Natural History Note

A Novel Terrestrial Fish Habitat inside Emergent Logs

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abstract: Reports of new habitats for a major group of organisms are rare. Fishes display diverse adaptations for temporary (amphibious) existence on land, but to our knowledge, none have ever been reported regularly living inside emergent logs. Here, we show that the mangrove killifish, *Kryptolebias marmoratus*, a species previously known to emerse (leave the water) regularly, is now known to emerse and aggregate in large numbers inside decaying mangrove logs that have been "galleried" by terrestrial insects. This behavior has now been documented in both Belize, Central America, and Florida, U.S.A., populations and represents the first known case of fishes entering terrestrial woody material. The dense packing of fish in the narrow log galleries may imply a novel social context in which intraspecific aggressive behaviors are reduced, possibly mediated by the physiological limitations imposed within this restrictive habitat.

Keywords: red mangrove, *Kryptolebias marmoratus*, emersion, amphibious fish.

Amphibious fishes are those known to utilize both aquatic and terrestrial habitats, and amphibious behavior is now known in at least 16 genera and 60 species of teleosts (Sayer 2005). Fishes display diverse adaptations for temporary (amphibious) existence on land, including species reported to climb trees (Sayer and Davenport 1991). Typically, amphibious behavior is correlated with a decline in water quality/quantity and/or biotic factors (e.g., aggression/predation; Taylor 2000). Amphibious fish may emerse for periods of a few minutes to a few days, and desiccation and thermal imbalance are likely the two factors limiting the duration of this behavior (Sayer and Davenport 1991).

The mangrove killifish, *Kryptolebias* (formerly *Rivulus*) *marmoratus* (Costa 2004), is a western Atlantic marine species with a range overlapping that of the red mangrove, *Rhizophora mangle*. It is known from southern Brazil to central Florida, U.S.A. (Taylor 2000). This small (60 mm maximum), cryptically colored fish typically is found in the upper reaches of mangrove forests, where it inhabits crab burrows, solution pits, and small ephemeral pools (Davis et al. 1990; Taylor et al. 2003). *Kryptolebias marmoratus* is the only known self-fertilizing hermaphroditic vertebrate (Harrington 1961), but more recently true males have been discovered in some populations, along with molecular evidence that sexual reproduction occurs (Turner et al. 1992; Lubinski et al. 1995; Mackiewicz et al. 2006). *Kryptolebias marmoratus* is tolerant of water quality extremes of salinity (maximum of 70–80 ppt; Taylor 2000) and H_2S (Abel et al. 1987) and occupies microhabitats that are marginal or inimical to most other fishes. One adaptation that it uses for survival in the variable and stressful mangrove habitat is emersion, or leaving the water for a damp terrestrial location. Both elevated H_2S and aggressive encounters between conspecifics are known to elicit emersion (Abel et al. 1987; Taylor 2000). Emersed fish generally move via serpentine wiggling or flipping to piles of leaf litter or under other damp debris and then become quiescent (Taylor 2000; Taylor et al. 2004). A number of unique physiological responses come into play during emersion. Opercular movements cease, and respiration occurs via an expanded network of capillaries on the skin and fins (Grizzle and Thiyagarajah 1987). Gill morphology changes during emersion (Ong et al. 2007), and some NH_3

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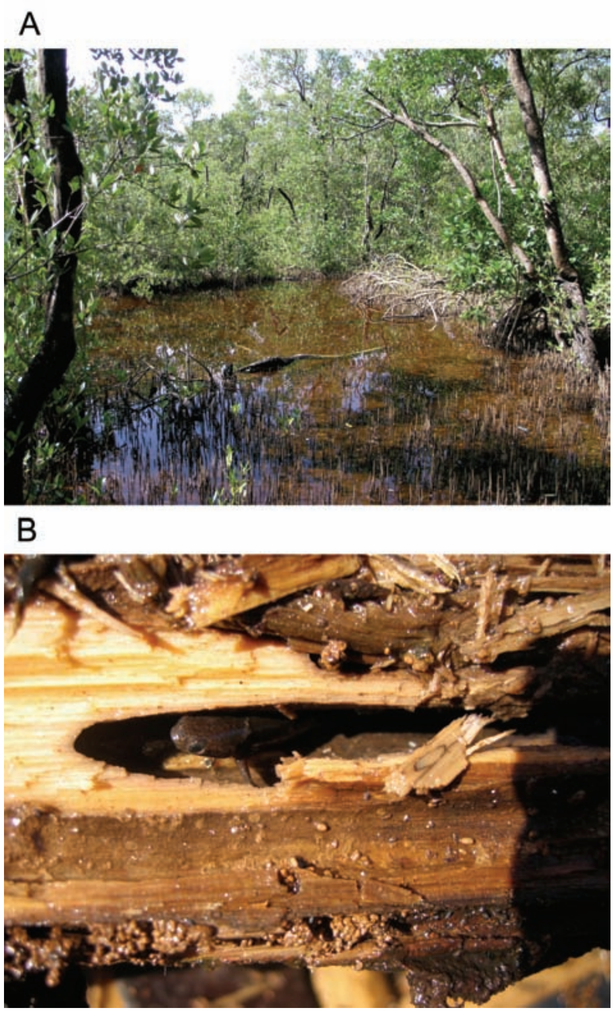

Figure 1: *A*, A flooded pool in the mangroves of the Belize Cays. During dry-down, *Kryptolebias marmoratus* will enter logs, such as the one seen in the foreground. *B*, A single fish peering out of an insect gallery inside a mangrove log.

is volatilized, probably through the skin (Frick and Wright 2002; Littwiller et al. 2006). *Kryptolebias marmoratus* is clearly well adapted for emersion and in the laboratory can survive for at least 66 days out of standing water (Taylor 1990). Emersion also plays a role in reproduction in this species, as hermaphrodites are known to oviposit on damp substrates while emersed (Taylor 1990), an option not available to related gonochoristic species requiring water for spawning embraces.

While we have observed emersion in a variety of locales in the field, these observations have always consisted of the fish being exposed (e.g., on the side of the interior of a crab burrow for presumably short-term emersion) or under inorganic (e.g., plastic) or organic (woody) material (Davis et al. 1990). However, we have now documented several cases in which *K. marmoratus* has left drying mangrove pools and entered rotting mangrove logs, occupying the galleries left by termites and beetle larvae. This behavior, which we have termed "log packing," has now been documented in both Belize, Central America, and Florida populations and represents the first known case of fishes entering terrestrial woody material. The dense packing of fish in the narrow log galleries may imply a novel social context in which intraspecific aggressive behaviors are reduced. It may also constrain the effectiveness of adaptations for cutaneous respiration and ammonia volatilization. In addition, the transport of such fish-laden logs by storm activity may represent a possible means of migration for these small fish, which are generally confined to small pools or fossorial habitats.

The first instance of this behavior was documented on the Belize Cays (Peter Douglas Cay), where in January 1991, we encountered a small drying pool (8 m × 3 m) in which at least four fish species (poeciliids/cyprinodontids) were stranded and dying (fig. 1*A*). We removed a 1.5-m-long log with a diameter of 9 cm from above the water line and on breaking it open discovered many *K. marmoratus* inside. The fish were packed heavily inside the galleried log, which remained quite moist in spite of being well above the water line. Fish were immediately active on being exposed, either flipping away from the log or attempting to enter deeper into the galleries. Ultimately, about 100 fish were collected from this log. During a sub-

Figure 2: Several fish exposed when a galleried log was broken apart. A video showing a log from Big Pine Key, Florida, as it was being slowly "dissected" open is available in the online edition of the *American Naturalist*.

Figure 3: A galleried mangrove log broken up to expose the interior. Rule shown is 15 cm.

sequent visit to the site (February 2000), the pool was completely dry and an additional 13 fish were found inside a different 5-cm-diameter log (Taylor et al. 2004).

In Florida, we have seen similar behavior at two locales: east-central Florida and the Florida Keys. At the east-central Florida sites (Melbourne Beach) at two different mangrove pools, *K. marmoratus* were found in galleried logs above the water line, and 17 fish were recorded from four different logs from October 1991 to March 1993. In one of these instances, a late-season cold spell in March 1993 resulted in mortality of several fish within one log. At these sites, pool salinity varied from 0 to 15 ppt. In the Florida Keys (Big Pine Key), in March 2007 we examined a 1.5-m portion of a 2.5-m-long log with a diameter of 9 cm from a drying pool (pool diameter = 3 m; salinity = 30 ppt). No fish were observed in the pool. The log was located several centimeters above the water line, with one end still immersed in water. When the log was "dissected," insect galleries 10–20 mm in diameter were noted, and frass, probably from beetle larvae, was abundant (figs. 1*B*, 2). Galleries were heavily packed with fish, with many individuals located 20–30 cm from obvious surface holes (fig. 3). Fifty-seven *K. marmoratus* were found within the galleries of this 1.5-m section. Fish actively flipped away from the log when exposed or attempted to penetrate farther into the galleries (see video in the online edition of the *American Naturalist*).

Our observations on *K. marmoratus* are the first documenting amphibious usage of the interior of logs by fishes. The number of *K. marmoratus* found therein is striking, and these types of logs may represent foci of populations in pool habitats during periods of dry-down. In a fish known for its aggressiveness in the aquatic realm (Taylor 2000), the density and close contact between these emersed individuals is unusual. The probable reduction in aggression in these terrestrial woody habitats may also be related to physiological limitations imposed by the limited size of insect galleries and restricted contact with outside air. In the laboratory, single emersed fish had metabolic rates comparable to those of fish in water (Ong et al. 2007), but close contact between individuals may alter individual metabolic rates. It is not known at what stage of dry-down fish choose to enter logs or how they navigate into the interior. However, local knowledge of and ability to navigate in terrestrial landscapes has been previously documented (Taylor 1990). Modeling log-packing behavior in a laboratory microcosm with an artificial log may provide some unique observations. This behavior has intriguing biogeographic implications as well. The geographic range of *K. marmoratus* is greater than that known for any other inshore-dwelling coastal fish species in North or South America and includes oceanic islands that undoubtedly were colonized by waif dispersal, possibly by a single free-swimming individual. However, if fish-packed logs can be transported by currents and winds, they could carry substantial numbers of fish across expanses of open sea, promoting colonization of new areas or mixture of otherwise isolated populations. It may not be a coincidence that the geographic ranges of *K. marmoratus* and the red mangrove itself are completely congruent.

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