

Reproductive Behavior in Banded Pygmy Sunfish, *Elassoma zonatum* (Elassomatidae), with Comments on Implications for Relationships of the Genus

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ABSTRACT: Reproductive behaviors and associated changes in color pattern are described for banded pygmy sunfish (Elassomatidae: *Elassoma zonatum*). Previous descriptions of behavior in the genus have been restricted to popular literature or were incidental to broader studies. Observations not previously reported include a striking change in male coloration during late courtship and spawning, a stereotyped “pointing” behavior by the male that resembles nest showing behavior in gasterosteid fishes, and a jerking behavior in the male that appears associated with sperm release. The behavior of *E. zonatum* is discussed in the context of recent studies suggesting that *Elassoma* may be closely related to the gasterosteids. Several aspects of courtship behavior in *E. zonatum* are reminiscent of the well-known behavior of gasterosteids.

RESUMEN: Los comportamientos reproductivos y cambios asociados en los patrones de coloración son descritos para la mojarrita de bandas *Elassoma zonatum* (Elassomatidae). Previa descripción sobre el comportamiento en el género han sido restringidas a literatura popular o incluidas en estudios más amplios. Las observaciones no previamente reportadas incluyen un cambio notable en la coloración del macho durante la última parte del cortejo y desove, un comportamiento de señalamiento del nido por el macho que se asemeja con aquel de exhibición del nido en los peces de la familia Gasterosteidae, y un comportamiento convulsivo del macho al parecer asociado con la expulsión de esperma. El comportamiento de *E. zonatum* es discutido considerando estudios recientes que sugieren que *Elassoma* puede estar cercanamente relacionado a Gasterosteidae. Varios aspectos del comportamiento de cortejo en *E. zonatum* son reminiscencias del comportamiento bien conocido de los Gasterosteidae.

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In this paper, we describe courtship and spawning in the banded pygmy sunfish, *Elassoma zonatum*, a small (generally <45 mm total length) inhabitant of heavily vegetated swamps, backwaters and springs in Atlantic and Gulf Coastal plains areas from North Carolina to eastern Texas (Walsh and Burr, 1984). Description of reproductive behavior in *Elassoma* has been restricted to hobbyist literature or included in studies with a broader emphasis. Miller (1963) described courtship (but not spawning) in *E. evergladei* as part of a study of centrarchid behavior. Taber (1965) and Walsh and Burr (1984) described courtship and spawning behaviors in *E. zonatum* in their studies of, respectively, eye development and life history. Mettee and Scharpf (1998) provided a general description of reproductive behavior, embryology, and larval development in four species of the genus, including *E. zonatum*. Probably because of the broader scope of these previous studies, certain aspects of reproductive behavior and associated color pattern changes seem to have been overlooked; our intent was to provide a more complete qualitative description for *E. zonatum*.

Relationships of pygmy sunfish have remained unresolved since the original description of the genus (Jordan, 1877). Until recently, the genus was considered a perciform and placed either in its own family or in the Centrarchidae. A close relationship to centrarchids has been discounted on the basis of both morphology and behavior (Branson and Moore, 1962; Johnson, 1984). More recently, the genus was removed from the Perciformes and placed in the Smegmamorpha,

which also includes synbranchiforms, mugilomorphs, atherinomorphs, and gasterosteiforms (Johnson and Patterson, 1993), and certain features of the skeleton suggest a sister relationship between *Elassoma* and gasterosteoids (D. Johnson, pers. comm.). Correspondingly, we find various components of courtship and spawning behavior in *E. zonatum* to be reminiscent of the well-known behavior of gasterosteids. Significantly, we reached this conclusion while observing pygmy sunfish in the spring of 1974, prior to the suggestion from morphology of a close relationship between *Elassoma* and gasterosteiforms.

Materials and Methods

In March of 1974 and 1994, adult *E. zonatum* were collected from, respectively, the city spring at Fort Towson, Choctaw Co., Oklahoma, and swampy pools near the Little River bridge N of Idabel, McCurtain Co., Oklahoma. Fish were maintained in various sizes of aquaria ranging from 20-80 liters. Observations were made from March through May in both years. Aquaria used for behavioral observation contained 2-3 males and 4-6 females. Seventeen males and 36 females were studied during approximately 155 hours of observations. In 1974, frequencies of various behaviors were recorded with a 20-channel Esterline-Angus event recorder. In 1994, courtship and spawning were documented with an 8-mm camcorder.

Aquaria were provided with aerators, gravel substrata, and vegetation from the natural habitat (1974) supplemented (1994) with artificial (plastic) aquarium plants "rooted" in the substratum. The simulated plants facilitated recording and did not notably alter reproductive behavior. Fish were fed, *ad libitum*, live aquatic invertebrates collected locally, augmented with live worms (*Tubifex*). Photoperiod was approximately 14 hours of light to 10 hours of darkness; water temperature varied from 18-26°C.

Results

Males defend territories centered around the preferred spawning site, typically a patch of dense vegetation (e.g., *Myriophyllum*) well off the bottom, but in the absence of such growths males will use a single sprig. The spawning site consists of a specific spot in the vegetation that the male preselects and generally guards against other pygmy sunfish except for spawning females and larvae; he uses this site day after day for spawning.

Territorial males frequently court females, and such activity was observed almost daily. Eleven courtship sequences that terminated with spawning were videotaped in 1994. Although less well documented, a similar amount of activity was observed in 1974. Fig. 1 shows some of the predominant behaviors in courtship and spawning; Fig. 2 shows frequencies of behaviors for a breeding male.

Females may initiate courtship by slowly approaching a male or moving directly to the male's spawning site. More frequently, the male initiates an encounter with a lateral display (Miller, 1963) or a sidling-threat display (Miller, 1963), both of which are important in agonistic interactions. Lateral display, with median fins fully spread, is performed while stationary and often develops into the more aggressive sidling-threat display, in which the male approaches the female sidewise. In sidling-threat display, median fins are bent away from the female and all fins vibrate rapidly. Subsequent behavior seems determined by the female's response. If she flees, the male is likely to chase her a short distance. If she maintains position, the male either terminates the encounter with a quick lunging attack or initiates courtship.

Courtship commonly begins with a complex display that Miller (1963) termed "wiggle waggle" for *E. evergladei* (Figs. 1A and 2); often, this is preceded by lateral display or sidling-threat display. Wiggle waggle is a conspicuous behavior involving several different fin movements added in a predictable sequence. Low intensity is typified by only a scissoring of the pelvics. At slightly higher intensities, the spinous portion of the dorsal fin collapses and the soft portions of the dorsal and anal fins are swung in unison from side to side as the pelvics are scissored. Finally, the caudal fin is swung from side to side, its motion opposing those of the dorsal and anal fins. At highest intensity, while either progressing forward or maintaining position, the male adds an up-down rocking motion in which his longitudinal axis is repeatedly tilted up, then down. In terms of frequency of occurrence, wiggle waggle is the predominant male reproductive behavior, both on days when spawning occurs and on days when it does not; however, the frequency of wiggle waggle is much higher on days when females seem more receptive and spawning occurs.

During the wiggle-waggle phase of courtship, the male typically initiates leading behavior by moving toward the spawning site and sometimes by alternately going toward the site and back toward the female. This is either a simple swimming movement or, more typically, it includes wiggle waggle/up-down displays. Responsive females haltingly follow the male, typically in a series of short glides accomplished

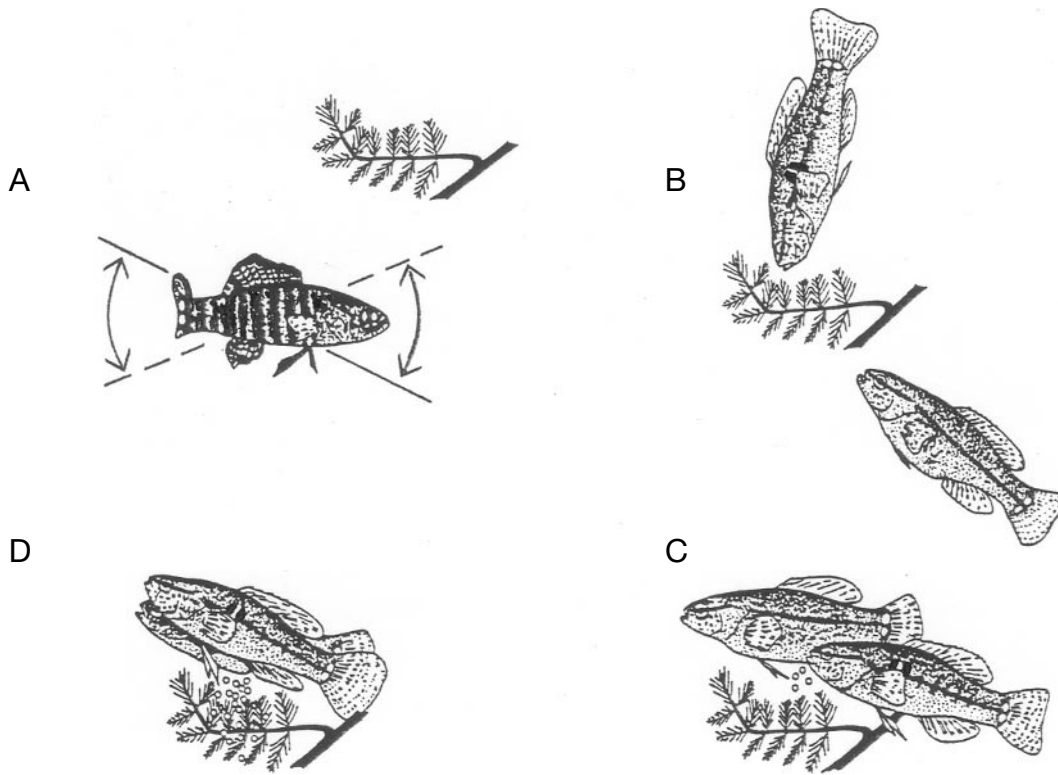


Fig. 1.

Courtship and spawning behaviors in *Ellassoma zonatum*. A = wiggle waggle (male); B = pointing (male) and following (female), C = nudging (male) and quivering and egg release (female), D = jerking (male) and quivering and egg release (female). Males are signified by the dark, broken scapular spot in B-D. Note the male color pattern change after he enters the spawning site (see Results for description).

solely by sculling with the pectoral fins. Between glides the female often tilts head up facing the male, either in midwater or on the substratum while supported by her caudal region and erected pelvic fins (a common resting posture).

As the female approaches the male in his spawning site, he shifts from wiggle waggle/up-down to pointing (Figs. 1B and 2). When pointing, the male quivers vigorously, head down, body nearly vertical, and snout directly over the spawning site. The caudal and pectoral fins vibrate rapidly, and the head is repeatedly jerked sidewise, mouth snapping open and shut.

During the male's pointing, the female moves to a position near his snout. He then reorients into a more horizontal position and initiates nudging (Figs. 1C and 2), fins and body quivering rapidly and snout repeatedly bumping the female ventrolaterally on her flank and genital area. While nudging, the male often moves from one side of the female to the other. After a second or two, the female begins an energetic quivering and then releases a shower of several to about 40 eggs.

When the first eggs emerge, the male, as if on visual cue triggered by egg release, quickly reorients and initiates jerking behavior (Figs. 1D and 2), which presumably is associated

with sperm release. Jerking, not previously reported for pygmy sunfishes, consists of a series of spasmodic, sidewise jerks of the head and body, often making a slight forward movement with each jerk. While jerking, the male's position is variable relative to the female. He may pass from one side of her to the other, or he may remain relatively stationary and parallel with the female at her level or slightly above, or he may orient directly beneath or above the female with his body crossing hers. During the male's jerking, the female continues to quiver while extruding eggs. Her quivering and particularly his jerking may extend a second or two beyond completion of egg release. The eggs are demersal and adhere to surrounding vegetation, although some usually fall to the bottom. Time from start of pointing to the end of jerking is approximately 30-40 seconds. After spawning, the male typically moves out of the area of egg release and returns to territorial defense. The female may rest quietly in the vegetation near the spawning site for 30 seconds or longer without being displaced by the male.

Color pattern changes during courtship and spawning are striking in the male and not apparent in the female. Males

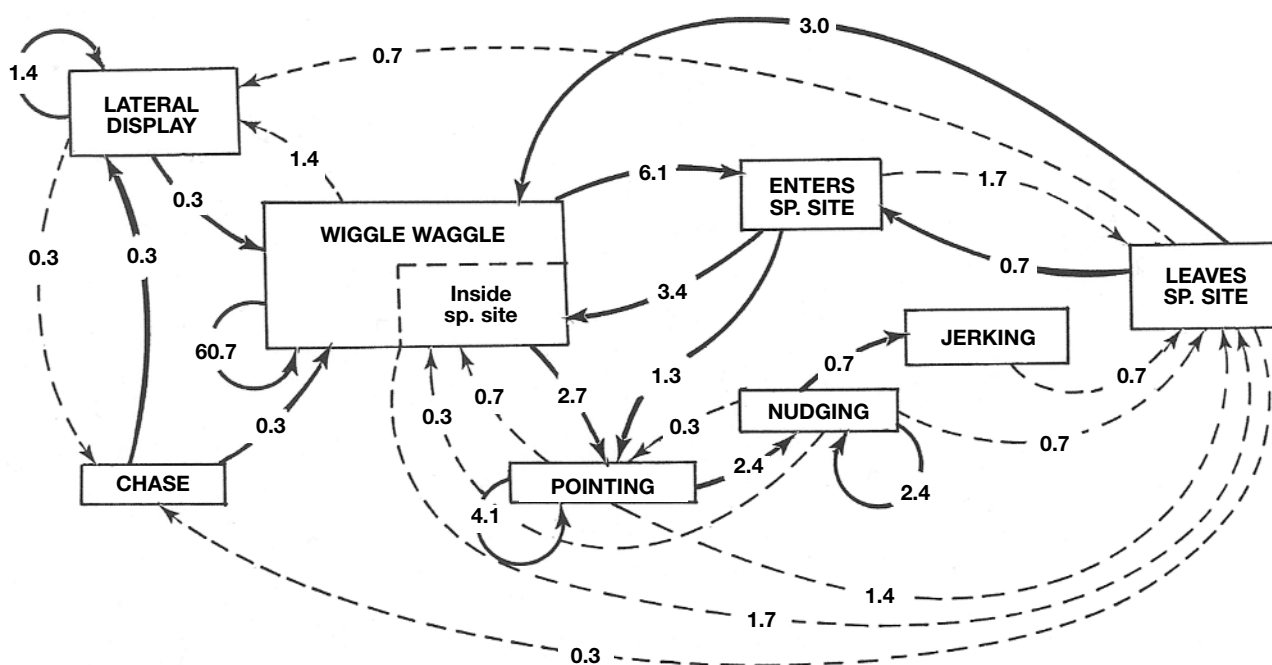


Fig. 2.

Percent frequency of occurrence of transitions between male courtship behaviors on a day when spawning occurred. Percentages represent the behavior of one male in 295 transitions during two hours of observation. Solid lines = transitions progressing toward the spawning act; dashed lines = transitions representing a reversion to earlier phases of courtship, or the breakdown of a courtship. Only interactions consisting of two or more transitions are considered.

actively engaged in territorial defense and in early courtship are typically blackish to dark brown with a barred pattern and a dark scapular spot broken by one or two iridescent turquoise bars. All fins are dark except the pectorals, which are clear. Outer edges of dorsal and anal fins are black; proximal halves of these fins are speckled with whitish to iridescent-turquoise. The pelvics are black with white spots near the bases. There are two small iridescent-turquoise bars under each eye and one behind the lower edge of the eye. A black hourglass-shaped bar passes through the center of the eye. The venter in front of the pelvics and the sides of the head are speckled, with black on a whitish or iridescent-turquoise background.

During the leading phase of courtship, the male's pattern begins to fade, and by the pointing and spawning phases it typically is light brownish and there is either a faint barring on the body or the barring disappears and the pattern resembles that of the female except for a remnant of the scapular spot. This spot generally is absent in females, except when they are aggressive toward other females. The eye of the male in this phase is white with no vertical bar and a small black pupil. As in females, the faded male has a narrow stripe extending from the tip of the snout to the margin of the

operculum, and sometimes to the base of the caudal fin. The male's dark, barred pattern may reappear within seconds after spawning and resumption of territorial defense.

On five occasions, we observed "sneaker behavior," an activity reported previously for *E. zonatum* (Poyser, 1919; Walsh and Burr, 1984). In such instances, an intruding male (often an adjacent territory-holder) moves into the spawning site and initiates jerking behavior, usually on the other side of the female from the resident male, but sometimes just above the spawning pair; once, a sneaker moved between a jerking male and the female. Such an intruder rarely encounters resistance until the resident male finishes spawning and chases him away. The color pattern of sneaking males resembles that of the female. On one occasion, a male stopped nudging a female and started nudging the abdomen of an intruding male.

Discussion

In agreement with other behavioral studies on the genus *Elassoma* (Miller, 1963; Taber, 1965; Walsh and Burr, 1984; Mettee and Scharpf, 1998), there apparently is no nest building by the male, although some workers suggest the possibility of such activity (Poyser, 1919; Hervey and Hems, 1952; Robison,

1971). We observed no parental care beyond the male's defense of his territory, which includes his spawning site.

Change in male color pattern from the dark, conspicuous phase characteristic of territorial defense and early courtship to the pattern typical of females in late courtship and spawning have not been previously documented for *Elassoma*, although other authors have noted that the pattern can change rapidly (Poyser, 1919; Miller, 1963; Walsh and Burr, 1984). Mettee and Scharpf (1998), in a general description of spawning in *Elassoma* (including *E. zonatum*), stated, "the male became brightly colored" when the female entered the spawning site. This is at variance with our observations in which the male pattern consistently faded to resemble that of the female. Such a change suggests reduced aggression in later phases of courtship and spawning. Correspondingly, spawning males showed no aggression toward sneaker males and were tolerant of sneakers and females for a brief period after spawning.

Overall, courtship and spawning behaviors in *E. zonatum* resemble those described for *E. evergladei* by Miller (1963) and Mettee and Scharpf (1998) and for two other species (Mettee and Scharpf, 1998), *E. okefenokee* and the recently described (Mayden, 1993) *E. alabamae*. However, we observed two behaviors, pointing and jerking, not described in previous reports on courtship and spawning in *Elassoma*, including the most recent description (Mettee and Scharpf, 1998) for *E. zonatum*. These behaviors, which were invariant in our observations, probably have been overlooked in *E. zonatum* and possibly also in the other species.

Some phases of courtship in *Elassoma* are at least superficially similar to comparable phases in gasterosteids (Wootton, 1976). In both groups, the territorial male preselects a specific spawning site, a nest constructed of vegetation by the male in gasterosteids and a small "patch" of vegetation in *Elassoma*. Also in both groups, territorial males exhibit a conspicuous behavioral display in early courtship (wiggle-waggle in *Elassoma*). Then, while positioned at the spawning site, the male gasterosteid or *Elassoma* (at least the species *E. zonatum*) shows the site by pointing toward it with his snout, and the female then enters. In both groups, egg release seems to require tactile contact between the male's snout/mouth and a posterior region of the female; nudging in *Elassoma* is similar to descriptions (Wootton, 1976) of quivering on the flank of the female by male threespine sticklebacks prior to egg release. Finally, in both groups the male does not move into position for sperm release until the female has either started to release eggs (*Elassoma*) or has completed egg deposition (gasterosteids).

McLennan et al. (1988) argued that behavior can provide useful, although frequently ignored, insight into phylogenetic relationships. McLennan et al. (op. cit.) then used the unusually rich background of knowledge on gasterosteid behavior to infer phylogenetic relationships among members of the group. With more information, such an analysis might provide broader insight into phylogenetic relationships and the evolutionary history of courtship and spawning behavior. For example, character-state distributions for gasterosteids and the gasterosteiform family Aulorhynchidae (McLennan, 1993) indicate that showing the nest is a potential synapomorphy uniting *Elassoma* and the gasterosteids. This, however, requires loss of a complex trait in *Elassoma*: namely, nest-building with a glue produced in the male's kidney (Wootton, 1976). Alternatively, showing is a plesiomorphy lost in aulorhynchids. Resolution of these and other conflicts awaits a more thorough analysis of the genus *Elassoma* and detailed comparative studies with other fishes.

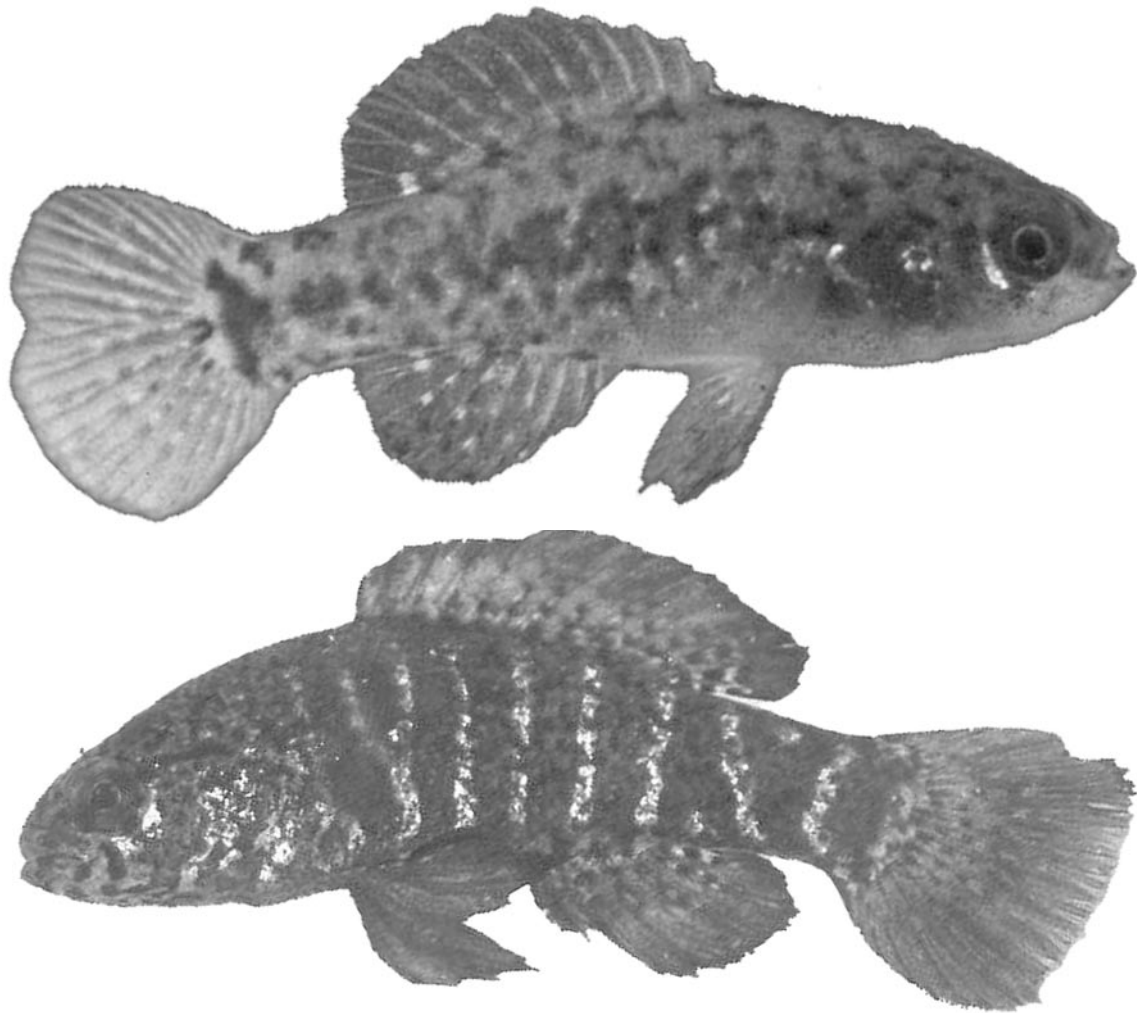
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Top: Everglades pygmy sunfish (*Elassoma evergladei*). Bottom: Banded pygmy sunfish (*Elassoma zonatum*). Photos by Fritz Rohde. For new information on the breeding behavior of *E. zonatum*, see the article on page one. For interesting nomenclatural trivia regarding all *Elassoma* species, see pp. 16-17.

Okefenokee pygmy sunfish (*Elassoma okefenokee*). This specimen hails from the Hillsborough River System of southwest Florida.



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