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OBSERVATIONS ON THE ECOLOGY OF THE KILLIFISH *Rivulus marmoratus* (CYPRINODONTIDAE) IN AN INFREQUENTLY FLOODED MANGROVE SWAMP

Rivulus, *Rivulus marmoratus* Poey, is a cryptic, solitary cyprinodont indigenous to mangrove swamps of the new world tropics. Rivulus was first reported from Florida by Harrington and Rivas (1958), however little has been published on its ecology and microhabitat preferences. Harrington and others have remarked on the rarity of the species in Florida, but more recently Huehner *et al.* (1985) described areas of localized abundance, where a collection of 51 individuals exceeded Harrington's (1958) original collection of 34 fish in Indian River County, Florida. Will Davis (pers. commun.) has since reported a collection of 140 ± specimens at night by several collectors in a mangrove site in Collier County, Florida.

The low collection rate of rivulus is related to the problems of collecting in a mangrove habitat as well as the fish's scarcity (Huehner *et al.* 1985). The terrain at most reported collection sites has made sampling difficult because of large logs, mangrove roots and heavy leaf litter.

Since the original discovery of this species in Florida in 1958 by Harrington and Rivas, and the subsequent elucidation of the fish's hermaphroditic traits (Harrington 1961), most of the published literature on the fish has dealt with the genetics, embryology and usage in bioassay and cancer research. Since rivulus is easily maintained in the laboratory and spawns readily, the demand for wild-caught specimens has been minimal.

Only two recent published accounts have contained field observations on the ecology of rivulus (Abel *et al.* 1987 and Huehner *et al.* 1985). Harrington and Rivas (1958) and Harrington (1961, 1971) made few remarks on the natural history of the species, but did note that some specimens of rivulus were collected in areas of high marsh where fish may be confined to small areas of poor quality water or crab holes isolated by dry terrain.

Emersion, the act of leaving the water for a temporary terrestrial existence, was first reported for rivulus by Kristensen (1970) and first documented in Florida by Brockmann (1975). Since then, both Huehner *et al.* (1985) and Abel *et al.* (1987) have observed emersion in the field and laboratory. Abel *et al.* (1987) found several fish hiding in moist mangrove leaves near the mouths of crab burrows and suggest that the fish readily leaves water containing adverse levels of hydrogen sulfide to take temporary refuge on land. Emersion of rivulus was induced by elevated levels of hydrogen sulfide, while decreasing the dissolved oxygen failed to elicit an emersion response. Rivulus is obviously fully capable of making limited terrestrial excursions. Huehner *et al.* (1985) observed rivulus capturing termites out of the water but returning to the water to swallow them. Emersed fish could not be induced to capture termites.

Abel *et al.* (1987) found that 17 of 20 fish survived 30 days in moist detritus and further reported the aerial deposition of eggs in the laboratory and their resistance to desiccation. Ritchie and Davis (1986) report circumstantial evidence for diapause and aestivation of rivulus eggs in mangrove swamp substrate during seasonal droughts.

Field accounts of this elusive fish are rare due to its diminutive size, cryptic coloration, and secretive behavior in the dense vegetation and leaf litter of its normal habitat, the mangrove swamp. The following account of rivulus using a previously undocumented habitat and a description of an easy method of collection adds valuable information on the ecology of this species.

MATERIALS AND METHODS

During September and October 1987, rivulus were found inhabiting burrows of the great land crab, *Cardisoma quanhumi*, at two locations on filled mangrove islands in the Indian River Lagoon, north of Vero Beach, Florida (Lat. 27°40′ N., Long. 80°23′ W.). A description of the two locations follows:

Site A: This site is located on what was formerly a mangrove island, used for dredge spoil deposition in the 1960's. Vegetation on the island is now dominated by the Australian pine (*Casurina equisetifolia*) and the Brazilian pepper (*Schinus terebinthifolius*). A few relict pockets of mangroves are left on the fringes of the island. Site A is one of these remaining mangrove areas, consisting of a shallow depression (5 m × 20 m) separated from the estuary by a sand-shell berm. Vegetation is composed of red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*), and the sea ox-eye (*Borrichia frutescens*). Heavy mangrove leaf litter covers the substrate. Floor elevation at this site is 0.7 ft (0.21 m) above mean sea level (NGVD).[1] The berm, which isolates the site from the adjacent estuary 4 m away except during the highest tides of the year, has an elevation of 1.8 ft (0.55 m) NGVD. One active *C. quanhumi* burrow, verified by fecal pellets and fresh mud castings, was studied at this site. The burrow was 10 cm in diameter and was the only *Cardisoma* burrow present.

Site B: This site is located on another filled mangrove island approximately 1 km NE of Site A. Site B is also an isolated mangrove stand in a larger depression, (10 m × 25 m), dominated by a thick growth of *B. frutescens* and pneumatophores from adjacent *A. germinans*. Leaf litter at this site is minimal. Two small 2 m and 3 m diameter ponds are present within the depression, and these ponds typically dry down during periods of drought and low tides. The elevation of burrow mouths studied here is 0.9 ft (0.27 m) NGVD and a berm, elevation 2.5 ft (0.76 m) NGVD, isolates this site from the lagoon 5 m away. Fifteen active and inactive *Cardisoma* burrows are present. Some burrows are directly adjacent to others, with apparent subterranean connections, as described by Herreid *et al.* (1965), and water displaced in one burrow rises in the adjacent burrow(s). Six 9 to 15 cm diameter burrows were found to contain rivulus and are located 6 m from the ponds.

The initial collections of rivulus were made with a small net dipped into the mouth of the burrow, but only smaller specimens were captured in this fashion. However, a unique method was devised allowing the capture of larger fish deep within the burrow. A 1 m length of 4 lb (1.8 kg) monofilament fishing line with a #12 hook was attached to a short stick. Bait consisted of a small earthworm hooked once through the middle and dropped into the burrow. Rivulus readily seized the worm, and if allowed a few seconds to partially swallow it, was easily lifted from the burrow into a waiting net or bucket without actually being hooked or physically damaged.

RESULTS

Rivulus were discovered at Site A during routine surveys for mosquito larvae. On 28 September, the area had dried following tidal flooding on 25 September by seepage through the berm. The only visible water remaining was in the mouth

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of the single *Cardisoma* burrow described above. Four rivulus (7-12 mm S.L.) were captured with a mosquito dipper inserted into the mouth of the burrow and retained for identification. On 30 September, 13 additional fish (10-29 mm S.L.) were captured from the same burrow with a small dip net, then measured and released. The water level in the burrow during this period was 5 cm below the mouth of the hole, and the burrow water salinity was 23 ppt., the same as the adjacent estuary. On 7 October, tidal amplitude in the estuary reached 1.4 ft (0.43 m) NGVD, the highest tide of the year to date, and the site was flooded to a depth of 12 cm. No fish were observed in the flooded burrow or in the standing water. On 9 October, estuarine water levels dropped, and the area again dried. Water levels receded within the mouth of the burrow, and rivulus were once again observed there. Eleven rivulus were captured by hand net and released. Five days later, a tropical disturbance briefly pushed tides to an unseasonal 2.4 ft (0.73 m) NGVD. Estuarine water crossed the berm and flooded the site to a depth of 20 cm. At least three additional fish species entered with this flooding: mosquitofish, *Gambusia affinis*, sailfin molly, *Poecilia latipinna*, and sheepshead minnow, *Cyprinodon variegatus*. The site remained flooded until mid-December with the seasonal rise in sea level. This is the typical inundation period for high marsh habitats in this region of Florida, and fall tides in the Indian River Lagoon remain elevated for several weeks.

Initial observations at Site B were made on 7 October during an estuarine tide of 1.4 ft (0.43 m) NGVD. The area was flooded by seepage to a depth of 5 cm, and standing water extended from the crab burrows to the adjacent ponds. Rivulus were observed retreating into the mouths of the submerged burrows, and seven individuals (25-40 mm S.L.) were captured from six burrows with the described hook and line method. Three specimens were retained, and one of these regurgitated a 9 mm juvenile rivulus. On 9 October, water levels had receded inside the burrows, within 18 cm of the burrow mouths. The two ponds still contained water (2-3 m dia), but no fish were observed or could be captured with a large dip net or the hook and line. However, twenty rivulus were easily captured from the same six crab burrows with the hook and line. Up to six individuals were obtained from a single burrow, and all were released after measurement. On 14 October, the berm at this site was topped by the same elevated tide that submerged Site A, and flooded the burrows to a depth of 20 cm. Four additional fish species, mosquito fish, sailfin molly, sheepshead minnow and marsh killifish, *Fundulus confluentus*, invaded Site B. Two rivulus were captured in the inundated burrows, and the area remained flooded until mid-December with seasonal high tides.

DISCUSSION

These two collection sites extend the known range of rivulus north on the east coast of Florida by 10 km. This region of East Central Florida is a zoogeographic transition zone between the Carolinian warm-temperate and tropical Caribbean fish faunas (Gilmore 1977), and these sites represent the northernmost reproducing population for this tropical species.

In addition, these collections are among the largest single-point collections in Florida. Seventeen individuals inhabiting a single crab burrow seems quite unusual, given the aggressive nature of this fish in captivity (Huehner *et al.* 1985 and Abel *et al.* 1987). The six larger specimens (20-40 mm S.L.) collected from a single burrow at Site B on 9 October are also an oddity, as larger fish have the potential to inflict more damage during aggressive encounters (W. Davis pers. commun.). Although at least ephemeral cohabitation is apparent, some intraspecific aggression and cannibalism is taking place, as witnessed by the regurgitated juvenile collected on 7 October.

An examination of tidal elevations for the Indian River Lagoon at Vero Beach (Florida Medical Entomology Laboratory)[2] over a 20 year period (1959-79) illustrates that at both sites mean high water exceeds the elevations of the burrow mouths (causing flooding by seepage through the berm) only during the period August-December. Unpredictable seasonal variations may occur due to rainfall, prevailing winds and the passage of tropical disturbances. Nevertheless, it is apparent that at both sites inundation is a somewhat infrequent event between January and August. Rainfall obviously offers an alternative source of flooding, but rainfall during the summer and fall preceding this observation period had been below normal. When major rainfall events do occur, it appears that there is little residual water at the study sites. The heaviest rainfall recorded during these observations was 3.2 cm in two hours, and no water was left standing at either location. Extremely high and low tides offer additional challenges to these fish. Tidal elevations were sufficient to exceed the berm at Site B at least once a year during 16 of 20 years (1959-79) and slightly more often at Site A. Therefore, during infrequent flooding directly from the adjacent estuary, new fish species are introduced and resident rivulus may disperse. Extreme low tides, encountered during late winter and spring (lowest recorded 1959-79: −1.1 ft (−0.33 m) NVGD could lower water levels deep within the burrows. It is not known whether the fish stay in the burrows during low water periods or leave for a damp terrestrial location.

The question of adequate food resources immediately arises when population levels of rivulus are as high as those encountered within a single crab burrow. A few of the captured fish were emaciated but most appeared healthy. The regurgitated juvenile demonstrates that this species is cannibalistic in the wild, although no account of this exists in the literature. Heuhner *et al.* (1985) found unidentified fish scales during gut analysis of rivulus, but a variety of invertebrate items were the mainstay of the diet. Abel *et al.* (1987) report that rivulus will eat its own eggs in captivity.

It is likely that rivulus preys on a variety of food resources and is not necessarily resource limited. During marsh flood periods, rivulus is least likely to be resource limited as a wide variety of estuarine and marsh invertebrates are available. During the dry season, existence in an isolated burrow may be more difficult, and any food material available may be consumed, including other rivulus. *Cardisoma quanhumi* burrows can be as much as 1.5 m in depth (Herreid and Gifford 1963), but the invertebrate fauna of the burrow has not been documented. Larvae and adults of the crabhole mosquito, *Deinocerites cancer*, could be a valuable food source for rivulus during burrow confinement. George O'Meara (pers. commun.) has observed larval counts of this mosquito up to 1000 per burrow, but the average is 25-30 per burrow. No crabhole mosquito larvae, however, were observed at either of the study sites. Materials brought back to the burrow or excreted by the scavenging

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crabs may be an important source of food for rivulus. All of these resources, however, may be able to support only a few rivulus per burrow, hence the rarity of the species and the cannibalism documented in this account.

The hook and line collection technique may indicate the voracity of burrow-dwelling rivulus in taking any available food. This technique was especially effective with larger fish which seem to reside deeper in the burrows. Often a wait of a few minutes was necessary before these larger individuals attacked the bait, implying that the odor or motion of the worm attracts them from greater depths.

Although Huehner *et al.* (1985) could not demonstrate strictly terrestrial foraging for rivulus, this could be a source of food for this species during long periods of burrow confinement. A related species, *Rivulus hartii*, has been observed foraging when emersed (Seghers 1978).

Emersion to avoid predation has not been observed in rivulus, although Abel *et al.* (1987) have seen *Rivulus brunneus* emerse to avoid predation in Panama. One specimen of rivulus at Site B, however, was seen to leap 10-12 cm out of the water up the side of a burrow to avoid a hand placed in an adjoining burrow.

· At both locations rivulus returned to the crab burrows after tidal inundations receded, although at Site A the only alternative would be to burrow under the leaf litter or enter the numerous *Uca* spp. burrows in the area. Two specimens, inadvertently dropped during collection, were observed entering *Uca* burrows. At Site B however, fish had access to the ponds on two occasions, but elected to return to the burrows and were even found in flooded burrows in preference to accessible ponds. The ponds were devoid of fish life prior to the extreme high tides, suggesting that they dry completely. Abel *et al.* (1987) reported rivulus in temporary pools with four fish species, mosquitofish, sailfin molly, sheepshead minnow and marsh killifish. When the pools dried, no rivulus were found among the dead fish.

The effect of burrow habitation on the life history of rivulus may be quite significant. This species is a self-fertilizing simultaneous hermaphrodite, a reproductive strategy which allows isolated individuals to successfully reproduce. If crab burrows are in fact the preferred microhabitat, simultaneous hermaphroditism would increase the chance of reproductive success to 100% for paired individuals, an advantage over the 50:50 opportunity for gonochorists. Thus, these observations indicate a life history condition for rivulus that may have been a major factor contributing to the evolution of its hermaphroditism.

CONCLUSION

Rivulus marmoratus has been rarely collected in Florida, due to its sporadic occurrence and ineffectiveness of conventional fish collection methods in capturing the species in mangrove swamps. Little is known about the ecology of rivulus, in contrast to extensive laboratory work on its hermaphroditism, genetics and immunochemistry. These observations reveal that an important microhabitat for this fish is the burrow of the great land crab, *Cardisoma quanhumi*, and that relatively high population levels can be found within a single burrow. Burrows can be easily sampled for rivulus with the hook and line method described. This microhabitat may have important implications in the evolution of the reproductive behavior of rivulus. Hopefully, these findings will spark additional interest and investigation into the life history and field behavior of this fascinating fish.

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[1] National Geodetic Vertical Datum, Vertical Control Data by the National Geodetic Survey, Sea Level Datum of 1929, U.S. Department of Commerce, National Oceanic and Atmospheric Administration.

[2] Tidal Records (Oslo Road 1959-1979), Florida Medical Entomology Laboratory, Institute of Food and Agricultural Sciences, University of Florida.

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