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How Long do Trinidad's Frogs Take to Reach Metamorphosis?

A key parameter in the life history of any amphibian is the time taken from spawning to metamorphosis. This is the phase when most species (terrestrial direct developers and some others are exceptions) require an aquatic habitat where they are faced by a range of potential predators. Many amphibians spawn in temporary water bodies where they are unlikely to suffer predation by fish, but such pools are inhabited by many invertebrate predators, notably odonate and coleopteran larvae. Temporary pools hold water for varying times, relating to speed of drainage and evaporation, depth profile and pattern of rainfall. Since few tadpole species can survive their pool drying up, we might expect species that breed in temporary pools to minimise the duration of the larval period, to improve their chances of metamorphosing before the pool disappears.

How long do Trinidad's amphibian species take to reach metamorphosis? It is not easy to answer this question since it requires knowing when a particular batch of eggs was laid, then following the larvae through to metamorphosis. In temperate regions where all spawning occurs over a short period in the spring, this task is straightforward; but in Trinidad, individual frogs may spawn whenever it rains and they are gravid, so new larvae can be entering the population throughout the wet season. Without marking individuals (generally not feasible for amphibian larvae), it is difficult to follow a particular batch to completion. Here I present observations of four species where the spawning and metamorphic times were known. Developmental staging is according to Gosner (1960).

In July 1982, I noted that a small isolated temporary pool on the University of the West Indies, St. Augustine campus contained a large number of hatchling *Rhinella beebei*, implying spawning within the previous 36 h. Twelve days later, with little intervening rain, the pool was almost dry. I captured a sample for staging (they were stage 36-37) and kept them in a small aquarium in the laboratory. Two days later, the pool dried up and all the tadpoles died. In the laboratory, two had completed metamorphosis after a further two days, so the time from spawning to initiation of metamorphosis was 17 days in a small pool with a large number of tadpoles, where intraspecific competition would have been intense.

In June 2012, I was able to obtain data for three further species. The spawning site was the foundation of an abandoned building site at Sunset Drive on the Lopinot Road, northern Trinidad. An extensive deep hole (dimensions: 21 x 13.7 m, depth below surrounding field 2.7 m) had an uneven concrete bottom with the result that the site holds water for some time following heavy rain. Small trees and bushes have grown up around the periphery of the site, providing some shade. The field around the pond site drains poorly and depressions there also hold water. Over the years that we have visited the site, it has been colonised by at least 10 frog species (*Trachycephalus typhonius, Hypsiboas crepitans, Scinax ruber, Phyllomedusa trinitatis, Dendropsophus microcephalus, Rhinella marina, Rhinella beebei, Elachistocleis ovalis, Engystomops pustulosus and Leptodactylus fuscus: names as in Frost 2013, except that I prefer <i>R. beebei* to *R. humboldti* as the name for the smaller of Trinidad's toads).

In 2012, I first visited the site on 8 June. Despite a little rain on the previous day and local reports that the dry season had been quite showery, the site was completely dry, with no sign of any amphibian larvae. On 10 June, heavy rains fell on north Trinidad from early to mid-morning. That night, I visited the site: it contained water over the main area to a depth of about 15 cm. A substantial chorus of T. typhonius was calling; also many E. pustulosus, L. fuscus and smaller numbers of S. ruber, D. microcephalus, H. crepitans and E. ovalis. I anticipated extensive spawning by some or all of these species. On 12 June, there had been more rain overnight; I checked the site in the morning and found plentiful well developed T. typhonius spawn which must have been deposited on the night of 10 June. More rain fell on 13 and 15 June and the water level became a little deeper but there followed a series of hot, dry days. I first sampled for tadpoles, using a hand net, on 19 June and found two species that were already well developed, T. typhonius and E. ovalis. These were found in deeper, cooler water towards the centre of the site. Netting also revealed an abundance of predatory insect larvae, mainly odonates and coleopterans. I returned a sample of both tadpole species to the laboratory for staging and measuring, using callipers. Further samples were taken on 21, 24 and

26 June (including on 26 June a third species, *S. ruber*). Since the furthest developed tadpoles were approaching metamorphosis on 26 June, I returned a sample of live tadpoles to the laboratory and maintained them in aquaria at ambient temperature to assess the earliest date for metamorphosis (See Table).

There was very little rain between 26 June and 2 July. On 2 July the water level was low, around 5 cm in most parts, and there was no sign of well developed *T. typhonius, E. ovalis* or *S. ruber.* Netting captured large numbers of odonate and coleopteran larvae. Presumably, the amphibian larvae resulting from the spawnings on 10 June had now metamorphosed or been predated. It is also possible that some larvae died from overheating. Following a sequence of dry days, we found early afternoon temperatures in the shallow water were above 40°C and some tadpoles appeared stressed and unhealthy.

From these observations, the minimum time to metamorphosis in field conditions, with abundant predator presence, is 19-20 days for *T. typhonius* and *S. ruber* and probably a little longer for *E. ovalis*, though for this species, the small initial numbers and high predation levels prevented us seeing completion.

Experimental rearings in Trinidad of *L. fuscus* and *E. pustulosus* tadpoles, both outdoors and in laboratory conditions (Downie *et al.* 2008; Hailey *et al.* 2006), have suggested that previous estimates (Kenny 1969) of larval period duration were too high, but it remained possible that these results were an artefact of field conditions. Here I show that this is not the case, at least for the fastest developing members of spawnings of four species, *R. beebei, T. typhonius, E. ovalis* and *S. ruber*. All reached metamorphosis in 20 days or less, whereas Kenny (1969) gave larval periods for these species as 28, 42, 56 and 42 days respectively.

All the species reported here primarily inhabit temporary water bodies as larvae and metamorphose at a relatively small size. In addition to re-investigating other

Table. The most advanced stages of development (Gosner 1960) and sizes (total lengths) reached in the field by three species of Trinidad tadpole following spawning on the night of 10 June, 2012. Column a = Gosner stage; column b = total length (mm). NS = not sampled; - = not found.

Species	Days after spawning								
	8.5		10.5		13.5		15.5		19.5
	а	b	а	b	а	b	а	b	а
T. typhonius	31	30.9	32	29.7	36	36.7	37	42.6	42
E. ovalis	28	14.4	31	19.4	-		-		-
S. ruber	NS		NS		NS		38	30.0	42

small temporary pond species, there is a need to assess larval periods in species inhabiting more permanent water bodies, such as streams, rivers and swamps, such as Mannophryne trinitatis, Hypsiboas boans and Hypsiboas geographicus, and those growing to large sizes at metamorphosis. Nutrition is another factor that needs investigation. The oligotrophic Northern Range rivers utilised by H. boans and H. geographicus may be very different in nutrient availability to temporary pools. Competition may also modulate tadpole growth. Under experimental conditions, we have demonstrated an inhibitory effect of one tadpole species, L. fuscus, on another, E. pustulosus, (Downie et al. 2008). Unravelling the complexity of such interactions where up to ten tadpole species may share the same pond with an abundance of invertebrates is a considerable challenge.

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