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Mating patterns and a test for female mate choice in *Etheostoma spectabile* (Pisces, Percidae)

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Abstract Neither size nor breeding color correlated with spawning success of male orangethroat darters, *Etheostoma spectabile* (Pisces, Percidae), under natural field conditions. When females were presented experimentally with a simultaneous choice they spent no more time in proximity to large than small males, and were subsequently no more likely to spawn with large than with small males. Females also displayed no preference for bright versus dull males. Males and females did not differ significantly in size. *Etheostoma spectabile* may lack sexual size dimorphism as a result of the lack of female choice for size and the ineffectiveness of male attempts to monopolize females, or selection may be for increased size of females. Males are not dwarfs because of sperm competition. Contest competition among males appeared to be important in initiating spawnings but many males obtained spawnings by participating in ongoing spawning events. *Etheostoma spectabile* is an example of a sexually dimorphic species with no evident female preference for male size or color.

Key words Female mate choice · Mating system
Fish · *Etheostoma spectabile*

Introduction

Male body size influences female mate preference (Downhower and Brown 1980; Berglund et al. 1986; Noltie and Keenleyside 1986; Hastings 1988; Cote and Hunte 1989; Jennings and Philipp 1992), male-male

competition (Downhower et al. 1983), and both female choice and male-male competition (Hughes 1985; Bisazza and Marconato 1988; McPeck 1992) in fish. Female choice for male color has been demonstrated in several species of fishes (Noble and Curtis 1939; Endler 1980; Kodric-Brown 1985; Houde 1987; Stoner and Breden 1988; Milinski and Bakker 1990). Females were found to prefer males with brighter or more coloration, suggesting that sexual selection may influence the evolution of male coloration in those species.

Many studies of female mate choice in fishes have been of species in which males perform some type of parental care (e.g., Downhower and Brown 1980; Grant and Colgan 1983; Marconato and Bisazza 1986; Knapp and Sargent 1989). In these species larger males were better able to defend territories, guard eggs, or win male-male contests (Downhower and Brown 1980). In such examples, male-male competition may allow larger males higher quality spawning sites or other resources upon which females might base their choice (Downhower and Brown 1980). Fewer species of fishes lacking male parental care have been tested for mate choice (but see Jarvi 1990; Haas 1976; Kodric-Brown 1983; Jones 1981; Warner and Schultz 1992).

In contrast with fish species in which males exhibit some type of parental care, orangethroat darters, *Etheostoma spectabile*, are egg buriers (Page 1985) lacking parental care and territorial guarding. The species is sexually dimorphic for color but not size. Males in breeding season develop blue and red stripes on the body and dorsal fins, and orange on the throat (male coloration varies moderately among subspecies – see Distler 1968). This darter inhabits small to medium-sized streams with gravel substrates (Robison and Buchanan 1988) and ranges across the central United States (Lee et al. 1980). In early spring, males move onto gravel riffles, followed by females that are ready to spawn (Winn 1958). A receptive female burrows into the substrate into a horizontal position with her head

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protruding. Her mate moves into position directly above and parallel to the female. Vibration of both presumably signals the release of gametes. Winn (1958) estimated that three to seven eggs are deposited per mating in a Michigan population. Both sexes leave the site after releasing gametes.

Under field conditions I observed male spawning success of orangethroat darters and tested the hypotheses that spawning is a function of a male's coloration, body size, and/or observed behaviors. I also conducted mate choice experiments to test the hypotheses that female *E. spectabile* prefer larger males, males with brighter coloration, or both when the effects of male-male competition are minimized.

Methods

Field site

I observed reproduction by *E. spectabile* in a spring in south-central Oklahoma, 4 km south of the town of Sulphur, Murray County. The spring flows into Buckhorn Creek, a tributary of the Washita River. Only two species of fish were typically present at the headwaters: *E. spectabile* and *Gambusia affinis* (mosquitofish). *E. spectabile* densities at the springhead were approximately 20–40/m² (personal observations). Water temperature in this spring was a constant 18°C and where reproduction was observed, water depth was 0.5 m. Substrate in the springhead pools consisted of sand, then became siltier farther from the springhead pools. Additional details of physical conditions are in Pyron (1994). At this site, *E. spectabile* has a reproductive season spanning 11 or 12 months (personal observations).

Field observations

From April to August 1991, 463 *E. spectabile* were captured and individually marked with tags (monofilament with paint beads) inserted through the dorsal part of the body (Chapman and Bevan 1990). Body standard length (snout to caudal peduncle) (SL), gender and an index of coloration (males only) were recorded prior to marking. Sex of mature *E. spectabile* was determined by the presence of genital papillae on females (Kuehne and Barbour 1983). Reproductive males had distinct coloration, ranging from dull to a bright striped pattern on the fins and body. Male coloration scores were as follows: 0, coloration indistinguishable from females, 1, only fins with color; 2, fins and a few body stripes with color; 3, fins and body stripes with bright color.

Focal male observations were made from 0900 to 1400 hours, during 29 June to 1 August 1992. Thirty individually marked males were observed underwater for 30 min each. Each individual was observed once. Males were classified as either small (< 38 mm SL) or large (> 40 mm SL). I recorded the following behaviors: "approach male" (male approaches another male), "approach female" (male approaches female), "lateral display" (male erects dorsal fins with body lateral to other fish), "flee" (target male is approached by another male, target male retreats), "approach spawn" (male approaches a spawning pair) and "spawn" (male vibrates above female that has burrowed into substrate). I contrasted behaviors, sizes, and color scores of large and small males, and by presence/absence of spawning with a Mann-Whitney *U* test. The variables approach male, approach female, display, flee, approach spawn, size (SL), and coloration index were tested using a discriminant function analysis to separate males that spawned from males that did not spawn.

Field experiments

Female preferences were tested in a 1 × 1 m screen (0.8 m high with 2-mm mesh) enclosure that was placed into the spring pool over sand substrate where spawning had been observed. To contain stimulus individuals, I placed along one side four plexiglass cubes (10 cm per side) with three holes (2 mm diameter) drilled in each side for water exchange. Only the shoreward side of the enclosure could be used for cube placement because elsewhere the sand substrate shifted continuously due to water flowing out of the spring. I sequentially rotated the positions of the cubes between trials to control for female choice of position within the enclosure. The cubes had two sides covered with black plastic to visually isolate stimulus individuals from each other.

To begin a trial, stimulus fish were placed into cubes and the cubes covered with opaque plastic boxes. After a 10-min adjustment period the opaque boxes were removed to start the trial. For 20 min I recorded the time the experimental female spent within 5-cm of the uncovered sides of each stimulus cube. I used a 5 cm distance to ensure that females were perceiving the fish in cubes. I defined choice as occurring when females spent significantly more time by one of the cubes. I tested this using a χ^2 analysis of summed times by each cube (converted into percentages for each individual). In addition I used a one-way ANOVA with time as the dependent variable and cube as the independent variable, as a more powerful test. I also used these data to examine female preference for cube position by comparing the times spent near the four cube positions with χ^2 and one-way ANOVA. I used an ANCOVA to test if females spent significantly more time by either stimulus cube containing a male, with coloration score or size as the covariate.

Test of female preference for male body size

This experiment was performed from 22 May to 2 July 1992. For each trial, each cube contained a stimulus consisting of a large male ($\bar{x} = 42$, SD = 3 mm SL), a small male ($\bar{x} = 30$, SD = 3 mm), a female conspecific ($\bar{x} = 34$, SD = 4 mm), or no fish. I performed 37 trials ($n = 37$ females) and replaced experimental females for each trial. Stimulus males were used only once and stimulus females were replaced daily. Males captured at the site by hand net were paired such that their minimum SL difference was at least 9 mm ($\bar{x} = 11.3$; SD = 1.9 mm). I always attempted to match males by color index (mean coloration index difference = 0.8 ± 0.6). This was not always possible because size correlated strongly with color index. Each experimental female, assumed to be gravid because of capture in the vicinity of spawning sites, was placed into the enclosure at the start of each trial.

After each trial, males were released from cubes, and all cubes were removed from the enclosure. Because a male could then spawn with the female, a successful spawning confirmed that the experimental female was receptive to mating. I recorded which male mated with her to determine if female discrimination under plexiglass predicted which males spawned. If spawning did not occur the trial was omitted from the analyses.

Test of female preference for male color

I performed 35 trials ($n = 35$ females) from 19 April to 5 May 1993 using the same procedure as in the previous experiment but the cubes with stimulus males contained either a bright male (coloration score of 3) or a dull male (coloration score of 1). Male color did not appear to fade as a result of handling. Males were as closely matched by size as possible (mean size difference = 4.9 ± 2.8 mm), but size was correlated with coloration, thus ANCOVA was used as above.

Results

Field observations

Males were not larger than females (independent *t*-test, $t_{461} = -0.687$, $P = 0.492$; Fig. 1). Male size was correlated with male coloration score for 368 marked fish ($r = 0.694$, $P < 0.001$). Spawning frequency among focal males averaged 0.4 per 30 min. Of the 30 focal males 8 spawned: 5 of them (17%) spawned once, 2 (7%) spawned twice and 1 (3%) spawned three times in 30 min. Spawning occurred in the sandy substrate surrounding springheads.

Large ($n = 10$, $\bar{x} = 48.2 \pm 4.44$ mm SL) and small focal males ($n = 20$, $\bar{x} = 34.5 \pm 2.60$ mm SL) differed significantly in the frequency of approach male, lateral display, and flee behaviors, but not in spawning frequency (Fig. 2a). Coloration scores were not significantly different for large ($\bar{x} = 2.8 \pm 0.42$) and small males ($\bar{x} = 1.8 \pm 0.81$), although large males did tend to be brighter than small males. Males that spawned used more approach female behavior than males that did not spawn (Fig. 2b). Approach female and spawning frequency were significantly correlated ($r = 0.399$, $P = 0.029$), because males often approached females that evaded them. No difference in coloration score or standard length was found for males that did ($\bar{x} = 2.5 \pm 0.76$) or did not spawn ($\bar{x} = 2.0 \pm 0.84$). A discriminant function correctly separated spawning from non-spawning males 27 out of 30 times (Wilks' lambda $F_{6, 23} = 4.126$, $P = 0.006$). The most important

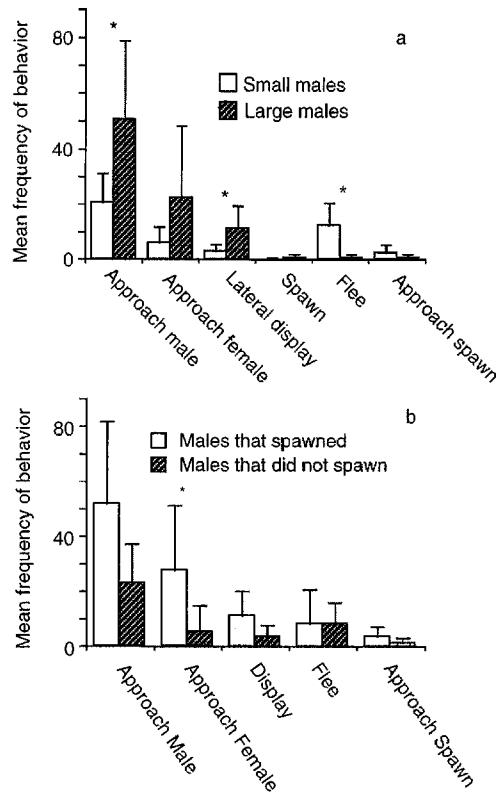


Fig. 2a Mean frequencies and SDs (error bars) of male behaviors from 30-min observations by size for 20 small and 10 large males. **b** Mean frequencies and standard deviations (error bars) of male behaviors from 30-min observations for 8 males that spawned and 22 males that did not spawn. * indicates significant differences using a Mann-Whitney *U*-test with Bonferroni adjustment of alpha level

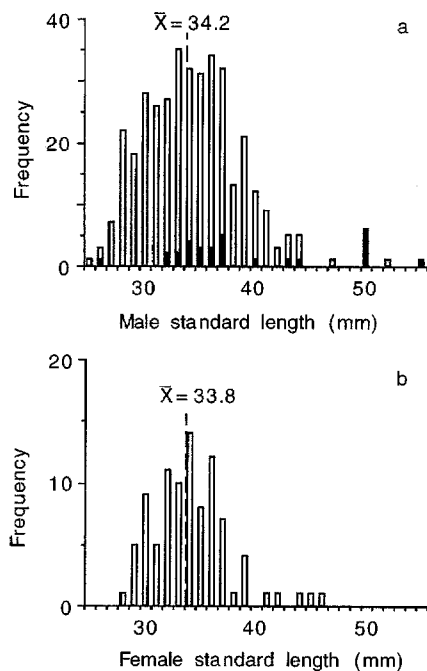


Fig. 1 Frequencies of standard lengths for **a** males and **b** females that were individually marked. Shaded bars represent males that were observed for 30-min intervals

variables (highest canonical loadings on discriminant function axis 1) were: approach female, approach male, and display (Table 1). Neither male body size ($r = 0.150$, $P = 0.428$) nor color index ($r = 0.142$, $P = 0.453$) were significantly correlated with spawning frequency. All males were sexually mature, and I observed even the smallest male (SL = 26 mm) mate. I did not detect any effect of color of the tags on reproductive success.

Field experiment for male body size

Females spawned in 32 of 37 trials with spawning occurring an average of 9.2 ± 9.1 min after release of males. In these 32 trials, females showed no preference for large ($\bar{x} = 39.1 \pm 49.3$ s), small ($\bar{x} = 27.9 \pm 45.8$ s), female ($\bar{x} = 43.2 \pm 39.2$ s), or the empty control cube ($\bar{x} = 27.4 \pm 39.2$ s, $\chi^2_3 = 0.54$, $F_{3, 124} = 0.564$, $P = 0.64$) or for cube location ($\chi^2_3 = 0.49$, $F_{3, 124} = 1.17$, $P = 0.32$). When time adjacent to cubes was adjusted for male color score, there was no preference for large versus small males (ANCOVA, $F_1 = 1.865$, $P = 0.177$). Experimental females spawned randomly with large (12) and small (20) males (χ^2 , $P > 0.05$). The time

Table 1 Canonical loadings on discriminant function axis 1. Probabilities are from discriminant function univariate *F*-tests

Variable	Loadings	<i>P</i>
Approach female	0.564	0.001
Approach male	0.584	0.001
Display	0.476	0.005
Approach spawn	0.283	0.081
Size (SL)	0.220	0.170
Body color	0.209	0.192
Flee	-0.012	0.939

before spawning occurred (latency) was not significantly different for large and small males ($t_{28} = -0.040$, $P = 0.968$). In five trials females burrowed into the substrate without approach behavior by a male. Male-male interactions occurred in six trials. In these trials, large and small males were equally successful in spawning (three trials each).

Field experiment for male color

Females spawned in 30 of 35 trials with spawning occurring an average of 9.8 ± 8.5 min after males were released. In these 30 trials, females showed no preference for bright males ($\bar{x} = 31.2 \pm 46.6$ s), dull males ($\bar{x} = 42.9 \pm 88.7$ s), females ($\bar{x} = 52.5 \pm 117.8$ s), or the empty control ($\bar{x} = 25.9 \pm 38.1$ s, $\chi^2_3 = 2.02$, $F_{3,87} = 0.755$, $P = 0.52$) or cube location ($\chi^2_3 = 1.59$, $F_{3,116} = 0.318$, $P = 0.81$). When time adjacent to cubes was adjusted for male size, there was no preference for either bright or dull males (ANCOVA, $F_1 = 0.022$, $P = 0.882$). Females spawned randomly with bright (16) and dull (14) males χ^2 , $P > 0.05$). The time before spawning occurred (latency) was not significantly different for bright and dull males ($t_{27} = -0.743$, $P = 0.464$). In two trials females burrowed into the substrate without approach behavior by a male. Male-male interactions occurred in three trials and bright males received all three spawnings. In one trial the dull male participated in spawning after the bright male initiated spawning.

Discussion

Size-based female mate choice is common in fishes, even when males are the same size or smaller than females (Hughes 1985, Berglund et al. 1986, Noltie and Keenleyside 1986, Hastings 1988, Cote and Hunte 1989, McPeck 1992). Many of these studies used species in which males perform some type of parental care. An absence of size-based female choice also has been identified in fishes that lack sexual size dimorphism (Petersen 1988), but few studies have found lack of choice in fishes with neither male parental care nor sexual size dimorphism. In orangethroat darters, a species without parental care and no sexual size dimorphism, large males did not have higher spawning success than

small males during field observations (Fig. 2a) or experimental manipulations, and there was no correlation between size and spawning frequency. Large males were not preferred over small males in field enclosure experiments. Although my field experiments had high variation in time that females spent near cubes, thus decreasing the power to detect differences, there is no suggestion that an increase in replication would result in female preference for large males.

Petersen (1988) suggested that in *Malacoctenus hubbsi*, a fish with no sexual size dimorphism, lack of female preference for larger males ultimately stems from the availability of a large supply of unpredictable oviposition sites. Oviposition sites for *E. spectabile* at this spring site seem spatially predictable but in low supply. Spawning sites are restricted to the immediate vicinity of springheads, which are predictably available and limited in number. Furthermore, spawning sites are probably too large to be successfully defended even by large males.

Females did not appear to choose males on the basis of color in the enclosure experiment. Coloration scores were not different for spawning and nonspawning males in field observations (Fig. 2b), and there was no correlation between coloration score and spawning frequency. In most animals with sexual color dimorphism females usually choose males based on color. The only exceptions known in fishes are lack of female choice for a color morph of *Cichlasoma citrinellum* (Barlow and Rogers 1978) and for black coloration in *Pseudolabrus celidotus* (Jones 1981). Other exceptions are variations in female choice among populations in which females in populations with different selection pressures have different mate preferences (e.g., Breden and Stoner 1987).

Male-male interactions in enclosures were minimal and had little influence over which male spawned with a female. This may have been due to the low density of males in enclosure trials (2 males/m²). The density in the spring area was greater (approx. 20–40 per m², personal observations). In my focal male observations, male-male interactions were common and were moderately important in the discriminant function predicting spawning: males that approached competitors more frequently and displayed more often were more likely to spawn. The focal male results also showed that large males were more likely to engage in these aggressive behaviors than small males. However, large and small males did not differ in spawning frequency (Fig. 2a), and males that spawned at least once were not significantly larger than unsuccessful males. The discriminant function analysis provided additional evidence that male size was not a good predictor of spawning success. Part of this paradox may stem from the overlap of aggressiveness and spawning success of large and small males. Many spawnings appear to occur opportunistically, with only one male present.

Approach female behavior (a form of courtship) was a good predictor of male spawning success in the size category comparison (Fig. 2b) and in the discriminant function analysis.

Parker (1992) predicted that males should be larger than females, with size-related fecundity of females held constant, in fishes with increased levels of male-male contests, and that sperm competition alone was unlikely to result in male-biased sexual size dimorphism. Sperm competition may be high in *E. spectabile* because many spawnings have multiple males. Males spawned individually with females in 15 of 21 matings and an average of 3.5 males participated in the other 6 matings (unpublished focal male observations). This provides a rough estimate that one third of all spawnings resulted from approach-spawn behavior. Males sometimes compete overtly for matings (male-male approach behavior was an important predictor of spawning) but once a mating has begun other males can participate (= sneakers), regardless of ability to dominate competitors. Large males initiating spawnings may get more fertilizations than sneakers due to their proximity to females. For chum salmon Schroder (1981) showed that the position of satellite males during spawning influenced the number of fertilizations they obtained.

In *E. spectabile* lack of sexual size dimorphism may be a product of a lack of female choice for size, only moderate levels of male contest behavior, and prevalent sperm competition. Selection acting on size (fecundity) of females is another alternative that could contribute to a lack of size dimorphism; larger female darters produce more eggs (Page 1983).

Bright coloration in *E. spectabile* males does not appear to have evolved as a result of female choice. Perhaps this bright coloration functions as a signal between males. These results suggest a stronger role of intraspecific than interspecific selection in this species. Or, depending on the survival costs of coloration, bright coloration in this fish may be present due to phylogenetic history (Brooks and McLennan 1991). All of the darters in the subgenus *Oligocephalus* have bright coloration (Page 1983).

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