NEOTROPICAL ANURANS AND FOAM NESTS WHY BREED ON LAND?

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Tropical rainforests are among the wettest of terrestrial environments: they harbour a rich fauna of frogs and toads, many of which, surprisingly, reproduce on land. The vast rainforests of Central and South America support the greatest diversity of anurans to be found anywhere on earth. Some of these inhabit the canopies of the trees; others live on the forest floor or even burrow underground, but very few of them spend all their lives in water.

Some day-active forms, such as the Arrow-Poison frogs *(Dendrobates* and *Phyllobates* spp.) are extremely poisonous and possess vivid warning (aposematic) coloration. These conspicuous amphibians walk boldly in the open, the males calling loudly from exposed positions. One small species, *P. terribilis*, is said to carry enough toxin in its skin to kill 1000 people if it were to enter the bloodstream: the poison is less lethal when swallowed, but must nevertheless be a powerful deterrent to predators (Forsyth & Miyata, 1984). Most Neotropical frogs and toads, however, are quite edible and so cannot afford to advertise themselves. Instead, they are inconspicuous; their concealing (cryptic) hues resemble the olive, brown or grey coloration of the background. The nocturnal, Panamanian toad illustrated in Plate 1 was photographed at night by flash. It could only be detected through its mating calls, for it was almost invisible, even in moonlight.

Although most brightly coloured species, especially those marked with yellow and red, are highly poisonous, bright colours are not always linked with toxic secretions. For instance, the dull-coloured *Ceratophrys americana* has a virulent poison, while the gaudy *C. dorsata* is innocuous (Noble, 1931). Is there a parallel here with the so-called Mertensian mimicry found among coral snakes?

Nursing habits are very common amongst the Anura, as Gadow (1901) emphasised, and the eggs of tropical species are frequently deposited out of water. In some frogs, they are laid in places from which they can be washed into standing water after the next heavy rain, or on leaves overhanging the water so that, on leaving their eggs, the larvae drop into it. In other species, the eggs are placed in damp situations on leaves, and hatch as tadpoles or immature air-breathing frogs. In many cases, the eggs are carried about during their development by the male or female parents. A classic example is afforded by the Marsupial Frogs (*Gastrotheca* spp.) in which the developing eggs are carried around in pouches on the females' back (Fogden & Fogden, 1988; Frazer, 1973).

The tadpoles of Arrow-Poison frogs develop in bromeliads, or in small holes in tree-trunks containing a few millilitres of water only. They are carried between these reservoirs of water on the backs of the males. In such cases, the tree-frogs remain safely in the higher vegetation of tropical forest, and need never descend to surface waters to breed, while the eggs and tadpoles are kept away from the many predators which might otherwise feast on them. Presumably the latter are less toxic than the adults, otherwise the argument would be paradoxical.

Foam nexts (Plate 2) are produced by a number of frogs of the genera *Rhacophorus, Leptodactylus, Physalaemus,* (= *Engystomops*) etc. They may be found in dry hollows on the ground, along the banks of streams, or even above ground and attached to bushes or the lower branches of trees. The tadpoles remain in them for a while after hatching until the nest liquifies. Downie (1988) has recently analysed the functions of foam nests of the common leptodactylid *Physalaemus pustulosus* (probably the species illustrated here). Unlike Gorzula (1977) and Dobkin & Gettinger (1985), he concluded that the foam has little thermal

Plate 1. – **Nocturnal ground-living Panamanian Toad.**

Plate 2. – Foam nest

significance. It may, however, help to protect the eggs and hatchlings from desiccation. It is also likely that it may have anti-predator properties.

This brings me to the problem that this article seeks to address. Why do so many tropical, and especially Neotropical, anurans reproduce on land? There are probably a number of adaptive advantages, operating simultaneously.

Rivers and their permanent streams apart, lakes, ponds, and standing water generally, are rare in the rainforest. At the same time, puddles and temporary pools in the tropics speedily acquire a rich fauna of predatory beetles, water-bugs, dragonfly and predaceous dipterous larvae. It may well be that the avoidance of insect predators is a more important selective factor than the lack of standing water. Certainly, insects are often extremely resistant to toxins that have a remarkably harmful effect upon vertebrates.

I would like to suggest, therefore, that the selective advantage to amphibians of reproducing on land rather than in water, in the tropics, may lie in the avoidance of predatory aquatic insects that are resistant to amphibian skin toxins, such as batrachotoxin, which have a paralysing action on, and are so effective as defences against, vertebrate enemies.

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