ineffective. Those smaller males, however, successfully courted females that were smaller than them. It appeared that all mature males were capable of mating, but high courtship success was only attained with a female of equal or lesser size. Therefore, the success of any given male is less a function of its absolute size and more related to its size relative to accessible females. Consequently, male reproductive success appears to be limited by the number of females in the population that are of equal or smaller size. This finding differs somewhat from the size-assortative mating documented in the closely related species *Micrometrus minimus* (Warner & Harlan, 1982) and *Cymatogaster aggregata* (DeMartini 1988), in that *B.*

Table 1. Results of factorial ANOVA testing for differences in the % time spent foraging by *B. frenatus* (males and females combined) during two time periods (morning and afternoon) and in two habitats (*Macrocystis*) and understory algae).

Source	df	F	P
Time	1, 59	7.5	0.008
Habitat	1, 59	24.7	<0.001
Habitat*Time	1, 59	6.6	0.008

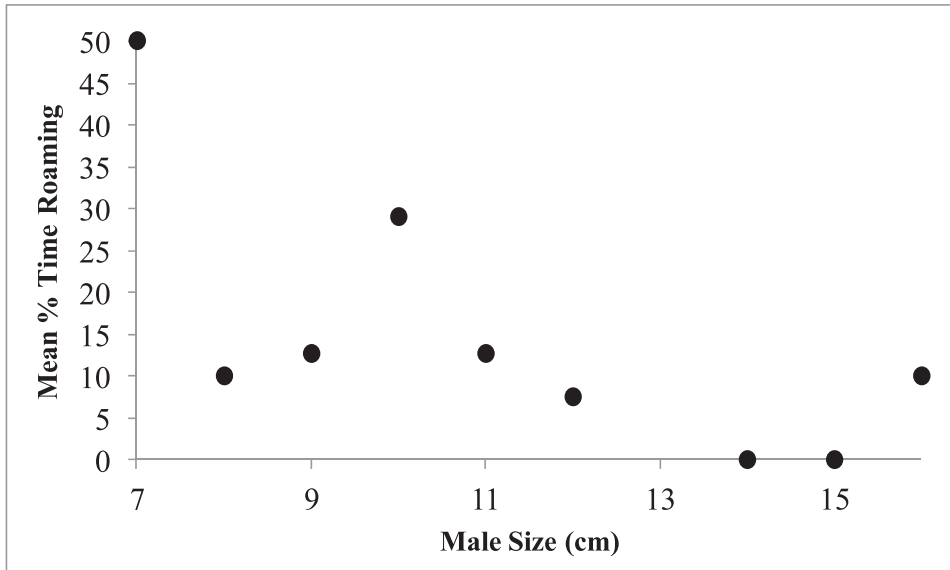


Fig. 3. Relationship between size and % of time spent roaming by male *Brachyistius frenatus*; $n=20$.

frenatus males will successfully court females similar in size and ones smaller than themselves.

Time budget observations revealed some evidence of a relationship between male size and time spent roaming, where smaller males roamed more often. This increased roaming may be a result of agonistic male-male interactions which forces small males to spend more time moving to avoid conflict with larger males, or smaller males may have to travel farther or more often than larger males in order to find receptive females. Regardless of the cause, since smaller males appear to roam more frequently, be slightly less successful during courtship than larger males, and perhaps mate with smaller females that will produce fewer offspring than large females, small male *Brachyistius frenatus* must have lower reproductive success than larger males.

The fact that aggressive interactions between males continued in the absence of courtship activity and only in the habitat where courtship occurred (understory algae) and not in the habitat used solely for feeding (giant kelp) indicates that agonism in kelp perch is primarily used as a mechanism to defend mating sites and access to females. DeMartini's (1988) study of kelp perch supports this conclusion, as do several other studies of embiotocid species, which have revealed similar aggressive behavior in males (Hubbs, 1921; Shaw & Allen, 1977; Hixon, 1981). The observations of male interruptions and agonism suggest that male-male interactions are governed by a size-based dominance hierarchy predicated on access to females, as has been widely noted in other fishes (e.g., Robertson & Choat, 1974; Downhower et al., 1983; Warner & Schultz, 1992). Because females did not search for mates (roam) or engage in agonistic interactions, they were able to spend more of their time foraging than were males.

It appeared that male size affected roaming behavior, though this pattern was marginally non-significant. Further study with higher replication may elucidate the actual associations between these factors in *B. frenatus*. Furthermore, previous work on marine fishes has shown that different size classes within a species may mate at different times of

the year (Hubbs, 1921; Baltz, 1984; Shultz, 1991), so repeated observations over a longer time period would be valuable in addressing this possibility in kelp perch.

It is noteworthy that courtship was only observed in the understory algae habitat and not in the *Macrocystis* bed habitat, especially given that the study species is called the kelp perch and DeMartini (1988) observed courtship in this species exclusively in giant kelp canopy. We suspect that this finding reflects mating habitat preferences that will only be expressed when *Macrocystis* and understory algae habitats are in close proximity, as was the case at our study site. At reefs surrounding Catalina Island, Anderson (1994) noted that adult *B. frenatus* were proportionally more abundant in understory algal habitats than were newly born offspring, which were found almost exclusively in the *Macrocystis* canopy habitat. One might therefore suspect that our finding of courtship occurring only in the understory algae habitat was the result of adults only occurring in this habitat and juveniles only in the *Macrocystis* habitat. This explanation, however, is incorrect. Adults were present in both habitats and there was no significant difference between the sizes of *B. frenatus* seen in the two habitats. The study sites at which DeMartini (1988) noted courtship behavior of *B. frenatus* occurring in the *Macrocystis* canopy habitat were much deeper (approximately 15 m) than our study site, and so the understory algae habitat was both more distant (vertically) from the canopy habitat and likely more sparse due to shading by giant kelp.

Results from this study conform to a common trend in marine fishes where larger mates are often preferred. Male preference for larger females is well documented and expected, as larger females are more fecund. Similarly, in species where males perform some role beyond fertilization for which large size is advantageous (e.g., defense of a nest site or offspring), larger males are expected to be preferred by females. DeMartini (1988) found that *B. frenatus* males prefer larger females and the present study indicates that large females also prefer larger males. Given that male *B. frenatus* do not defend their offspring nor provide females access to any limited resource, females may prefer larger males because their offspring are more fit, whereas males may choose larger females because they produce more offspring.

Acknowledgements

This study was made possible by the Marine Biology Semester program of the Ocean Studies Institute. We thank the staff of the Wrigley Marine Science Center for excellent logistical support of this work. This is contribution # 249 from the Wrigley Marine Science Center.

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