Notes on the breeding biology of four species of mantellid frogs from Madagascar

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The breeding biologies of the mantellid frogs from Madagascar include an unusual mode of fertilization with eggs commonly laid on surfaces above water. Oviposition behavior and an understanding of clutch structure obtained only by observing oviposition and hydration of the milky white egg arrays of *Guibemantis depressiceps* (Boulenger 1882) are described. Multiple males are involved, and the females acted quite lethargic during the process. The much smaller egg arrays of *Blommersia cf. domerguei* (Guibé 1974), calling behaviors of *G. liber* (Peracca 1893), and nocturnal egg guarding by male *Mantidactylus majori* (Boulenger 1896) are also reported.

KEY WORDS: *Mantidactylus*, *Guibemantis*, *Blommersia*, Mantellidae, Madagascar, breeding, eggs.

INTRODUCTION

Egg morphologies and clutch structures are variable and poorly understood among amphibians (Altig & McDiarmid 2007), but these sorts of data added to descriptions of the courtship and ovipositional behavior increase our understanding of the complexity and diversity of breeding biologies. The addition of clutch structure to the concept of breeding mode would increase
the resolution of this concept. One can best understand these variations by observing amplexus, oviposition and eventual hydration of the clutch rather than only the end result. Most mantellid frogs of Madagascar oviposit arboreal eggs on surfaces over either lentic or lotic sites (Glaw & Vences 1992).

Field observations on the breeding biology of four species were made between 14 December and 18 January in 1991 through 1993 from sites about 8 km west of the village of Ranomafana within the Ranomafana National Park, Fianarantsoa Province, Madagascar. The terminology of eggs and clutches follow Altig & McDiarmaid (2007), and staging follows Gosner (1960).

**Guibemantis** cf. *depressiceps* (Boulenger 1882)

The breeding site was a triangular temporary, forest pool about 25 m on a side with about 40 cm of clear water and 50 cm of organic debris. There was almost no emergent vegetation, and the pool was heavily shaded by primary forest. Several other mantellids and the microhylids *Paradoxophyla palmata* (Guibé 1974) and *Scaphiophryne spinosa* Steindachner 1882 bred here, and *Mantidactylus guttulatus* (Boulenger 1881) were transients from a neighboring stream.

A few clutches of *G. depressiceps* were found on the morning of 15 December 1991, and most of the observations occurred that night during light rain. Numerous, active males calling from atop leaves 0.5–3 m above the water often changed position. The bright white vocal sac contrasted sharply with the brown frog and the green leaves, and the call was a series of harsh squawks. Oviposition is described as a composite from several situations observed during various stages of the lengthy process.

All observed females had chosen oviposition sites when they were first found and were flattened on the upper surface of vertically-oriented leaves with all legs spread. Whereas males were active, females seemed catatonic, moved infrequently in a slow, lethargic fashion, and showed no response to lights or being touched by me or approaching males. The female least advanced in oviposition had deposited 10-12 eggs and a male was not present. Whether there had been a male present earlier or not, how males find females, and how many males visit a given female is not known. During the next 45 min, two different males amplexed with the female. The males turned quickly ahead of the female and backed up slightly until their vents were above her scapulas. Males were motionless without clasping her head or limbs. Times were not recorded, but as noted by Bloemers-Schlösser (1975) for *Guibemantis liber*, the males remained in position for a few seconds to a few minutes; the rain inhibited verification of sperm release. Between the visits by two males and after the second one left, the female continued a number of ovipositional bouts: standing up slightly on widely-spread hind legs, bending her body ventrally so that the cloacal opening was nearly parallel with the leaf surface, and slowly swiping anteriorly as a few eggs were extruded. Usually one swipe was made per bout, and 3-5 eggs were released each time. Another event involved three males sitting one on top of the successive male’s head with the bottom individual sitting on a female’s head.
These frogs frequently shuffled positions, a fourth individual attempted to sit on top of the first male, and one of the original three that was displaced tried to push into position beneath the hind legs of the bottom male. The female appears to participate very little in the mating processes. Except by apparently choosing an ovipositional site somehow associated with a calling male, mate choice seems to be largely influenced by males. The occurrence of more than one male associating with a female at one time and multiple males amplexing with one female at different times assures mixed paternity (e.g., Jennions et al. 1992). This result is enhanced because the mode of fertilization forbids mobility of the pair, and the strange catatonic behavior of the female surely enhances the probability of her remaining in one spot for some time.

Once an entire clutch was deposited, females remained with the clutch for at least an hour. They remained adpressed against the eggs with all legs spread; sometimes the hind legs were fully extended, and one female hung off the edge of a leaf by her front legs for several minutes. Ensuring firm adhesion of the eggs to the leaf, aiding the spreading of sperm throughout the clutch, or channeling the flow of rain water over the eggs for jelly hydration are possible functions of these behaviors. There were a number of empty egg jellies at the periphery of the egg array (Fig. 1A), but the females never manipulated the eggs (e.g., Aichinger 1987) or added fluid (e.g., Cadle & McDiarmid 1990). In the three-dimensional groups of eggs wrapped in a leaf produced by phyllomedusine hylids, empty egg capsules atop the mass are a possible source of water to protect from dehydration (Pyburn 1980). Empty capsules in the laminar arrays of these mantellids with one side fully exposed to the air tended to be more peripheral and perhaps function similarly. Arrays always occurred on living leaves and clutches moved to the laboratory did not develop well if left on the leaf as it wilted. It is tempting to hypothesize that living leaves modulate gas and hydric environments of arboreal frog eggs. Eggs moved to the laboratory immediately after oviposition without additional water did not hydrate, although they would hydrate slowly but incompletely within 3-4 hr if water was added. Nonhydrated eggs did not develop, and three such clutches found in the field apparently resulted when rain stopped too soon. These observations suggest that the female does not provide any or sufficient water to the clutch for adequate hydration.

At the end of oviposition, a clutch was composed of the large white eggs more or less centered within a dense field of numerous, smaller capsules that were empty or contained small ova. Heights of clutches above the ground were estimated to be 0.3-10 (most \( \leq 2 \) m) m, and clutch size of hydrated arrays ranged from 50-120 (n = 3); there certainly were errors in counting because of the opacity of the milky white jelly. Individual ova (2.3-3.0 mm diameter) were bright white. Immediately after jelly hydration, the eggs were positioned deep within the jelly, but as development proceeded, the embryos were nearer the surface. The outer parts of the jelly drooped beyond the leaf as development proceeded. The hydrated jelly (Fig. 1B) had a peculiar consistency because it was composed of a rather gelatinous peripheral part and a firmer and somewhat clearer basal layer; the jelly distorted considerably when the leaf was tilted but could not be easily removed from the leaf because of the dense, adhesive, basal layer. A 5-mm cross-
section cut by hand from a hydrated array preserved in 10% formalin was stained with 0.1% Toluidine Blue for 30 min (Steinke & Benson 1970) and immediately observed with transmitted light and photographed. The jelly of individual eggs extended as an elongate stalk (Fig. 1C) from the leaf to the surface of the array, and the outer jellies either adhered to each other or melded imperceptibly. Although it could not be discerned with staining, there must be a mosaic pattern on the surface of the clutch formed by the exposed surfaces of adjacent egg jellies. As often happens with formalin-preserved eggs, the jelly of these eggs eventually deteriorated, but the pattern of disintegration emphasizes the complicated structure of these egg jellies. At first, all material surrounding an ovum was lost so that the ovum fell to the bottom of the container, but a strand representing an apparently dens-
er jelly of the columns with concave distal ends where the ova were seated remained attached to the leaf.

The bright white, opaque egg jelly is unusual; the jelly of the related *Guibemantis tornieri* (Ahl 1928) becomes somewhat milky with age (Glaw & Vences 1992). The white jelly of some populations of *Ambystoma maculatum* (Shaw 1802) is perhaps the closest analog, and this whiteness is caused by protein crystals dispersed in the jelly (Hardy & Lucas 1991, Ruth et al. 1993). Functions of the white jelly, which makes the clutches very conspicuous but perhaps hides the ova, are not known. Hydration of the mucopolysaccharide jelly of frog eggs involves an influx of water modified by ionic content of the water (Beattie 1980), and because there is so little protein (Folkes et al. 1950) in egg jelly, typical eggs will hydrate in 10% formalin. The eggs of *G. depressiceps* submerged in water hydrated very slowly and incompletely, and one nonhydrated mass preserved in formalin did not hydrate. Of several mechanisms that might be involved in these differences, a higher protein content in the jelly of *G. depressiceps* is a possibility. If proteins were more common, formalin would cross-link them and this likely would inhibit hydration, and elevated protein concentrations also could contribute to the unusual consistency of the jelly.

At stages 22-23, the embryos hatched from their individual jelly layers, positioned themselves head-up, and moved about near the surface of the jelly by slow, exaggerated body undulations. Embryos could enter the jelly if they were removed manually, and they dropped into the water at about stage 25. Tadpoles that fell onto soil moved to water by tail flips of up to 20 cm/flip. A wasp was seen landing on these eggs, and an unidentified snake commonly raked the eggs from jelly masses by sweeping its head sideways through the jelly. In 1992-1993, rains were erratic and sparse, and none of 20 clutches hatched successfully. Most of these were not fully hydrated, and most of the somewhat dehydrated ova had been eaten.

**Blommersia** cf. *domerguei* (Guibé 1974)

Breeding was observed at the site described above. Males produced quiet, squeaky calls from the tops and bottoms of grassy leaves about 15-20 mm wide and close to or emerging from the water. Oviposition was similar to that described above; males spent short periods of time sitting on the heads of females, females continued to oviposit when males were not present, and 1-3 males amplexed successively or simultaneously. One male was observed sitting on an egg mass during the day. Egg arrays (Fig. 1D; about 10 × 37 mm, 51-82 eggs, ova = 1.3-1.7 mm diameter) of yellow eggs arranged in an oval monolayer of clear jelly were usually positioned on the bottoms of leaves. Clutches commonly were predated, and none survived in the drier year of 1992-1993.

**Guibemantis liber** (Peracca 1893)

Blommers-Schlösser (1975) described the breeding behavior and tadpoles of this species. Although variable in color, most males at night are uni-
formly dark brown dorsally with a brilliant white vocal sac and a black or
dark gray venter. Females usually have a medium green ground color with
purplish markings at night. Intense breeding activity was observed in a large
bush at the edge of an ephemeral basin before it actually filled.

Males called from and moved about on the tops of leaves of the large
bush up to 3 m above the ground. Because of the cacophony of the multispe-
cies chorus, it was difficult to determine accurately, but it seemed that some
males inflated the vocal sac without calling or left it inflated after calling as
if the bright white marble-sized sac provided a visual signal. There were
numerous small green frogs presumed to be females moving about through
the chorus. One wrestling encounter between a male and a small green frog
was observed, and one small green frog tried to push into an amplectic posi-
tion from the rear of an amplectic male. In 1992-1993, wrestling matches were
observed among three pairs of males, and one male sat in an amplectic posi-
tion on another male's head (both sexed by color) for at least 8 min. No egg
masses were present and no breeding occurred that night. These cursory obser-
vations are presented as a notice. The behaviors suggest unusual male-female
interactions, female interruption of amplexus, or the presence of some form of
satellite (e.g., BACKWELL & PASSMORE 1991) or other alternative male strategies.

*Mantidactylus majori* (Boulenger 1896)

This common frog occurs along slower parts of forested streams and
produces long series of quiet, chirping calls from calling stations on sticks and
rocks near the water during the day. At night the frogs sit quietly a few centi-
meters to about 5 m above the water, perhaps as protection against the preda-
tory *Mantidactylus guttulatus* that usually sits in or near the water and arbo-
real, nocturnal snakes that forage in streamside vegetation. These observa-
tions add to those of VENCES & DE LA RIVA (2005) and WOODHEAD et al. (2006).
Six males were seen guarding egg arrays positioned on the upper surfaces
of leaves or vertical twigs. Guarded clutches were seen on three visits dur-
ing both clear and rainy nights, but clutches were rarely guarded during the
day. In all cases, the male sat with the eggs under his abdomen. Clutch sites
ranged from 0.15-3 m above the water, and in three cases they were accessible
only by the frog moving onto the bank, up the trunk of a tree and then down
a small limb. Comparable situations are known for female *Phrynobatrachus
sandersoni* (Parker 1935) (Cameroons; AMIET 1981), male *Oreophryne* sp. (New
Guinea; JOHNSTON & RICHARDS 1993), and male centrolenids.

**SUMMARY**

Although seldom documented, the structure of egg jellies and clutches
provides useful information, and researchers are urged to collect these mate-
rials. Variations and consistencies among the mantellid frogs of Madagascar
would be particularly informative. In the cases presented herein, the true
clutch structure could not have been realized without observing oviposition and hydration. Also, archival fixation of eggs remains a problem, and the fixative recommended by McDIARMID & ALTIG (1999: 15) is now known not to be as effective as originally presumed. I am testing alternatives but I urge others to experiment with this process.

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