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THE BREEDING SYSTEM OF AN ENDANGERED PUPFISH
(*CYPRINODON ELEGANS*)

John K. Leiser[1] and Murray Itzkowitz[1]

ABSTRACT.—We examined the breeding behavior of the endangered Comanche Springs pupfish (*Cyprinodon elegans*) during 3 separate breeding seasons in a pool of springwater originating in Phantom Cave, near Balmorhea State Park, Texas, in relation to behaviors reported for the species in swift-flowing canals (Itzkowitz 1969). In the quiet pool, unlike in swift water, the breeding system was characterized by 3 different male mating tactics: territorial defense, satellite positioning, and sneak spawning. Although the breeding strategies adopted by the males were conditional, mating tactics generally reflected male size. Territorial residents were the largest, satellites were medium-sized, and sneakers were the smallest adult males observed in the population. Territorial males traversed the least amount of area, defending compact territories, while satellites and sneakers covered more area in attempts to spawn. Although preferred territories in swift water centered on algal mats, territorial residents in quiet water seemed to prefer territories around large rocks. Males defending rocks had higher reproductive successes than males occupying other substrate types. The flexibility of the males' tactics was exhibited during one year of study when large males appeared to be absent from the population. During that year, medium-sized males switched from the satellite to territorial tactic, while small males remained sneakers.

Key words: pupfish, Cyprinodon elegans, *breeding, Texas, conditional mating tactics.*

The Comanche Springs pupfish, *Cyprinodon elegans* Baird and Girard, was originally described from a population inhabiting the artesian pool of Comanche Springs near Fort Stockton in Pecos County, Texas. Before the end of the 1950s, however, depletion of groundwater caused the spring to fail, leading to the extinction of this pupfish from its type locality (Hubbs and Echelle 1972). The only remaining natural populations of this species inhabit spring-fed waters in and near Balmorhea State Park in Toyahvale, Reeves, and Jefferson Davis Counties, Texas (Echelle 1975, Davis 1979). As a result of substantial declines in populations of this pupfish, this species has been listed as endangered.

Although the breeding behavior of *C. elegans* was described in swift-flowing, cement-lined canals (Itzkowitz 1969), little has been done to document its reproductive behaviors in its primary habitat of quiet springs and slowly flowing canals. Here, we describe the breeding system of a population of *C. elegans* occurring in a pool of spring water originating in Phantom Cave, located approximately 8 km west of Balmorhea State Park. The breeding grounds of the population comprised a small cove and adjacent shallow waters (<30 cm deep) with silt and sand substrate interspersed with submerged rocks and mats of filamentous algae around which many of the males' territories occurred. Total area of the breeding grounds was approximately 50 m^2, accommodated the territories of nearly 20 males, and was bounded by dry land or deeper areas of the spring. Although all apparent breeding occurred in the shallows, the deeper water housed most of the population. Fish were observed during the last week in April 1996 and the first 2 weeks in May 1998 and 1999. We attempt to characterize the behaviors seen in this population in relation to behaviors observed in swift water (Itzkowitz 1969). Although the future status of the Phantom Cave population is questionable due to failure of the spring, healthy populations of this species remain in 2 refuges within the state park (Hubbs 2001).

Members of the genus *Cyprinodon* are typically small in size with stout bodies and short fins (Itzkowitz 1974); in both swift and quiet water, *C. elegans* has a similar but more elongate body plan (Itzkowitz 1969, Echelle 1975). Individuals of this species are generally grey and drab with dark speckled coloration and

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blotches that form a faint lateral "stripe"; the species lacks the dark grey-brown vertical barring characteristic of many *Cyprinodon* (Page and Burr 1991). In addition, adult males generally exhibit some blue blotches of nuptial coloration on their anterior dorsa, although this is not as brightly developed as in other species of *Cyprinodon* (Kodric-Brown 1983). Adult body size reaches a maximum of about 60 mm total length (Gehlbach et al. 1978, Davis 1979). Reproductively active males observed at Phantom Cave varied in total length from 30 to 60 mm (mean $\pm s_{\bar{x}}$: 45.5 $\pm$ 1.12 mm; N = 67). The size of each fish was estimated by placing a ruler in the water as near as possible to the fish without disturbing the fish's behavior. The breeding season of *C. elegans* appears typical for the genus; most pupfish breeding seasons encompass the warmer months of the year, beginning in late March or early April and extending into October, with their peaks in July (e.g., Itzkowitz 1974, Kodric-Brown 1986).

The mating system of *C. elegans* is territorial, generally promiscuous, and similar to that of its congeners (for review, see Kodric-Brown 1981). During our observations, spawning sequences typically began with a female entering the territory of a male. Following the male's approach, the female would bite the substrate; the male then positioned himself alongside the female with his snout directly behind her operculum. The pair would form an S-shape and complete spawning with a rapid, jerking movement (Itzkowitz 1969). A single demersal egg was assumed to have been deposited during the jerk, as is typical in pupfish (Barlow 1961). Substrate biting by the female occurred at times without the pair's spawning, and the spawning sequence was not necessarily initiated by substrate biting. After the initial spawning event, 1 of 3 behaviors was frequently observed. First, the male and female might repeat the spawning sequence, resulting in several sequential spawns. Second, the female could leave the male's territory and enter the territory of another male, spawning with this 2nd male. Third, the female could leave the territory and disappear from view, often leaving the breeding grounds. Spawning sequences were consistent with those reported by Itzkowitz (1969), with the exception that females in calm water often spawned more than once with a given male. No direct parental care of offspring was exhibited, although defense of the territory by the male

provides indirect care of developing eggs (Kodric-Brown 1981).

Male *C. elegans* were each observed for 15 minutes, or for as long as the focal male could be followed. As some non-territorial males ranged widely, they were difficult to follow for the entire 15 minutes. Observations were recorded onto audiotape and later transcribed for analysis. Due to errors in recording, some data from several observed males were missing (e.g., the habitat type occupied may have been erased or recorded over by data from the next observation). These males were then excluded from appropriate analyses. Analyses were conducted using the statistical software package STATISTICA, 1998 edition, by StatSoft Inc.

During 1996 and 1999 we observed 3 qualitatively different male mating tactics in *C. elegans*; males were divided into 3 size categories, reflecting the 3 tactics. The largest males present defended territories, while medium-sized and small males adopted satellite and sneak-spawn tactics, respectively. During spring 1998 large males appeared to be absent from the population, and only 2 tactics were observed. Medium-sized males defended territories, while small males remained as sneakers.

During all years the largest males present on the breeding grounds defended territories. In 1996 and 1999 territorial residents ranged in size from 50 to 60 mm (mean $\pm s_{\bar{x}}$ total length: 55.53 $\pm$ 0.85 mm, N = 19; 50.0 $\pm$ 1.18 mm, N = 9 for 1996 and 1999, respectively). In 1998 territorial residents ranged in size from 40 to 50 mm (43.61 $\pm$ 1.06, N = 18). Territorial males often defended sections of submerged rocks or algal mats in shallow water (<30 cm deep), but they also occupied territories covering sand or silt. Unlike *C. elegans* occurring in fast-flowing water which were more likely to defend algal mats (Itzkowitz 1969), territorial males in quiet water tended to defend territories that included rocks. In addition, territories that included rocks were preferentially visited by females. That is, across the 3 years of observation, males that occupied rocks spawned significantly more times than males with territories that did not include at least 1 rock (median test: $\chi^2(1)$ = 6.96, P < 0.01; Fig. 1). This was the case even though the number of spawns was significantly different among years (Kruskal-Wallis 1-way ANOVA:
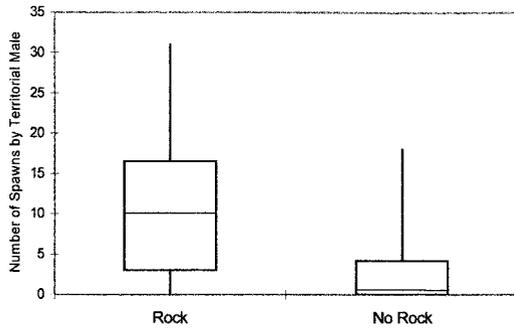
Fig. 1. Medians, 1st and 3rd quartiles, and ranges for the number of spawns in which territorial males engaged during spring 1996, 1998, and 1999 (median test, $P < 0.01$).
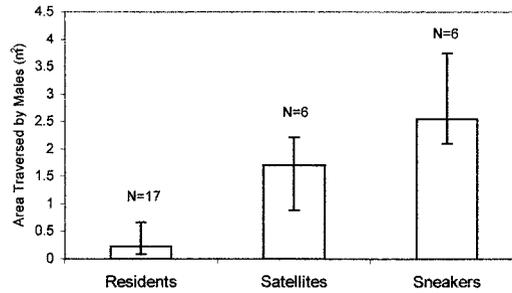

Fig. 2. Medians and 1st and 3rd quartiles for the amount of area covered by males engaging in each of the 3 conditional breeding tactics during 1996 (Kruskal-Wallis 1-way ANOVA, $P < 0.01$).

$H_{2,43} = 8.29$, $P < 0.05$). The number of spawns was similar for 1996 and 1998 (post hoc comparison: $Q = 2.01$, NS; Zar 1999) and 1996 and 1999 (post hoc comparison: $Q = 0.81$, NS), but significantly fewer spawns were observed in 1998 compared to 1999 (post hoc comparison: $Q = 2.60$, $P < 0.05$). This result was most likely due to differences in the operational sex ratio of the population during the different years (Leiser and Itzkowitz 2002).

As in swift-flowing canals (Itzkowitz 1969), territorial residents in quiet pools spent much of their time defending the territory against non-territorial conspecific intruders. In addition, male *C. elegans* were observed chasing heterospecific intruders, including *Astyanax mexicanus* as well as *Gambusia* sp. These species occur in the same habitat as *C. elegans* and may be egg predators; heterospecific fish were not seen attacking *C. elegans.* Although we observed territorial males chasing intruders beyond their territorial boundaries, the residents quickly returned to the center of their territories. Because of the quiet water, males neither positioned themselves at an upstream edge of the territory nor oriented themselves in any particular direction as they had in flowing water (Itzkowitz 1969). Unlike in canals (Itzkowitz 1969), territories were contiguous with relatively stable boundaries, although boundary fights did occur. Median territory size in 1996 was 0.225 m^2 (Fig. 2).

Intrusions by smaller males into territories of large males were common. Both medium-sized (40–45 mm) and small males (30–35 mm) were seen entering the territories of larger males in attempts to spawn with females.

Quantitative data on conditionally breeding males were taken during 1996 only. During that year, medium-sized intruders engaged in a "satellite" tactic. The largest satellite males were shorter than the smallest territorial males but longer than the largest small males (sneakers), ranging in size from 40 to 45 mm (mean $\pm s_{\bar{x}}$ total length: 43.57 ± 0.92 mm; $N = 7$). Satellite males exhibited nuptial coloration qualitatively similar to territorial males and initiated aggression against smaller males but infrequently attacked larger opponents. The satellite tactic was characterized by the males' positioning themselves in the water column above the territories of up to 6 larger males (range: 2–6 territories), patrolling an area that encompassed up to several square meters (median area traversed: 1.71 m^2; Fig. 2). There were significant differences in the areas covered by males engaging in the 3 different tactics (Kruskal-Wallis 1-way ANOVA: $H_{2,43} = 17.85$, $P < 0.001$), and satellite males covered significantly more area than territorial males (ad hoc comparison: $Q = 2.74$, $P < 0.05$). Satellite males attempted to gain spawning opportunities by interrupting a territorial male's spawns or by sneaking spawns with females when the territorial male was absent. The average percentage of spawns engaged in by satellites by interrupting large males was $76.02 \pm 15.3\%$; on average, $23.98 \pm 15.3\%$ of spawns were achieved during the territorial males' absences.

The smallest adult males in the population engaged in a sneak-spawning tactic; males exhibiting this "sneaker" strategy ranged in size from 30 to 35 mm (mean $\pm s_{\bar{x}}$ total length: 31.54 ± 0.667 mm; $N = 13$). Sneaker males

initiated little aggression while on the breeding grounds. These males retained a cryptic, female-like coloration and attempted to gain reproductive opportunities by either spawning with a female in the territory of a large male while that male was preoccupied elsewhere (11.88 ± 6.54%) or by sidling with a female while she spawned with either a territorial male (54.38 ± 15.28%) or a satellite male (8.75 ± 6.40%). Sneakers ranged widely, covering significantly more ground than territorial males (ad hoc comparison: $Q = 3.81$, $P < 0.05$), but not satellite males (ad hoc comparison: $Q = 0.88$, NS). Sneaker males traversed an area as large as 16 m^2 (median area traversed: 2.55 m^2; Fig. 2). These males entered and exited the breeding grounds frequently. The presence of conditionally breeding males has not been documented in *C. elegans* (Itzkowitz 1969), but it has been reported in congeners (e.g., *C. pecosensis*; Kodric-Brown 1986). However, Kodric-Brown (1986) described sneak-spawning as a strictly "opportunistic breeding tactic" adopted by "individuals, irrespective of size" and not as a tactic adopted by particular males. The tactics exhibited by *C. elegans* males were clearly conditional; however, *C. elegans* provides the first example of small males primarily adopting a sneaker strategy.

Although the spring habitat of *C. elegans* has been dramatically modified (Winemiller and Anderson 1997), the breeding behavior of the Phantom Cave population more closely resembles that typical of other *Cyprinodon* (for review, see Kodric-Brown 1981) than did the breeding behavior in swift water (Itzkowitz 1969). For example, territorial residents spent much of their time patrolling their territories in defense against both conspecific and heterospecific intruders, and aggressive interactions between contiguous neighbors were common. In addition, non-territorial males attempted to acquire spawns in the territories of resident males through alternative tactics (satellite-positioning and sneaking) not observed in swift water.

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