

## Review Article

# Coloration of Anuran Tadpoles (Amphibia): Development, Dynamics, Function, and Hypotheses

**Giselle Thibaudeau<sup>1</sup> and Ronald Altig<sup>2</sup>**

<sup>1</sup>*Institute for Imaging and Analytical Technologies, Mississippi State University, Mississippi State, MS 39762, USA*

<sup>2</sup>*Department of Biological Sciences, Mississippi State University, Mississippi State, MS 39762, USA*

Correspondence should be addressed to Ronald Altig, [raltig@biology.msstate.edu](mailto:raltig@biology.msstate.edu)

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Colorations of anuran tadpoles surely function in many of the same ways that have been ascribed to color and pattern in other animals, but the paucity of data forces one to look to other groups to generate hypotheses. Such an action often occurs because of the difficulty of defining specific fitness parameters to larval forms. The commonly muted colorations of tadpoles are typically considered to function only in some form of crypsis, but we discuss other functions in the particular context of behavioral ecology and changes induced by various kinds of coinhabitants. We review the development, terminology, diversity, and functions of coloration in tadpoles and then pose various questions for future research. We strongly support a broad-based perspective that calls for an integration of several fields of research.

## 1. Introduction

The literature on coloration, the visual impression gained from color and pattern, is very incomplete for tadpoles, probably because colorations used in aggressive interactions, territorial maintenance, and species and sex recognition are presumed to be absent. Also, it seems that for many years we accepted ideas from major summaries [1] as intuitive fact. Studies of sexual selection, community ecology, and developmental genetics have changed the research landscape immensely. We are at least approaching a respectable understanding of the development, genetics, and evolution of coloration of several model organisms. Studies of the coloration of birds and fishes obviously sit near the top of the knowledge base, and the data on all larval amphibians certainly sits near the bottom.

After we review the formation and ontogeny, diversity, and functions of the colorations of tadpoles, we discuss possible ways to use larval coloration to better understand several facets of the behavioral ecology of tadpoles. The potential ramifications of inducible changes in coloration that are stimulated by coinhabiting competitors and predators [2] are a major focus. One must use various surrogates

of fitness in evaluating larval forms, and we attempted to supply information and identify questions more than supplying answers [3]. These authors rightfully warn that an “uncritical interpretation of supposedly adaptive features presents dangers of properties being mistaken for function...” Another pertinent comment [4] was “I have assumed that eyespots have a function but do not wish to be so adamantly adaptationist as to suggest that we ignore the null hypothesis that eyespots are not adaptive and currently have no function.” There is much to be learned about intra- and interspecific differences in the ecobehavior of anuran larvae, and the recognition of an increase in the relevance of coloration in the interpretations of such studies is surely warranted.

Other than descriptive and typically speculative notes, actual tests of the functions, including crypsis via several means, thermoregulation, ultraviolet protection, and modifications of social interactions of those taxa that aggregate, of coloration of larvae [5] are rare; survival rates of larvae are often quite low and in most reproductive modes, large numbers of offspring are produced. The probable occurrences of many behavioral and social components have not been investigated. Fitness components throughout the amphibian

biphasic life cycle have obvious underpinnings long before the actual consequences of a breeding event. Surrogates of larval fitness include size at stage, survivorship, growth, time to metamorphosis, and size at metamorphosis; vulnerability [6, 7], viability, or especially various measures of energetics through developmental stages [8, 9] and coloration might be more immediately productive concepts. Various facets of coloration may be viable indicators of fitness if we understood the ecobehavioral aspects of tadpole biology more completely.

There are summaries of coloration in adult frogs [10] and a few tadpoles [11], but attempts to integrate the ecobehavioral and coloration of tadpoles are lacking. We emphasize ecobehavioral and phylogenetic correlations, and the large databases involving biochemical, endocrinological, and immunological [12] factors that are surely very influential are not included. The visual perception of infrared [13, 14] and ultraviolet [15–22] wavelengths was not addressed. Amphibian larvae can use polarized patterns of light at least for orientation [23].

## 2. Development and Genetics

The neural crest is an ectodermal derivative of all of vertebrate embryos that gives rise to cells of the cranial facial structures, paraendocrine system, peripheral nervous system, enteric ganglia, and all pigment cells. Unlike the single type of pigment cell in mammals, amphibians have melanophores (containing melanin that produce browns and blacks), xanthophores (lipophores of older literature, containing purine and pteridine pigments like drosoperin and sepiapterin [24] and carotenoids [25] that produce yellows and oranges), and iridophores (guanophores of older literature, containing crystalline purines that produce structure colors of various types). The pigment-containing organelles found in each of these cell types are melanosomes, pterinosomes, and reflecting platelets [26]. Cells giving rise to these three lineages are assumed to contain primordial vesicles originating from the endoplasmic reticulum that become the various pigment-containing organelles [27]. Unlike mammalian pigment cells, which deposit pigment-containing organelles into keratinocytes of the skin and hair follicles, amphibian pigment cells retain the pigment-containing organelles, and the ability of the organelles to be rearranged within the cells allows metachrosis (i.e., change color and pattern). We do not include details of carotenoids, which must be sequestered from the environment and serve many other functions besides color [28, 29]. Although amphibian chromatophores are found in both the epidermis and the dermis, it is primarily the dermal chromatophores that produce the colors and patterns among different stages and taxa [30]. Melanin deposited in the animal pole of an ovum by the mother during oogenesis does not contribute to larval pigmentation.

Presumptive neural crest cells are detectable within the neural folds prior to the closure of the neural folds. These cells form a wedge-shaped ridge or crest in the neuroepithelium along the dorsal midline. The crest remains intact a relatively short time before the cells migrate to

various locations throughout the embryo and differentiate into the cell types noted above. In general, amphibian trunk neural crest cells migrate between the neural tube and somites and give rise to such cells as the paraendocrine system and the enteric ganglia. Other trunk neural crest cells migrate dorsolaterally between the epidermis and somites and give rise to most pigment cells of the body [31, 32]. Some crest-derived pigment cells that migrate medially end up in the coverings of the body cavity and viscera.

Morphogenesis, migration, and differentiation of neural crest derivatives are dependent on interactions of the cell/extracellular matrix, cell/cell, and cell/diffusible factors. Classical studies suggest a significant role played by the extracellular matrix (ECM) in the timing of dispersal, direction of migration, and differentiation of neural crest cells [33–36]. Somites, the lateral line, other neural crest cells, and other pigment cell types can influence neural crest cell activities through physical interference or cell signaling events. Pigment cell interactions contribute to the barred, banded, and striped patterns seen in many amphibian larvae [31, 33, 36, 37]. Sorting [38] and differential adhesion of specific pigment cell types [39] are also influential. The influence of cell/diffusible factor interactions in dispersal of neural crest cells or aggregation of pigment cells during early patterning events is implied in some studies [35, 39–41].

In general, differentiation of pigment cells occurs after-chromoblast (i.e., pigment cell precursors) reach their destinations in the embryo, and melanophores disperse away from the neural tube and differentiate before other pigment cell types. Xanthophores begin to differentiate shortly after the melanophores and the iridophores differentiate significantly later [26]. Melanophores and xanthophores are primarily responsible for pigment patterns seen shortly after hatching [35]. The three primary populations of chromatophores eventually become arranged in (a) chromatophore unit ([30, 42]; Figures 1(a)–1(d)). Melanophores positioned at the base of the chromatophore unit have dendritic processes that extend upwards through layers of xanthophores and iridophores and often travel along the underside of the epidermis.

Collectively, it is the deposition and quantity of pigment, the arrangement of pigment organelles within the cells, and the quantity and arrangement of the different pigment cell types in the skin that result in the observed coloration. A larger quantity of pigment per organelle or organelles per cell results in a higher intensity of black or yellow in a melanophore or xanthophore, respectively. Melanosomes of melanophores and pterinosomes of xanthophores can aggregate to the cell body or disperse radially by means of microtubules [43] when stimulated by melanocyte stimulating hormone, epinephrine, or melatonin [27]. Reflective platelets do not aggregate or disperse, but they do contribute to structural colors and pattern by reorienting within the iridophores [44]. Structural colors [45] are produced by refraction of incident light and selective absorption based on the orientation of reflective platelets and the disposition of other adjacent chromatophores. For example, green in amphibians usually is a structural color, although the green in centrolenids and some hylids is pigmentary [46]. Green

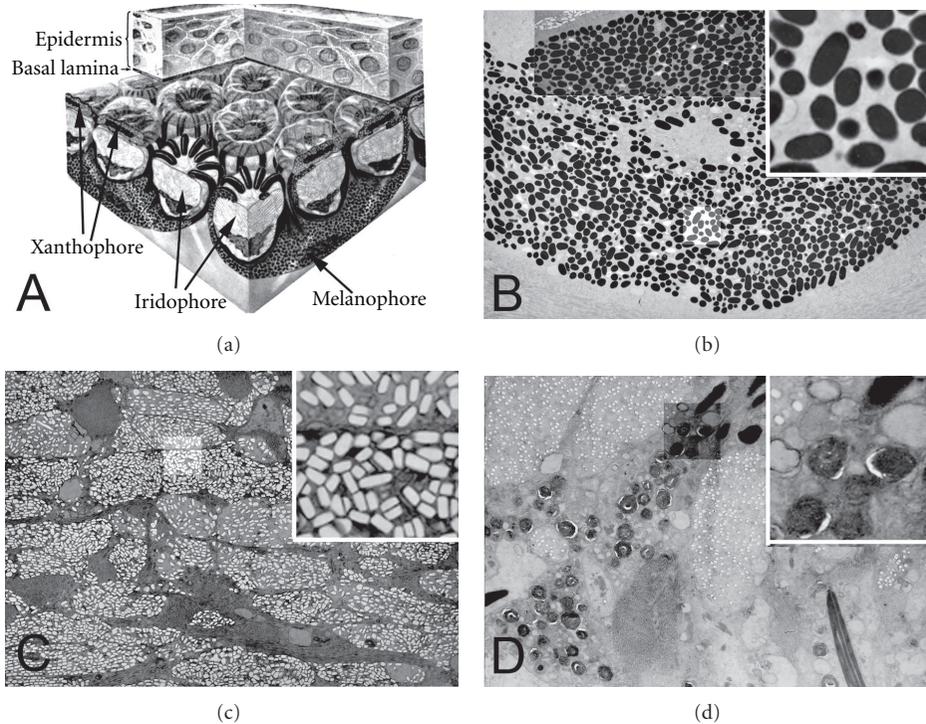


FIGURE 1: (a) The chromatophore unit, modified from [30], composed of layers of melanophores, iridophores, and xanthophores, that provides the basis for color, pattern, and metachrosis in amphibians. Transmitting electron photomicrographs of pigment-containing organelles in (b) melanophores (melanin granules in a melanosome; part of darkened area in upper left enlarged in inset), (c) iridophores (guanine reflecting platelets, part of lightened area in center enlarged in inset), and (d) xanthophores (carotenoids in pterinosomes, darkened area in upper center enlarged in inset).

color in larvae is relatively rare, is seldom bright [47], and typically appears late in ontogeny even in tadpoles that metamorphose into green frogs. Carotenoids as pigments in larval amphibians have not been studied extensively but seem to be important components of induced color changes. Examples of pigmentation that result from carotenoids occur in the fins of some North American *Hyla* [2], the *Dendropsophus minuta* group of South America, and *Hemisus* of Africa. All these tadpoles have lateral eyes, tall fins, and compressed bodies and spend considerable time in midwater. An alternate color is presented if all three populations of chromatophores are not present. For example, if xanthophores are either absent or nonpigmented, a normally green frog is blue [48–50]. A number of pigment mutations exist in amphibians, and because eye and body pigmentation are controlled by different genetic systems, individuals with normal eye color and altered body color do occur.

During early stages of development, the distribution of melanophores seems to be closely regulated to produce fixed numbers of cells in definite subepidermal positions [51]. Later in development, the distribution of pigment cells is less precise and melanophores can be found in such locations as spinal ganglia, peritoneum, and gut. Populations of neural crest stem cells likely remain within the skin and differentiate at later larval stages, during metamorphosis, or throughout adult life [26, 36, 37, 52]. This accounts for the often dramatic changes in coloration during and

after metamorphosis. Cell migration and restructuring of the skin at this time is certainly influenced by endocrine changes associated with metamorphosis. Consistent with the metamorphic effects triggered by thyroid hormones, the ECM is reorganized, and specific pigment cell types are surely affected.

Patterns are produced by differential migrations of the various chromatophores. Using melanophores as the simplest example, imagine two cell populations residing near the midline of an early embryo. Cells of the first population start to migrate laterally and ventrally, and because some stop at various places, a uniformly dark color is produced. All stop at some specific ventrolateral plane and thus delimit the darker dorsal and lateral coloration from the paler venter. The boundary is distinct if no cells migrate beyond one specific plane or diffuse if diminishing numbers of cells stop at various distances. Conversely, no cells of the second population stop until they are beyond the first migration boundary so that a dark dorsum, a lateral pale stripe, and a ventrolateral dark area are results. Iridophores and xanthophores migrate similarly. Regenerated parts of tails typically have a modified coloration [53] with smaller, more numerous contrasting marks than in the original tail, or such marks may be absent.

Other commonly used terms include “leucophore” (i.e., an iridophore that produces white) and “erythrophore” (i.e., a xanthophore that produces red). In addition, there are

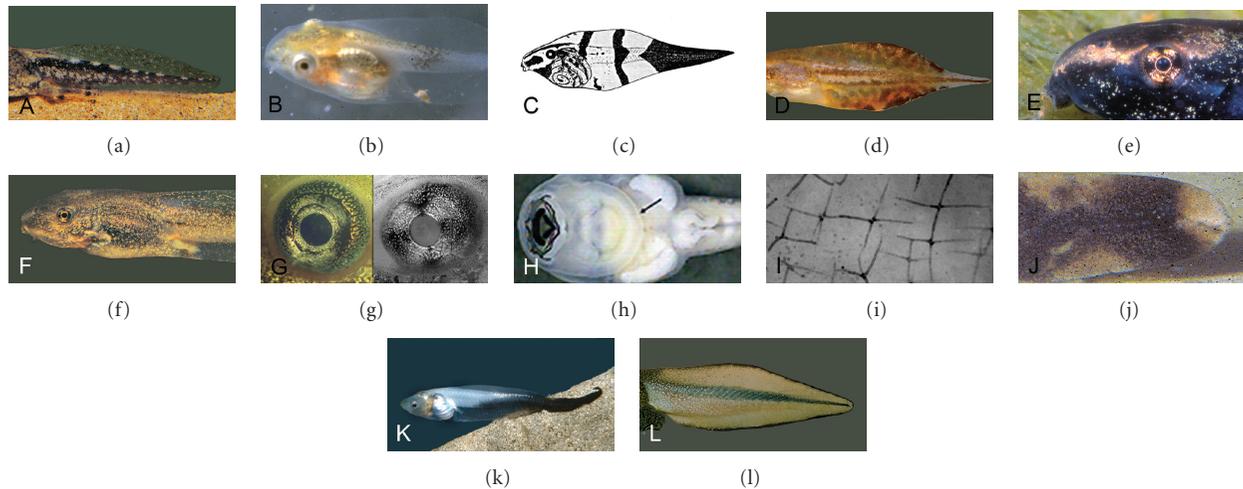


FIGURE 2: Illustrations of color and pattern of anuran tadpoles: (a) pale bands on the tail of the tadpole of *Incilius nebulifer*, Bufonidae, (b) single dark band on tail of young tadpole of *Hyla gratiosa*, Hylidae, (c) barred pattern of young tadpole of *Pseudis paradoxa*, Hylidae, modified from [72], (d) striped tail of *Hyla femoralis*, Hylidae, (e) eye line of *Hyla avivoca*, Hylidae, (f) lip line of *Lithobates sylvaticus*, Ranidae, (g) iridial patterns of (left) *Hyla chrysoscelis*, Hylidae and (right) *Amietia vertebralis*, Pyxicephalidae; photo: E. D. Van Dijk, (h) abdominal sucker (arrow) bordered by large integumentary glands of *Amolops* sp., Ranidae, (i) melanophores of *Bombina orientalis*, Bombinatoridae, arranged in a net pattern, (j) eyespot at the tail tip of *Ascaphus truei*, Leiopelmatidae, (k) white body, silver peritoneum, and black tail of *Calluella guttulata*, Microhylidae, and (l) tail fin rimmed with black and fins frosty white in *Lithobates hecksheri*, Ranidae.

other types of chromatophores with unique pigments that are seemingly restricted to specific taxa [14, 54]. Reviews of many of the classical studies of pigment pattern development in amphibians have been written [34–36, 55–58]. Although chromatophores in the amphibian integument end up in both the epidermis and the dermis, it is primarily the dermal chromatophores that are responsible for the specific pigment patterns.

Studies of the biochemistry and cellular mechanisms of pigmentation usually do not offer information needed to understand the influence of coloration on behavioral ecology. Also, the genetics of coloration stems primarily from research on normal and mutant adult individuals of model species (e.g., Caudata: *Ambystoma mexicanum* [59]; Anura: *Bombina orientalis* [60]; *Lithobates pipiens* “burnsi” and *L. pipiens* “kandyohi” [61]). As is so often the case, the use of models stems from the ease of laboratory propagation and not necessarily from the most interesting cases of coloration. Also, these studies usually involve only adult colorations. There are discussions of genetic analysis of an aposematic pattern [62] and the genetics of adaptive coloration in reptiles [63]. The tail bands of *Ambystoma mexicanum* do not coincide with the distribution of the myotomic musculature [64].

Laboratory hybridizations were usually done to reveal genetic relationships among taxa and not for the examination of specific traits, especially color, but some basic ideas can be extracted from studies that include larvae. Tadpoles of *Incilius nebulifer* have a banded tail muscle (Figure 2(a)), and hybrids involving *I. nebulifer*, *Anaxyrus americanus*, and *A. terrestris*, both of the latter with uniformly pigmented tail muscles [65], had nonbanded tail muscles. F<sub>1</sub> tadpoles from crosses of various hylids always had the pattern of one

or the other parent [66]. With the likelihood that sufficient F<sub>1</sub> crosses, let alone the more informative later generations, will ever be made, the information content of embryo and hatchling colorations needs more attention so that we have at least some understanding of the initial development and diversity. The banding in cyprinid fishes resulted from a monogenic, recessive autosomal gene [67–69]. Various genetic mechanisms have been noted in coloration of frogs [70], and evaluations of sequential changes in pattern and color [71] would be helpful.

The energetic costs of producing coloration have not been well studied [73]. One must first distinguish between those pigments that are manufactured versus those that are sequestered. Different pigment types (e.g., melanins, pteridines) and the two classes of melanins (eumelanin, pheomelanin) may differ in costs of production; melanins may have evolved first in response to their antioxidant properties [74, 75] and only secondarily provided body color.

### 3. Terminology and Functions

Pattern descriptors do not enjoy a standardized terminology that can be used for organisms of different shapes [76], and we use the various terms as follows. A band, limited to the body and tail musculature, is a pale transverse, symmetrical pattern within a dark field or vice versa that crosses the sagittal plane and often occurs in a series (Figure 2(a)). A single band at midbody is not uncommon in tadpoles, but the single dark band midway along the dorsum of the tail muscle of small *Hyla gratiosa* (Figure 2(b)) is a rarity. *Phasmahyla cruzi* [77] has a white band on the dorsum of the dark tail muscle at about three-quarters of the tail length. Bands are formed during early embryology [65, 78], and

most banded embryos and hatchlings lose the pattern as they grow. Tail bands remain throughout ontogeny in *Acris* spp. and a number of other hylids. *Lysapus limellus* [47] has a definite band near the tail:body junction, another less distinct band at about midtail, and a terminal black tail tip.

A bar [79], often extending the height of both fins, extends perpendicular to the longitudinal axis and may or may not cross the sagittal plane or be matched uniformly with a bar on the other side (e.g., *Litoria micromembrana* [11]; small *Pseudis paradoxus* [72]; Figure 2(c)). The single tail spot (semibar of [80]) of *Hysiboas hutchinsi* [81]) is likely an abbreviated bar, and a black tail tip is actually a bar with only an anterior boundary. The number of bars increases by additions on both the anterior and posterior end of a series in centrarchid fishes [79], but it appears that the number of bars and bands is fixed during early development in amphibians.

A stripe is a longitudinal or diagonal (e.g., naris to eye in many hylids, diagonal body stripe) contrasting mark on the body or tail (Figure 2(d)). Stripes may be restricted to the tail or extend from the naris onto the tail, and, as with a band, may be formed from the presence or absence of pigment in surface tissue or deeper layers. The juncture of dorsal dark pigmentation and ventral pale pigmentation on the body or on a bicolored tail muscle (i.e., dark dorsally, pale ventrally in lateral view) is not considered a stripe because there is only one delimiting margin.

Other common descriptors of patterns are less distinct and apply to larger surfaces of the body. These appear disorderly and are defined much more subjectively: blotched—multiple haphazardly shaped spots, usually relatively large; dotted—a small spot, usually with discrete borders; marbled—similar to mottled but more likely to produce a random circuitry of marks, as if swirled; mottled, dappled or variegated—random markings of different darker and paler shades; speckled or flecked—similar to dotted but many small marks involved whether randomly or uniformly arranged; spotted—sizeable contrasting marks, often approximately circular with reasonably discrete boundaries; and unicolored—grossly appearing one color. The impressions of all such patterns sometimes change when viewed at different magnifications and may change ontogenetically.

The various functions for eye lines (i.e., pale or dark lines extending through the eye; Figure 2(e)) include camouflaging the eye, protecting the eye from glare, and serving as sighting line during feeding [82, 83]. Lip lines (Figure 2(f)) extend from near the snout posteriorly below the eye. Isolated pale spots may occur on the snout of *Polypedates leucomystax* [84] or between the eyes (*Microhyla heymonsi* [85]). Irises [86, 87] have metallic colors (Figure 2(g)) in several notable patterns when viewed in living individuals; like other patterns produced by iridophores, these pigments disappear in preservatives. A common pattern among several families produces a pupillary rim and patches in the ciliary zone that produces a cross with the pupil at the center. Large tadpoles of *Hyla gratiosa* often have a uniformly silver iris, and those of *Lithobates heckscheri* and some hylids have a red iris. Subtle patterns of corneal pigmentation and iridial projections ([88], elygium and umbraculum) that are presumed to protect the eye from downwelling light have not

been studied sufficiently to know the taxonomic distribution. Eye size is an associated feature that has not been studied [89–91]. Nektonic forms have large, protrusive eyes that are usually positioned more laterally than benthic forms with smaller, dorsal eyes. The most protrusive and proportionally largest eyes occur in several convergent, semiterrestrial tadpoles in South America (*Thoropa*, Cycloramphidae), Africa (*Petropedetes*, Petropedetidae), and Sri Lanka (*Nannophrys*, Dicroglossidae).

Our preliminary observations of pieces of preserved skin with bright-field, dark-field, and polarized lighting suggest differences in the perceived structure of melanophores that would be useful in identification of larval amphibians; a classification of chromatophore shapes [92] is a useful guide. For example, the arrangement of the melanophores that form the dots on the dorsum of tadpoles of *Lithobates catesbeianus* and *L. clamitans* (Ranidae) differs in spatial orientation. The ornate melanophores of *Gastrophryne* (Microhylidae) tadpoles are foliose. Many neotropical, stream-inhabiting hylid tadpoles have rodular melanophores arranged in bundles of 4–8 cells arranged at 90° to each other. The melanophores of bombinatorid and discoglossid tadpoles are arranged like a net (Figure 2(i)).

Talking about the functions of coloration in amphibian larvae is almost entirely supposition based on substantiated cases in other taxa, and often the best we can do is recognize the habitats or other circumstances in which specific patterns occur. Coloration likely involves both intra- and interspecific functions, but with our present understanding of behavioral ecology of tadpoles, detecting and deciphering these conditions are difficult. Even so, the fact that larval coloration surely functions differently than that of the adults in most cases seems real, and it must be kept in mind that a given coloration may serve more than one function [80]. Finding circumstances where the coloration and associated behaviors are decoupled may be a productive venture [93]. Also, predators view [94] larvae with optical systems of specific abilities and in water. Thermoregulation may play a role in ecobehavior and color at times, but lying near the surface on top of dense vegetation or in shallow water may also be an escape from low oxygen tensions. In any case, seeking warmer water [95] surely takes precedence over the actual effects of coloration on the body temperature. Correlations of pattern with habitat (e.g., bars in structurally complex habitats and stripes in piscivorous fishes and those that shoal [96–98]) present interesting research questions. Most macrocarnivorous tadpoles (e.g., Ceratophryidae: *Lepidobatrachus*; Scaphiopodidae: *Spea*) are unicolored.

Only some of the suggested functions [99–101] of eyespots pertain to nonreproductive larvae (e.g., attack displacement to more dispensable parts of the body). It could be argued that a black tail tip (e.g., *Acris*, Hylidae [5], some hyperoliid *Hyperolius*, and the microhylid *Calluella*) functions as an eyespot. An eyespot occurs on the tail tip of *Ascaphus truei* (Figure 2(j)) at some sites, and because these tadpoles adhere to rocks in fast flowing water, these tadpoles may be expected to be attacked from the rear most often [102]. The bright yellow torus-shaped marks on the sides of

the tail muscle of the social tadpoles of *Clinotarsus alticola* form the impression of an iris and pupil and sometimes increase in number with the size of the tadpole. Does the single band in small tadpoles of *Hyla gratiosa* and the single, abbreviated bands of *Hypsiboas hutchinsi* [81] and *Atelopus mittermeieri* [103] act as eyespots? The frequency of tail damage [104] indicates that this motile structure is a common predatory target. Aposematism in larval amphibians has been suggested but never tested specifically (see [105]), and judgements have been assumed based on the presence of contrasty colorations of individuals that are either toxic or noxious (*Anaxyrus* [106]; *Hypsiboas geographicus* [107]; *Phrynobatrachus maculiventris* [108]). Integumentary glands that produce either toxic or noxious secretions likely occur throughout the skin of most tadpoles, but large, multicellular glands are less common (Figure 2(h)). These occur behind the eye, dorsolaterally and ventrolaterally on the body and elsewhere, and often these glands are contrasty in color and texture relative to the local surfaces.

Discussions of reflectivity [109–113] and transparency [114–118] as methods of crypsis have been addressed in larval amphibians. Rhinophrynid, pipid and some Old World microhylid tadpoles range from white to transparent, and the body and basal part of the tail of the tadpoles of *Calluella* are white to transparent relative to the long, black tail (Figure 2 (k)). Tadpoles of *Scaphiophryne* (Microhylidae) are amazingly transparent and have large, fluid-filled lymph sinuses between the skin and body tissue [119]. Fins of many species are often transparent and commonly have contrasty dark marks that appear isolated in space. Discussions of transparency have to address the whole body versus parts of bodies or patterns, but outline disruption seems like the most likely functions; tadpoles that have such coloration often remain stationary for long periods in midwater. Various other forms of crypsis are commonly assumed to represent background matching, but countershading (i.e., dark dorsum and pale venter [120, 121]) and disruptive of the body shape or edges must be incorporated into the concept; crypsis is a particular concept that would benefit from quantitative rather than qualitative evaluations [122]. Behavioral changes associated with ontogenetic color changes are known in only a few cases, but many more will likely be found. Some form of sociality is often involved in the behavioral changes. A number of studies with distinctly different motives show that tadpoles can preferentially recognize and associate with others of their own species, siblings, or half-siblings [123, 124], but the terms that describe these associations are vague and often ill defined because we do not know the functions involved or the reaction stimuli. There is a huge database on schooling in fishes, but perhaps no tadpoles congregate in the same contexts. To understand the potential function of a group and the benefits to its members, one needs to gather at least the following information: single or uncommonly multiple species [125, 126], age or size distributions, group including single or multiple sibships, individuals maintaining position independent of but in response to others, group polarized (individuals somehow aligned and oriented) or not, group mobile or stationary and group occurring on the bottom,

in midwater, or at the surface. Potential functions (e.g., predator avoidance, feeding, and seeking amiable microenvironments) are diverse, and several of the traits suggest some form of sociality [127]. Ontogenetic behavioral changes, sometimes associated with differences in color, have been noted.

#### 4. Diversity and Ontogeny

A general pattern of morphological diversity among larval anurans has been recognized for a number of different structures (e.g., diversity of labial tooth rows [128]; diversity of labial tooth morphology [129]). A large morphospace of relative commonality that encompasses taxa from across the order in many habitats and geographic regions is accompanied by novelties of various kinds at various points. Taxonomic and ecological distributions of coloration are surely similar, and potential reasons for the large area of commonality and the novelties both beg for answers. For example, the average ranid tadpole has a somber, mottled coloration, but *Lithobates hecksheri* has a golden body band and a black rim around an opaque white fin (Figure 2(1)). Tadpoles of the 18 species of *Pseudacris* are typically somber, but those of *P. brimleyi* and *P. ocularis* are prominently striped. The average bufonid tadpole is uniformly dark with no or minor patterning, but the torrent-dwelling tadpoles of the Asian *Ansonia* [130] and neotropical *Atelopus* include some taxa that are uniformly colored and some that are brightly banded. All centrolenid tadpoles [131, 132], burrowers in leaf mats of mountain streams, are nearly uniformly white, tan or red; the ranid tadpole of *Staurois natator* is similar in coloration and behavior. There are often specific patterns in hatchlings that may be retained throughout larval life or modified in later stages. Metamorphs commonly but not always (e.g., some hylids) have a similar coloration as the adults. All references to stage that follow are based on the table by Gosner [133].

In general, larger, darker, more contrasty, or complex colorations develop with increases in body size, especially in the tail fins. The single tail band of *Hyla gratiosa* tadpoles that develops embryologically [134] either disappears or becomes incorporated into the uniform tail pattern of older tadpoles. Also, clear fins of younger individuals of *H. gratiosa* become populated with melanophores near the base that do not dilate at night, and the melanophores in the distal two-thirds of the tail dilate to jet black at night (also [135]; phyllomedusine hylids; [136]; *Xenopus*; [137]). Small tadpoles of *Lithobates hecksheri* have uniformly jet black bodies with a bright golden band at midbody, a tail muscle that is black dorsally, and clear fins. By the time the tadpole reaches about 25 mm total length, an intensely black rim starts to form around the fins, and the remainder of the fin becomes translucent, frosty white. Young tadpoles of *Lithobates grylio* and *L. virgatipes* are patterned similar to *L. hecksheri* but less contrasty, and the diagnostic line of dots in the dorsal fins of these two species does not develop until about stage 28. The bands of small tadpoles of *Dendropsophus berthalutzae* [138] become connected as a large, haphazard blotch in larger tadpoles. Metamorphs that have a discrete metamorphic pattern attain

the adult pattern before sexual maturity is attained (e.g., some *Gastrotheca*, some mantellids).

Variation in ventral coloration, whether transparent in younger stages or uniformly pale in older individuals, is much less diverse than are dorsal colorations and may vary with stage or life history. For example, the pale bellies [121] of tadpoles of *Lithobates chiricahuensis* have few melanophores while those of adults are densely populated with melanophores [139]. Microhylid tadpoles (e.g., *Dasylops schirchi* [140]; *Gastrophryne carolinensis*) are quiescent, midwater suspension feeders at night; they commonly have bellies that are crudely striped or mottled. Some megophryid (e.g., *Megophrys*, quiescent, surface film feeders in streams during the day) tadpoles have ornately banded bellies. We tend to notice the black markings, but it is likely the pale markings that break up the body outline when viewed from below against the brightness of the surface.

Because of its mode of development [141], the back of the oral disc usually is pigmented uniformly like the adjacent body surfaces but usually lacks iridophores. The oral (outer) face of the oral disc is typically translucent and nonpigmented. Both surfaces of the oral flaps of microhylids are pigmented. The spiracle(s), nares, and neuromasts sometimes influence pattern. Pigment in the nasal sac that is often visible through the skin gives the impression that the nares are more darkly pigmented than the surrounding surface. Structural ornamentations of the narial aperture (e.g., megophryids, [142]) vary widely and change ontogenetically, and some of these structures contrast with the local color. The viscera of larval amphibians [143] are usually not pigmented or at least not until late in ontogeny [144–146]. Even then, the melanophores associated with the viscera are usually sparse and respond to stimuli much more slowly than do the integumentary chromatophores. A classification of viscera pigmentation of adult frogs [147] could be easily adapted for use with larvae. Melanophores in tadpole tails may be photoreceptive [137]. The amount of visceral pigmentation may correlate with body color [148], and various functions or at least correlations (e.g., gonad protection [149]) have been suggested for visceral pigmentation. Diet can affect the color of frogs [60], and even though similar responses are expected in larvae, no one has made the pertinent observations. The causes of common pale versus dark individuals among cultured tadpoles [150], as if some have aggregated melanosomes and some have dispersed ones under the same conditions, are not known.

## 5. Inducible Changes in Coloration

The potential ramifications of inducible changes in coloration was a primary concept that stimulated the writing of this paper. We propose that with the addition of the correct data, we could use ontogenetic changes [151] and those colorations that are inducible as a predictor of larval fitness; the use of coloration as an indicator of fitness is a common theme in other animals but has never been applied to larval amphibians.

Differences in coloration of tadpoles of the same species from adjacent ponds is often obvious to the casual observer,

and until recently, these differences were assumed to be caused by light regimes, turbidity, and tannin content; animals from turbid pools are pale to almost albinistic in appearance, and those from clear to tannin-stained waters are much more brightly colored. Also, colors are usually more brilliant or contrasty during the day and paler at night. Sometimes specific parts of the body and melanophores of specific shapes may produce different patterns (e.g., *Hyla gratiosa*; [137]).

Inducible reactions, including morphological, behavioral, and biochemical responses, have been shown in many organisms, and after early studies of tadpoles [2, 152], a whole new variable in our understanding of coloration, morphology and ecology came to light. Variations in color and pattern result from the presence of predators and competitors. The effects of shape changes on pattern in larvae [153] have not been examined. The most notable fact of the known inducible color changes is that the inducible responses vary among individuals. We suggest that the significance of this variation has not been fully realized.

Tadpoles with modified colors and shapes perform better in a predatory encounter, but we suggest that this is just a minor indication of the potential fitness of these individuals. We need to know something about the breeding adults [154] that are derived from tadpoles that respond differently to inducible stimuli. The survival of a tadpole and the attainment of metamorphosis is a viable fitness signal, but in fact these features are rather uninformative stations relative to the overall goal of reproduction [155]. As difficult as it would be to conduct the experiment, we would be much further ahead if we had even the slightest indication of whether a tadpole judged to be ecologically robust at any given moment in its ontogeny has a better chance to grow into a fecund adult than a tadpole in its cohort that is judged to be less robust. That is, how well do the qualities of individual larvae indicate eventual fitness responses? Discussing the various options, let alone actually doing such an experiment, would be very lengthy, but we suggest that the ultimate experiment should be done on field populations to avoid the many limitations imposed by any laboratory test. Studies based on naturalistic mesocosms are a more feasible option, but we question if proper mesocosms can be prepared and replicated. In either case, a benign, long-lasting mark [156] of many previously evaluated tadpoles would be required to guarantee that at least a few individuals with a known ontogenetic and ecological history would be encountered as breeding adults.

To state the premise in another way, are the tadpoles that produce either the most vivid colors or the largest area of such colors under specific test circumstances likely to have higher adult fitness than those that respond minimally? Various ecobehavioral and genetic correlations seem possible (e.g., differential exposure to inducing stimulus because of differences in individual behavioral traits or differential acquisition of carotenoids). For example, do variations in innate behavior within a species and the duration of a given stimulus and its spatial sphere [157] influence the degree of induction? Are individuals that shun social contact somewhat exempt from the inducing stimuli? Behavioral

differences among species only amplify this idea. Also, most interesting to this discussion, genotypic responses related to individual quality are surely at play. Might we find exciting correlations with coloration if we tested for individual differences in aggression and stress responses [158, 159], competitive ability, foraging skills, disease resistance, and particularly immune responses [160–163]? In summary, we suggest that looking at trait changes among individuals in experiments of inducible mechanisms would be as or more productive than looking at species responses.

Does the ability to be induced vary geographically or intraspecifically, and if so, what does this say about the functions of color? For example, the variations between *Hyla chrysoscelis* tadpoles from North Carolina [2] and those from Mississippi (R.A., unpublished data) are distinct. In North Carolina the tadpoles were collected from permanent ponds, and these animals typically responded with a profound but variable color change in the presence of predators. In Mississippi this species most commonly breeds in temporary pools, and in over 35 years of general observations by the second author, the slightest hint of an orange color in the fins has been observed only four times. Potential differences in these responses range from genetics of the tadpoles to differences in the habitats (e.g., relative amounts and available carotenoids) to differences in coinhabitants. Also, at least the tadpoles in Mississippi are quite aggressive to intraspecific and heterospecific individuals with very obvious individual variations (R.A., unpublished data). Are aggressive individuals also the ones who might experience the most inducible color? Might the aggression representative of specific genotypes of tadpoles also be manifested in various behaviors of the adults (e.g., territoriality, diurnal retreat protection, calling station maintenance, and feeding and breeding success)? Being able to properly formulate better definitions of fitness components throughout the amphibian biphasic life cycle would be very informative. As an ancillary note, almost all studies of induced morphology has been done on bufonid, hylid, and ranid tadpoles of the northern hemisphere; photos of *Microhyla butleri* [164, 165] show the first microhylid tadpole with probable induced red color in the fins that we have seen. The tadpole of *Litoria aurifera* (Hylidae, [166]) may show considerable red color in the distal part of the tail, and this is an uncommon feature of stream-dwelling tadpoles.

Are stream tadpoles subject to the same kinds and degrees of inducible changes as pond forms? Because of the constraints of maintaining position in fast-flowing water, these kinds of tadpoles may be less plastic. Is coloration of those tadpoles that aggregate or are tended to by a parent less likely to be inducible? What about tadpoles that are known to or seem to have chemical defenses? Social species often are contrasty even if unicolored dark (e.g., *Schismaderma carens*, “*Bufo*”), uniformly bright (*Phyllomedusa vaillanti*), or boldly patterned (e.g., *Lithobates heckscheri*, *Clinotarsus alticola*). Knowing species-specific and individual temperaments that probably have a genetic basis would be helpful, and this idea certainly extends to interspecific comparisons. Also, the carnivore: omnivore scenario in some scaphiopodid tadpoles [167] is another case where unnoticed behavioral differences

surely exist; oddly, the huge morphological changes [168] in these species are not accompanied by notable color changes. Imagine a mixed population of equal numbers of several tadpoles that are not suspected of being strong competitors based on morphology or spatial usages (e.g., *Hyla*, pelagic rasper; *Lithobates*, benthic, rasper; *Gastrophryne*, midwater suspension feeder) and predators are absent. If there are induced changes in any members of this hypothetical community, one has to ask what the competitive factor might be. To what degree can tadpoles of different ecomorphological types function as competitors?

With all known and suspected influences on coloration, discussing geographic variation per se (i.e., genotypic differences in strict response to abiotic factors [169] is either difficult or impossible. The few studies that claim to address geographic variation of larvae [170, 171] likely represent actual responses to different kinds or degrees of induced changes. Larvae do learn substrates [172–175], and commonly seen variations are likely responses to substrate color that would change in relation to a new substrate or lighting regime. Tadpoles of *Lithobates grylio* and *R. virgatipes* have a single row of longitudinal dots in the dorsal fin; some tadpoles (e.g., *Lithobates clamitans* from northeastern United States) have such a pattern that has not been noticed elsewhere. Considerable geographic variation exists in general coloration (e.g., ground color yellow, mottled to black; presence and completeness of the eyespot on the tail tip *Ascaphus truei*). Perhaps an actual analysis as with centrachid fishes [79] would resolve what appear to be inexplicable differences, but at least a first glance, and assuming some similarities in the developmental genetics of coloration, the feasibility of such a study with tadpoles would often seem to have some large hurdles to cross. Is absolute size of a tadpole ever a constraint on color or pattern (e.g., banded tail muscles of members of the diminutive members of the *Anaxyrus debilis* group and hatchlings in some hylids)? Finally, do the appearance of similar colorations in disparate taxa indicate a common selective influence [176]?

## 6. Discussion

For obvious reasons, the study of the evolution of coloration has been largely focused on sexual and species traits of reproductive individuals, and many facets of the behavioral ecology of amphibian larvae are poorly known. For example, of the many studies that examine competitive outcomes among various combinations of species [177], behavioral factors are essentially never suggested as contributing to which species wins. In this light, this discussion is a synthesis of circumstances and queries that need to be addressed to enhance our understanding of many interrelated subjects of amphibian larval biology.

It is obvious that individuals and species vary in temperament, and it seems that we should make a controlled adjustment to our phobia of anthropomorphisms so that we can describe and talk about behavioral differences more easily with our human lexicon. We say “innate behavioral differences” to avoid sounding anthropomorphic, but this is quite uninformative. Some might cringe at “tadpole bullies”

[178] and “fishes acting recklessly” [179], but lengthy similes are annoying. We could do fine if we keep our notions in the realm of fitness and avoid descriptors that require empathy or an ability to project into the future. With such caution, we can more accurately evaluate and describe species and individuals behaviorally. For example, fish culturalists [180] strive to understand variations in behavior, growth, and survival so as to maximize production, and judgements of temperament are common. Many kinds of data that these researchers have are not available for amphibians.

Most larval and adult amphibians deposit most of their stored energy reserves in discrete fat bodies attached to the anterior end of the kidney. These reserves are commonly measured relative to reproduction of adults [181], but equivalent data on larvae and metamorphs are not common [182]. Individual trout from three populations differed relative to trade-off situations involving predator cues and food [179]. Genetically more variable fishes showed more risk-prone behavior. Having this kind of information on amphibian larvae would propel our thinking forward a great deal [183–186]. Individual and interspecific differences in coloration and behavior related to genotype and hormones have bases in a number of research areas. Based on our own observations, there are behavioral features of tadpoles (e.g., overt aggression in nektonic hylids, passive aggression in ranids [178]; escape responses, tendencies to aggregate, and details of the part of the water column that is inhabited most commonly) that surely contribute to species interactions. Many of these factors involve some expression of sociality, and coloration is surely a factor to consider.

Not long ago [152] and relative to the numerous papers on the subject that have followed [187, 188], no one considered that coloration was inducible ontogenetically or that the strength and quality of certain signals involved in coloration were likely indicators of fitness. Variations were apparent, but mechanisms for this variation beyond the immediate environment were not suspected. It is likely for the present and for some time in the future that we will continue to consider a given larva typologically just to manage the wide diversity that is present, but in many ecobehavioral cases we need to change our perspectives. Speculations and subjective evaluations are often useful, but in absolutely all cases, we need a lot of additional data that is gathered very accurately. The amounts and kinds of variation and periods during which they occur during larval ontogeny are likely quite pervasive. By an extension of this progression of understanding, one can easily predict that there are numerous ontogenetic and interspecific aspects of the behavior, ecology, and effects of coloration on the biology of amphibian larvae that have gone unnoticed [189, 190]. The effects of aggressive intra- and interspecific interactions (RA, personal observations) that are not observable by casual observations and the causes, consequences, and dynamic structure of aggregations and schools are all fertile fields for research; coloration is a potential influence in all these cases, and understanding the presumed genotypic variations associated with these occurrences would be most exciting.

Phylogenetic [191, 192] and statistical [193–196] analyses of patterns are a great adjunct to the use of the

rather inexact descriptive terms. Patterns that are presumed to be random (e.g., mottling and spotting) may not be [197]; these studies would be particularly useful because the developmental processes involved often are unknown. The common banded patterns in fishes as a mean of camouflage via selection for background matching [198] without regarding the distinct possibility that the patterns are influenced by body shape [199, 200] need evaluation. Spectroradiometric quantifications [201] would improve or calibrate our subjective visual interpretations. Better understanding of hunting tactics and optical systems of various predators in and outside the water [202] would be helpful. In many respects, understanding the functions of coloration is actually an understanding of community structure and function.

Quantitative procedures for evaluating behavior are needed. Bailey et al. [203] generated an index of aggression for charr ( $I_A = \text{Agg}^+ / \text{Agg}^+ + \text{Agg}^-$  where  $+$  = bites given and  $-$  = bites received). This index and the amount of food consumed by individuals produced estimates of a given fish's fitness. Similar relationships involving activity, time spent feeding, location in water column, and coloration could be devised. A means of marking individuals during such tests will be required so their behavior can be correlated with growth and size at stage [158]. In summary, coloration is a potential means to evaluate the temperament of individuals and species.

Escape responses relative to color, site characteristics, sizes, and taxa are poorly known, and our understanding of the interactions of morphology, coloration, and characteristics of the site and relevant predators remain elusive. Tadpoles of *L. catesbeianus* often rest in shallow water near the bank and escape perpendicular to the bank; they often make a 90° turn at the end of such runs and wiggle into the substrate. Small tadpoles of *Hyla gratiosa* have a unique pattern that likely breaks up the body outline, and they remain motionless in stands of vegetation during the day and night. Larger tadpoles of the same species with a different color pattern, at least at night, hang at middle depths in open water. If touched from the top, they usually escape toward the bottom; if touched from the rear or below, they escape to other areas in midwater and momentarily swing vertically as they coast to a stop.

There are a number of brightly colored tadpoles or at least ones with contrasty patterns [166], and in some cases, there appears to be some correlation with sociality [204] and perhaps toxicity or noxiousness [205]. We know of no verified cases of mimicry among larval amphibians, and suppositions of aposematism need verification. We certainly do not understand the mechanisms of all behaviors that have been lumped under the concept of schooling [206, 207]. Crypsis by outline disruption seems like a viable option for some contrasty patterns, but sociality must also be considered. Tadpoles of *Lithobates heckscheri* change their schooling behavior with size. Small ones, with a clear, unmarked fin and bright gold band on a densely black body, maintain a stationary school which appears polarized. The group moves by short swim-and-coast sequences by small groups of individuals within the school. Larger individuals

form huge, mobile schools during the day travel long distances. At some sites, tadpoles of *Hyla andersonii* and *H. squirella* look as if they are gilded. What causes this color and what might be its function? Because the taxa and conditions that have been tested is small, we simply do not have a thorough understanding of all possible effects of the many factors that may influence coloration.

In summary, we must be cautious not to underestimate the functions of coloration or automatically assign them to the most handy classical function. At least in larval amphibians, we have a tendency to pass coloration off as functioning only in some form of crypsis or occasionally aposomatism [106], but testing such assumptions are rare. Coloration may have multiple and modifiable functions [208], and even though larval coloration does not directly signal reproductive potential at the moment, there is every reason to ask if larval coloration involves profound fitness signals that we fail to recognize. A phylogenetic analysis is an alternative approach, but we predict that there would be a strong ecological signal and little or no phylogenetic signal.

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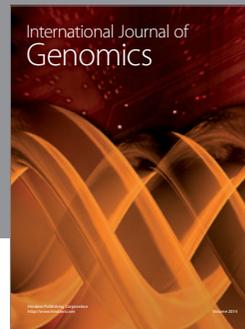
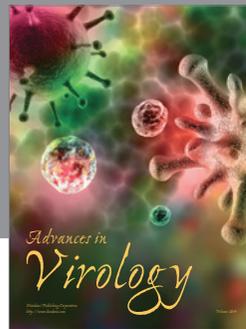
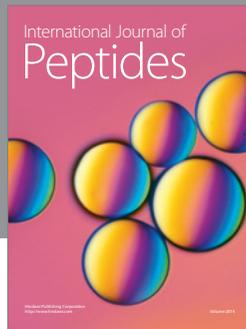
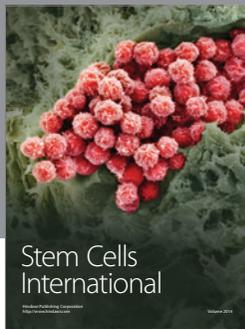
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