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Article in *The Southwestern Naturalist* · January 2009

DOI: 10.1894/0038-4909(2007)52[371:RSDACB]2.0.CO;2

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REVERSED SEXUAL DIMORPHISM AND COURTSHIP BY FEMALES IN THE
TOPAZ CICHLID, *ARCHOCENTRUS MYRNAE* (CICHLIDAE, TELEOSTEI),
FROM COSTA RICA

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ABSTRACT—*Archocentrus myrnae* is a small Central American cichlid that breeds in crevices. This study describes reproductive behavior and associated changes in color patterns in this species. Unlike most other cichlids from that area, female *A. myrnae* establish territories and actively court males before spawning. During courtship, females exhibit a distinct coloration. Whereas presence of courtship by females and the reversed sexual dimorphism usually is connected to reversal of sex roles in other fishes, females of *A. myrnae* intensively care for their brood after spawning through the free-swimming stage. Males are less active during brood care. In the context of the high reproductive investment of females, the evolution and maintenance of courtship and ornamentation of females is not yet understood.

RESUMEN—*Archocentrus myrnae* es un cíclido pequeño centroamericano que se aparea en grietas. El presente estudio describe la conducta reproductiva y los cambios asociados en los patrones de color en esta especie. A diferencia de muchos otros cíclidos en esta área, las hembras de *A. myrnae* establecen territorios y cortejan activamente a los machos antes del desove. Durante el cortejo, la hembra exhibe una coloración distinta. Mientras que la presencia de cortejo por la hembra y el dimorfismo sexual invertido son usualmente asociados a la inversión del papel sexual en otros peces, las hembras de *A. myrnae* cuidan intensamente a sus huevos y a sus crías después del desove, incluyendo hasta cuando las crías nadan por sí mismas. Los machos son menos activos en el cuidado de los huevos y las crías. En el contexto de una alta inversión de la hembra en la reproducción, la evolución y el mantenimiento del cortejo por la hembra y su ornamentación todavía no se entienden.

Central America harbors a diverse fish fauna consisting of North and South American clades that radiated into numerous unique species (Miller, 1976). Characteristic of the Central American fish fauna is the family Cichlidae, represented by almost 100 species of the tribe Heroini that range from southern Panama to the Rio Grande system in the southern United States (Kullander, 1996; Stawikowski and Werner, 1998; Reis et al., 2003; Hulsey et al., 2004). Although Central American cichlids are fairly well described at the species level, little is known about their behavior, especially in natural habitats. Previous studies focused on reproductive and aggressive behavior of *Herotilapia multispinosa* (Baylis, 1974), *Archocentrus nigrofasciatus* (e.g., Keenleyside et al., 1990; Wisenden, 1995), and species of the genus *Amphilophus* (e.g., McKaye et al., 2002), as well as the foraging behavior of other species (e.g., Swanson et al., 2003, 2005; Tobler, 2005).

The reproductive behavior of all Central American cichlids follows the same general pattern (Baerends and Baerends-van Roon, 1950; Stawikowski and Werner, 1998). Almost all species appear to be monogamous and show no or little sexual dimorphism. If sexual dimorphism is present, males usually are larger and more colorful than females. Pairs form during a courtship period, in which males play the more active role. Eggs are laid on plants, solid surfaces, or in crevices and are attended by both parents. After hatching, parents care for their brood for ≤ 10 weeks before it becomes autonomous. During brood care, various degrees of division of labor between sexes can be observed among species, ranging from no division of labor in sexually monomorphic species to pronounced differences in more dimorphic species, where females usually spend more time attending the fry and males defending the periphery.

A well-studied exception to this general pattern is *Archocentrus nigrofasciatus*, a sexually dimorphic species in which males grow larger (McKaye, 1986) and have a different fin morphology (Stawikowski and Werner, 1998). Females exhibit a conspicuous coloration not found in males (Wisenden, 1995; Beeching et al., 1998; Jackson, 2001). Both sexes have black vertical bars on light gray background, but females also have gold or orange flecks on the abdomen, and iridescent blue, orange, and yellow hues on the throat, chin, dorsal fin, and anal fin (Wisenden, 1995; Bussing, 1998). This reversed sexual dimorphism was associated with intrasexual aggression among females (Beeching et al., 1998), as well as active courtship by females (Wisenden, 1995).

This study concentrates on the congeneric Topaz cichlid, *Archocentrus myrnae*. I studied the behavior and changes in color patterns of *A. myrnae* during different phases of reproductive activity in the laboratory. Laboratory observations were supplemented by observations in the natural habitat.

METHODS—Study species—*Archocentrus myrnae* (Loiselle, 1997), formerly known as *A. septemfasciatus* "Topaz," is a small species (≤ 80 mm SL) endemic to the Río Sixaola drainage in the borderland of Costa Rica and Panama (Bussing, 1998). According to Fromm (1988), the species also occurs further north up to the Río Estrella. However, extensive sampling in 2002 did not reveal any populations of *A. myrnae* north of the Río Sixaola drainage. Thus, field work concentrated on populations in small tributaries of the Río Sixaola. Little is known about the ecology of the species. Bussing (1998) notes that *A. myrnae* commonly is found in waters of little current and eats plant detritus and ooze.

Fieldwork—Fish collections and observations were performed 6–11 March 2002 in the Río Uatsi, a tributary of the Río Sixaola, southwest of Bribri (9°36.85'N; 82°51.76'W; Fig. 1). Banana plantings were common in this region, but the headwaters of the Río Uatsi and all other upstream tributaries of the Río Sixaola are in the Talamanca Range and the La Amistad National Park (both protected as UNESCO World Heritage). Thus, the habitats examined are relatively unaffected by human activities.

The Río Uatsi is a small river about 15–20 m wide and <1.3 m deep. River substrates are cobble and boulder in areas with higher current, and broad expanses of sand in areas with lower current. Macrophytes were absent, but dense algal mats covered the bottom. The shore on both sides of the river was overgrown by reeds; trees were lacking so that the water was exposed to the sun almost the whole day. Water analyses on 6 March 2002 (1130 h) provided the

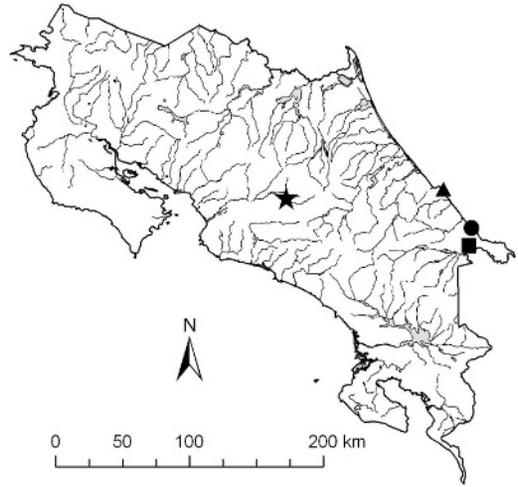


FIG. 1.—Map of Costa Rica showing the study site (■) near Bribri in the Southeast: the cities of San José (★), Puerto Limón (▲), and Cahuita (●).

following values: temperature, 28°C; pH, 8.45; specific conductivity, 242 μ S; O₂, 9.1 mg/l.

Fish were collected using a seine (6-mm stretch mesh, 6 × 2 m), a cast net (9-mm stretch mesh) and dip nets (1-mm stretch mesh). Species were determined using keys provided by Bussing (1998). Nomenclature follows Reis et al. (2003). Besides *A. myrnae*, a number of other species of fishes were recorded in the Río Uatsi (*Astyanax* cf., *aeneus*, *Agonostomus monticola*, *Alfaro cultratus*, *Poecilia gillii*, *Centropomus undecimalis*, *Pomadasys croco*, *Amphilophus bussingi*, *Archocentrus nigrofasciatus*, *Gobiomorus dormitor*, *Awaous banana*, *Sicydium* sp.). Underwater observations of *A. myrnae* were made during snorkeling.

Observation in the laboratory—Fifteen individuals of *A. myrnae* (8–14 mm TL) from 4 different broods were collected, transported to Switzerland, and raised in a 300-L tank. After they reached maturity, the group was split up and fish were kept in pairs or larger groups in 5 tanks containing 80–300 L of water, and *Poecilia gillii* (Poeciliidae, 4–10 individuals depending on size of tank) as tanks mates. To mimic the natural habitat, tanks were equipped with a layer of sand and cobble, as well as driftwood for shelter. Temperature was maintained at 26°C. A 12L:12D artificial light cycle was maintained using fluorescent tubes. Fish were fed 5 times/week with spinach, frozen *Cyclops*, and commercially available fish food. Observations of reproductive behavior were made over 2.5 y on wild-caught *A. myrnae* and their direct descendants.

RESULTS—Reproduction in Captivity—A total of 53 breeding events was recorded involving ≥ 15 different pairs. Size of breeding females ranged from 32 to 62 mm standard length. Reproduction took place year-round. The reproductive behavior of *A. myrnae* can be classified into five phases:

- (1) Establishment of a territory: Females ready to spawn, recognizable by their girth and a slight protuberance of their genital papilla, start to defend a territory, the center of which usually lies underneath a rock. The territories defended never exceeded 50 cm in diameter and were considerably smaller in smaller females. Females maintained in groups with other *A. myrmae* seemed to have smaller territories than those kept with a single male. Not only conspecific females but also males are displaced by chasing them out of the territory. Establishment of a territory usually was accompanied by digging activities. Females sometimes moved considerable amounts of sand by picking it up with their mouth and spitting it out at the edge of their territories.
- (2) Courtship: Breeding activity was invariably initiated by females and announced by a pronounced color change (see below). Aggression toward conspecific females and small males peaked during this time, whereas larger dominant males were actively courted. Females approached such males quickly and stopped at a right angle to and directly in front of the male, then curved and slightly canted over on one side presenting their abdomen to the male. At the same time, dorsal, caudal, and anal fins were maximally erect. Sometimes females performed tail beats in the direction of the male; in doing so, the female remained stationary in the right-angle position in front of the male. Females then returned to their crevice. These displays were repeated several times a minute and were often interrupted when females chased away other individuals or even the male she was previously courting. During displays by females, males usually remained stationary with erect fins. After the display, males either turned away or followed the female into the crevice, but most often females would then immediately chase the male out of the crevice. Courtship behavior normally could be observed over only one or maximally 2 d before spawning occurred.
- (3) Spawning: The act of spawning was never observed because it took place hidden in the crevice. As spawning approached, females tolerated the presence of the male in the crevice for increasingly longer periods. Clutches usually were laid on the overhead surface of the crevice. Clutch size (determined post hoc by the number of free-swimming fry) ranged from 15 to about 60 and was positively correlated with size of female. Some clutches were inspected before hatching and only a few eggs were not developing.
- (4) Care of clutch and larvae: After spawning, females did not tolerate males in or near the crevice entrance. Males were chased away or kept at a distance with bites to their flanks. Whereas some males defended the wider periphery around the crevice, others showed no signs of guarding. Consequently, only females cared for clutch and larvae. Larvae hatched about 3 d after spawning.
- (5) Care of free-swimming fry: As soon as fry started to swim free (about 7 d after spawning), males became more active in brood care. Although females usually had the closest contact to the offspring, males aggressively defended the periphery against intruders. In addition to aggressive behavior, a suite of specific behavioral patterns (either shown by both sexes or only females) was observed during this phase of reproduction. In the 10 d after free-swimming, females diligently kept the fry together in a compact shoal. Individual fry that left the shoal were immediately picked up with the mouth and spit back into the shoal. Whenever other fish approached the fry, females positioned themselves directly over the shoal with erected fins and quivered their head, at which time fry immediately became motionless on the substrate. In the evening hours, females retreated with their fry to the crevice, usually picking up most individuals one-by-one. After about 10 d, the shoal of fry loosened up, parents were observed to pick up fry less frequently and instead, defended the wider area around the shoal. Both males and females were observed providing food to fry during the whole time of brood care. Large pieces of flake food were picked up, chewed, and spit directly into the shoal of fry. Furthermore, parents stirred up detritus with tail

beats on the substrate. Males stopped caring for their offspring after 2–4 weeks, whereas females continued to provide care ≤ 10 weeks after spawning. Pairs that were kept separately tended to guard their fry for a shorter period of time than pairs that were kept in a group with other *A. myrnae*.

Changes in Color Patterns—Non-reproductive *A. myrnae* typically had parallel lines of yellow to coppery dots on the lower half of the body. Head and breast also were coppery, whereas the upper half of the body was brownish gray. The lower lip, the lower edge of the operculum and the iris were blue. Especially in adult animals, blue hues also could be found in the dorsal, caudal, and anal fin, as well as along the ventral part of the body. The anal fin had a dark edge. The dorsal fin of the female sometimes showed a fine red edge. In non-reproductive coloration, both sexes showed a prominent black lateral blotch, and a second less conspicuous one on the caudal peduncle. In terms of color, the main difference between sexes was presence of a black blotch interfused with blue iridescent spots on the center of the dorsal fin of the female (see Figs. 2a and 2b). Below, color patterns during the different phases of the reproductive cycle are described. The numbers correspond to the respective phases described above.

- (1) Coloration before and during establishment of a territory: During establishment of a territory, females and males showed their non-reproductive color pattern, but especially in females the copper coloration on the head and lower part of the body, as well as the blue hues, increased in intensity.
- (2-3) Courtship coloration: Whereas coloration of males remained normal and only increased in intensity, coloration of females changed during courtship and spawning. The caudal peduncle blotch disappeared and a dark area developed, reaching from the bases of the pelvics and pectorals to the lateral blotch of the body and the base of the anal fin. This darkening was caused by an increase in black coloration on the edge of each scale in this area. A prominent blue color also developed around the genital area. The copper coloration on the head and the lower part of the body and the blue hues on the whole body reached maximum intensity during this period (Fig. 2c).

- (4-5) Breeding coloration: Immediately after spawning, females lost their bright courtship coloration, returning quickly to the non-reproductive coloration with a ground coloration of faint gray. The copper coloration, as well as the blue hues and the blotch on the dorsal fin and on the caudal peduncle, disappeared completely. The black lateral blotch, the head and the breast up to the base of the pelvic fins, and the pelvic fins themselves, turned completely black (Fig. 2d). Contrary to females, males changed colors just after the free-swimming of the fry. Males also developed black coloration on the head and breast, but the other colors were not suppressed to the extent that they were in females, so coloration of males appeared less rich in contrast.

Other color patterns observed: Besides the different color patterns observed in adults during different phases of the reproductive cycle, some further variation could be observed, especially in juvenile and subadult individuals. Juveniles often showed a lateral band reaching from the blotch on the caudal peduncle through the lateral blotch to the edge of the operculum. In subdominant males this lateral line is expressed only partly, breaking into a series of blotches. A second line of blotches could be found on the back of such individuals, whereas mostly only the first 3 of these blotches were shown clearly.

Complementary Field Observations—In natural habitats, *A. myrnae* was present only in areas with boulder and cobble that provided shelter. During the observations, all size classes were present. Through most of the observation period, animals foraged in algal mats covering rocks. Color patterns of *A. myrnae* in natural habitats were identical to those observed in captivity. No courting female was observed, but breeding females were abundant and caring for fry ranging from a few millimeters to 1.5 cm TL. Except for one case, females always were guarding fry without a male present. All females and the only male observed performing brood care showed the color patterns described from aquaria observations.

Many shoals of fry guarded by the female contained similar-sized fry of a different cichlid species. Three out of four shoals caught

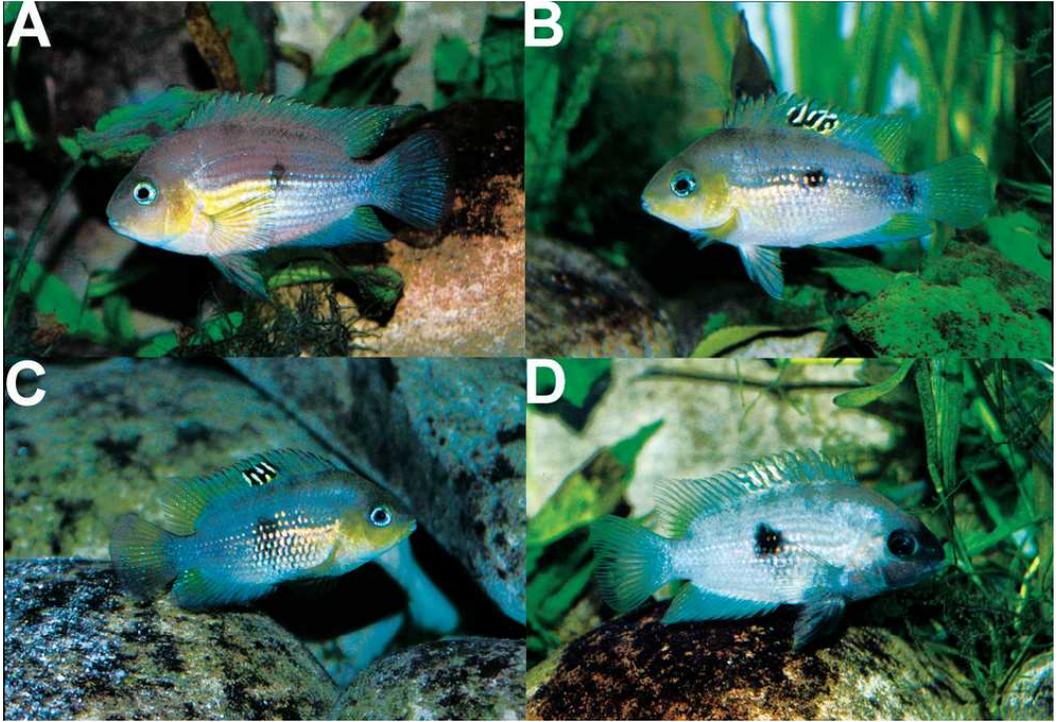


FIG. 2—Color patterns of *Archocentrus myrnae* during different stages of the reproductive cycle: A) non-reproductive male; B) non-reproductive female; C) courting female; D) female guarding fry.

contained fry of *A. bussingi*; breeding pairs of which were observed in the same area.

DISCUSSION—During the process of pair formation in the laboratory, female *Archocentrus myrnae* showed a unique color pattern and actively courted males. Other than this reversed sexual dichromatism and courtship by females, *A. myrnae* follows the general pattern of reproductive behavior of other Central American cichlids. Reversed sexual dichromatism and courtship by females has been observed in the related species *Archocentrus nigrofasciatus* (Wisenden, 1995; Beeching et al., 1998), and other species of *Archocentrus* (*A. nanoluteus*, *A. septemfasciatus*—M. Tobler, pers. observ.). It should be noted that the phylogenetic history of species currently assigned to *Archocentrus* is as yet unresolved and previous studies have yielded conflicting results (Hulsey et al., 2004; Concheiro Pérez et al., 2007). Both studies, however, indicate that *Archocentrus* sensu Reis et al. (2003) is polyphyletic and, thus, ornamentation and courtship of females might have evolved more than once.

In *A. nigrofasciatus*, it was shown that ventral coloration of females plays a role in intrasexual competition (Beeching et al., 1998). The same study determined that males do not choose females on the basis of their color intensities. Nonetheless, females actively courted males in *A. nigrofasciatus* (Wisenden, 1995) and other *Archocentrus* (this study), indicating that coloration of females most likely also plays a role in intersexual selection.

Reversed sexual dimorphism and courtship by females is common in systems with reversal of sex roles (e.g., in pipefish where males gestate eggs in a brood pouch—Berglund et al., 1997), and some blennies, in which exclusively males provide brood care (Goncalves et al., 2002). Female ornamentation and courtship in *Archocentrus*, as well as in some African cichlids (e.g., in the genera *Pelvicachromis* and *Nanochromis*—Jackson, 2001), seems to be uncoupled from reversal of sex roles. In these, increased investment by males is not coupled with reduction of investment by females because most of these cichlids are assumed to be monogamous with a high participation of females during brood care

(Stawikowski and Werner, 1998; Jackson, 2001). It is unclear what drove evolution of courtship by females in these cichlids, because apparently females do not reduce their investment in reproduction (they not only produce the eggs, but still provide more brood care) and males do not seem to provide additional investment compared to related taxa lacking courtship by females.

A potential solution to this paradox might be that the mating system in *Archocentrus* is more plastic than generally assumed, which may be suggested by the delayed assumption of breeding coloration by males. A delayed assumption of breeding coloration by males also was described for other *Archocentrus* (e.g., *A. septemfasciatus*—Stawikowski and Werner, 1998).

Keenleyside et al. (1990) noted that although *A. nigrofasciatus* usually is monogamous, males sometimes deserted females or simultaneously mated with multiple females. Desertion by males may also play a role in *A. myrnae*. Whereas males in captivity always participated in brood care, most females in the natural habitat were observed to care for their brood alone. Contribution of males to brood care could be dependent on quality of females. If courtship by females is an honest signal indicating quality, courting females could get good mates contributing more brood care.

Alternatively, courtship by females could evolve as a response to a female-biased, operational sex ratio. *Archocentrus* is dependent on a crevice to breed and breeding territories could be limited in natural populations (McKaye, 1977). Furthermore, in many Central American cichlids, males establish territories first (Baylis, 1974; Perrone, 1978; Wisenden, 1995). The resulting bias of operational sex ratio toward females can increase female-female competition and promote evolution of courtship by females. In captivity, female *A. myrnae* established territories, so it is not clear if a sex-ratio-bias mechanism is working. The evolution and function of courtship by females in this group of Central American cichlids warrants further investigation.

The occurrence of mixed broods is an interesting observation from the field. Alloparental care of fry, where guarding parents adopt conspecific offspring, is known from many species of fishes (Wisenden, 1999). If the adoption of fry of *Amphilophus bussingi* by *A. myrnae* is adaptive in terms of reduced predation

on their own offspring (Wisenden, 1999), or if heterospecific fry just lost connection to their own shoals and associated with the next group available, is not known.

Field work, collections, and export of animals were permitted by the Ministerio del Ambiente y Energía Costa Rica (Permit 068-2002-OFAU). I thank T. Schmid for help in the field and R. Guggenbühl for providing equipment. N. Franssen helped to create the map. Two anonymous reviewers provided valuable comments on an early version of the manuscript.

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Submitted 16 June 2006. Accepted 20 February 2007.
Associate Editor was Gary Garrett.