Nest Site Habitat Preference and Competition in Gasterosteus aculeatus and G. wheatlandi

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Gasterosteus aculeatus and G. wheatlandi are sympatric stickleback species that compete for suitable nest sites and nest material. Gasterosteus aculeatus, the dominant competitor, is a specialist species and will nest only in the presence of vegetation. Gasterosteus wheatlandi is a generalist species and nests successfully in the absence of these materials. Gasterosteus wheatlandi may find a competitive refuge in this generalist behavior which allows for the coexistence of the two species in the estuaries.

In competition with G. aculeatus in experimental pools, G. wheatlandi built significantly fewer nests, nested further away from its preferred nest site, and shifted its preference from Enteromorpha sp. to other nest habitats in combined species pools with G. aculeatus. The presence of G. wheatlandi in combined species pools had no measurable effect on G. aculeatus' nesting success.

COMPETITION occurs when organisms inhibit each other's access or ability to use common resources which are actually or potentially limiting (Birch, 1957). One presumption of competition is that, in any group of similar species, careful study will reveal interspecific differences in resource use (Hutchinson, 1957), following the Volterra-Gause principle that two species utilizing, and limited by, the same resource cannot coexist indefinitely. Much theoretical work has been directed at how species divide their environment to coexist (Schoener, 1974; Slatkin, 1974; Grant and Schluter, 1984).

One hypothesis suggested by Hutchinson (1953) to explain coexistence was for one or more of the competing species to persist as a fugitive using less preferred resources when competition was severe. Under this model, resource partitioning need not occur; the fugitive species need only avoid interaction with the superior competitor. If the environment is sufficiently unpredictable, a fugitive species should still be able to obtain some of a limiting resource, demonstrated for marine fishes (Sale, 1975; Hixon, 1980; Larson, 1980). Little research has been directed at the concept of fugitive behavior, although it is a plausible alternative to resource partitioning as a means of coexistence. There exists a pair of sympatric species of Gasterosteus to which this type of study is well suited.

Gasterosteus aculeatus (three-spine stickleback) and G. wheatlandi (black-spotted stickleback) are sympatric stickleback species commonly found in tide pools and estuaries from Newfoundland to Long Island (Coad and Power, 1973; Wootton, 1976). Males of both species are territorial nest builders that spawn in shallow water (Breder and Rosen, 1966; Wootton, 1976). Morphologically, these species are very similar (Bigelow and Schroeder, 1953); phylogenetic analysis has demonstrated that G. aculeatus and G. wheatlandi are sister species (McLennan et al., 1988). Gasterosteus aculeatus is the larger species with males averaging 50 mm standard length vs 30 mm for G. wheatlandi (Rowland, 1983a; Walsh and FitzGerald, 1984). Both species are sexually dimorphic: male G. aculeatus develop red nuptial coloration with blue eyes; G. wheatlandi males become bright green. Their natural diets are similar (Walsh and FitzGerald, 1984; Whoriskey and FitzGerald, 1985) although competition for food may not occur because of the abundance of prey and morphological constraints on feeding behavior (Delbeek and Williams, 1988).

Interspecific aggression and dominance in G. aculeatus and G. wheatlandi have been demonstrated in the laboratory and in the field. In the laboratory, G. aculeatus consistently displaces G. wheatlandi from G. wheatlandi nests and then goes on to construct nests of its own (Rowland 1983a). Gaudreault and FitzGerald (1985) found that, in tidal pools, 10-66% of G. wheatlandi nests were destroyed by G. aculeatus. Rowland (1983a, 1983b) suggested that interspecific competition for nest sites occurs among sticklebacks. FitzGerald and Whoriskey (1985) found that only 30% of the available males of either species in tidal pools in Quebec established territories and built nests. Here, I report experimental evidence supporting Hutchinson's concept of fugitive species to explain coexistence of G. aculeatus and G. wheatlandi.

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MATERIALS AND METHODS

Gasterosteus aculeatus and G. wheatlandi were collected from Succotash Marsh in South Kingstown, Rhode Island, by repeatedly seining one 100-m section of tidal creek with a 0.3-cm mesh 6-m seine. The species were housed separately in aquaria at the University of Rhode Island in Kingston, at a salinity of 32 ppt on a 12:12 light: dark schedule, which approximated local conditions at the time of collection, for a minimum of five days. All fish were in breeding condition at the beginning of each experiment. Breeding condition was defined by the presence of nuptial coloration in males and swollen abdomens in females. The fish were fed 100 ml of Artemia daily for the duration of the study. The study was conducted from 10 April-20 May 1986, the limits of peak breeding season for Gasterosteus in Rhode Island.

Laboratory experiments were conducted in 1.7 m² wading pools which contained 15 cm of water over 4 cm of sand. Each pool contained either 10 males and 10 females of the same species, or five males and five females of each species, depending on treatment, for a total pool population of 20 fish (12 fish/m²).

Single species experiments.-Nest site location preference (treatment A): Ten males and 10 females of one species, in breeding condition, were placed in a pool devoid of vegetation. Two areas of the pool were distinguished-"near edge," i.e., the outer half of the pool area; and "open," i.e., the inner half of the pool areafor recording position preference within the pool. After introduction, fish were allowed 6 hr to become accustomed to their surroundings prior to observation. Because most males nest within two to three days (Rowland 1983a), each pool was observed from behind a partition for 1 hr each day for at least 4 days. During each observation, I recorded the following: (1) number of nests built in each pool, (2) distance from the nest to the nearest edge, and (3) distance between nests. This experimental set up was replicated five times for each species.

Vegetation preference (treatment B): Ten clusters each of Zostera marina, Enteromorpha sp., and Fucus sp., for a total of 30 clusters, were randomly placed in each pool; 50% of each plant species was placed in the near edge area, and 50% was placed in the open area of the pool. Zostera marina and Enteromorpha sp. were chosen because they are the dominant vegetation in Succotash Marsh. Fucus sp. was chosen as an additional plant choice because it is plentiful in certain Rhode Island estuaries where Gasterosteus is found (pers. obs.). Ten males and 10 females of one species, in breeding condition, were introduced into the pools and observed on the schedule outlined in treatment A. Data recorded were as follows: (1) number of nests built per pool; (2) distance from nest to nearest edge; (3) distance to base, and species of, nearest plant; and (4) distance between nests. Four replicate *G. aculeatus* pools and five replicate *G. wheatlandi* pools were observed.

Combined species experiments.—Vegetation not limiting (treatment D): Replicate pools (n = 8)of five males and five females of each species were set up in which 10 clusters of each vegetation type had been placed as above. Information recorded included the following: (1) number of nests constructed per species; (2) distance to nearest edge; (3) distance to base, and species of, the nearest plant; and (4) distance between conspecific and heterospecific nests.

Vegetation preference.—Limited vegetation (treatment E): Five males and five females of each species were introduced into a pool in which eight clusters of *Enteromorpha* sp. had been placed; four clusters were placed in the inner half and four clusters were placed in the outer half of the pool. Information was recorded as in treatment D.

Behavioral observations.—Each pool was observed for one hour per day for nest-building activities, aggressive interactions, and courtship. These behaviors were not quantified and are only reported anecdotally.

Statistical analyses.—Distance measurements met the assumptions of normality (Kolmogorov-Smirnov test) and homogeneity of variance (Hartley's F-max test), thus the data were analyzed using a two-way ANOVA to determine significance and a Duncan's multiple range test statistic to determine which treatments were different from one another (Sokal and Rohlf, 1981). In instances where the interaction between species and treatments was significant, a one-way ANOVA within a species group was then used. The behavior of individual fish in the experimental pools did not meet the criteria of independence necessary for chi-square analysis. Rather, the proportion of males nesting per species in each pool was arcsin transformed and then analyzed using a two-way ANOVA and Duncan's multiple range test statistic. Distribution of nest sites in the inner versus outer



Fig. 1. The proportion of males nesting per treatment. Numbers above the histobars indicate the number of replicates per treatment. Histogram bars that share symbols do not differ significantly (two-way ANOVA, P < 0.05).

areas, and vegetation preference, data were also analyzed in this manner.

RESULTS

Number of nests per species.—The most striking result of this experiment is that G. aculeatus failed to nest in the absence of vegetation, yet G. wheatlandi males built an average of 5.4 nests per pool under the same conditions (Fig. 1). Observations were continued on one pool of G. aculeatus for 14 days. During that period, four of the males lost their nuptial coloration, and all the fish in the pool continued to school; there was no evidence of nest-building, aggression, or courtship behavior. There were no significant differences in the number of nests built by G. aculeatus in the three other treatments (two-way ANOVA, P = 0.0009, df = 5,22). There was no difference in the number of nests built by G. aculeatus and G. wheatlandi males in the single species experiment where vegetation was provided; however, significantly more G. aculeatus males built nests than did G. wheatlandi in combined species experiments. Gasterosteus wheatlandi males built more nests in single species pools than they did in combined species pools (two-way ANOVA, P = 0.0009, df = 5,22, Fig.1).

Distance to nearest edge.—Gasterosteus wheatlandi nested significantly nearer to the edge than did G. aculeatus in every treatment (ANOVA, P =0.0001, df = 5,22, Fig. 2A). The distance from the edge at which G. aculeatus nested did not differ among treatments whereas G. wheatlandi in single species pools nested farther from the edge in the presence of vegetation (ANOVA, P = 0.0001, df = 5,22) than it did in the other three treatments (Fig. 2A). An ANOVA of dis-



Fig. 2. (A) The average distance to the nearest edge. (B) The number of nests built in the inner vs outer one-half of the pool. Numbers above the histobars indicate the number of replicates per treatment. Histogram bars that share symbols do not differ significantly (two-way ANOVA, P < 0.05).

tance to nearest edge data indicates a significant (P < 0.05, df = 5,22, Fig. 2B) tendency for both species to nest closer to the edge than in the open areas of the pool.

Distance to vegetation.—There were no significant among-treatment differences (ANOVA, P = 0.4847, df = 2, Fig. 3A) in how close to vegetation G. aculeatus nested. The distance to the nearest vegetation differed significantly (ANO-VA, P = 0.0112, df = 2) among treatments for G. wheatlandi.

Vegetation preference.—Gasterosteus aculeatus showed a significant preference for Enteromorpha sp. as nest cover (Duncan's multiple range test, P = 0.0045, df = 2) over both Fucus sp. and Z. marina in both single species and combined species treatments (Fig. 3B). Gasterosteus wheatlandi displayed no tendency to utilize one plant species as cover more often than the others (Duncan's multiple range test, P = 0.8904, df = 2). Although the majority of nests of both species was built of sand, Enteromorpha or glass wool from the pool filters were used in several



Fig. 3. (A) The average distance from a nest to the nearest vegetation cluster. (B) Vegetation type chosen as nest cover. (C) Material used in nest construction. Numbers above the histobars indicate the number of replicates per treatment. Histogram bars that share symbols do not differ significantly (two-way ANOVA, P < 0.05).

nests (Fig. 3C). Neither Fucus sp. nor Zostera marina were used in nest construction.

Internest distances.—There were no significant differences in how far *G. aculeatus* built its nest from either conspecific (ANOVA, P = 0.3002, df = 2) or heterospecific (ANOVA, P = 0.8480, df = 1) fish (Fig. 4). However, at the 10% level in treatment D (combined species with unlim-



Average Distance between Con- and Heterospecific Nests Fig. 4. The average distance between conspecific and heterospecific nests. Numbers above the histobars indicate the number of replicates per treatment. Histogram bars that share symbols do not differ significantly (two-way ANOVA, P < 0.05).

iting vegetation) G. aculeatus appeared to be nesting closer to G. wheatlandi ($\bar{x} = 79.3$ cm, SE = 12.4 cm) than to other G. aculeatus ($\bar{x} = 98.2$ cm, SE = 15.1 cm).

Gasterosteus wheatlandi nested farther away from both conspecifics (ANOVA, P = 0.0129, df = 3) and heterospecifics (ANOVA, P =0.0116, df = 1) when vegetation was limited (treatment E) than it did in the other treatments (Fig. 4); distances between conspecific G. wheatlandi nests among the other treatments were not significantly different from each other.

Behavioral observations.—In the single species pools without vegetation (treatment A), G. aculeatus males continued to school with females and showed no signs of aggressiveness or territorial behavior. In addition, 40-60% of these males lost their nuptial coloration. Gasterosteus wheatlandi males became aggressive and territorial within six hours of introduction into the pools. In all five G. wheatlandi pools, males had begun to build nests within six to 12 hours. In two of the five G. wheatlandi pools for treatment A, six males were eventually able to establish nests although the sixth nest was in the center of the pool in each case. The owner spent a considerable amount of time defending the nest and much less time in courtship and nest maintenance behavior. It appears that five nests per pool, or three nests/m², is the maximum density for these pools.

In the single species pools with vegetation (treatment B), aggression and nesting behavior were observed in both species. In one *G. aculeatus* replicate pool, two males nested within 34 cm of each other (mean conspecific internest distances were 93.8 cm). These two fish showed no aggression toward each other once their nests were established yet both fish would chase away other intruders, often simultaneously.

Gasterosteus aculeatus appeared to defend larger territories (approximately 30–40 cm diameter) than did G. wheatlandi (15–20 cm diameter). These territory sizes were essentially the same in all treatments although they were not quantified. Exact measurement of territory size was not possible without disturbing the fish, and thus visual estimates were made by noting how far a fish would travel to defend its nest site.

In combined species pools with limiting vegetation, *G. wheatlandi* males spent more than 50% of their time in aggressive behaviors, thus leaving less time for nest building and care of eggs. Most of the aggression by the *G. wheatlandi* males was directed at conspecifics. This may result from *G. wheatlandi*'s competing for space away from *G. aculeatus*. Forty percent of the *G. wheatlandi* males in this treatment lost their nuptial coloration.

CONCLUSIONS

Existence of competition.—The success of the fish in the experimental pools, measured in number of nests built per pool, was influenced by both the habitat and the presence of other fish. Gasterosteus wheatlandi succeeded in building nests in the absence of vegetation, yet G. aculeatus never initiated reproductive behavior under these conditions. Once plant material was added, G. aculeatus males successfully built and defended nests. Vegetation appears to be crucial to G. aculeatus for nest site concealment rather than as nest material; the nests were often constructed of sand yet were located under the cover of vegetation. Jenni (1972) and Sargent and Gebler (1980) discuss the role of nest site concealment on nesting success in G. aculeatus. Males nesting in flower pots spawned earlier and had greater hatching success than did males without pots. Males also nested closer together in the presence of vegetation, possibly because of decreased visibility of neighbors. Rowland (1983a) and Gaudreault and FitzGerald (1985) found that G. aculeatus is more aggressive, issuing more attacks per minute than G. wheatlandi. If this is the case, G. aculeatus may be subject to attack from neighboring conspecifics, and less successful, when nesting without concealment. Selection would then favor males who nest only under protective cover. Gasterosteus wheatlandi, being less aggressive, may not have the same requirements for concealment and thus will build and defend nests in the absence of vegetation.

The presence of heterospecific males had no

effect on G. aculeatus, yet it negatively impacted the number and location of G. wheatlandi nests. Gasterosteus wheatlandi built fewer nests in the presence of G. aculeatus and was pushed further away from preferred nest sites under these conditions. Gasterosteus wheatlandi also shifted its preference for Enteromorpha sp. as vegetative cover to less preferred vegetation or to the pool edge when in combined pools with G. aculeatus. The differences between G. wheatlandi's choice of nest site location in single species and combined species pools demonstrates the potential for competition among the congeners for nesting space and preferred habitat. This competition has been demonstrated in the field. Fitz-Gerald and Whoriskey (1985) found significantly more G. aculeatus nested in sympatry with G. wheatlandi than in allopatry, where the reverse was true for G. wheatlandi. Gaudreault and Fitz-Gerald (1985) found that, at low nesting densities, G. aculeatus would not destroy G. wheatlandi nests, but at high densities of nesting G. aculeatus, 10-66% of G. wheatlandi nests were destroyed.

Mechanisms for coexistence.—If G. aculeatus is the dominant competitor in this system, why does it not competitively exclude G. wheatlandi? A key observation is that G. aculeatus is a specialist species, whereas G. wheatlandi is a generalist. This is supported both by G. aculeatus's requirement for nest concealment to begin reproductive behavior and in its preference for Enteromorpha sp. for cover. Gasterosteus wheatlandi did not show a significant preference for vegetative cover type and was able to nest in the absence of vegetation, a condition observed frequently in Rhode Island salt marsh tidal pools (pers. obs.). In a continually changing system such as a seasonal salt marsh, the generalist regime of G. wheatlandi could facilitate coexistence with a dominant competitor. If there was reduced vegetational growth, or G. aculeatus arrived at a site in the estuary without much vegetation, it may experience decreased reproductive success. Indirect evidence has demonstrated this. Weeks (1985) found no G. aculeatus in pools lacking Enteromorpha sp. and W. H. Krueger (pers. comm.) found a decrease in G. aculeatus with the loss of Z. marina beds in Rhode Island estuaries. Although my data show G. aculeatus's preference for Enteromorpha sp., Z. marina could be preferred when the former is absent. Second choices were not investigated in this study. These differences in habitat would not have as great an impact on the generalist G. wheatlandi.

Additional evidence supports the specialist/ generalist concept of coexistence. Gasterosteus *aculeatus* may return to its natal site within the estuary with greater fidelity than G. wheatlandi. Gasterosteus aculeatus appears capable of detecting natal sites within an estuary whereas G. wheatlandi appears to only recognize the estuary itself (unpubl. data). Because G. aculeatus is the competitive dominant, it can afford to be more specific in its homing behavior; it can presumably displace any G. wheatlandi it encounters. Gasterosteus wheatlandi cannot afford to be so rigid with its reproductive behavior. If G. wheatlandi is not capable of locating areas in the salt marsh where G. aculeatus is predictably rare, it is advantageous to be more flexible; G. wheatlandi may distribute itself more uniformly throughout the estuary locating preferred habitat as yet undiscovered by G. aculeatus.

The persistence of G. wheatlandi can also be explained by its being a fugitive species (Hutchinson, 1953). It is clear that coexistence cannot be explained by the species' finely partitioning a limiting resource (Schoener, 1974; Diamond, 1978). In single species pools, both species use and prefer the same nest habitat. Gasterosteus wheatlandi exhibits a partial niche shift in combined species pools by switching to a less preferred habitat. However, G. wheatlandi was still able to use some of the preferred habitat in combined pools because the two species engage in interference competition. Because of the nature of intraspecific interactions among G. aculeatus, some clusters of Enteromorpha sp. were not used by G. aculeatus, presumably because they were too close to another G. aculeatus territory.

Connell's (1978) hypothesis of intermediate disturbance and gradual change in a nonequilibrium system could also explain the Gasteros*teus* congeners' coexistence. Suitable nesting sites are generated unpredictably in the salt marsh as a result of predation, emigration, and mortality. FitzGerald and Dutil (1981) and Tremblay and Ellison (1980) discuss selective predation on the larger G. aculeatus, which may diminish competition for nest sites [although Whoriskey and FitzGerald (1985) found that birds preved upon both species equally]. Paine (1966), Slatkin (1974), and Roughgarden and Feldman (1975) demonstrated theoretically that selective predation on a dominant competitor could facilitate coexistence of competing species. Whoriskey et al. (1986) found that male G. aculeatus in breeding condition did not necessarily remain in a pool if they did not have a nest; as a result, the pool population and species composition was constantly changing. By combining emigration with selective predation of territory holders, the system may be sufficiently

unpredictable to generate available nesting sites for *G. wheatlandi*. This pattern of coexistence has been demonstrated by Hixon (1980) and Larson (1980) for temperate marine reef fish competing for territories.

This work clearly indicates, however, that interspecific competition among adult males for suitable nest site locations is an important factor in determining stickleback breeding success. It appears that *G. wheatlandi* is able to coexist with its competitive dominant *G. aculeatus* because *G. wheatlandi* is a generalist species and a fugitive competitor.

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