

## FORUM

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# HYPOTHESIS: FUNCTIONAL SIGNIFICANCE OF COLOUR AND PATTERN OF ANURAN TADPOLES

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In the absence of sexual selection, the modest array of colours and patterns of anuran tadpoles function primarily in camouflage and specific intra- (e.g. school cohesion) and interspecific (e.g. antipredator) interactions. We suggest that the paucity of observations (e.g. Voris & Bacon, 1966) and tests (e.g. Caldwell, 1982) involving tadpole colours result in part from the lack of a summarisation and synthesis of the variations present. We present such a summary and submit three general hypotheses concerning the colours and patterns of tadpoles.

An effective terminology must represent preserved and live specimens and distinguish among patterns formed by the presence, absence and dispersion of both melanin (persist in preservative) and non-melanin (mostly disappear in preservative) pigments. Non-melanin pigments often overlie gaps in melanin patterns, and patterns commonly are formed, sometimes almost entirely in younger stages, by pigment deposited in subintegumentary structures.

(1) *Dorsal and ventral colour and pattern correlate with the ecology and behaviour of tadpoles.* Patterns of tadpoles are more diverse than the relatively low variety of colours. We divided these patterns that are assumed to function in various forms of crypsis in specific macro- and microhabitats into 11 components that often occur in combinations. (1) Both uniformly dark (e.g. many *Bufo*, some *Rana*, some *Rhinophrynus*, some *Scaphiopus*) and light (e.g. various microhylids, some *Rhinophrynus*, some *Scaphiopus*, some *Xenopus*) dorsal colourations are common. Sparse pigmentation (e.g. some *Scaphiopus*, *Rhinophrynus* and *Xenopus*) or transparency of all (e.g. some hylids, some microhylids) or part (e.g., some phyllomedusine hylids) of the body are common in midwater forms. Multiple objects, such as gut and eyes surrounded by translucent areas move together but appear separated, and tracking such objects is more difficult because receptive eyes look at the parts alternately. Ventral colouration varies from uniformly dark to translucent (benthic forms) or white (= countershading) in nektonic forms. (2) Stripes (i.e. longitudinal or oblique) may be positioned on the sagittal line of the body (e.g. *Hypopachus variolosus*, *Kaloula rugifera* and *Rana pleuraden*), laterally on the tail (e.g. *Hemismus guttatus*, *Hyla andersoni*, *H.*

*femoralis*, *Phrynohyas venulosa*, *Semnodactylus weali*) or obliquely from eye to naris (e.g. *Hyla avivoca*) or extend from the body onto the tail and often through the eye (e.g. *Hyla microcephala* group, *H. picta*). Both melanin and non-melanin pigments may be involved, and a bicoloured tail muscle (upper dark, lower light, many *bufo*) is a type of stripe. Faint dots formed by pigment around neuromasts (e.g. *Rana grylio*, *R. virgatipes*) can form a discontinuous, faint stripe. (3) Bands (i.e. transverse or vertical: across body, between eyes, or vertical, height of tail muscle and fins) may occur on the tail (e.g. *Atelophrynus chrysophorus* and *Litoria micromembrana*, Fig. 1B, *Litoria "bicolor"*) or body (e.g. between eyes of *Hyla avivoca*; tail of small *Rana palmipes*, tail and body of small *Pseudis*). (4) Saddles, partial bands limited to the dorsum of the tail muscle, may be single (e.g., young *H. gratiosa*) or multiple (e.g. *Acris* spp., *Bufo valliceps*, *Hyla avivoca*, Fig. 1C, *Pseudacris crucifer*). Stripes, bands and saddles probably serve to break up the body outline in different views. Stripes may provide camouflage or disruptive effects in linearly arranged habitats (e.g. submerged grasses) and probably modify a predatory attack because the speed of striped objects is often over-estimated. Bands offer crypsis by disruption of outline and confusion during movement because of the inability to track specific bands. (5) Mottling, dark reticulations and irregular blotches on light ground colour or vice versa, occurs in many species (e.g. *Rana*). (6) Maculate (i.e., multiple, dark, isolated spots, dots and blotches on light background or vice versa (e.g. *Boophis microtypanum*, *Rana catesbeiana*, Fig. 1D) and (7) freckled (i.e. smaller, usually evenly distributed spots or dots; *Boophis tephraeomystax*, *Phyllomedusa marginata* and large *Hyla cinerea*) differs only in the size of mark. Mottling, spots and dots all function as camouflage in a dappled environment caused by vegetation. (8) Light or dark lip-lines extend posteriorly to posteroventrally from near the lateral base of the oral disc. (9) Light fins with darkened areas at or near the edges and lighter or unpigmented zones adjacent to the tail muscle (*Phrynomerus bifasciatus*, *Calluella yunnanensis*, and *Rana heckscheri*, Fig. 1E) probably serve a disruptive function. (10) Fake eyes or ocelli, light, usually circular areas surrounded at least partially by darker borders or vice versa, are assumed to be deflection marks. Crude ocelli with indistinct proximal borders occur on the tail tips of suctorial tadpoles of *Ascaphus* (Fig. 1F) and *Staurois* that move relatively little; attacks from within the water presumably come from the rear, and aerial attacks would presumably be directed at the tail rather than the cryptically coloured body. The large (c. 100 mm) gregarious tadpoles of *Rana alticola* have a single (Sahu & Khare, 1984) or multiple (Annandale, 1912) bright enamel yellow rings surrounding intense black situated on each side of the tail muscle (Fig. 2B). The ocellus may make the tadpole look like the head of a much larger, big-eyed beast, and large glands occur dorsolaterally and ventrolaterally on the body. Selection should favour characteristics of ocelli that enhance apparent size or prominence of the "eye." Over-estimation of the size of the inner of concentric circles (= large "pupil") and underestimation of the outer circle is greatest when the two diameters are in a ratio of 1.5:1 (Oyama, 1962). High contrast enhances the effect. The ratio of ocellar components of four specimens of *R. alticola* (CAS 111532) ranged from 1.15 - 1.29. Black tail tips without surrounding light areas are assumed to serve as deflection patterns (e.g. *Acris* (Fig. 2A), *Chirixalus doriae*, *Hemismus*

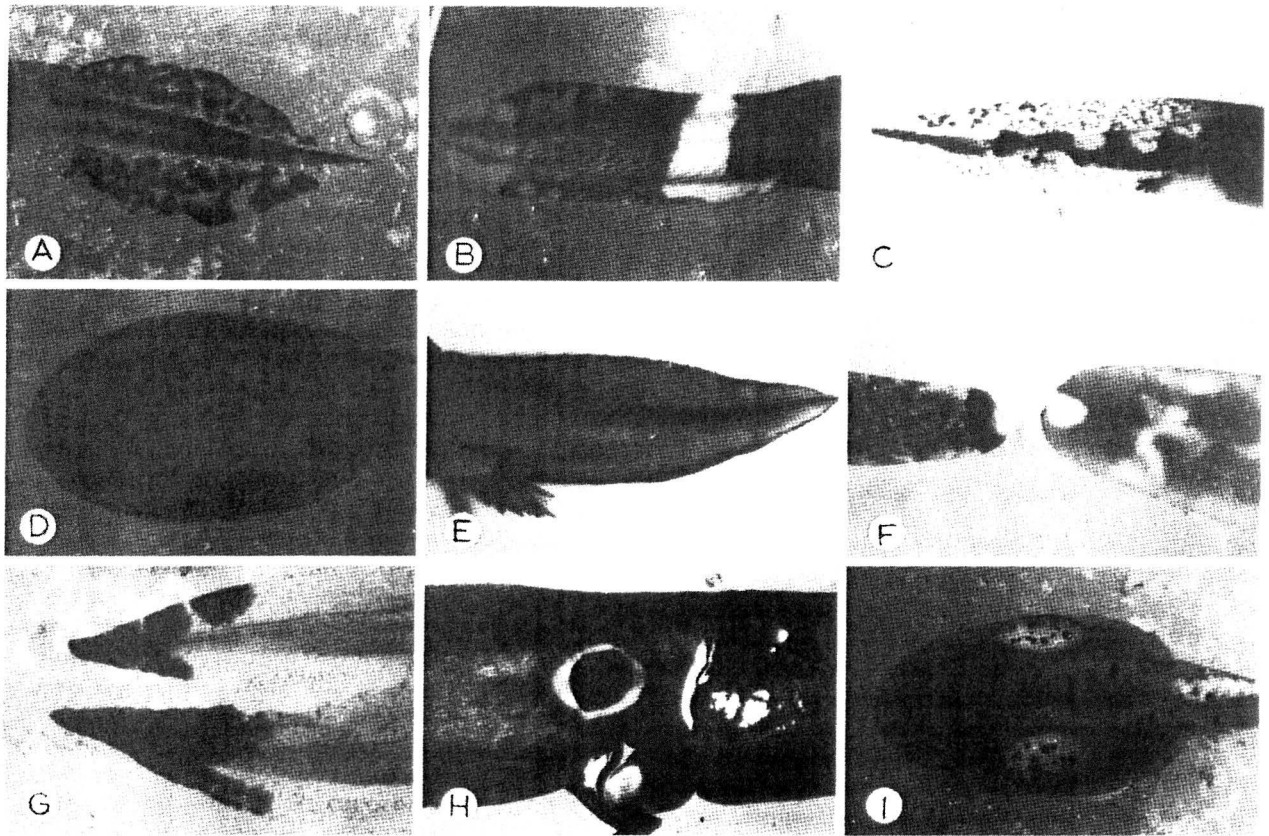


Fig. 1. Pigment patterns of selected tadpoles: (A) striped tail muscle of *Hyla avivoca*; (B) banded tail of *Litoria micromembrana*; (C) saddles on tail of *Hyla avivoca*; (D) maculate body of *Rana catesbeiana*; (E) dark margin on the tail fins of *Rana heckscheri*; (F) tail tip ocellus of *Ascaphus truei*; (G) black tail tip of *Acris gryllus*; (H) yellow ocelli at the base of the tail of *Rana alticola*; and (I) integumentary glands of an Indian ranid tadpole.

*guttatum*, *Hyla smithii*, some *Hyperolius*, some *Lysapsus* and some *Rana*; Caldwell, 1982). (11) Isolated clear areas along the periphery of the tail fin (e.g. *Hyla berthalutzae*) and isolated dark spots, often in the tail fins and usually surrounded by transparent or lightly-pigmented tissue (e.g. phyllomedusine hylids) in tail fins and muscle may serve as ocelli but more likely serve for outline disruption. Tadpoles of *Hyla hutchinsi* have a pinkish tail with a single large black spot with diffuse margins at about midlength. Unicoloured dark (benthic) or light (mobile nektonic) ventral coloration are common. Tadpoles that remain motionless in midwater, often among dense vegetation, commonly have banded (e.g. *Megophrys carinensis*), mottled (e.g. *Gastrophryne*, some *Microhyla*, some phyllomedusine hylids) or striped (*Hyla leucophyllata* and *H. parviceps* groups) throats and bellies.

(2) *Changes in colour and pattern as a function of time of day, ontogeny and site are accompanied by changes in behaviour and ecology.* Diel changes usually involved nocturnal blanching of all or part of the body, but the distal third of the tail of large tadpoles of *H. gratiosa* (Altig, 1972) becomes darker at night. Changes in intensity of the diffuse spot in the middle of the ventral fin of some phyllomedusine hylids is correlated with light intensity.

Ontogenetic colour changes usually occur between hatchling and tadpole stages or between small and large tadpoles. Tail saddles of many hatchlings are lost by the time the tadpole is free-swimming but retained throughout larval life in *Acris*, *Hyla avivoca*, *Pseudacris cadaverina* and some *Bufo*. The yellow body band of young tadpoles of *Rana grylio*

and *R. heckscheri* disappears in the benthic tadpoles of *R. grylio* (Altig, 1972) but remains throughout larval life in the nektonic, schooling tadpoles of *R. heckscheri*. Likewise, small tadpoles of *R. heckscheri* lack the dark edges on the fins that are present in larger tadpoles. Until about a third grown, tadpoles of *Hyla gratiosa* have a single dark saddle at midlength of the tail muscle that is not derived from the pattern of hatchlings; these small tadpoles tend to stay among vegetation. After this saddle dissipates, a sharp demarcation between proximal punctate and distal stellate melanophores becomes apparent, and the tadpoles are more pelagic in open water. Small tadpoles of *Rana palmipes* have bands at midbody and at the tail-body junction that disappear in larger tadpoles, and young tadpoles of *Pseudis paradoxa* are boldly banded on the body and tail, while large specimens are rather uniformly greenish-black to faintly mottled. Multiple ocelli on the tails of *Rana alticola* tadpoles disappear with age until only one remains (Annandale, 1912). Some pigmentary traits respond as dominants in  $F_1$  progeny (Fortman & Altig, 1973), but there are no definitive data on the genetics of larval colours.

The implications of colour differences among sites largely are enigmatic. Successive cohorts of *Rhinophrynus dorsalis* in the same pond in Costa Rica were uniformly light or almost black (R. W. McDiarmid, pers. comm.). *Rana alticola* tadpoles from streams were lighter than those from ponds (Sahu & Khare, 1984). Tadpoles growing in clear water, especially if darkly stained by tannins, are more prominently coloured than individuals in turbid water (e.g. Bragg, 1957), and the red tail colouration of tadpoles in the *Hyla versicolor* group only

occurs when the tadpoles live in clear waters: if this colouration functions in chromostereopsis (inability of a lenticular system to focus all wavelengths in one plane simultaneously), the red and melanin pigments should appear at different distances from the viewer. The normally darkly-pigmented tadpoles of *Spea* living in turbid water appear silvery in life and largely transparent in preservative.

(3) *Associated structures and behaviours are correlated with colour and pattern.* A fright reaction in response to cutaneous substances has been shown only for ranid (Altig & Christensen, 1981) and bufonid (Hews & Blaustein, 1985; Pheiffer, 1974) tadpoles. The intense blackness of most *Bufo* tadpoles may be an aposematic colouration associated with a tendency to aggregate and cutaneous toxicity during part of larval ontogeny (Brodie & Formanowicz, 1987). The organized schools of golden, nektonic tadpoles of *Phyllomedusa vaillanti* are segregated by size, and school formation is governed by ambient light (Branch, 1983). Large mobile aggregations of tadpoles of *Rana heckscheri* appear unorganized, contain hundreds of individuals, occupy a number of cubic meters, and along a bank they move in a rotational manner as described by Duellman & Lescure (1973) for tadpoles of *Osteocephalus taurinus*. Tadpoles in stationary or slowly-moving, mid-water schools of small tadpoles of *R. heckscheri* all face one direction, and the schools appear spatially organized (pers. observ.). Bursts of swimming interspersed with quiet periods appear to occur after a neighbour moves and stops, and it is tempting to suggest that the golden band contrasted against the black body serves as a motivational cue to sustain orientation within the group.

Escape by swimming or immobility are viable modes of defence for individuals or a group that are presumed to vary with colour, age and site. Escape behaviours are poorly understood but usually involve moving away and often downward from the stimulus regardless of the starting position. Ending positions usually are at or near the bottom or within bottom debris. Large tadpoles of *Hyla gratiosa* and *Pseudacris nigrita* commonly escape temporarily to the surface in clear water at night, and tadpoles of *Rana sphenoccephala* often escape upward in turbid water during the day or night. Skin glands assumed to produce toxic or noxious substances upon contact occur in hylids (e.g. *Hyla fimbrimembra*), leptodactylids (e.g. *Physalaemus petersi*), ranids (e.g. *Amolops* spp. *sensu lato*, *Rana alticola*, *R. chalconota*) and rhacophorids (e.g. *Boophis* cf. *majori*). Some *Amolops sensu lato* have epidermal spines on the dorsum.

Judged relative to human visual perception and based on the contingencies of lens, sensory structures and interpretative centres, probably no visual interpretation is exactly the way the scene exists. The primary functions of colour in tadpoles probably involve: (1) background matching, (2) disruptive patterns and (3) countershading for crypsis plus (4) deflection marks and (5) perhaps mimicry or aposematic colouration. Benefits of colour and pattern probably stem from (1) failure of a predator to detect or recognize the prey, (2) a delay in a predatory attack while proper identification and location of the prey is evaluated, and (3) misdirection of attack. A colour pattern of a given tadpole may employ more than one technique and function differently with (1) different predators, (2) at different times of day, (3) in different habitats, and (4) at different ages. The success of anti-predator features need not be totally effective to enhance selection. The effects of foraging strategies (e.g. sit-and-wait vs. pursuit hunters; attacking from above or within

water column) and sensory abilities (e.g. binocular vs. monocular vision, foveate vs. non-foveate eyes, electroreceptive vs. not, colour vs. black and white vision, and olfactory acuity) of predators are poorly understood modifiers.

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