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On the Comparative Palatability of Some Dry-Season Tadpoles from Costa Rica

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ABSTRACT: Tadpoles of eight species of frog were tasted in a standardized procedure by 11 volunteers. The tadpoles were rated in their palatability from "tastes good" to "highly unpalatable." It is suggested that palatability in tadpoles may correlate inversely with vulnerability.

INTRODUCTION

Tadpoles are poor swimmers in both speed and agility. Anuran larvae have had to evolve defenses other than fleeing from predators. Many kinds of tadpoles are cryptically colored or, if mid-water swimmers, largely pigmentless. Several are secretive and hide individually under rocks or vegetation.

Some tadpoles, however, are remarkably conspicuous. *Bufo marinus*, a uniformly black tadpole, forms tight aggregates of hundreds or thousands of individuals in open shallows. These aggregations may be visible from many meters and would seem highly susceptible to heavy predation. The fact that they are not conspicuously attacked by larger vertebrates suggests that some defense is operative. Often conspicuous animals are noxious and it can be hypothesized that conspicuous tadpoles may be so.

The following experiment was undertaken to compare the palatability of tadpoles with diverse ecology.

MATERIAL AND METHODS

The eight species used in this experiment represent four families and six genera. All are common as tadpoles during the latter half of the dry season on the Osa Peninsula, Puntarenas Province, Costa Rica. They were all collected on the morning of 6 March 1970, in the neighboring few miles accessible by road from Rincon de Osa. An effort was made to collect tadpoles of equal size and stage although this was not always possible. Pertinent information on these tadpoles is given in Table 1.

The tadpoles were kept alive in clear fresh water for several hr before the experiment was actually run, from 3:45 - 6:15 in the afternoon.

The mock predator in this experiment was a sample of 11 students and faculty of the 1970 Dry Season course, Tropical Biology: An Ecological Approach, offered by the Organization for Tropical Studies. The volunteers were two females and nine males aged 22 to 36 ($\bar{X} = 27.5$). The experiment was run at least 2½ hr since the last meal for the volunteer tasters. Each taster was tested separately and asked not to discuss the test until the experiment was over. The tadpoles, which were assigned a number, were presented individually to each subject one at a time and by number rather than name. The tasters did not know which tadpole had which number. This was done to prevent preconceived notions about how any certain tadpole

TABLE 1.—Characteristics of the experimental tadpoles

Tadpole with reference to accounts of descrip. and/or ecol.	Stage by Gosner, 1960	X snout-vent (mm) (N=11)	Snout-vent range (mm)	Approximate H ₂ O temp. in C. when collected	General habitat where collected
Leptodactylidae <i>Engystomops pustulosus</i> Breder, 1946; Starrett, 1960	31-41	6.5	5- 8	30-32	Shallow standing pools such as those made by flooded tire tracks; drying cattle ponds.
Hylidae <i>Agalychnis callidryas</i> Gage, 1936 Stuart, 1948	32-33	17	15-20	30-34	A permanent but turbid pond of some 2000 sq. m. surface area.
<i>Smilisca sordida</i> Duellman and Trueb, 1966	26-28	10	9-11	27	Under rocks in a shallow but flowing area of the Rio Rincon, a major drainage channel for the area.
<i>Smilisca phaeota</i> Duellman and Trueb, 1966	30-32	7	6- 8	25-26	Collected with <i>E. pustulosus</i> in tire tracks and pools.
<i>Hyla rosenbergi</i> Noble, 1927 Breder, 1946	27-29	8.5	8- 9	30-32	Collected in submerged shallow pocket-like depressions adjacent to flooded tire tracks.
<i>Hyla rufitela</i> Duellman, 1970	28-38	18	15-20	34-36	Very shallow, highly turbid, drying puddles overgrown with grass in an open marshy area.
Dendrobatidae <i>Colostethus nubicola</i> Dunn, 1924	30-34	8	7- 9	26	Under leaves and rocks in water no deeper than the tadpole itself in rapidly flowing tributary to Rio Rincon.
Bufonidae <i>Bufo marinus</i> Ruthven, 1919 Breder, 1946	30-32	8.5	8- 9	36-38	In dense aggregates in quiet open pools adjacent to Rio Rincon.

should taste influencing the results. Also, the order of presentation was varied in an attempt to balance any biasing caused by the after-taste of an especially distasteful tadpole.

The tasters were asked to rate the palatability of each tadpole's skin, tail and body on a 1 to 5 scale: 1, tastes good; 2, no taste; 3, only slightly disagreeable; 4, moderately disagreeable, and 5, very strongly disagreeable. They were also asked to make comments about the taste as they went along and to note the most and least palatable tadpole at the end of the experiment. The standardized tasting procedure included several steps. A tadpole was rinsed in fresh water. The taster placed the tadpole into his or her mouth and held it for 10-20 sec without biting into it. Then the taster bit into the tail, breaking the skin and chewed lightly for 10-20 sec. For the last 10-20 sec the taster bit firmly and fully into the body of the tadpole. The participants were directed not to swallow the tadpoles but to spit them out and to rinse their mouths out at least twice with fresh water before proceeding to the next tadpole.

RESULTS AND ANALYSIS

The results are presented in Table 2 and Figure 1. The median is the only meaningful statistic here because the taste scale is not a continuum. The sample size is nine rather than 11 because two subjects had to be eliminated; both were heavy cigarette smokers. The heavier smoker of the two was unable to taste anything throughout the test, while the other smoker fell outside of the range of values gathered from the other subjects 13 out of 24 times. Interestingly, 9 of those 13 times he found the taste less displeasing than did the rest of the tasters.

The most distasteful tadpole was clearly *Bufo marinus*. This tadpole has distasteful skin, a condition that could not be demonstrated in any of the other tadpoles. The distastefulness of *Bufo marinus* tadpoles

TABLE 2.—Results of the palatability tests. Total scale runs from 1 to 5 with 1 representing opinion category "tastes good," and 5 representing "very strongly disagreeable"; 2 indicates "no taste"*

	Skin		Tail		Body	
	Range	Median	Range	Median	Range	Median
<i>Engystomops pustulosus</i>	2-3	2	2-4	2	2-4	3
<i>Agalychnis callidryas</i>	2-3	2	1-4	2	2-5	3
<i>Smilisca sordida</i>	2	2	1-2	2	2-3	2
<i>Smilisca phaeota</i>	2	2	1-4	2	1-5	3
<i>Hyla rosenbergi</i>	2-3	2	1-3	2	1-5	3
<i>Hyla rufitela</i>	2	2	2-3	2	2-5	3
<i>Colostethus nubicola</i>	1-2	2	1-4	2	2-5	2
<i>Bufo marinus</i>	3-5	4	2-5	3	2-5	4

* Number of tasters = 9

is present as one bites into the animal but this may be the result of a lingering of the taste from the skin. The increase in range (see Table 2) between the taste of the skin and the taste of the tail and body shows that at least one subject felt that the distastefulness was solely centered in the skin. *Bufo marinus* was rated the most distasteful tadpole by six of nine subjects. Of those who chose to comment on the distastefulness of this or any other tadpole, bitterness was always mentioned.

The other tadpoles recorded as most distasteful were *Smilisca phaeota*, *Hyla rufitela* and *Colostethus nubicola*, each once. However, none of the tasters who specified these tadpoles as the most distasteful rated them higher than No. 4 on the scale. In all these cases it was only the body that they found distasteful.

The most palatable tadpoles, based on the subjective rating of "best," were *Smilisca sordida* and *Colostethus nubicola* in that order. *Smilisca sordida* was rated "best" three times and tied for that honor twice. *Colostethus* was twice chosen as the most palatable. Other

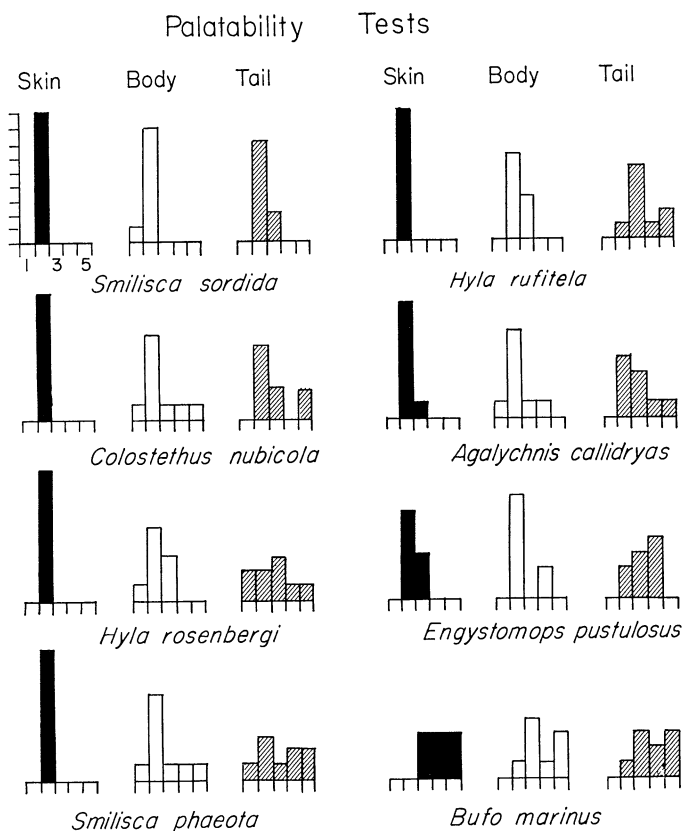


Fig. 1.—Horizontal axis scale runs from 1 to 5, with 1 representing opinion category "tastes good" and 5, "very strongly disagreeable"; 2 indicates "no taste." Each vertical increment represents response of one taster

species to appear on the most palatable list are: *H. rufitela*, once; *H. rosenbergi*, two ties; *S. phaeota*, once.

The other four species of tadpoles rest between these extremes. These evaluations of the tadpoles tended to be "tasteless" on the skin and tail but "slightly disagreeable" within the body. This distastefulness may result from food in the gut rather than some innate distasteful property of the tadpole. The body cavity of tadpoles is almost entirely occupied by gut in which tadpoles process large volumes of detritus. One taster specifically commented on the grittiness of the gut contents.

The scale used to rate the tadpoles, namely, "tastes good" to "very strongly disagreeable," is somewhat regrettable in that it does not form a continuous span. The scale is subjective and does not lend itself readily to precise comparisons. There is clearly a wide range of opinion on tadpole taste; there are two instances where tadpole bodies were rated from 1 to 5. Also, with three species, *S. phaeota*, *C. nubicola* and *H. rufitela* appearing on both the most and least palatable list, it is obvious that these results can only serve to convey a general impression. No attempt has been made to put these data to any more rigorous statistical tests.

DISCUSSION

The knowledge that some anurans have unpalatable developmental stages is not new. True toads (Bufonidae) are well known for their toxins. Of the species used in this study the adults of *Bufo marinus* are known to be unpalatable. Some species of the phyllomedusine hylids are assumed to be unpalatable. Cei and Erspamer (1966) assayed large quantities of bradykinin and physalaemin-like polypeptides from the skin of the adult *Agalychnis callidryas*. The highly potent steroidal alkaloids of the Dendrobatidae have received much attention (see Daly and Myers, 1967), although it has yet to be established that frogs of the genus *Colostethus* are in any way toxic or unpalatable.

Phisalix (1922) demonstrated that *Bufo bufo* eggs were toxic to *Rana temporaria* when injected into that frog. Licht (1967) reported the deaths of two Peruvian natives after the accidental ingestion of *Bufo* (probably *Bufo marinus*) eggs. He then initiated two studies on the palatability of anuran eggs. *Bufo boreas* and *Bufo valliceps* eggs were consistently rejected by both the leech *Batrachobdella picta* and a diverse group of vertebrates that might normally feed on amphibian eggs (Licht, 1968, 1969). In comparison, eggs of *Rana aurora*, *Rana catesbeiana*, *Rana clamitans* and *Hyla regilla* were accepted willingly by the same group of potential predators.

In 1959, Liem suggested that what he recognized as poison glands in *Rana chalconota* tadpoles served to protect these larvae from attack by carnivorous fishes. He later showed (Liem, 1961) that the carnivorous *Fluta alba* and *Tilapia mossambica* would starve rather than eat tadpoles of this species. At the same time these fish would readily eat tadpoles of *Rhacophorus leucomystax*, *Rana limnocharis*, *Rana cancrivora* and *Rana erythraea*, all of which lack the poison glands. In the other previous experiment done on the comparative palatability of tadpoles, Voris and Bacon (1966) clearly demonstrated that the bluegill fish, *Lepomis macrochirus*, greatly preferred the hylid tadpoles,

Pseudacris triseriata, to those of *Bufo americanus*. Like Liem, they suggest that unpalatability may be an important defense against predation.

In attempting to interpret the ecological significance of the present results, the objection that man is not a natural predator will doubtless be raised. Cott (notably 1951, 1952, 1953, 1954) did massive comparisons of the palatability of birds' eggs and found a startling amount of agreement between the preferences of natural predators and members of the Egg Panel set up in England to grade the quality of eggs. He gives, as one example, the "unanimous verdict of unpalatability by animals with such widely differing feeding-habits and diets as spiders, frogs, lizards and various birds, bats and man." In assessing relative palatability he found broad agreement among the hedgehog, rat, ferret, cat and man. Man is easy to condition, inquisitive and offers subjective opinions that cannot be obtained from other species. In this sense, it is not unreasonable to use man as an experimental predator. Cott concluded that there was an inverse correlation between palatability and vulnerability for birds' eggs. He considers size, weapons of defense, powers of offense, availability of the clutch, habits, sociability and visibility as factors relevant to vulnerability. He found that the birds' eggs that were most palatable were the largest, least accessible, most cryptic ones often belonging to social birds. Obviously, powers of defense, offense and sociability of the adult frog are of little consequence to the tadpoles of this experiment. The other parameters, however, may be significant and are worth some inspection.

Whereas large size seems to afford some protection to birds' eggs, from the few data here it does not appear that there is any correlation between size and palatability of tadpoles. *Bufo marinus*, *Smilisca sordida* and *Colostethus nubicola* are all in the same size range and are not too far apart in developmental stage. The tadpoles of *Agalychnis callidryas* and *Hyla rufitela* were considerably larger than the other tadpoles and several of the tasters expressed a natural aversion to masticating such a large live animal. This makes the size factor difficult to interpret.

Availability of the clutch (or, in this case, the tadpoles), habits, sociability and visibility are all factors that are difficult to separate and can be treated broadly together. On one extreme there are the *Bufo* tadpoles. As mentioned in the introduction, these tadpoles form large aggregates and are highly visible. When disturbed, they exhibit no special evasive action, but a chain reaction of disorganized activity takes place. By aggregating in shallow water, these tadpoles may avoid larger aquatic predators, but at the same time they become more susceptible to aerial and terrestrial predation. Interestingly, Liem (pers. comm.) has informed me that *Rana chalconota* tadpoles also aggregate and form mobile schools that he would consider quite conspicuous to aerial or terrestrial predators.

On the other extreme there are the tadpoles of *Colostethus nubicola* and *Smilisca sordida* which never seem to aggregate. Whereas all the other tadpoles used in this study could be collected in masse with a net, both of these species had to be searched out singly. In part, this could reflect the simple fact that it is energetically difficult to maintain group

organization in a strong current. However, the cryptic nature of these tadpoles is noteworthy. When exposed, these tadpoles would lie still rather than move, and when prodded into moving, they would move with a single short fast motion, then immediately lie still again. They both matched the color of their habitat perfectly and tadpoles over 2 cm long could not be observed from more than a half meter away.

The above observations, although based on but three species, tend to verify the general rule that the least vulnerable animal is the most palatable and the most vulnerable is the least palatable. The other four species could be said to lie between the two extremes of vulnerability although this is impossible to quantify. Most of the species seem moderately visible from above, but in color, *E. pustulosus*, *S. phaeota*, *H. rufitela* and *H. rosenbergi* all seem to blend in well with their background. *E. pustulosus* and *S. phaeota* would burrow into the mud when disturbed; Duellman and Trueb (1966) also observed this response in *S. phaeota*. The tadpoles of *H. rufitela* were especially difficult to see in the muddy, weed-choked areas where they were collected.

The nest built by the male *H. rosenbergi* for its tadpoles is likely an effective defense against aquatic predators. However, they would not seem so effective against nonaquatic predators.

Agalychnis callidryas is somewhat of an enigma. These tadpoles seem less visible than Stuart (1948) reported, but they form dense mobile aggregations that are conspicuous during their regular surfacing. I spent several hours watching a kingfisher sit on a branch by the pond where these were collected. As the tadpoles surfaced, the kingfisher swooped down and picked off individuals.

A final correlation to be discussed is between temperature and palatability. *B. marinus* occurred in the warmest water, *S. sordida* and *C. nubicola* in the coolest water, and the other tadpoles somewhere in between. It may appear that standing water, which was the warmest, was more likely to be stagnant. This in turn, one might claim, would impart a foul taste to the tadpoles. This supposition could have some validity since *A. callidryas* and *H. rufitela* live in quite stagnant pools. The water where *B. marinus* was collected was relatively clear compared to that where these last two species were found. A correlation between temperature and palatability is doubtful and cannot be established with the sparse data here. At best such a correlation would be most indirect. The apparent palatability to some tasters of the *Agalychnis* tadpoles suggests that the unsavory dermal compounds for this genus are not produced until metamorphosis.

In conclusion, data presented here for tadpoles, although slight, support the general rule that the most palatable organisms are those least vulnerable to predator attack, while the most distasteful are those most susceptible to such an attack. Hopefully, this will someday be better verified with a larger sample of tadpoles and a different, more natural predator.

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