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FOAM NEST CONSTRUCTION IN THE LEPTODACTYLID FROGS *LEPTODACTYLUS PENTADACTYLUS* AND *PHYSALAEMUS PUSTULOSUS* (AMPHIBIA, ANURA, LEPTODACTYLIDAE)

The purpose of this paper is to present for the first time descriptions of foam nest construction in *Leptodactylus pentadactylus* and *Physalaemus pustulosus* based on motion pictures.

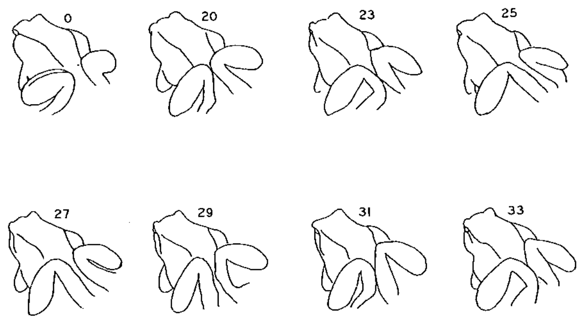

FIGURE 1. *Leptodactylus pentadactylus* foam nest construction. Numbers are number of frames, first frame in sequence diagrammed being zero.

Foam nest construction was photographed on 16 mm Kodachrome movie film at a speed of 24 frames per second at Barro Colorado Island. The films were analyzed on a Vanguard motion analyzer.

Leptodactylus pentadactylus, Fig. 1

The foam nest is built in a series of acts, alternating with periods of rest. The filming sequence began when much of the foam nest had been constructed. Initiation of the nest formation activity starts with the male and female in a resting amplectic position, with the female head well out of the water and the vent presumably under the water (the presence of considerable foam obscures the position of the vent relative to the water). In the space of one frame of film (approx. 0.04 s) the amplexing pair rock forward, with most of the female's head submerged in foam and water. The male back is arched and it appears as though the male is exerting more squeezing pressure on the female at this time. As the pair rock forward, the vents are elevated. At this time, the positions of the male legs are at approximate right angles to the body (Fig. 1, frame 0). This position is assumed for a brief time. It may be during this period that the female prepares to discharge eggs and jelly. The next change in male position is raising the legs anteriad along the sacral region (Fig. 1, frames 20, 23). With the femur and tibia remaining relatively fixed, the feet and tarsi are moved back and forth in lateral motions, very similar in appearance to the windshield wiper action of an automobile (Fig. 1, frames 25 to 33). A single complete "wipe" takes an average of 0.42 s. In the three sequences filmed, 7 or 8 complete back and forth motions are made by the male, at the end of which the head of the female rises, and the legs of the male drop to normal resting amplectic position. The total time for a sequence ranges from 5.1 to 5.2 s in the three filmed sequences. The amount of foam already present obscured much of the female's activity. The movement of the male's feet mixes air into the jelly surrounding the now fertilized eggs producing the foam of which the nest is constructed.

Physalaemus pustulosus, Figs. 2, 3

As for *L. pentadactylus,* the nest is built in bouts of activity and rest. The first motion in each sequence is the female arms moving posteriorly. During this movement, the female appears to be undergoing an abdominal squeezing motion (Fig. 2, frames 0, 5). At the peak of the female squeeze, the head of the female is often completely under water. The female then brings her arms forward, at which time the male places his feet down and across the vent of the female (Fig. 2, frame 7). The male rapidly draws his feet up over the vent (approx. 0.08 s) and places his feet and legs in a kicking position (Fig. 3, frame 0). This action probably 1) draws the eggs and jelly up and out that the female has just extruded or is still extruding, and 2) facilitates fertilization, as the eggs probably are fertilized before

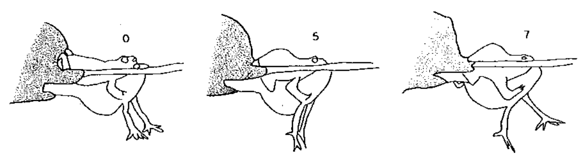

FIGURE 2. *Physalaemus pustulosus* foam nest construction. Numbers are number of frames, first frame in sequence diagrammed being zero.

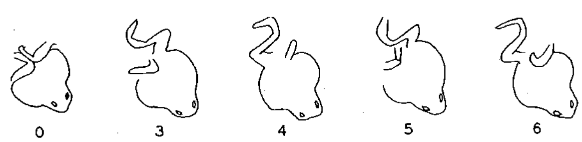

FIGURE 3. *Physalaemus pustulosus* foam nest construction. Numbers are number of frames, first frame in sequence diagrammed being zero.

the next sequence in the activity begins. The male then initiates a series of rapid kicks, alternating legs, kicking backward and noticeably upward (Fig. 3, frames 3-6). The initial kicks are rapid, a double kick involving both legs approx. 0.08 s. The rapid kicks seem to beat air into the jelly and form the foam. The last two to three double kicks in the sequence are noticeably slower and more lateral. The total number of kicks (both legs) in a given series ranges from 14 to 19 in the sequences filmed. The female legs are spread laterally on the water surface during the entire sequence, mostly in the already formed foam. The female legs in the foam appear to anchor the amplexing pair during the male kicking behavior. The female arms are essentially motionless during most of the time the male is kicking. During the last few male kicks, the female arms begin a swimming motion at the end of which her head is clearly above the water. When the head of the female clearly rises above the water, the male stops his kicking activity. A given sequence ranges from 3.1 to 4.3 seconds in those filmed. It is clear that the female initiates male activity. It also appears that the swimming motion of the female arms toward the end of the sequence signals the male to make the last two to three slow, more lateral kicks.

DISCUSSION.—Breder (1946) has presented the most complete observations on the foam nests of both *Leptodactylus pentadactylus* and *Physalaemus pustulosus.* Breder (1946) did not see the construction of the foam nest in *L. pentadactylus,* but his description of foam nest construction in *P. pustulosus* is as complete as possible for what can be observed without benefit of film. Rivero and Esteves (1969) describe the nest construction in *L. pentadactylus.* The descriptions presented here extend the previous descriptions.

Sexton and Ortleb (1966) postulated that *P. pustulosus* preferred a foam nest construction site that consisted of a solid vertical plane or curved surface intersecting and perpendicular to the water surface because the female needed a submergent arm support to maintain the position of the amplectant pair during the kicking activity. All of the filmed sequences were in open water, where the female did not have any contact with the substrate with her arms. In the filmed sequences, the female clearly did not need any arm support to maintain the position of the amplectant pair. The only use of the female arms came at the end of the sequence when the swimming motions brought her head above the water. This last activity might well be facilitated by having a submerged support that the female could push upwards against to raise her head. Sexton and Ortleb (1966) clearly demonstrated a behavioral preference for certain kinds of habitats on the part of *P. pustulosus.* Their hypothesis as to why certain specific sites were selected must be modified to incorporate the fact that the female arms remain motionless during the most violent kicking period in our filmed sequence.

The major difference in foam nest construction between the Australian and Neotropical foam nesting liptodactyloids has been pointed out previously (e.g. Martin, 1970). In the Australian leptodactyloids, the females beat up the foam with their hands, while in the Neotropical leptodactyloids, the males beat up the foam with their legs. We are struck by the very different ways that *L. pentadactylus* and *P. pustulosus* construct the foam nest. Two explanations seem possible. First, the differences may be due to size, as *L. pentadactylus* are very large and *P. pustulosus* are very small. Second, the differences may be phylogenetic. The choice between these alternatives can be made by observation of foam nest construction in a small *Leptodactylus* species. There are no such observations at present. The only observations we are aware of are those made by one of us (WRH) on *L. melanonotus* in Western Mexico, in which only the initial sequence was seen. The starting sequence of *L. melanonotus* involves the male placing his feet over the female vent and drawing the feet up, exactly as described here for *P. pustulosus.* Although foam obstructed the view in the *L. pentadactylus* films, it is reasonable to conclude a similar initial male movement due to positioning of the visible portions of the legs. Thus, the initial sequence of foot placement over the female vent appears to be uniform in the Neotropical foam nest builders. Whether the kick and wiping differences are size dependent or phylogenetically based remains an unanswered question.

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