

CHAPTER 12

Amphibian Coloration: Proximate Mechanisms, Function, and Evolution

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INTRODUCTION

Amphibians have been commonly studied in relation to their physiology and life history strategies, due to the fascinating changes they undergo throughout their complex life cycle, and to their communication, predominantly acoustic for anurans and chemical for urodeles. Furthermore, some species, such as the axolotl (*Ambystoma mexicanum*) and frogs of the genus *Xenopus*, have become important models for biomedical research. Since the late 19th and early 20th century, there has also been considerable interest in the ontogenetic and cellular/molecular aspects of amphibian pigmentation (e.g., DuShane 1935, Cabello Ruz 1943, Bagnara 1968), as well as the frequent intraspecific variation in color patterns (e.g., Hargitt 1912, Hairston and Pope 1948, Dunlap 1955). More recently, and after a relatively slow start, the number of studies on the adaptive value of amphibian coloration has also been rapidly increasing, particularly in the context of anti-predator strategies (reviewed in Rudh and Qvarnström 2013, Rojas 2017).

Some of the first studies on amphibian coloration were related mostly to the incredible polymorphism observed in some cryptic frogs (reviewed in Hoffman and Blouin 2000). The great diversity in vibrant and conspicuous coloration of some

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Neotropical poison frogs also started to be documented recurrently in taxonomic descriptions, travel diaries and natural history notes as early as 1874 (e.g., Belt 1874), but it was only until the late 1990's when the function and evolution of such diversity started to be increasingly addressed. Studies on the function of salamander warning coloration, on the other hand, seem to have bloomed a little earlier (Huheey 1960, Huheey and Brandon 1974, Brandon and Huheey 1975, Brandon et al. 1979a, b, Brodie and Brodie 1980).

Over the last two decades, research on the (potential) role of coloration in amphibian sexual selection has also been proliferating, albeit with the overrepresentation of some taxa (e.g., *Oophaga pumilio*, the strawberry poison frog, Maan and Cummings 2008, 2009, Crothers and Cummings 2013). There have been numerous accounts of the existence of sexual dichromatism (e.g., Bell and Zamudio 2012, Bell et al. 2017) and, in some cases, the influence of colour patterns on mate choice or intra-sexual competition (e.g., Maan and Cummings 2008, Crothers et al. 2011, Acord et al. 2013), both in anurans and urodeles. Coloration in gymnophionans has been studied much less but, given their fossorial lifestyle, instances of conspicuous coloration in species of this group (Wollenberg and Measey 2009) continue to puzzle researchers.

Here, we provide an overview of the research conducted on amphibian coloration to understand its functional basis, antipredator function, and role in sexual selection. We review the available knowledge and provide suggestions for avenues of research yet to be explored when seeking to understand color in amphibians.

The Functional Basis of Amphibian Coloration

A long history of physiological, behavioral, ecological, and evolutionary studies of coloration phenotypes in animals, together with the ease with which they are scored, has resulted in a profound understanding of the mechanisms governing pigmentation development and evolution in vertebrate model systems (Bennett and Lamoreux 2003, Sturm 2009, Irion et al. 2016, Patterson and Parichy 2019) and, increasingly, in non-model systems (Hofreiter and Schöneberg 2010, Hubbard et al. 2010, Kronforst et al. 2012, Thibaudeau and Altig 2012, Kuriyama et al. 2020). Since at least the late 1800s, studies using amphibians have contributed to our understanding of several mechanistic aspects of vertebrate pigmentation, such as the ontogenetic origin (Ehrmann 1892, Eycleshymer 1906, DuShane 1935), structure and function of pigment cells (Bagnara et al. 1968, Bagnara and Matsumoto 2006), the role of hormones in pigmentation (Allen 1916, Smith 1916, Houssay 1925, Parker 1948), the mechanisms underlying rapid color change (Parker 1948, Tuma and Gelfand 1999, Sköld et al. 2013), and the role of non-cellular chromophores (i.e., color-producing molecules) in green (Cabello Ruz 1943, Barrio 1965) and fluorescent (Taboada et al. 2017) coloration. In this section, we review the current knowledge and open questions on the molecular, cellular, and physiological mechanisms underlying color patterns and their evolution in amphibians.

Chromatophores: the Building Blocks of Vertebrate Coloration

In vertebrates, skin coloration is produced by chromatophores, a group of cells that originate in the neural crest (DuShane 1935, Fujii 1993), and can be classified

in two broad groups based on the physical mechanisms through which they produce color (Bagnara 1968, Ligon and McCartney 2016). First are pigmentary chromatophores, which produce color via the absorption of particular wavelengths of light by pigments within them. Three kinds of pigmentary chromatophores are predominant in vertebrates: melanophores, which contain melanic pigments and are black or brown, and xanthophores and erythrophores, which are yellow or red, respectively, and contain carotenoid and pteridine pigments. The second type are structural chromatophores, which contain cellular nanostructures that produce color by scattering and reflecting certain wavelengths of light. Iridophores, which contain purine crystalline platelets, are the most widespread kind of structural chromatophore in vertebrates (Bagnara 1966, Fujii 1993, Bagnara and Matsumoto 2006). In most vertebrates, chromatophores are arranged three-dimensionally within the dermis, forming structures known as dermal chromatophore units, which consist of stacked xanthophores, iridophores and melanophores. Xanthophores are at the outermost end (i.e., closest to the epidermis) followed by iridophores and finally melanophores, which are found near the base of the dermis. Melanophores, in addition, have dendritic processes that extend around and over iridophores (Fig. 1A; Bagnara et al. 1968). A notable exception to this pattern are mammals and birds, in which pigment cells (mostly melanocytes, homologous to melanophores) are in the dermis, and transport pigments into neighboring keratinocyte cells, which may retain them or deposit them into hairs or feathers (Weiner et al. 2007, Mills and Patterson 2009).

Chromatophores dictate an animal's coloration in two ways: through the actual colors produced by their pigments or nanostructures (i.e., color), and through the spatial organization of these colors in the skin (i.e., pattern). In pigmentary chromatophores, color is determined by the metabolic pathways involved in either the production of pigments, or their uptake from the diet and posterior modification (Goodwin 1984, d'Ischia et al. 2015). In structural chromatophores, in contrast, color is determined by the morphology and organization of the reflective platelets within cells (Fujii 1993, Ligon and McCartney 2016). Below we detail how color is produced in the main chromatophore types.

Melanophores

Melanic pigments are produced within melanophores, by organelles called melanosomes, through a pathway that is relatively conserved across vertebrates (d'Ischia et al. 2015). Melanosomes can produce different types of related pigments, whose relative quantities produce different colors. The best-studied among them are eumelanin and pheomelanin, which reflect different colors and are responsible for multiple instances of coat and plumage color variation in mammals and birds (Bennett and Lamoreux 2003, Hoekstra 2006, Hubbard et al. 2010). Melanocytes that produce higher levels of the darker eumelanin relative to pheomelanin result in darker coat or feather colors, and vice versa. Amphibians were traditionally thought to produce only eumelanin, leading to the view that variation in melanic pigmentation is solely due to the amount, color and distribution of eumelanin in melanophores (reviewed by D'Alba and Shawkey 2019). This, however, contrasts with the notion that pheomelanin is a more straightforward product of the melanogenesis pathway, and requires less regulatory/catalytic proteins than eumelanogenesis (Schallreuter

et al. 2007, Ito and Wakamatsu 2008, McNamara et al. 2021). In fact, pheomelanin was recently uncovered in the skin of the pipid frog *Hymenochirus boettgeri* (Wolnicka-Glubisz et al. 2012), suggesting that this pigment may play an unappreciated role in amphibian coloration.

In some anuran species the pigment pterorhodin, which produces a wine-red coloration, is produced in a specialized kind of melanophore (Bagnara et al. 1973). This pigment is thought to be unique to frogs, and has only been found in species of the Neotropical subfamily Phyllomedusinae and the Australo-Papuan family Pelodyadidae, which appear to have convergently evolved pterorhodin-containing melanophores (Bagnara et al. 1973, Bagnara 2003). Although these melanosomes display similar cellular structure and early development to melanin-containing ones, very little is known about pigment synthesis in these organelles (Bagnara 2003), or their prevalence among other groups of amphibians or vertebrates in general. Future pigment surveys of amphibian skins will most likely reveal the extent to which pheomelanin, pterorhodin, and perhaps other uncharacterized melanosome-derived pigments contribute to coloration in amphibians.

Xanthophores

Pteridines are also synthesized metabolically in xanthophores (Obika and Bagnara 1964, Stackhouse 1966), and variation in the pteridine synthesis pathways has been shown to produce noticeable changes in amphibian pigmentation (Bagnara et al. 1978). For example, experimentally inhibiting the enzyme *xdh* (xanthine dehydrogenase) in tiger salamanders (*Ambystoma tigrinum*) results in reduced pterin content in xanthophores, which translates to a much darker appearance, devoid of the characteristic yellow pigmentation of this species (Frost and Bagnara 1979). Recent work has shown differential expression of genes involved in pteridin synthesis between different color morphs of some frog species (Stuckert et al. 2019, Rodriguez et al. 2020, Stuckert et al. 2021).

Carotenoids, on the other hand, cannot be synthesized by most animals, except for a few arthropod species that have acquired carotenoid synthesis genes via horizontal transfer from fungi (Moran and Jarvik 2010, Altincicek et al. 2011, Cobbs et al. 2013). They are instead obtained from dietary sources, and sometimes modified before deposition in their target tissue (Goodwin 1984). In vertebrates, variation in carotenoid-based coloration is usually achieved either through modulation of pigment uptake and/or deposition rates, or through chemical modification of carotenoids to alter their light absorption properties (Goodwin 1984, Toews et al. 2017). For instance, within a population of *Oophaga pumilio*, the skin concentration of some carotenoids (but not others) is strongly correlated with skin brightness (Crothers et al. 2016). In the polytypic frog *Ranitomeya sirensis*, red and yellow populations differ markedly in skin expression levels of the cytochrome P450 enzyme CYP3A80, which is part of a protein family known to convert yellow dietary carotenoids into red ketocarotenoids. The higher expression of this enzyme in red frogs is thought to result in much higher accumulation of red than yellow carotenoids in xanthophores (Twomey et al. 2020), providing a clear example of how punctual changes in carotenoid metabolism pathways can produce coloration differences. Similar mechanisms have been shown or suggested to underlie red/yellow/orange

variation across vertebrate taxa, including birds (Lopes et al. 2016, Mundy et al. 2016, Twyman et al. 2018, Hooper et al. 2019), squamates (Andrade et al. 2019), and fish (O'Quin et al. 2013), which suggests that metabolic carotenoid modification may be a common route in vertebrate color evolution.

Iridophores

While pigmentary chromatophores produce color by absorbing light at specific wavelengths, iridophores do so by reflecting or refracting white or specific spectra of light. These cells contain stacks of reflective platelets, usually made of guanine, which are effectively transparent but have very high refractive indices. Their stacked arrangement in the cytosol, which has a lower refractive index, results in particular wavelengths being reflected. Multiple aspects of the guanine platelets, such as their width, separation, and orientation, or the height of platelet stacks determine the wavelengths reflected by iridophores (Bagnara 1966, Land 1972). For example, in dendrobatid poison frogs, iridophores have been shown to be a major contributor to hue variation, with thicker guanine platelets being associated with longer wavelength (i.e., redder) hues, and thinner platelets associated with shorter wavelength (i.e., bluer) hues (Twomey et al. 2020).

In the majority of documented cases, the color of a patch of skin results from the combined action of the three chromatophore types. For instance, green can be obtained by combining the absorption of short wavelengths by yellow xanthophores and long wavelengths by melanophores with the amplification of medium wavelengths by iridophores. Blue is often achieved when melanophores absorb long wavelengths and iridophores selectively reflect short wavelengths (Bagnara et al. 2007). Therefore, to understand the mechanisms underlying color variation, it is necessary to consider both the nature of individual chromatophores and their interactions.

Physiological Chlorosis and Fluorescence

Although the majority of variation in amphibian coloration is thought to be mediated by the arrangement of chromatophores in the epidermis, there is mounting evidence that other mechanisms play an important role in the coloration of multiple species. Chief among these is physiological chlorosis: the accumulation of the biliverdin in the blood, lymph, bones, and soft tissues, whose green/blue-green color is visible through translucent skin (Fig. 1B), which at least partially lacks chromatophores (Cabello Ruz 1943, Barrio 1965). Biliverdin is a green pigment that results from the catabolism of heme from senescent red blood cells. In humans, this pigment accounts for the greenish color of aging bruises. In most vertebrates, biliverdin is either directly excreted (fish, amphibians, birds, non-avian reptiles; Colleran and O'Carra 1977, Cornelius 1991) or reduced to bilirubin and further broken down for excretion (mammals; Colleran and O'Carra 1977). In chlorotic frogs, on the other hand, biliverdin is accumulated, with some species exhibiting biliverdizing plasma concentrations orders of magnitude higher than those found in non-chlorotic vertebrates (Barrio 1965). This is achieved through the action of a recently identified group of serpin proteins that bind biliverdin, presumably preventing its excretion. Furthermore, these biliverdin-binding serpins modify the spectral properties of

biliverdin, which at least in one species (*Boana punctata*) results in a fine-tuning of the frogs' color to very closely match the leaves on which they perch, most likely to enhance camouflage (Taboada et al. 2019).

Chlorosis mediated by biliverdin and its associated serpins has been experimentally demonstrated in 11 species of the families Hylidae and Centrolenidae, but at least 430 species across 11 families are known to accumulate green pigments in their blood, lymph, bones, or soft tissues. The phylogenetic distribution of these species points to more than 40 convergent origins of physiological chlorosis in anurans (Taboada et al. 2017b, Taboada et al. 2019). Many of the biliverdin-binding serpins that have been identified in Hylid frogs appear to be paralogous, suggesting that different, closely related proteins have repeatedly evolved the ability to bind biliverdin in different lineages (Taboada et al. 2019). This scenario points to mechanisms other than chromatophore-based coloration as underappreciated avenues for the evolution of coloration in anurans, and perhaps other amphibians.

In addition to green coloration, chemicals in the lymph and other tissues have recently been shown to produce fluorescence in two species of hylid frogs, *Boana punctata* and *B. atlantica* (Taboada et al. 2017a,b). A combination of newly discovered fluorophore molecules called hyloins, found in the frogs' lymph and serous cutaneous glands, produce green fluorescence when excited by UV-A/blue light. Under dawn and moonlight conditions, fluorescence was estimated to account for 18-30% of a frog's reflectance (Taboada et al. 2017a). Based on other traits that appear to be correlated with fluorescence, Taboada et al. (2017b) speculated that this phenomenon may be present in over 200 species across seven anuran families. Since then, several additional examples of fluorescence have been reported across the amphibian phylogeny (Goutte et al. 2019, Lamb and Davis 2020), but the mechanisms underlying fluorescence in these cases remain largely unstudied. The fact that entirely new groups of fluorescent molecules and biliverdin-binding proteins associated with amphibian coloration have been discovered in the last few years underscores the importance of functional research to acquire a more complete understanding of evolution of coloration (and other phenotypes).

The Molecular Basis of Macroscopic Color Patterns

Color patterning, the spatial organization of an organism's color patches, is driven by differential expression of genes involved in pigmentation (or other coloration) pathways, and by chromatophore interactions in different regions of the skin. Although less well understood than the mechanisms governing color itself, the molecular basis of some common patterns have been characterized (Mills and Patterson 2009, Irion et al. 2016). For example, in the frogs *Xenopus laevis* and *Rana forreri*, ventrally-expressed inhibitors suppress ventral melanization, resulting in much lighter ventral than dorsal pigmentation (Fukuzawa and Ide 1988, Fukuzawa et al. 1995). This same mechanism underlies the lighter ventral patterns of multiple species of mice and fish (Millar et al. 1995, Zuasti 2002). In both mice and fish the gene *agouti* (or its orthologs) has been identified as the melanization suppressor (Millar et al. 1995, Zuasti 2002). This also seems to be the case in at least some species of frogs (Fukuzawa et al. 1995, Goutte et al. 2021), but has not been fully confirmed.

The molecular mechanisms underlying striped color patterns in amphibians and fish have received considerable attention. In several species of salamanders, newts, and zebrafish of the genus *Danio*, dark stripes are produced by dense aggregations of melanophores, which are absent or nearly absent in the lighter inter-stripes (Mills and Patterson 2009, Irion et al. 2016). For some salamander species, the melanophore-free region is formed as melanophores migrate away from the lateral line primordium during larval development (Parichy 1996a,b). In zebrafish, stripe position is also achieved through chromatophore migration during development. In addition to interactions between chromatophores and the tissue environment, interactions between different chromatophore types, both over short (Watanabe et al. 2006, Eom et al. 2012) and long (Eom et al. 2015) distances, play an important role in defining the spatial localization of color patches. Iridophores initially establish the location of the inter-stripe, and serve as a reference for posterior xanthophore and melanophore migration and differentiation to produce the final color pattern (Maderspacher and Nüsslein-Volhard 2003, Frohnhöfer et al. 2013, Patterson and Parichy 2019). Although the cellular and molecular processes responsible for defining color patterns have not been studied in detail in most species of amphibians, we anticipate that the renewed interest in the functional underpinnings of coloration among herpetologists, facilitated by recent technological advances for functional biology, should yield important advances on this subject in the near future. This can be evidenced by recently increasing influx of studies on the genetic (e.g., Goutte et al. 2021) and transcriptomic (e.g., Burgon et al. 2020, Rodriguez et al. 2020, Stuckert et al. 2021) bases of amphibian color pattern variation.

Coloration Change through Ontogeny

The life cycle of most amphibian species is marked by drastic phenotypic changes over time given its biphasic nature, in which larvae transition from an aquatic to a terrestrial lifestyle and body plan. Accordingly, coloration changes widely across an individual's lifetime, with larval and adult forms displaying considerably different colorations. Embryos acquire visible coloration patterns early in development, as chromatophore cells originating in the neural crest, become differentiated, and migrate to different parts of the body to produce a given color pattern (Bagnara et al. 1978). As tadpoles hatch and continue to grow, they eventually reach their “characteristic” larval coloration, with darker, more complex, or more contrasting coloration tending to appear at later stages of development (Thibaudeau and Altig 2015). As with other phenotypes, tadpoles of some species exhibit considerable phenotypic plasticity in coloration. For example, tadpoles of the hylid frog *Dryophytes chrysoscelis* develop considerably different tail pigmentation when reared in the presence or absence of predators or their cues (McCollum et al. 1996, 1997), and larvae of the Tiger Salamander *Ambystoma mavoritum nebulosum* develop darker or paler colorations depending on the substrate and water turbidity where they are reared (Fernandez and Collins 1988).

The metamorphic climax involves an organism-wide remodeling of tissues and functions as tadpoles transition into frogs. In the stages surrounding metamorphosis, as the skin is remodeled, pigmentation changes drastically (Kemp 1961,

Heatwole and Barthalmus 1995, Parichy 2006). During this period, both existing and newly differentiated pigment cells migrate extensively, organizing themselves in dermal chromatophore units (Fig. 1A), and usually culminating in the individual's adult coloration (e.g., DuShane 1943, Sterner 1946, Bagnara et al. 1968, 1978,

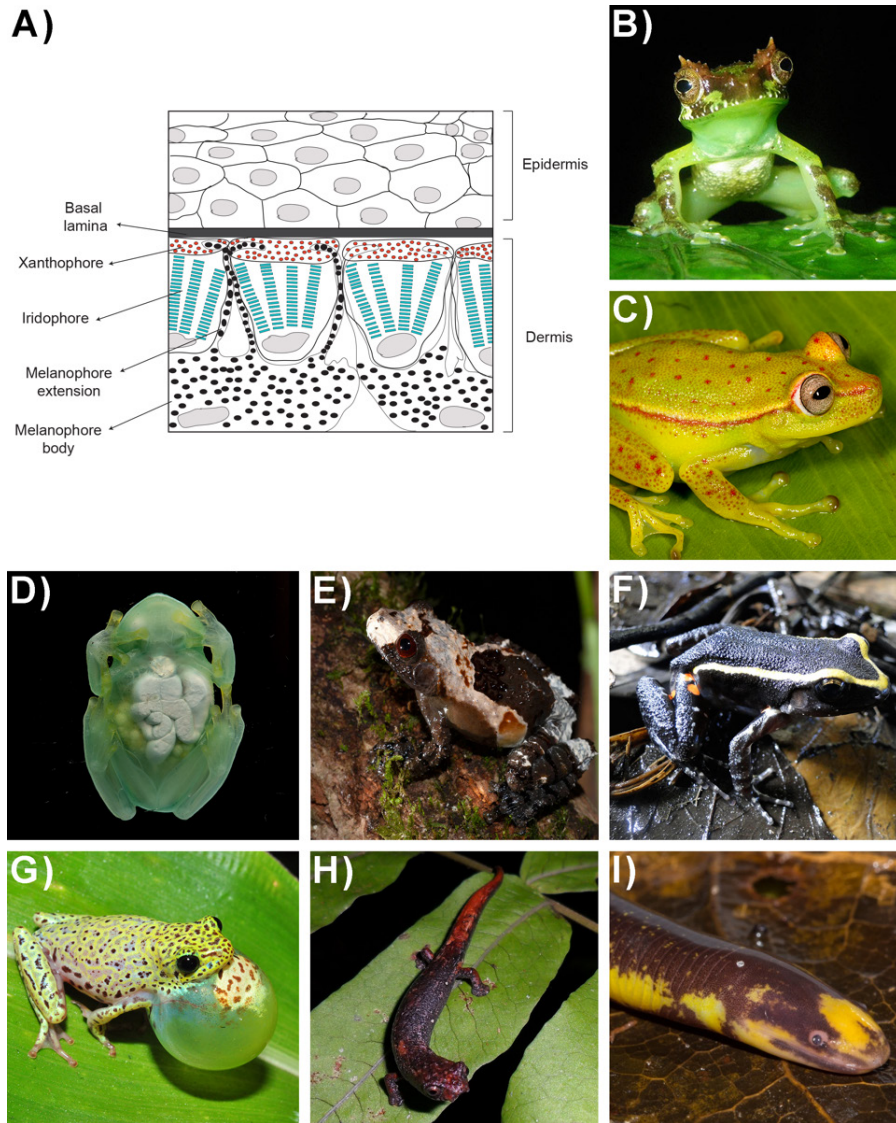


Figure 1. (A) Structure of dermal chromatophore units on a sagittal skin section. Melanosomes on the left melanophore are scattered, while those on the right are retracted. (B) Physiological chlorosis in *Gracixalus supercornutus*; (C) Biofluorescence in *Boana punctata*; (D) Transparent skin in *Hyalinobatrachium fleishmanni*; (E) *Theloderma asperum* displaying bird-dropping-like coloration; (F) Putative mimetic coloration of *Leptodactylus lineatus*; (G) Conspicuous sac coloration in *Hyperolius* sp. (H) Conspicuous coloration in *Bolitoglossa tamaense* I) Conspicuous coloration in *Rhinatrema bivittatum*. Jodi Rowley B, E; J.P. Lawrence C, D; Bibiana Rojas F; Daniela Rößler G; Aldemar A. Acevedo H; Antoine Fouquet I.

Yasutomi 1987, Lechaire and Deneffe 1991). Although the precise mechanisms underlying these transformations have not been characterized, they are thought to be mediated by endocrine hormones, many of which mediate metamorphic changes in the skin (Heatwole and Barthalmus 1995, Parichy 2006). For instance, thyroxine, one of the thyroid hormones known to trigger several metamorphic changes, induces melanophore migration from the dermis to the epidermis of frog integument tissue cultures (Yasutomi 1987). Work on zebrafish showing that thyroid hormones regulate pigment cell maturation (Saunders et al. 2019) is in line with this notion.

Although most amphibian species do not experience considerable changes in coloration past metamorphosis, there are several documented instances of post-metamorphic color change in frogs (e.g., Richards and Nace 1983, Duellman and Ruiz-Carranza 1986, Vaisi et al. 2018, Bueno-Villafane et al. 2020, and reviewed by Hoffman and Blouin 2000) and salamanders (e.g., Fernandez and Collins 1988). In most cases, changes in coloration consist of a general darkening or lightening of an individual's colors, or the loss/gain of pattern elements such as spots or stripes (Hoffman and Blouin 2000), with some species experiencing quite drastic changes. The majority of ontogenetic coloration change reports are in the family Hyperoliidae, especially the genus *Hyperolius*. Juveniles of multiple species in this genus are pale green and transition to dark-green or brown coloration in adulthood, often gaining or losing pattern elements. In other species, juveniles are brown with an hourglass pattern which fades or is otherwise modified over time (reviewed in Hoffman and Blouin 2000). It is frequent for only one sex to experience ontogenetic color change in hyperoliids (Schjötz 1967, Richards 1976). Studies on the hormonal underpinnings of sexual dimorphism in these species have shown that the adult pattern can be induced at metamorphosis by exposing tadpoles to estrogen and/or testosterone, suggesting that ontogenetic color change is intrinsically linked to sexual maturation (Richards 1982, Hayes and Menéndez 1999).

Aside from *Hyperolius*, there are a few noteworthy examples of drastic ontogenetic coloration change in other taxa. Perhaps the most commonly cited case is that of the newt *Notophthalmus viridescens*, where post-metamorphic juveniles (i.e., efts) are bright-red or orange, while adults display dark olive-green coloration (Kelly 1878, Gage 1891). Color change is accompanied by morphological change in several other traits, including tail and limb morphology. In fact, efts and adults differ so much in appearance that taxonomists considered them separate species for over half a century (Rafinesque 1820, Kelly 1878). Given the toxins present in both eft and adult skins, eft coloration is often considered aposematic (Hurlbert 1970, see Aposematism section below for further information). Similarly, in the microhylid frog *Oreophryne ezra* juveniles display yellow spots contrasting against a glossy black background, and gradually transition into plain apricot/brown adults (Kraus and Allison 2009). Adults are nocturnal and call from concealed perches while juveniles are diurnal and perch on conspicuously exposed locations. Although they do not seem to secrete toxic/distasteful chemicals, their coloration closely resembles that of a putatively toxic beetle of the genus *Pantorhytes*, which has led to the idea that *O. ezra* mimic *Pantorhytes* sp. as juveniles, and transition to a cryptic lifestyle as adults (Bulbert et al. 2018). A third case occurs in poison frogs of the genus *Phyllobates*, where metamorphs are black with a thin yellow, green or orange dorsolateral stripe.

In two species, *P. bicolor* and *P. terribilis*, the black background gradually gives way to a yellow suffusion and eventually a solid bright-yellow coloration, while in all other species coloration remains unchanged after metamorphosis (Myers et al. 1978, Silverstone 1976). A similar situation is present in the centrolenid genus *Nymphargus*, where *N. anomalus* and *N. rosada* display the chlorotic green skin and bone coloration characteristic of glass frogs, but over time become tan brown with white bones (Rada et al. 2017). In both *Phyllobates* (Márquez et al. 2020) and *Nymphargus* (Castroviejo-Fisher et al. 2014, Guayasamin et al. 2020), very similar instances of ontogenetic color change appear to have evolved independently in closely related (but not sister) species, suggesting that relatively small modifications of the developmental program of these species may trigger appreciable ontogenetic coloration changes.

Although the molecular and cellular basis of chromatophore differentiation and migration during embryonic and larval development have been studied to a considerable extent (see citations in previous paragraphs), the mechanisms underlying coloration ontogeny around and (especially) after metamorphosis still remain an open field. Evidence from *Ambystoma* salamanders suggests that pre- and post-metamorphic color patterns may be functionally decoupled (Parichy 1998), suggesting that larval and adult coloration may be regulated by at least partially distinct genetic networks. Recent work on *Salamandra* salamanders however showed that environmentally-induced changes in larval coloration influence adult coloration (Sánchez 2018), suggesting at least some degree of coupling. Further studies on the functional basis of coloration ontogeny across amphibian life cycles have the potential to yield interesting insights on multiple aspects of evolutionary biology, ranging from the evolution of life stage-specific ecological strategies to the role of ontogenetic modularity in phenotypic evolution.

Short-term Plastic Color Change

In addition to ontogenetic change, vertebrate color patterns can also change over shorter time scales, and in a reversible manner. Famous examples of color change include the many polar birds and mammals that seasonally molt their coats or feathers to match their highly seasonal environment, or reptiles (e.g., chameleons) that can drastically change their coloration within seconds. In birds and mammals, most color change occurs through the shedding and posterior re-growth of hairs or feathers, which allows for the formation of a new color pattern at each molt (Zimova et al. 2018). In all other vertebrate groups, rapid color change is generally achieved through the transport and rearrangement of chromophores (i.e., pigments, platelets), usually within chromatophores (Sköld et al. 2012, Ligon and McCartney 2016), or through changes in chromatophore cell shape.

The best studied example of this phenomenon is melanosome aggregation and scattering, in which melanosomes are transported between the melanophore body and its periphery through a network of microtubules (Nascimento et al. 2003, Aspögren et al. 2009). When melanosomes are scattered throughout the cytosol, the cells convey a darker appearance than when melanosomes are aggregated at the center. This effect is accentuated if melanosomes travel up the cell's dendritic processes

and occlude the iridophores and xanthophores above them (Bagnara 1968, Tuma and Gelfand 1999, Aspöngren et al. 2009, Sköld et al. 2012). This process has been replicated *in vitro*, and is often used as a model system to study intracellular transport and molecular motors (reviewed by Tuma and Gelfand 1999). In amphibians, melanophore movement has been shown to underlie rapid color change in multiple contexts, such as the lightening and darkening of frog skin during background matching (e.g., Bagnara et al. 1968, Nielsen 1978a), and possibly thermoregulation (e.g., Fernandez and Bagnara 1991), as well as changes from dull to bright colors during breeding (e.g., Kinderman and Hero 2016).

Xanthophores can also produce short-term color changes through microtubule-guided scattering and aggregation dynamics similar to those observed in melanophores, which are also mediated by a similar set of hormones (reviewed by Ligon and McCartney 2016). However, the movement patterns of pigment-containing vesicles seem to be different to those of melanophores, possibly due to differences in microtubule arrangement (Byers and Potter 1977, Beckerle and Potter 1983). The majority of research on this subject has, however, occurred on non-amphibian taxa, mostly teleost fish. Iridophores, on the other hand, can effect rapid color change through the sliding and re-orientation of platelets, as well as their vertical expansion or compression. For example, changes in iridophore shape and platelet orientation accompany plastic changes from light to darker green colors in *Hyla cinerea* and *H. arborea* (Nielsen 1978a). Again, beyond a few examples (e.g., *H. cinerea* and *H. arborea*; Nielsen, 1978a, Nielsen 1978b), most studies on iridophore-mediated color change have focused on fish (Sköld et al. 2012, Ligon and McCartney 2016) or reptiles (e.g., Teyssier et al. 2015), while amphibian systems remain relatively unstudied.

The Genetic Basis of Variation in Coloration

In addition to the functional mechanisms that produce phenotypic traits, from an evolutionary perspective, it is important to understand the genetic basis of variation in such traits, for example between species or within a population. In amphibians, most studies of the genetic basis of variation in coloration have focused on species with discrete morphs that vary within populations (i.e., polymorphic species), and have been aimed at elucidating the mode of inheritance of these morphs (e.g., Moriwaki 1953, Goin 1950, Fogleman et al. 1980, Richards and Nace 1983, Summers et al. 2004, O'Neill et al. 2010, Richards-Zawacki et al. 2012, reviewed by Hoffman and Blouin 2000). A generality that can be drawn from these studies is that the absence of certain colors (e.g., in albinistic morphs) or pattern elements (e.g., spots or stripes) tends to be recessive, which points to an association with loss-of-function alleles. The majority of studied polymorphisms seem to be controlled by one or a few loci, which is expected considering that the maintenance of discrete morphs is greatly facilitated by simple (i.e., Mendelian) modes of inheritance. The genetic basis of more complex (i.e., quantitative) variation has received much less attention, even though it putatively accounts for a large percentage of variation both within and between populations. Notably, Vastegaard and co-authors (2015) studied color pattern variation in a hybrid zone between two morphs of *Ranitomeya imitator*

to estimate the number of genes that underlie color and pattern differences in this system. Their results indicate that one or two loci of major effect may be responsible for most of the pattern differences between morphs. Whether this is a general pattern among amphibians remains unknown.

Beyond characterizations of their mode of inheritance, the genetic basis of differences in coloration has been sparsely studied in amphibians. A salient avenue of research in this regard is identifying the genetic elements that underlie coloration variation. The identity and history of the loci underlying phenotypic variation provide key insights on multiple aspects of phenotypic evolution, such as the origin of adaptive variants (e.g., mutation, introgression, selection on standing variants) or the timing and nature of selection they've experienced, and can inform functional studies by pointing to candidate genes or pathways. To the best of our knowledge, to date, only two studies have identified candidate genes for color pattern differences within species in the wild. Posso-Terranova and Andrés (2017) sequenced a region of the *mc1r* gene, a well-known member of the vertebrate melanogenesis pathway that underlies melanin-based coloration variants in multiple species, in the poison frogs *Oophaga histrionica* and *O. lehmani*. They found an association between background color (black vs. brown) and *mc1r* alleles, with black frogs in both species carrying alleles exhibiting premature stop codons, which resulted in considerably shorter proteins that lacked multiple functional domains present in most other vertebrates. Truncated *mc1r* proteins have been mostly associated to albinistic or otherwise pale-colored forms in other species (e.g., Everts et al. 2000, Gross et al. 2009, Xiao et al. 2019) and are usually considered to be non-functional. Further work to understand how the truncated *Oophaga mc1r* alleles function in melanin pathways could provide interesting insights into the functional basis of melanic pigmentation, and trans-membrane receptor proteins in general. Goutte et al. (2021), on the other hand, conducted a genome-wide association study aimed at identifying the genetic basis of vertebral stripe presence/absence in the grass frog *Ptychoadena neumanni*, and found a strong signature of association between vertebral stripes and genetic variants surrounding an ortholog of *agouti*, which is also part of the melanogenesis pathway, and has been associated to melanic pigmentation variants across vertebrate taxa. Although vertebral stripes are polymorphic in several species of *Ptychoadena*, the history of *agouti* variants in the genus suggests that the alleles behind each morph are not the same across species, pointing to a dynamic evolution of this polymorphism over the genus's history.

The size and repetitive content of amphibian genomes (e.g., Rogers et al. 2018, Sun et al. 2020) make the genome-wide association approaches often used to map phenotypes to genomic regions costly and methodologically challenging. A commonly used approach to partially circumvent this limitation is comparing gene expression profiles between relevant tissues (different regions of the skin, for example) or developmental stages (e.g., Burgon et al. 2020, Stuckert et al. 2021). Although these studies are limited in the extent to which they can pinpoint the genetic variants directly responsible for (heritable) phenotypic variation, they can certainly identify candidate genetic pathways and even genes for further exploration. Furthermore, they can also provide functional validation for genetic association studies. As sequencing and functional genetic (e.g., genome editing) technologies

continue to advance, we expect to see an increase in functional evolutionary genetic studies of coloration in amphibians, which should lead to more solidly bridging our understandings of the molecular, developmental, ecological, and evolutionary drivers of coloration evolution.

Interactions Between Predators and Amphibian Prey

Considerable research on amphibian coloration has focused on its ecological function, with particular emphasis on antipredator defenses. Coloration can broadly be viewed on a gradient from cryptic to conspicuous, and the opposite ends of the spectrum could be considered camouflage or aposematism, although recent research has highlighted the multi-functionality of coloration that may belie this spectrum as overly simplistic (Reynolds and Fitzpatrick 2007, Bell and Zamudio 2012, Barnett et al. 2018). Because of their ubiquity and wide range of functional coloration, amphibians are model systems for understanding the evolution and function of color. For example, a large part of what is currently known on the evolution of aposematism derives from research on dendrobatid poison frogs (e.g., see Summers and Clough 2001, Santos et al. 2003, Saporito et al. 2007, Wang and Shaffer 2008, Maan and Cummings 2012, Rojas et al. 2014a,b, Santos et al. 2014, Lawrence et al. 2019, Carvajal-Castro et al. 2021). Other aspects of coloration, such as deimatic displays, have been considerably less studied despite appearing to be somewhat common in amphibians (Fig. 4), particularly in some taxa (e.g., tree frogs, myobatrachid frogs). In this section, we will discuss some of the particularly notable examples of antipredator coloration, the research surrounding them, and what is yet unknown.

Camouflage

Camouflage, where species display coloration meant to avoid detection or recognition by predators (Nokelainen and Stevens 2016), can largely be classified in three main categories: background matching, disruptive coloration, and masquerade (but see Ruxton et al. 2018 for further description of camouflage). In short, animals that employ background matching aim to blend in with their surroundings (e.g., Fig. 2A), while those that employ disruptive coloration aim to prevent their shape from being discerned by predators (e.g., Fig. 2E). Those that employ masquerade, in contrast, aim to look like an inedible object in the environment (i.e., stick, rock, leaf; Skelhorn et al. 2010). While camouflage is the most common anti-predator strategy among amphibians, what type of camouflage they exhibit is largely variable among different groups of amphibians.

Frogs that employ camouflage are extremely variable in body plan, which allows them to capitalize on different strategies. When at rest, for example, frogs in the genus *Cruziohyla* look like leaves, a resemblance further accentuated by fringed extensions on their legs that make them appear to be the insect-damaged edges of leaves and light blotches reminiscent of lichens on their dorsum (Toledo and Haddad 2009). These particular frogs however, when active, may display startle coloration as well (see below) as their flanks have bright orange coloration (Gally et al. 2014), as in other phyllomedusine frogs (but see Robertson and Green 2017 for possible social function of these colors). Frogs such as cricket frogs (*Acris*) exhibit impressive

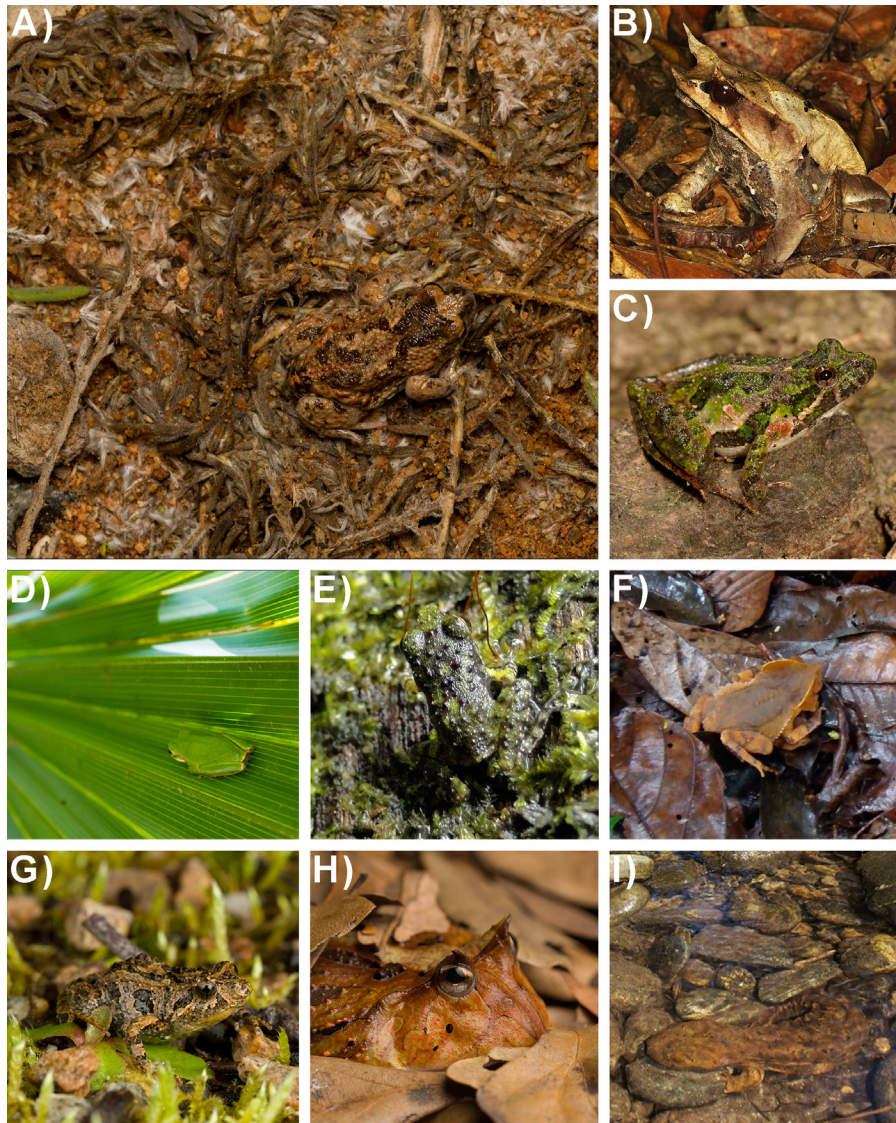


Figure 2. Examples of (putative) camouflage in amphibians. (A) *Pseudophryne guentheri*, (B) *Megophrys nasuta* (C) *Acris crepitans*, (D) *Hyla cinerea*, (E) *Pristimantis zeuctotylus*, (F) *Rhinella aff. margaritifera*, (G) *Crinia signifera*, (H) *Ceratophrys cornuta*, (I) *Cryptobranchus alleganiensis*. Image Credits: J.P. Lawrence A, B, C, D, G, H. Todd Pierson I; Bibiana Rojas E, F.

background matching that is accentuated by jump behavior. These frogs will jump a long distance, and upon landing, will change their body orientation. This feature, coupled with their cryptic coloration makes them exceptionally difficult for predators to detect (Cox et al. 2020).

While frogs seem to show greater variability in body plan which can help them camouflage, salamanders have relatively little variation in body form (Bonett and

Blair 2017). This may be because most salamanders are fossorial or aquatic, thus extra extensions of skin might make those lifestyles difficult. As such, camouflage in salamanders could perhaps be best characterized as masquerade or background matching. With their elongated and slender shape, many resemble sticks or roots, and likely can avoid detection from would-be predators. Perhaps the most impressive example of putative masquerade in salamanders occurs in the cryptobranchids, which include the Chinese and Japanese Giant Salamanders, and the North American Hellbender (*Cryptobranchus alleganiensis*, Fig. 2I). These aquatic salamanders have fringes of skin along their flanks meant to increase surface area for oxygen exchange in cool waters (Guimond and Hutchison 1973). However, coupled with their mottled brown and black coloration, these salamanders appear to be little more than waterlogged pieces of decaying wood. Thus far, however, the function of this coloration is largely speculative and warrants further research.

As mentioned above, a particular case of camouflage is masquerade, where an organism looks like an inanimate object in its environment (Skelhorn et al. 2010). Masquerade is common in insects (i.e., leaf-mimicking katydids and walking sticks), and, while it appears to also be rather common in a number of species of amphibians (i.e., *Phyllomedusa*, *Cruziohyla*, and *Theloderma*), formal examination has largely been overlooked. An exception is *Rhinella margaritifera* (Barnett et al. 2021), an Amazonian toad whose coloration and body shape make it resemble dead leaves in the leaf litter (Fig. 4F). Other species appear to mimic bird droppings (i.e., *Theloderma asperum* or *Dendropsophus marmoratus*, Fig. 1E), but no research to our knowledge has tested whether this is indeed an example of masquerade.

As camouflage relies on the idea that predators will have difficulty in detecting or recognising prey, within-population variability in prey color (i.e., polymorphism) is evolutionarily favorable (Bond and Kamil 2002). Variability in phenotype among individuals results in predators having difficulty in developing a search image for prey species, thus making detection more difficult (Bond and Kamil 2002, Bond and Kamil 2006, Bond 2007). Cryptic coloration is characterized by slow diversification rates compared to conspicuous coloration. Despite this, crypsis appears to be the more evolutionarily favorable state, as there are numerous instances of conspicuous lineages reverting to crypsis, but relatively few of the opposite (Arbuckle and Speed 2015). Furthermore, polytypic conspicuous lineages appear to be more likely to revert to crypsis than the reverse, supporting the idea that variation is evolutionarily favorable in cryptic species (Arbuckle and Speed 2015)

Aposematism

Aposematism is a widespread strategy in which a warning signal (e.g., conspicuous coloration) is coupled with a secondary defense (i.e., noxious smell, distasteful secretions, poisonous compounds; Poulton 1890) to warn predators about prey unprofitability. Thus, this defensive strategy relies on predator learning and/or biases towards conspicuous signals to protect prey species (Endler and Mappes 2004, Mappes et al. 2005). Notably, social animals such as birds, many of which feed on amphibians, have been shown to be capable of learning to avoid aposematic signals through social cues and observation without direct experience (Thorogood et al. 2017, Hämäläinen et al. 2020).

Among amphibians, frogs are the most well-studied in terms of understanding the role of aposematic coloration. Aposematic signaling has evolved multiple times in a number of frog families including, but not limited to, Dendrobatidae (Summers and Clough 2001, Fig. 3A, E), Mantellidae (Vences et al. 2003, Fig. 3D), Bufonidae (Bordignon et al. 2018, Fig. 3B-C), and Myobatrachidae (Lawrence et al. 2018, Fig. 3F). Warning signals are widespread in these families, but other families have evolved aposematic signals as well, though usually among individual lineages (e.g., *Eleutherodactylus iberia*; Rodriguez et al. 2011). Perhaps the best known and most studied example of aposematism in frogs is in the poison frogs in the family Dendrobatidae (e.g., Santos et al. 2003, Saporito et al. 2007, Rojas et al. 2014a, b, Casas-Cardona et al. 2018). There are more than 300 species in the family and the vast majority of species display aposematic signaling. With colors that span the entire visible spectrum, dendrobatids have received disproportionate attention to understanding the evolution and ecology of aposematic signaling. However, numerous other groups are notable. Frogs in the genus *Mantella* are restricted to the island of Madagascar and have evolved conspicuous coloration independently. *Mantella* and dendrobatids offer perhaps one of the best examples of convergent evolution in the animal kingdom (Vences et al. 2003). These two taxa shared a common ancestor approximately 170 MYA (Feng et al. 2017), yet are convergent in numerous traits. They evolved the same methods of sequestering defensive alkaloids from invertebrate prey (including many of the same types of toxins; Clark et al. 2005, Moskowicz et al. 2018); they have convergent phenotypes within the taxon (Chiari et al. 2004, Stuckert et al. 2014) as well as show considerable diversity in aposematic phenotypes (Santos et al. 2003, Klonoski et al. 2019); and they have evolved similar sizes and diurnality, as well as similar locomotion (hopping, as opposed to jumping). Furthermore, some species in both groups exhibit egg-feeding behavior, through which mothers pass on toxins to their offspring (Stynoski et al. 2014, Fisher et al. 2019). While dendrobatids are well represented in the literature, *Mantella* are less well-studied, largely due to dwindling populations (Harper et al. 2007, Randrianavelona et al. 2010).

Many species of aposematic amphibians display considerable variation in aposematic signaling within (polymorphism; Rojas and Endler 2013, Beukema et al. 2016) and among populations (polytypy; Summers et al. 2003, Twomey et al. 2016, Klonoski et al. 2019). This seems perplexing, as aposematic signaling is thought to be maintained via positive frequency-dependent selection (Endler 1988, Mallet and Joron 1999, Rönkä et al. 2020). Under the assumptions of positive frequency-dependent selection, novel signals will be removed by predators unfamiliar with new signals (Mallet and Barton 1989). Polymorphism and polytypy are, however, common in aposematic frogs, with numerous species displaying variation in color patterns. The best-studied example of such variation are dendrobatid frogs. Species in this group derive their defensive skin secretions from invertebrate prey, so as invertebrate communities vary across geographic space, so too do defensive compounds of these frogs (Saporito et al. 2007, Saporito et al. 2006). Thus, honest signaling, where signal is predictive of severity of secondary defense (Sherratt and Beatty 2003, Blount et al. 2009, Summers et al. 2015, White and Umbers 2021), has been suggested as driving regional phenotypic variation in this group. However,



Figure 3. Aposematism found in amphibians. (A) *Eleutherodactylus iberia*; (B) *Atelopus* sp.-dorsal; (C) *Atelopus* sp.-ventral; (D) *Mantella baroni*; (E) *Dendrobates tinctorius*; (F) *Pseudophryne corroboroeae*; (G) *Taricha granulosa*; (H) *Tylotriton shanjing*; (I) *Salamandra salamandra*; (J) *Notophthalmus viridescens*; (K) *Pseudotriton ruber*. Image Credits: Ariel Rodríguez A; Daniela Rößler B, C; J.P. Lawrence D, E, F, G, J, K; Jodi Rowley H; Christoph Leeb I.

experimental evidence of honest signaling has resulted in a convoluted picture. In some species, more conspicuous colors are more toxic (i.e., *Oophaga pumilio*; Maan and Cummings 2012), but in others, the inverse is true (i.e., *O. granulifera*; Wang 2011). Importantly, this toxicity has been measured via injections on mice and/or via quantification of the amount of alkaloids in the frogs' skin, which may yield different results than when palatability of defensive alkaloids is examined

(Bolton et al. 2017, Lawrence et al. 2019). Thus, these patterns of alkaloid variation and predator response warrant further investigation.

Aposematism is less well-studied among salamanders, and most examples of warning signals come from species in the family Salamandridae. Newts and salamandrid salamanders are notable for their potent skin secretions, which in some genera (i.e., *Taricha*, *Tylotriton*; Fig. 3G-H), are among the most toxic substances naturally produced by animals (Brodie 1968, Brodie et al. 1974, Lorenz et al. 2016). Furthermore, some of these salamanders have an interesting ontogenetic color change throughout their lives. The eastern newt (*Notophthalmus viridescens*) is notable for having a terrestrial subadult phase called an “eft.” Efts are bright red and could be considered a classic example of aposematism (Shure et al. 1989; Fig. 3J). This terrestrial phase allows them to disperse across the landscape. When newts leave this subadult phase, they change to a green color (see the Color Change through Ontogeny section above about the proximate mechanisms underlying this ontogenetic color change). The only vestige of the conspicuous coloration of their previous stage are small red spots along the dorsum. While the adults are still toxic, their toxicity is reduced compared to their eft phase. Therefore, it is unclear how much their subdued coloration protects them (Brodie 1968), but the low number of reports of predation of adults suggests that they are protected, too. Aposematic signaling in other salamander families is likely, although much less studied. Many plethodontid salamanders generate sticky or distasteful skin secretions (particularly on their tails) that are known to dissuade predation (Brodie 1977, von Byern et al. 2017), and many species do appear to have conspicuous coloration (von Byern et al. 2017). Future research in salamanders should focus on the evolutionary ecology of coloration in these and other salamander species to better understand the function of conspicuous signals in the group.

Among the three amphibian orders, the ecology, natural history and behavior of gymnophionans (i.e., caecilians) is least understood. This includes, of course, understanding the use of coloration in these animals. Some species do appear to display conspicuous coloration (i.e., *Ichthyophis kohtaoensis*, *Rhinatrema bivittatum*; Fig. 1I), but the function of this coloration is unclear, partly because these and most species of caecilians are fossorial; understanding why fossorial species would display conspicuous coloration is conceptually difficult (Wollenberg and Measey 2009). However, given that most species of caecilians have reduced eyes and likely have poor vision, it is tempting to assume that their conspicuous coloration, when present, is likely used in antipredator defense as opposed to conspecific signaling. Indeed, current research suggests that conspicuous coloration in caecilians is largely driven by natural selection for when they are above surface, suggesting a mix of aposematic and cryptic defenses (Wollenberg and Measey 2009). Some species, such as *Siphonops annulatus*, do have enlarged poison glands reminiscent of macroglands found in frogs and salamanders, which suggests chemical defense (Arun et al. 2020). However, this is evidently a research area which warrants further investigation.

One interesting aspect of aposematism is that it has been suggested to provide benefits to prey beyond protection from predators, for example allowing prey to gather resources while wandering around freely in their environment (Speed et al. 2010). Using ancestral state reconstruction and multivariate phylogenetic analyses,

Carvajal-Castro et al. (2021) tested this idea and demonstrated that warning coloration and the possession of skin toxins allowed dendrobatid poison frogs to start using phytotelmata instead of larger bodies of water, thus diversifying their tadpole deposition sites. Despite the importance of *both* coloration and chemical defenses in the success of this antipredator strategy, most studies on aposematism continue to focus on coloration in isolation, and to neglect selective pressures other than predation (i.e., sexual selection) in its evolution (Rojas et al. 2018).

Mimicry

Mimicry, which can be broadly classified as either Batesian (defended model, undefended mimic) or Müllerian (defended model, defended mimic), allows species to capitalize on predator experience to improve fitness (Speed 1999). In amphibians, evidence of mimicry is rather sparse. Perhaps the best example of Müllerian mimicry in amphibians is with the imitator poison frog (*Ranitomeya imitator*; Chouteau et al. 2011, Stuckert et al. 2014, Twomey et al. 2016), a species which shows considerable polytypy in the Peruvian Amazon. Phenotypes of this species covary with a number of other congeners with impressive fidelity to phenotype.

Batesian mimicry, however, appears to be less common among amphibians. In salamanders, two potential examples exist. First, highly toxic eft phases of the eastern newt (*Notophthalmus viridescens*; Fig. 3J) have a number of putative mimics that co-occur with this species including red salamanders (*Pseudotriton ruber*; Howard and Brodie 1973, Huheey and Brandon 1974; Fig. 3K) and red-backed salamander (*Plethodon cinereus*; Kraemer and Adams 2014, Kraemer et al. 2015). Notably, erythristic populations exist of the red-backed salamander, and it has been hypothesized that such a population may be a mimic of sympatric newts (Tilley et al. 1982). The other putative example of Batesian mimicry in salamanders is the red-cheeked salamander (*Plethodon jordani*) and red-legged salamander (*Plethodon shermani*) and their potential mimic, the imitator salamander (*Desmognathus imitator*, *sensu lato* *D. ochrophaeus*; Tilley et al. 1978). Neither *Plethodon* species has overlapping ranges with one another, but where *D. imitator* is sympatric with either species, it either has an orange cheek patch, mimicking *P. jordani* or orange legs, mimicking *P. shermani* (Labanick and Brandon 1981). On the west coast of North America, *Ensatina eschscholtzii* forms a ring species complex (Moritz et al. 1992). Some of the subspecies of *E. eschscholtzii* (i.e., *E. e. xanthopicta*) have been implicated as part of a mimicry complex with sympatric rough-skinned newts (*Taricha*; Kuchta 2005, Kuchta et al. 2008). By and large, however, little work has been recently conducted on mimicry in salamanders.

Among frogs, Batesian mimicry is poorly understood, too. Perhaps the only example thought to illustrate that phenomenon is that of *Ameerega picta* and *Leptodactylus lineatus* (Fig. 1F). These two species are relatively similar in phenotype and, while *A. picta* does produce defensive compounds (Mebs et al. 2010), *L. lineatus* was long assumed to be nontoxic. However, recent evidence suggests that *L. lineatus* may be defended (Prates et al. 2012), which would make this system an (other) example of Müllerian mimicry. This, and other putative mimicry systems, are yet to be confirmed with rigorous experiments where predator response to the

species involved is assessed (e.g., Bolton et al. 2017, Winters et al. 2018, Lawrence et al. 2019).

Mimicry in amphibians, as a whole, is an area of considerable opportunity for novel research. Convergent phenotypes are common across taxa, particularly conspicuous taxa (e.g., *Mantella baroni*/*M. madagascarensis*, *Notophthalmus viridescens* efts/other red salamander species) but, with a few exceptions discussed above, little work has been conducted to determine if such convergent phenotypes are mimetic. Mimicry confers a fitness advantage on mimics that breaks down when models are in low numbers or absent (Valkonen and Mappes 2014). While phenotypic similarity does suggest mimetic complexes, further research is necessary to determine whether it is predation or other selective pressures driving phenotypic similarity.

Deimatic Displays

Deimatic displays, or startle displays, are those that use bright or contrasting coloration to startle a predator, thus giving the prey species opportunity for escape (Umbers et al. 2015, Umbers et al. 2017). Such displays are well documented in insects (Umbers and Mappes 2015, O’Hanlon et al. 2018), but only beginning to be understood in amphibians. Perhaps the best-known putative example of a deimatic display in amphibians is the “unken” reflex, first described in the fire-bellied toads (*Bombina*) of Europe (Löhner 1919, Bajger 1980). While normally cryptic above, fire-bellied toads are characterized by highly conspicuous color blotches across their venter. According to the reports (Bajger 1980), this coloration is normally hidden until the toad is disturbed, at which point it raises its head and reads up with the palms of its feet facing upward, exposing the conspicuous ventral coloration to potential predators. As *Bombina* produce toxic peptides (Michl and Kaiser 1963, Csordas and Michl 1969), this may allow them to capitalize on aposematic coloration that predators can learn from (Kang et al. 2017) while avoiding excessive predation due to the cryptic dorsal coloration. This behavior has also been reported in species of the South American genus *Melanophryniscus* (Bordignon et al. 2018) and Australian *Pseudophryne* (Williams et al. 2000).

Other amphibians also display the so-called unken reflex, particularly salamandrid salamanders. The rough-skinned newts (*Taricha*) are characterized by dull reddish-brown dorsal coloration and bright orange ventral coloration (Johnson and Brodie 1975). Other salamandrids, such as the eastern newt (*Notophthalmus viridescens*), lift their head and tail up to expose the bright coloration when disturbed, presumably to advertise the potent tetrodotoxins that they harbor in their skin (Brodie 1983, Fig. 4A). Other salamanders (i.e., the slimy salamander [*Plethodon glutinosus*] complex) will show similar behavior while excreting sticky white secretions from their tails (von Byern et al. 2017).

In insects, some of the most common deimatic displays involve using false eyespots (Stevens 2005). Some amphibians appear to employ similar tactics, although the effects of putative eyespots as an antipredator defense are poorly understood. In insects, false eyespots are thought to mimic predator eyes, thus startling predators into thinking that the prey may in turn be their predator (De Bona et al. 2015).



Figure 4. Putative deimatism in amphibians. (A) *Notophthalmus viridescens*; (B) *Edalorhina perezii*; (C) *Phyllomedusa* sp.; (D) *Pseudophryne dendyi*; (E) *Pseudophryne semimarmorata*; (F) *Melanophryniscus admirabilis*; (G) *Litoria adelaidensis*; (H) *Dendropsophus marmoratus*; (I) *Pleurodema brachyops*. Image Credits: J.P. Lawrence A, B, D, E, G, H; Daniela Rößler C; Natália D. Vargas F; Luis Alberto Rueda I.

Several species of frogs are known to have eye spots in their groin which are made visible when the frog inflates itself in defense and raises the inferior part of its body. The best examples of these putative deimatic displays using eye spots seem to occur in Leiuperinae, with a number of species displaying coevolution of lumbar glands and eye-like coloration (Ferraro et al. 2020). *Physalaemus nattereri* has black eye spots that correspond with poison glands (Ferraro et al. 2020). Likewise, *Pleurodema*

brachyops (as well as other *Pleurodema*) have lumbar glands with contrasting colors resembling eye spots (Fig. 4I, Martins 1989). *Edalorhina perezii*, notably, has conspicuous black spots in its groin surrounded by yellow which could serve as a reasonable mimic for eyes (Fig. 4B), and thus may protect them from predation. While most research into eye spots in *E. perezii* and other frogs suggests defensive purposes, little empirical work has been conducted to examine the effect of these displays on predators.

Visual Illusions

Visual illusions, where pattern (often coupled with movement) causes difficulty in identification of prey species or their trajectory, are another form of protection against predators. Many snakes, for example, display longitudinal stripes which, when moving through vegetation like grass, may hamper predators' ability to identify the head of the snake (Murali and Kodandaramaiah 2016). Furthermore, many snakes have latitudinal bands which may produce a flicker fusion effect when in movement (Jackson et al. 1976); this illusion can confuse predators, too (Titcomb et al. 2014).

While such patterns are not common in amphibians, they may still employ visual illusions. The dyeing poison frog (*Dendrobates tinctorius*, Fig. 3E), while aposematic, has a highly variable pattern, from longitudinal stripes to interrupted markings, which appear to be associated to different types of movement (i.e., frogs with longitudinal elongated patterns move directionally and at a higher speed than frogs with blotched patterns; Rojas et al. 2014). This association has been suggested to be able to generate the so-called motion dazzle, which is thought to create an illusion of immobility or reduced speed that makes difficult for aerial predators to strike a successful attack on the moving prey (Stevens et al. 2011). While a recent experimental approach did not find support for striped patterns to get increased protection from predators in comparison to interrupted patterns, the authors found that patterned prey are harder to catch than their pattern-less counterparts (Hämäläinen et al. 2015). Similarly, the brightly-colored yellow-and-black striped southern corroboree frog (*Pseudophryne corroboree*) was originally thought to be aposematic, but recent evidence suggests that the pattern may actually be cryptic, particularly from a distance, in the alpine grasses in which they are typically found (Umbers et al. 2019). Notably, Umbers et al. (2019) proposed the potential crypsis of corroboree frog (Fig. 3F) patterns using stationary models. Given the longitudinal dorsal stripes of this species, however, it could be that such a pattern allows for a visual illusion. Among the different types of anti-predator coloration discussed, visual illusions in amphibians is likely least known, though may be most fruitful for research given the broad array of color and pattern found in amphibians.

Sexual Selection on Amphibian Coloration

Sexual selection is perhaps the least-studied aspect in relation to amphibian coloration, possibly because of the prevalence of other sensory modalities (e.g., chemical, acoustic; see Chapters 10 and 11) in mating interactions among amphibians. To date, some of the studies addressing the potential link between colour patterns and sexual selection in urodeles have demonstrated that colors are used in interactions between

males and females (Rojas 2017). For example, Secondi et al. (2012) showed the role of UV reflectance in mate choice in the newt *Lissotriton vulgaris*, whereby males appeared less attractive in the absence of UV (Secondi et al. 2012). Eastern red-backed salamanders (*Plethodon cinereus*) are polymorphic for color patterns (striped and unstriped) throughout part of their range. Field and laboratory experiments suggest that striped males are more attractive to females, which may contribute to positive assortative mating in the wild (Acord et al. 2013).

While acoustic signals are known to be the prominent signal type used during anuran mating (Chapter 11), there is growing evidence that colors may be involved in mating, too, particularly in diurnal species. Among diurnal frogs, *Oophaga pumilio* is inarguably the species in which visual mate choice has stimulated most research (Fig. 5F). In choice experiments done in the laboratory under controlled conditions, *O. pumilio* females have been shown to prefer males with higher dorsal brightness (Maan and Cummings 2009), suggesting that females pay attention to males' dorsal coloration when choosing a mate (Summers et al. 1999, Maan and Cummings 2008, Dreher et al. 2017). Given their extensive geographic variation in coloration, a few studies have also directly addressed whether this variation is maintained via assortative mating for colors. When presented with males from two different color morphs, representing two different populations, females were more likely to spend time with the male from their own population (Summers et al. 1999, Reynolds and Fitzpatrick 2007). A series of studies addressing similar questions using molecular pedigrees (Richards-Zawacki et al. 2012) or intensive field observations (Yang et al. 2019) indicate that the assortative mating found in the laboratory does not necessarily reflect the patterns seen in the field, and that assortative mate preferences might occur among (some) populations, but not within the same population (Yang et al. 2016, Dreher et al. 2017, but see Gade et al. 2016 for an example of color assortative mating operating in the wild, in a mainland population). This has highlighted the need for more field studies to get a better idea of the role of color patterns in mating interactions under natural conditions. Interestingly, it has been recently shown that *Oophaga pumilio* males and females can imprint on coloration, which has important and previously unexplored implications in potential speciation processes (Yang et al. 2019).

Colors have also been shown to play a role in mate choice of non-diurnal frog species. This is not as surprising as it intuitively seems, as frogs have been shown to use a dual rod system to discriminate colors at the visual threshold (Yovanovich et al. 2017, Donner and Yovanovich 2020), and to respond to some color cues under low light (Gomez et al. 2010). For instance, Gomez et al. (2009) used video playbacks of frogs emitting identical calls but differing in the color and brightness of their vocal sac to demonstrate that female *Hyla arborea* are more attracted to males with a more colorful sac and salient lateral stripe (Fig. 5G); these two traits are thought to enhance male conspicuousness when combined. Interestingly, the authors hypothesized that carotenoid-based colors in the vocal sac may provide information about male quality, given that carotenoid production has proven to be costly (Gomez et al. 2009). Female *Hyla squirrella* appear to be more attracted to males with larger lateral stripes when presented with two models differing in the size of lateral stripes but emitting identical calls (Taylor et al. 2007) and in *Scaphiopus couchii*, male color patterns are reliable



Figure 5. Amphibian species which display sexual dichromatism or engage in sexual selection based on color. (A) *Hoplobatrachus tigerinus*; (B-C) *Rana arvalis*; (D) *Incilius luetkenii*; (E) *Ambystoma opacum*; (F) Pair of *Oophaga pumilio* in courtship; (G) *Hyla arborea*. Image Credits: Doris Preininger A; Christoph Leeb B, C; Daniel Mennill D; J.P. Lawrence E; Andrius Pašukonis F; Susi Stückler G.

indicators of body size, which may in turn be used as an indicator of male quality by females. Indeed, females have been shown to prefer brighter males (Vasquez and Pfennig 2007). In the Puerto Rican cave-dwelling frog, *Eleutherodactylus cooki*, males with larger proportions of their venter covered with yellow had the highest reproductive success (Burrowes 2000). Interestingly, those males with the highest amount of yellow coloration suffer, too, the highest parasitization by ticks (Longo et al. 2020). For some other species the role of color patterns is not as clear cut, but there is increasing evidence pointing at an important role in species recognition, female choice and male-male competition in species such as *Agalychnis callidryas* (Jacobs et al. 2017) and, possibly, other phyllomedusines (Robertson and Greene 2017).

Interesting cases highlighting the role of coloration in sexual selection involve species with so-called dynamic sexual dichromatism, a term first coined by Doucet and Mennill (2010). These species, which are often explosive breeders (i.e., species that breed during just one or a few days during the year, following torrential rain),

exhibit some of the most fascinating behavioral and phenotypic changes to ensure either species or sex recognition, or both (e.g., Ries et al. 2008, Szatecsny et al. 2012). The Neotropical toad *Incilius luetkenii* (Fig. 5D), for example, forms breeding aggregations around temporary ponds at the start of the rainy season. Males call to attract females and, along with their vocalizations, they change their color from a dull brown to bright yellow (Doucet and Mennill 2010). Using frog models with brown or yellow coloration, the authors demonstrated that, regardless of the time of the day (i.e., both during the day and during the night), males were more likely to attempt amplexing brown models than their brown counterparts, suggesting that color plays a crucial role in sex discrimination in the large aggregations formed during their brief breeding period (Rehberg-Besler et al. 2015). Females, on the other hand, do not seem to show any preference for either yellow or brown males, indicating the female choice is not a driver of male color change (Gardner et al. 2021).

Sex differences in coloration have been reported for numerous amphibian species (e.g., Bell and Zamudio 2012, Bell et al. 2017) but, despite an increasing number of studies, the function, evolution and mechanisms of maintenance of amphibian sexual dichromatism are still poorly understood. Darwin's frogs (*Rhinoderma darwinii*), for example, are sexually dimorphic for color patterns, such that males, particularly at the brooding stage, are greener. Females, on the other hand, are mainly brown (Bourke et al. 2011). Reed frogs (Hyperolidae) have striking sexual dimorphism in coloration, which is linked to rapid diversification and, presumably, speciation by sexual selection (Portik et al. 2019), and *Epidalea calamita* toads (Zamora-Camacho and Comas 2019) exhibit a sexual dichromatism in which differences in coloration also seem to be linked to habitat, morphology and locomotor performance. However, the function of these differences in coloration between males and females remain unknown. Interestingly, in the golden rocket frog (*Anomaloglossus beebei*), females are the colorful sex, exhibiting a bright golden coloration that contrasts with the brownish coloration of males (Engelbrecht-Wiggans and Tumulty 2019). While the authors suggest that these colors may serve intraspecific communication purposes, no evidence has been provided yet to confirm their hypothesis.

That is also the case in urodeles where, despite the occurrence of sexual dichromatism, conclusive evidence on the significance of such differences between the sexes is, for most part, still lacking. In the spotted salamander, *Ambystoma maculatum*, males have a larger spotted dorsal area and less bright yellow than females (Morgan et al. 2014), while in the marbled salamander, *A. opacum*, males exhibit whiter and a higher proportion of dorsal white coloration (Todd and Davis 2007, Pokhrel et al. 2013, Fig. 5E). Male fire salamanders, *Salamandra salamandra*, exhibit significantly larger yellow spots (Balogová and Uhrin 2015) and a larger yellow-to-black ratio than females, but no differences between the sexes have been found in color traits such as hue, saturation or brightness (Balogová and Uhrin 2015).

Intra-specific Competition in Relation to Coloration

Colors can influence the outcome of agonistic interactions in several taxa, where they are known to be reliable signals of status (e.g., Gerald 2001, Pryke et al. 2001, Whiting et al. 2006). Among amphibians, this aspect has been less studied than

in other groups, but there are a few examples going in the same direction. Again, possibly the most studied species in that respect is *Oophaga pumilio*, whose coloration (brightness, in particular) appears to be a reliable indicator of aggressiveness that influences the outcome of agonistic encounters (Crothers et al. 2011, Galeano and Harms 2015, Crothers and Cummings 2015). However, field observations seem to point at factors (e.g., prior residency status) other than color as the determinants of the outcome of agonistic interactions (Yang et al. 2020). Also, populations with individuals conspicuously colored tend to have higher levels of aggressiveness than populations with duller individuals (Rudh et al. 2013). Interestingly, these trends about the role of color in agonistic encounters do not apply only to males. A recent review on frogs of the genus *Mannophryne* reported the females of all known species have a yellow throat with a dark collar whereas in eight of them males change their color to black when vocalizing, showcasing interesting instances of both ontogenetic and dynamic color change, which warrants further investigation (Greener et al. 2020). In *Mannophryne trinitatis*, for example, agonistic encounters between females involve a female adopting an upright posture and pulsating her yellow-colored throat facing an intruder (Wells 1980). However, the role of coloration on female aggressive behavior remains an understudied topic, particularly considering the many instances of reported agonistic interactions between females in species of colorful frogs (e.g., *Dendrobates auratus*, Summers 1989; *Oophaga pumilio*, Meuche et al. 2011; *D. tinctorius*, Rojas and Pašukonis 2019).

Areas of Future Research

Amphibians use coloration in a number of different ways, many of which are very well studied, but we would like to highlight a few areas deserving further research, as well as caution for inferences without further research. Biofluorescent animals have been increasingly discovered in recent years, garnering headlines in scientific and popular media (e.g., platypus, Anich et al. 2020; geckos, Protzel et al. 2021). Amphibians joined the ranks of biofluorescent animals when researchers discovered that the polkadot tree frog (*Boana punctata*, Fig. 1C) fluoresces under moonlight conditions (Taboada et al. 2017a; see section Physiological Chlorosis and Fluorescence). Further work has shown that fluorescence is widespread across amphibians, at least under artificial UV stimulation (Lamb and Davis 2020). These discoveries are intriguing and novel, and open promising future research avenues on both the organismal and ecological functions of fluorescence in amphibians. For example, work to determine how much fluorescent light is emitted under biologically relevant ambient light conditions, or whether animals interacting with fluorescent signals alter behavior based on the presence or absence of such signals could provide insights on whether amphibian biofluorescence is involved in inter- or intraspecific communication.

Notably, understanding coloration in amphibians where color is not obviously advantageous (i.e., fossorial or nocturnal species) appears to be particularly challenging. For example, the most fossorial group of amphibians, the caecilians, are poorly understood in this regard, which as noted above, is likely due to their secretive nature. Like many caecilians, a number of fossorial frogs (i.e., many

myobatrachids and microhylids) display distinct coloration that could potentially serve important functionality in their survival. Conspicuous coloration in fossorial, or even nocturnal, species is a puzzling phenomenon ripe for further research on how amphibians use coloration. Likewise, salamanders show remarkable diversity in coloration, but with the exception of a few notable species (i.e., *Taricha granulosa*, *Plethodon cinereus*), relatively little study has been conducted on the wide multitude of salamander species, most of whom are fossorial or nocturnal.

As mentioned above, an emerging area of research elsewhere in the field of color biology is that of deimatic displays. These remarkably effective displays are common in other taxa, particularly insects, but have received relatively little attention in amphibians, offering an exciting avenue of research that can provide insight into the dynamic function of coloration.

Our understanding of color, its use and evolution in amphibians, is derived from a relatively small sampling of one of the largest animal clades, which has a particular overrepresentation in frogs. Indeed, even this has been instrumental in providing understanding of everything from cell function and ontogeny to evolution of coloration across the animal kingdom. Amphibians, with their broad array of habits and lifestyles, are frequently models in understanding biology. No different should this be for understanding coloration, its development, evolution, and function.

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References

- Acord, M.A., C.D. Anthony and C.-A.M. Hickerson. 2013. Assortative mating in a polymorphic salamander. *Copeia* 2013: 676–683.
- Allen, B.M. 1916. The results of extirpation of the anterior lobe of the hypophysis and of the thyroid of *Rana pipiens* larvae. *Science* 44: 755–758.
- Altincicek, B., J.L. Kovacs and N.M. Gerardo. 2012. Horizontally transferred fungal carotenoid genes in the two-spotted spider mite *Tetranychus urticae*. *Biol. Lett.* 8: 253–257.
- Andrade, P., C. Pinho, G.P. i de Lanuza, S. Afonso, J. Brejcha, C.J. Rubin et al. 2019. Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. *PNAS* 116: 5633–5642.
- Anich, P.S., S. Anthony, M. Carlson, A. Gunnelson, A.M. Kohler, J.G. Martin et al. 2021. Biofluorescence in the platypus (*Ornithorhynchus anatinus*). *Mammalia* 85: 179–181.
- Arbuckle, K. and M.P. Speed. 2015. Antipredator defenses predict diversification rates. *PNAS* 112: 13597–13602.
- Arun, D., S. Sandhya, M.A. Akbarsha, O.V. Oommen and L. Divya. 2020. An insight into the skin glands, dermal scales and secretions of the caecilian amphibian *Ichthyophis beddomei*. *Saudi J. Biol. Sci.* 27: 2683–2690.
- Aspengren, S., D. Hedberg, H.N. Sköld and M. Wallin. 2009. New insights into melanosome transport in vertebrate pigment cells. *Int. Rev. Cell Mol. Biol.* 272: 245–302.

- Bagnara, J.T. 1966. Cytology and cytophysiology of non-melanophore pigment cells. *Int. Rev. Cytol.* 20: 173–205.
- Bagnara, J.T., J.D. Taylor and M.E. Hadley. 1968. The dermal chromatophore unit. *J. Cell Biol.* 38: 67–79.
- Bagnara, J.T., J.D. Taylor and G. Prota. 1973. Color changes, unusual melanosomes, and a new pigment from leaf frogs. *Science* 182: 1034–1035.
- Bagnara, J.T., S.K. Frost and J. Matsumoto. 1978. On the development of pigment patterns in amphibians. *Am. Zool.* 18: 301–312.
- Bagnara, J.T. 2003. Enigmas of pterorhodin, a red melanosomal pigment of tree frogs. *Pigm. Cell Res.* 16: 510–516.
- Bagnara, J.T. and J. Matsumoto. 2006. Comparative anatomy and physiology of pigment cells in nonmammalian tissues. pp. 11–59. *In: Nordlund, J.J., R.E. Boissy, V.J. Hearing, R.A. King, W.S. Oetting and J. Ortonne [eds.]. The Pigmentary System.* Blackwell Publishing Ltd, Oxford, UK.
- Bagnara, J.T., P.J. Fernandez and R. Fujii. 2007. On the blue coloration of vertebrates. *Pigm. Cell Res.* 20: 14–26.
- Bajger, J. 1980. Diversity of defensive responses in populations of fire toads (*Bombina bombina* and *Bombina variegata*). *Herpetologica* 36: 133–137.
- Balogová, M. and M. Uhrin. 2015. Sex-biased dorsal spotted patterns in the fire salamander (*Salamandra salamandra*). *Salamandra* 51: 12–18.
- Barnett, J.B., C. Michalis, N.E. Scott-Samuel and I.C. Cuthill. 2018. Distance-dependent defensive coloration in the poison frog *Dendrobates tinctorius*, Dendrobatidae. *PNAS* 115: 6416–6421.
- Barnett, J.B., C. Michalis, N.E. Scott-Samuel and I.C. Cuthill. 2021. Colour pattern variation forms local background matching camouflage in a leaf-mimicking toad. *J. Evol. Biol.* 34: 1531–1540.
- Barrio, A. 1965. Cloricia fisiológica en batracios anuros. *Physis* 25: 137–142.
- Beckerle M.C. and K.R. Porter. 1983. Analysis of the role of microtubules and actin in erythrophore intracellular motility. *J. Cell Biol.* 96:354–62.
- Bell, R.C. and K.R. Zamudio. 2012. Sexual dichromatism in frogs: natural selection, sexual selection and unexpected diversity. *Proc. R. Soc. B* 279: 4687–4693.
- Bell, R.C., G.N. Webster and M.J. Whiting. 2017. Breeding biology and the evolution of dynamic sexual dichromatism in frogs. *J. Evol. Biol.* 30: 2104–2115.
- Belt, T. 1874. *The naturalist in Nicaragua: a narrative of a residence at the gold mines of Chontales; journeys in the savannahs and forests. With observations on animals and plants in reference to the theory of evolution of living forms.* J. Murray, London, UK.
- Bennett, D.C. and M.L. Lamoreux. 2003. The color loci of mice--a genetic century. *Pigm. Cell Res.* 16: 333–344.
- Beukema, W., A.G. Nicieza, A. Lourenço and G. Velo-Antón. 2016. Colour polymorphism in *Salamandra salamandra* (Amphibia: Urodela), revealed by a lack of genetic and environmental differentiation between distinct phenotypes. *J. Zool. Syst. Evol. Res.* 54: 127–136.
- Blount, J.D., M.P. Speed, G.D. Ruxton and P.A. Stephens. 2009. Warning displays may function as honest signals of toxicity. *Proc. R. Soc. B* 276: 871–877.
- Bond, A.B. and A.C. Kamil. 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* 415: 609–613.
- Bond, A.B. and A.C. Kamil. 2006. Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *PNAS* 103: 3214–3219.
- Bond, A.B. 2007. The evolution of color polymorphism: Crypticity searching images, and apostatic selection. *Annu. Rev. Ecol. Evol. Syst.* 38: 489–514.
- Bolton, S.K., K. Dickerson and R. Saporito. 2017. Variable alkaloid defenses in the dendrobatid poison frog *Oophaga pumilio* are perceived as differences in palatability to arthropods. *J. Chem. Ecol.* 43: 273–289.
- Bonett, R.M. and A.L. Blair. 2017. Evidence for complex life cycle constraints on salamander body form diversification. *PNAS* 114: 9936–9941
- Bordignon, D.W., V.Z. Caorsi, P. Colombo, M. Abadie, I.V. Brack, B.T. Dasoler et al. 2018. Are the unken reflex and the aposematic colouration of Red-Bellied Toads efficient against bird predation? *PloS One* 13: e0193551.
- Bourke, J., K.C. Busse and T.M. Bakker. 2011. Sex differences in polymorphic body coloration and dorsal pattern in Darwin's frogs (*Rhinoderma darwinii*). *Herpetol. J.* 21: 227–234.

- Brandon, R.A. and J.E. Huheey. 1975. Diurnal activity, avian predation, and the question of warning coloration and cryptic coloration in salamanders. *Herpetologica* 31: 252–255.
- Brandon, R.A., G.M. Labanick and J.E. Huheey. 1979a. Learned avoidance of brown efts, *Notophthalmus viridescens louisianensis* (Amphibia, Urodela, Salamandridae), by chickens. *J. Herpetol.* 13: 171–176.
- Brandon, R.A., G.M. Labanick and J.E. Huheey. 1979b. Relative palatability, defensive behavior, and mimetic relationships of Red Salamanders (*Pseudotriton ruber*), Mud Salamanders (*Pseudotriton montanus*), and Red Efts (*Notophthalmus viridescens*). *Herpetologica* 35: 289–303.
- Brodie, E.D. 1968. Investigations on the skin toxin of the red-spotted newt, *Notophthalmus viridescens viridescens*. *Am. Midl. Nat.* 80: 276–280.
- Brodie, Jr., E.D., J.L. Hensel Jr. and J.A. Johnson. 1974. Toxicity of the urodele amphibians *Taricha*, *Notophthalmus*, *Cynops* and *Paramesotriton* (Salamandridae). *Copeia* 506–511.
- Brodie, Jr., E.D. 1977. Salamander antipredator postures. *Copeia* 523–535.
- Brodie, E.D., Jr. and E.D. Brodie 3rd. 1980. Differential avoidance of mimetic salamanders by free-ranging birds. *Science* 208: 181–182.
- Brodie, E.D. 1983. Antipredator adaptations of salamanders: evolution and convergence among terrestrial species. pp. 109–133. In *Adaptations to terrestrial environments*. Springer, Boston, MA, USA.
- Bueno-Villafane, D., A. Caballero-Gini, M. Ferreira, F. Netto, D.F. Rios and F. Brusquetti. 2020. Ontogenetic changes in the ventral colouration of post metamorphic *Elachistocleis haroi* Pereyra, Akmentins, Laufer, Vaira, 2013 (Anura: Microhylidae). *Amph.- Rept.* 41: 191–200.
- Bulbert, M.W., T.E. White, R.A. Saporito and F. Kraus. 2018. Ontogenetic colour change in *Oreophryne ezra* (Anura: Microhylidae) reflects an unusual shift from conspicuousness to crypsis but not in toxicity. *Biol. J. Linn. Soc.* 123: 12–20.
- Burrowes, P.A. 2000. Parental care and sexual selection in the Puerto Rican cave-dwelling frog, *Eleutherodactylus cooki*. *Herpetologica* 56: 375–386.
- von Byern, J., C. Müller, K. Voigtländer, V. Dorner, M. Marchetti-Deschmann, P. Flammang et al. 2017. Examples of bioadhesives for defence and predation. pp. 141–191. In: Gorb, S.N. and E.V. Gorb [eds.]. *Functional Surfaces in Biology III*. Springer, Cham, Switzerland.
- Byers, H.R. and K.R. Porter. 1977. Transformations in the structure of the cytoplasmic ground substance in erythrocytes during pigment aggregation and dispersion: I. a study using whole-cell preparations in stereo high voltage electron microscopy. *J. Cell Biol.* 75: 541–558.
- Cabello Ruz, J. 1943. Biliverdinemia del sapo. *Rev. Soc. Arg. Biol.* 19: 81–93.
- Carvajal-Castro, J.D., F. Vargas-Salinas, S. Casas-Cardona, B. Rojas and J.C. Santos. 2021. Aposematism facilitates the diversification of parental care strategies in poison frogs. *Sci. Rep.* 11: 19047.
- Casas-Cardona, S., R. Márquez and F. Vargas-Salinas. 2018. Different colour morphs of the poison frog *Andinobates bombetes* (Dendrobatidae) are similarly effective visual predator deterrents. *Ethology* 124: 245–255.
- Castroviejo-Fisher, S., J.M. Guayasamin, A. Gonzalez-Voyer and C. Vilà. 2014. Neotropical diversification seen through glassfrogs. *J. Biogeogr.* 41: 66–80.
- Chiari, Y., M. Vences, D.R. Vieites, F. Rabemananjara, P. Bora, O. Ramilijaona et al. 2004. New evidence for parallel evolution of colour patterns in Malagasy poison frogs (*Mantella*). *Mol. Ecol.* 13: 3763–3774.
- Chouteau, M., K. Summers, V. Morales and B. Angers. 2011. Divergence in Mullerian mimicry: the case of the poison dart frogs of Northern Peru revisited. *Biol. Lett.* 7: 796–800.
- Clark, V.C., C.J. Raxworthy, V. Rakotomalala, P. Sierwald and B.L. Fisher. 2005. Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the Neotropics. *PNAS* 102: 11617–11622.
- Colleran, E. and P. O'Carra. 1977. Enzymology and comparative physiology of biliverdin reduction. pp. 69–80. In: Berk, P.D. and N.I. Berlin [eds.]. *Chemistry and Physiology of Bile Pigments*. Dept. of Health, Education, and Welfare, Public Health Service, National Institutes of Health, Bethesda, Md, U.S.
- Cornelius, C.E. 1991. Bile pigments in fishes: A review. *Vet. Clin. Pathol.* 20: 106–116.
- Cox, C.L., J. Bowers, C. Obialo, J.D. Curlis and J.W. Streicher. 2020. Spatial and temporal dynamics of exuberant colour polymorphism in the southern cricket frog. *J. Nat. Hist.* 54: 2249–2264.

- Crothers, L., E. Gering and M. Cummings. 2011. Aposematic signal variation predicts male–male interactions in a polymorphic poison frog. *Evolution* 65: 599–605.
- Crothers, L., R.A. Saporito, J. Yeager, K. Lynch, C. Friesen, C.L. Richards-Zawacki et al. 2016. Warning signal properties covary with toxicity but not testosterone or aggregate carotenoids in a poison frog. *Evol. Ecol.* 30: 601–621.
- Crothers, L.R. and M.E. Cummings. 2013. Warning signal brightness variation: sexual selection may work under the radar of natural selection in populations of a polytypic poison frog. *Am. Nat.* 181: E116–E124.
- Crothers, L.R. and M.E. Cummings. 2015. A multifunctional warning signal behaves as an agonistic status signal in a poison frog. *Behav. Ecol.* 26: 560–568.
- Csordas, A. and H. Michl. 1969. Primary structure of two oligopeptides of the toxin of *Bombina variegata* L. *Toxicon* 7: 103–108.
- D’Alba, L. and M.D. Shawkey. 2019. Melanosomes: Biogenesis, properties, and evolution of an ancient organelle. *Physiol. Rev.* 99: 1–19.
- D’Ischia, M., K. Wakamatsu, F. Cicoira, E. Di Mauro, J.C. Garcia-Borrón, S. Commo et al. 2015. Melanins and melanogenesis: From pigment cells to human health and technological applications. *Pigm. Cell Melan. Res.* 28: 520–544.
- De Bona, S., J.K. Valkonen, A. López-Sepulcre and J. Mappes. 2015. Predator mimicry, not conspicuousness, explains the efficacy of butterfly eyespots. *Proc. R. Soc. B* 282: 20150202.
- Donner, K. and C.A. Yovanovich. 2020. A frog’s eye view: Foundational revelations and future promises. *Semin. Cell Dev. Biol.* 106: 72–85.
- Doucet, S.M. and D.J. Mennill. 2010. Dynamic sexual dichromatism in an explosively breeding Neotropical toad. *Biol. Lett.* 6: 63–66.
- Dreher, C.E., A. Rodríguez, M.E. Cummings and H. Pröhl. 2017. Mating status correlates with dorsal brightness in some but not all poison frog populations. *Ecol. Evol.* 7: 10503–10512.
- Duellman, W.E. and P.M. Ruiz-Carranza. 1986. Ontogenetic polychromatism in marsupial frogs (Anura: Hylidae). *Caldasia* 15: 617–627.
- Dunlap, D.G. 1955. Inter- and intraspecific variation in Oregon frogs of the genus *Rana*. *Am. Midl. Nat.* 54: 314–331.
- DuShane, G.P. 1935. An experimental study of the origin of pigment cells in Amphibia. *J. Exp. Zool.* 72: 1–31.
- DuShane, G.P. 1943. The embryology of vertebrate pigment cells. Part I. Amphibia. *Q. Rev. Biol.* 18: 109–127.
- Ehrmann, S. 1892. Beitrag zur Physiologie der Pigmentzellen nach Versuchen am Farbenwechsel der Amphibien. *Archiv Dermatol. Syph.* 24: 519–539.
- Endler, J.A. 1988. Frequency-dependent predation, crypsis and aposematic coloration. *Phil. Trans. R. Soc. Lond. B* 319: 505–523.
- Endler, J.A. and J. Mappes. 2004. Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* 163: 532–547.
- Engelbrecht-Wiggans, E. and J.P. Tumulty. 2019. “Reverse” sexual dichromatism in a Neotropical frog. *Ethology* 125: 957–964.
- Eom, D.S., S. Inoue, L.B. Patterson, T.N. Gordon, R. Slingwine, S. Kondo et al. 2012. Melanophore migration and survival during zebrafish adult pigment stripe development require the immunoglobulin superfamily adhesion molecule Igsf11. *PLoS Genetics* 8: e1002899.
- Eom, D.S., E.J. Bain, L.B. Patterson, M.E. Grout and D.M. Parichy. 2015. Long-distance communication by specialized cellular projections during pigment pattern development and evolution. *eLife* 4: 1–25.
- Everts, R.E., J. Rothuizen and B.A. van Oost. 2000. Identification of a premature stop codon in the melanocyte-stimulating hormone receptor gene (MC1R) in Labrador and Golden retrievers with yellow coat colour. *Anim. Gen.* 31: 194–199.
- Eycleshymer, A.C. 1906. The development of chromatophores in *Necturus*. *Am. J. Anat.* 5: 309–313.
- Feng, Y.-J., D.C. Blackburn, D. Liang, D.M. Hillis, D.B. Wake, D.C. Cannatella et al. 2017. Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *PNAS* 114: E5864–E5870.
- Fernandez, P.J. and J.P. Collins. 1988. Effect of environment and ontogeny on color pattern variation in Arizona tiger salamanders (*Ambystoma tigrinum nebulosum* Hallowell). *Copeia* 1988: 928–938.

- Fernandez, P.J. and J.T. Bagnara. 1991. Effect of background color and low temperature on skin color and circulating α -MSH in two species of leopard frog. *Gen. Comp. Endocrinol.* 83: 132–141.
- Ferraro, D.P., M.O. Pereyra, P.E. Topa and J. Faivovich. 2021. Evolution of macroglands and defensive mechanisms in Leiuperinae (Anura: Leptodactylidae). *Zool. J. Linn. Soc.* 193: 388–412.
- Fischer, E.K., A.B. Roland, N.A. Moskowitz, C. Vidoudez, N. Ranaivorazo, E.E. Tapia et al. 2019. Mechanisms of convergent egg provisioning in poison frogs. *Curr. Biol.* 29: 4145–4151.
- Fogleman, J.C., P.S. Corn and D. Pettus. 1980. The genetic basis of a dorsal color polymorphism in *Rana pipiens*. *J. Hered.* 71: 439–440.
- Frohnhofer, H.G., J. Krauss, H.M. Maischein and C. Nüsslein-Volhard. 2013. Iridophores and their interactions with other chromatophores are required for stripe formation in zebrafish. *Development* 140: 2997–3007.
- Frost, S.K. and J.T. Bagnara. 1979. Allopurinol-induced melanism in the tiger salamander (*Ambystoma tigrinum nebulosum*). *J. Exp. Zool.* 209: 455–465.
- Fujii, R. 1993. Cytophysiology of fish chromatophores. pp. 191–255. *In: Jeon, K.W., M. Friedlander and J. Jarvik [eds.]. International Review of Cytology (Vol. 143).* Academic Press, Cambridge, MA, USA.
- Fukuzawa, T., P. Samaraweera, F.T. Mangano, J.H. Law and J.T. Bagnara. 1995. Evidence that MIF plays a role in the development of pigmentation patterns in the frog. *Dev. Biol.* 167: 148–158.
- Fukuzawa, T. and H. Ide. 1988. A ventrally localized inhibitor of melanization in *Xenopus laevis* skin. *Dev. Biol.* 129: 25–36.
- Gade, M.R., M. Hill and R.A. Saporito. 2016. Color assortative mating in a mainland population of the poison frog *Oophaga pumilio*. *Ethology* 122: 851–858.
- Gage, S.H. 1891. Life-history of the Vermilion-Spotted Newt (*Diemictylus viridescens* Raf.). *Am. Nat.* 25: 1084–1110.
- Galeano, S.P. and K.E. Harms. 2016. Coloration in the polymorphic frog *Oophaga pumilio* associates with level of aggressiveness in intraspecific and interspecific behavioral interactions. *Behav. Ecol. Sociobiol.* 70: 83–97.
- Gally, M., J. Zina, C.V. de Mira-Mendes and M. Solé. 2014. Legs-interweaving: An unusual defense behaviour of anurans displayed by *Agalychnis aspera* (Peters, 1983). *Herpetol. Notes* 7: 623–625.
- Gardner, K.M., D.J. Mennill, L.M. Savi, N.E. Shangi and S.M. Doucet. 2021. Sexual selection in a tropical toad: Do female toads choose brighter males in a species with rapid colour change? *Ethology* 127: 475–483.
- Gerald, M.S. 2001. Primate colour predicts social status and aggressive outcome. *Anim. Behav.* 61: 559–566.
- Goin C.J. 1950. Color pattern inheritance in some frogs of the genus *Eleutherodactylus*. *Bull. Chic. Acad. Sci.* 9: 1–15.
- Gomez, D., C. Richardson, T. Lengagne, S. Plenet, P. Joly, J.P. Léna et al. 2009. The role of nocturnal vision in mate choice: females prefer conspicuous males in the European tree frog (*Hyla arborea*). *Proc. R. Soc. Lond. B* 276: 2351–2358.
- Gomez, D., C. Richardson, T. Lengagne, M. Derex, S. Plenet, P. Joly et al. 2010. Support for a role of colour vision in mate choice in the nocturnal European treefrog (*Hyla arborea*). *Behaviour* 147: 1753–1768.
- Goodwin, T.W. 1984. *The Biochemistry of the Carotenoids (Vol. II: Animal)*. Springer, Dordrecht, Netherlands.
- Goutte, S., I. Hariyani, K.D. Utzinger, Y. Bourgeois and S. Boissinot. 2021. Coloring inside the lines: genomic architecture and evolution of a widespread color pattern in frogs. *BioRxiv*, 2021.10.28.466315.
- Goutte, S., M.J. Mason, M.M. Antoniazzi, C. Jared, D. Merle, L. Cazes et al. 2019. Intense bone fluorescence reveals hidden patterns in pumpkin toadlets. *Sci. Rep.* 9: 428.
- Greener, M.S., E. Hutton, C.J. Pollock, A. Wilson, C.Y. Lam, M. Nokhbatolfighahai et al. 2020. Sexual dichromatism in the neotropical genus *Mannophryne* (Anura: Aromobatidae). *PLoS One* 15: e0223080.
- Gross, J.B., R. Borowsky and C.J. Tabin. 2009. A novel role for Mc1r in the parallel evolution of depigmentation in independent populations of the cavefish *Astyanax mexicanus*. *PLoS Genetics* 5: e1000326.

- Guayasamin, J.M., D.F. Cisneros-Heredia, R.W. McDiarmid, P. Peña and C.R. Hutter. 2020. Glassfrogs of Ecuador: Diversity, evolution, and conservation. *Diversity* 12: 222.
- Guimond, R.W. and V.H. Hutchison. 1973. Trimodal gas exchange in the large aquatic salamander, *Siren lacertina* (Linnaeus). *Comp. Biochem. Physiol. A* 46: 249–268.
- Hairston, N.G. and C.H. Pope. 1948. Geographic variation and speciation in Appalachian salamanders (*Plethodon jordani* group). *Evolution* 2: 266–278.
- Hämäläinen, L., J. Valkonen, J. Mappes and B. Rojas. 2015. Visual illusions in predator–prey interactions: birds find moving patterned prey harder to catch. *Anim. Cogn.* 18: 1059–1068.
- Hämäläinen, L., J. Mappes, H.M. Rowland, M. Teichmann and R. Thorogood. 2020. Social learning within and across predator species reduces attacks on novel aposematic prey. *J. Anim. Ecol.* 89: 1153–1164.
- Hargitt, C.W. 1912. Behavior and color changes of tree frogs. *J. Anim. Behav.* 2: 51–78.
- Harper, G.J., M.K. Steininger, C.J. Tucker, D. Juhn and F. Hawkins. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environ. Conserv.* 34: 325–333.
- Hayes, T.B. and K.P. Menendez. 1999. The effect of sex steroids on primary and secondary sex differentiation in the sexually dichromatic reedfrog (*Hyperolius argus*: Hyperolidae) from the Arabuko Sokoke forest of Kenya. *Gen. Comp. Endocrinol.* 115: 188–199.
- Heatwole, H. and G.T. Barthalmus. 1995. *Amphibian Biology*, vol. 1, The Integument. Surrey, Beatty and Sons, Norton, New South Wales, Australia.
- Hoekstra, H.E. 2006. Genetics, development and evolution of adaptive pigmentation in vertebrates. *Heredity* 97: 222–234.
- Hoffman, E.A. and M.S. Blouin. 2000. A review of colour and pattern polymorphisms in anurans. *Biol. J. Linn. Soc.* 70: 633–665.
- Hofreiter, M. and T. Schöneberg. 2010. The genetic and evolutionary basis of colour variation in vertebrates. *Cell. Mol. Life Sci.* 67: 2591–2603.
- Hooper, D.M., S.C. Griffith and T.D. Price. 2019. Sex chromosome inversions enforce reproductive isolation across an avian hybrid zone. *Mol. Ecol.* 28: 1246–1262.
- Houssay, B.A. 1925. Factores que regulan la pigmentación de la rana “*Leptodactylus ocellatus*” (L) Gir. Imprenta de la Universidad.
- Howard, R.R. and E.D. Brodie, Jr. 1973. A Batesian mimetic complex in salamanders: responses of avian predators. *Herpetologica* 29: 33–41.
- Hubbard, J.K., J.A.C. Uy, M.E. Hauber, H.E. Hoekstra and R.J. Safran. 2010. Vertebrate pigmentation: from underlying genes to adaptive function. *Trends Genet.* 26: 231–239.
- Huheey, J.E. 1960. Mimicry in the color pattern of certain Appalachian salamanders. *J. Elisha Mitchell Sci. Soc.* 76: 246–251.
- Huheey, J.E. and R.A. Brandon. 1974. Studies in warning coloration and mimicry. VI. Comments on the warning coloration of Red Efts and their presumed mimicry by Red Salamanders. *Herpetologica* 30: 149–155.
- Hurlbert, S.H. 1970. Predator responses to the Vermilion-Spotted Newt (*Notophthalmus viridescens*). *J. Herpetol.* 4: 47–55.
- Irion, U., A.P. Singh and C. Nüsslein-Volhard. 2016. The developmental genetics of vertebrate color pattern formation: lessons from zebrafish. *Curr. Top. Dev. Biol.* 117: 141–169.
- Jackson, J.F., W. Ingram III and H.W. Campbell. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. *Am. Nat.* 110: 1029–1053.
- Jacobs, L.E., A. Vega, S. Dudgeon, K. Kaiser and J.M. Robertson. 2017. Local not vocal: assortative female choice in divergent populations of red-eyed treefrogs, *Agalychnis callidryas* (Hylidae: Phyllomedusinae). *Biol. J. Linn. Soc.* 120: 171–178.
- Johnson, J.A. and E.D. Brodie, Jr. 1975. The selective advantage of the defensive posture of the newt, *Taricha granulosa*. *Am. Midl. Nat.* 93: 139–148.
- Kang, C., T.N. Sherratt, Y.E. Kim, Y. Shin, J. Moon, U. Song et al. 2017. Differential predation drives the geographical divergence in multiple traits in aposematic frogs. *Behav. Ecol.* 28: 1122–1130.
- Kelly, H.A. 1878. Identity of *Diemictylus miniatus* with *Diemictylus viridescens*. *Am. Nat.* 12: 399.
- Kemp, N.E. 1961. Replacement of the larval basement lamella by adult-type basement membrane in anuran skin during metamorphosis. *Dev. Biol.* 3: 391–410.

- Kindermann, C. and J.M. Hero. 2016. Pigment cell distribution in a rapid colour changing amphibian (*Litoria wilcoxii*). *Zoomorphology* 135: 197–203.
- Klonoski, K., K. Bi and E.B. Rosenblum. 2019. Phenotypic and genetic diversity in aposematic Malagasy poison frogs (genus *Mantella*). *Ecol. Evol.* 9: 2725–2742.
- Kraemer, A.C. and D.C. Adams. 2014. Predator perception of Batesian mimicry and conspicuousness in a salamander. *Evolution* 68: 1197–1206.
- Kraemer, A.C., J.M. Serb and D.C. Adams. 2015. Batesian mimics influence the evolution of conspicuousness in an aposematic salamander. *J. Evol. Biol.* 28: 1016–1023.
- Kraus, F. and A. Allison. 2009. A remarkable ontogenetic change in color pattern in a new species of *Oreophryne* (Anura: Microhylidae) from Papua New Guinea. *Copeia* 2009: 690–697.
- Kronforst, M.R., G.S. Barsh, A. Kopp, J. Mallet, A. Monteiro, S.P. Mullen et al. 2012. Unraveling the thread of nature's tapestry: the genetics of diversity and convergence in animal pigmentation. *Pigm. Cell Melan. Res.* 25: 411–433.
- Kuchta, S.R. 2005. Experimental support for aposematic coloration in the salamander *Ensatina eschscholtzii xanthoptica*: implications for mimicry of Pacific newts. *Copeia* 2005: 265–271.
- Kuchta, S.R., A.H. Krakauer and B. Sinervo. 2008. Why does the Yellow-eyed *Ensatina* have yellow eyes? Batesian mimicry of Pacific newts (genus *Taricha*) by the salamander *Ensatina eschscholtzii xanthoptica*. *Evolution* 62: 984–990.
- Kuriyama, T., A. Murakami, M. Brandley and M. Hasegawa. 2020. Blue, black, and stripes: Evolution and development of color production and pattern formation in lizards and snakes. *Front. Ecol. Evol.* 8: 232.
- Labanick, G.M. and R.A. Brandon. 1981. An experimental study of Batesian mimicry between the salamanders *Plethodon jordani* and *Desmognathus ochrophaeus*. *J. Herpetol.* 15: 275–281.
- Lamb, J.Y. and M.P. Davis. 2020. Salamanders and other amphibians are aglow with biofluorescence. *Sci. Rep.* 10: 2821.
- Land, M.F. 1972. The physics and biology of animal reflectors. *Prog. Biophys. Mol. Biol.* 24: 75–106.
- Lawrence, J.P., M. Mahony and B.P. Noonan. 2018. Differential responses of avian and mammalian predators to phenotypic variation in Australian Brood Frogs. *PLoS One* 13: e0195446.
- Lawrence, J.P., B. Rojas, A. Fouquet, J. Mappes, A. Blanchette, R.A. Saporito et al. 2019. Weak warning signals can persist in the absence of gene flow. *PNAS* 116: 19037–19045.
- Lechaire, J.P. and J.P. Deneffe. 1991. Dermal breaks: Migratory cell pathways opened in anuran tadpole skin at climactic metamorphosis. *Tiss. Cell* 23: 307–315.
- Ligon, R.A. and K.L. McCartney. 2016. Biochemical regulation of pigment motility in vertebrate chromatophores: A review of physiological color change mechanisms. *Curr. Zool.* 62: 237–252.
- Löhner, L. 1919. Über einen eigentümlichen Reflex der Feuerunken nebst Bemerkungen über die "tierische Hypnose". *Pflüger's Archiv für die gesamte Physiologie des Menschen und der Tiere* 174: 324–351.
- Longo, A.V., C.A. Rodríguez-Gómez, J.P. Zegarra, O. Monzón, H.J. Claudio-Hernández, R.L. Joglar et al. 2020. Tick parasitism as a cost of sexual selection and male parental care in a Neotropical frog. *Ecosphere* 11: e03010.
- Lopes, R.J.J., J.D. Johnson, M.B.B. Toomey, M.S.S. Ferreira, P.M.M. Araujo, J. Melo-Ferreira et al. 2016. Genetic basis for red coloration in birds. *Curr. Biol.* 26: 1427–1434.
- Lorentz, M.N., A.N. Stokes, D.C. Röbber and S. Lötters. 2016. Tetrodotoxin. *Curr. Biol.* 26: R870–R872.
- Maan, M.E. and M.E. Cummings. 2008. Female preferences for aposematic signal components in a polymorphic poison frog. *Evolution* 62: 2334–2345.
- Maan, M.E. and M.E. Cummings. 2009. Sexual dimorphism and directional sexual selection on aposematic signals in a poison frog. *PNAS* 106: 19072–19077.
- Maan, M.E. and M.E. Cummings. 2012. Poison frog colors are honest signals of toxicity, particularly for bird predators. *Am. Nat.* 179: E1–E14.
- Maderspacher, F. and C. Nüsslein-Volhard. 2003. Formation of the adult pigment pattern in zebrafish requires leopard and obelix dependent cell interactions. *Development* 130: 3447–3457.
- Mallet, J. and N. H. Barton. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution* 43: 421–431.
- Mallet, J. and M. Joron. 1999. Evolution of diversity in warning color and mimicry: Polymorphisms, shifting balance, and speciation. *Annu. Rev. Ecol. Syst.* 30: 201–233.

- Mappes, J., N. Marples and J.A. Endler. 2005. The complex business of survival by aposematism. *Trends Ecol. Evol.* 20: 598–603.
- Márquez, R., T.P. Linderoth, D. Mejía-Vargas, R. Nielsen, A. Amézquita and M.R. Kronforst. 2020. Divergence, gene flow, and the origin of leapfrog geographic distributions: The history of colour pattern variation in *Phyllobates* poison-dart frogs. *Mol. Ecol.* 29: 3702–3719.
- Martins, M. 1989. Deimatic behavior in *Pleurodema brachyops*. *J. Herpetol.* 23: 305–307.
- McCollum, S.A. and J. Van Buskirk. 1996. Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla chrysoscelis*. *Evolution* 50: 583–593.
- McCollum, S.A. and J.D. Leimberger. 1997. Predator-induced morphological changes in an amphibian: Predation by dragonflies affects tadpole shape and color. *Oecologia* 109: 615–621.
- McNamara, M.E., V. Rossi, T.S. Slater, C.S. Rogers, A.L. Ducrest, S. Dubey et al. 2021. Decoding the evolution of melanin in vertebrates. *Trends Ecol. Evol.* 36: 430–443.
- Mebs, D., M. Jansen, G. Köhler, W. Pogoda and G. Kauert. 2010. Myrmecophagy and alkaloid sequestration in amphibians: a study on *Ameerega picta* (Dendrobatidae) and *Elachistocleis* sp. (Microhylidae) frogs. *Salamandra* 46: 11–15.
- Michl, H. and E. Kaiser. 1963. Chemie und biochemie der amphibiengifte. *Toxicon* 1: 175–228.
- Millar, S.E., M.W. Miller, M.E. Stevens and G.S. Barsh. 1995. Expression and transgenic studies of the mouse agouti gene provide insight into the mechanisms by which mammalian coat color patterns are generated. *Development* 121: 3223–3232.
- Mills, M.G. and L.B. Patterson. 2009. Not just black and white: Pigment pattern development and evolution in vertebrates. *Semin. Cell Dev. Biol.* 20: 72–81.
- Moran, N.A. and T. Jarvik. 2010. Lateral transfer of genes from fungi underlies carotenoid production in aphids. *Science* 328: 624–627.
- Morgan, S.K., M.W. Pugh, M.M. Gangloff and L. Siefferman. 2014. The Spots of the spotted salamander are sexually dimorphic. *Copeia* 2014: 251–256.
- Moritz, C., C.J. Schneider and D.B. Wake. 1992. Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. *Syst. Biol.* 41: 273–291.
- Moriwaki, T. 1953. The inheritance of the dorso-median stripe in *Rana limnocharis* Wiegmann. *J. Sci. Hiroshima Univ. (Zoology)* 14: 159–164.
- Moskowitz, N.A., A.B. Roland, E.K. Fischer, N. Ranaivorazo, C. Vidoudez, M.T. Aguilar et al. 2018. Seasonal changes in diet and chemical defense in the Climbing Mantella frog (*Mantella laevigata*). *PLoS One* 13: e0207940.
- Mundy, N.I., J. Stapley, C. Bennison, R. Tucker, H. Twyman, K.W. Kim et al. 2016. Red carotenoid coloration in the zebra finch is controlled by a cytochrome P450 gene cluster. *Curr. Biol.* 26: 1435–1440.
- Murali, G. and U. Kodandaramaiah. 2016. Deceived by stripes: conspicuous patterning on vital anterior body parts can redirect predatory strikes to expendable posterior organs. *R. Soc. Open Sci.* 3: 160057.
- Nascimento, A.A., J.T. Roland and V.I. Gelfand. 2003. Pigment cells: a model for the study of organelle transport. *Annu. Rev. Cell Dev. Biol.* 19: 469–491.
- Nielsen, H.I. 1978. Ultrastructural changes in the dermal chromatophore unit of *Hyla arborea* during color change. *Cell Tiss. Res.* 194: 405–418.
- Nielsen, H.I. and J. Dyck. 1978. Adaptation of the tree frog, *Hyla cinerea*, to colored backgrounds, and the role of the three chromatophore types. *J. Exp. Zool.* 205: 79–94.
- Nokelainen, O. and M. Stevens. 2016. Camouflage. *Curr. Biol.* 26: R654–R656.
- Obika, M. and J.T. Bagnara. 1964. Pteridines as pigments in amphibians. *Science* 143: 485–487.
- O’Hanlon, J.C., D.N. Rathnayake, K.L. Barry and K.D.L. Umbers. 2018. Post-attack defensive displays in three praying mantis species. *Behav. Ecol. Sociobiol.* 72: 1–7.
- O’Neill, E.M. and K.H. Beard. 2010. Genetic basis of a color pattern polymorphism in the coqui frog *Eleutherodactylus coqui*. *J. Hered.* 101: 703–709.
- O’Quin C.T., A.C. Drilea, M.A. Conte and T.D. Kocher. 2013. Mapping of pigmentation QTL on an anchored genome assembly of the cichlid fish, *Mtreaclima zebra*. *BMC Genomics.* 14: 287.
- Parichy, D.M. 1996a. Pigment patterns of larval salamanders (Ambystomatidae, Salamandridae): the role of the lateral line sensory system and the evolution of pattern-forming mechanisms. *Dev. Biol.* 175: 265–282.

- Parichy, D.M. 1996b. When neural crest and placodes collide: Interactions between melanophores and the lateral lines that generate stripes in the salamander *Ambystoma tigrinum tigrinum* (Ambystomatidae). *Dev. Biol.* 175: 283–300.
- Parichy, D.M. 1998. Experimental analysis of character coupling across a complex life cycle: pigment pattern metamorphosis in the tiger salamander, *Ambystoma tigrinum tigrinum*. *J. Morphol.* 237: 53–67.
- Parichy, D.M., M.V. Reedy and C.A. Erickson. 2006. Regulation of melanoblast migration and differentiation. pp. 108–139. *In: Nordlund, J.J., R.E. Boissy, V.J. Hearing, R.A. King, W.S. Oetting and J.-P. Ortonne [eds.]. The Pigmentary System and its Disorders (2nd Edition).* Oxford University Press, Oxford, UK.
- Parker, G.H. 1948. Animal colour changes and their neurohumours: a survey of investigations 1910–1943. *Q. Rev. Biol.* 23: 368–369.
- Patterson, L.B. and D.M. Parichy. 2019. Zebrafish pigment pattern formation: insights into the development and evolution of adult form. *Annu. Rev. Genet.* 53: 505–530.
- Pokhrel, L.R., I. Karsai, M.K. Hamed and T.F. Laughlin. 2013. Dorsal body pigmentation and sexual dimorphism in the marbled salamander (*Ambystoma opacum*). *Ethol. Ecol. Evol.* 25: 214–226.
- Portik, D.M., R.C. Bell, D.C. Blackburn, A.M. Bauer, C.D. Barratt, W.R. Branch et al. 2019. Sexual dichromatism drives diversification within a major radiation of African amphibians. *Syst. Biol.* 68: 859–875.
- Posso-Terranova, A. and J. Andrés. 2017. Diversification and convergence of aposematic phenotypes: truncated receptors and cellular arrangements mediate rapid evolution of coloration in harlequin poison frogs. *Evolution* 71: 2677–2692.
- Poulton, E.B. 1890. *The Colours of Animals: their Meaning and Use, especially Considered in the Case of Insects.* Kegan Paul, Trench, Trubner, UK.
- Prates, I., M.M. Antoniazzi, J.M. Sciani, D.C. Pimenta, L.F. Toledo, C.F.B. Haddad et al. 2012. Skin glands, poison and mimicry in dendrobatid and leptodactylid amphibians. *J. Morphol.* 273: 279–290.
- Prötzel, D., M. Heß, M. Schwager, F. Glaw and M.D. Scherz. 2021. Neon-green fluorescence in the desert gecko *Pachydactylus rangei* caused by iridophores. *Sci. Rep.* 11: 297.
- Pryke, S.R., M.J. Lawes and S. Andersson. 2001. Agonistic carotenoid signalling in male red-collared widowbirds: aggression related to the colour signal of both the territory owner and model intruder. *Anim. Behav.* 62: 695–704.
- Rafinesque, C.S. 1820. *Annals of nature or annual synopsis of new genera and species of animals, plants, etc., discovered in North America.* Thomas Smith, Lexington, KY, USA.
- Randrianavelona, R., H. Rakotonjoely, J. Ratsimbazafy and R.K.B. Jenkins. 2010. Conservation assessment of the critically endangered frog *Mantella aurantiaca* in Madagascar. *Afr. J. Herpetol.* 59: 65–78.
- Rehberg-Besler, N., D.J. Mennill and S.M. Doucet. 2015. Dynamic sexual dichromatism produces a sex signal in an explosively breeding Neotropical toad: a model presentation experiment. *Behav. Proc.* 121: 74–79.
- Reynolds, R.G. and B.M. Fitzpatrick. 2007. Assortative mating in poison-dart frogs based on an ecologically important trait. *Evolution* 61: 2253–2259.
- Richards, C.M. 1976. The development of color dimorphism in *Hyperolius v. viridiflavus*, a reed frog from Kenya. *Copeia* 1976: 65–70.
- Richards, C.M. 1982. The alteration of chromatophore expression by sex hormones in the Kenyan reed frog, *Hyperolius viridiflavus*. *Gen. Comp. Endocrinol.* 46: 59–67.
- Richards, C.M. and G.W. Nace. 1983. Dark pigment variants in anurans: classification, new descriptions, color changes and inheritance. *Copeia* 1983: 979–990.
- Richards-Zawacki, C.L., I.J. Wang and K. Summers. 2012. Mate choice and the genetic basis for colour variation in a polymorphic dart frog: inferences from a wild pedigree. *Mol. Ecol.* 21: 3879–3892.
- Ries, C., J. Spaethe, M. Sztatecsny, C. Ströndl and W. Hödl. 2008. Turning blue and ultraviolet: sex-specific colour change during the mating season in the Balkan moor frog. *J. Zool.* 276: 229–236.
- Robertson, J.M. and H.W. Greene. 2017. Bright colour patterns as social signals in nocturnal frogs. *Biol. J. Linn. Soc.* 121: 849–857.
- Rodríguez, A., D. Poth, S. Schulz and M. Vences. 2011. Discovery of skin alkaloids in a miniaturized eleutherodactylid frog from Cuba. *Biol. Lett.* 7: 414–418.

- Rodríguez, A., N.I. Mundy, R. Ibáñez and H. Pröhl. 2020. Being red, blue and green: the genetic basis of coloration differences in the strawberry poison frog (*Oophaga pumilio*). *BMC Genomics* 21: 301.
- Rogers, R.L., L. Zhou, C. Chu, R. Márquez, A. Corl, T. Linderoth et al. 2018. Genomic takeover by transposable elements in the Strawberry poison frog. *Mol. Biol. Evol.* 35: 2913–2927.
- Rojas, B. and J.A. Endler. 2013. Sexual dimorphism and intra-populational colour pattern variation in the aposematic frog *Dendrobates tinctorius*. *Evol. Ecol.* 27: 739–753.
- Rojas, B., P. Rautiala and J. Mappes. 2014a. Differential detectability of polymorphic warning signals under varying light environments. *Behav. Proc.* 109: 164–172.
- Rojas, B., J. Devillechabrolle and J.A. Endler. 2014b. Paradox lost: colour pattern and movement are associated in an aposematic frog. *Biol. Lett.* 10: 20140193.
- Rojas, B. 2017. Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biol. Rev.* 92: 1059–1080.
- Rojas, B., E. Burdfield-Steel, S.P. Gordon, C. De Pasqual, L. Hernández, J. Mappes et al. 2018. Multimodal aposematic signals and their emerging role in mate attraction. *Front. Ecol. Evol.* 9: 93.
- Rojas, B. and A. Pašukonis. 2019. From habitat use to social behavior: natural history of a voiceless poison frog, *Dendrobates tinctorius*. *PeerJ* 7: e7648.
- Rönkä, K., J. Valkonen, O. Nokelainen, B. Rojas, S.P. Gordon, E. Burdfield-Steel et al. 2020. Geographic mosaic of selection by avian predators on hindwing warning colour of a polymorphic aposematic moth. *Ecol. Lett.* 23: 1654–1663.
- Rudh, A. and A. Qvarnström. 2013. Adaptive colouration in amphibians. *Semin. Cell Dev. Biol.* 24: 553–561.
- Rudh, A., M.F. Breed and A. Qvarnström. 2013. Does aggression and explorative behaviour decrease with lost warning coloration? *Biol. J. Linn. Soc.* 108: 116–126.
- Ruxton, G.D., W.L. Allen, T.N. Sherratt and M.P. Speed. 2018. *Avoiding Attack. The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry.* Oxford University Press, Oxford, UK.
- Sanchez, E., H. Pröhl, T. Lüddecke, S. Schulz, S. Steinfartz and M. Vences. 2019. The conspicuous postmetamorphic coloration of fire salamanders, but not their toxicity, is affected by larval background albedo. *J. Exp. Zool. B* 332: 26–35.
- Santos, J.C., L.A. Coloma and D.C. Cannatella. 2003. Multiple, recurring origins of aposematism and diet specialization in poison frogs. *PNAS* 100: 12792–12797.
- Santos, J.C., M. Baquero, C.L. Barrio-Amorós, L.A. Coloma, L.K. Erdtmann, A.P. Lima et al. 2014. Aposematism increases acoustic diversification and speciation in poison frogs. *Proc. R. Soc. B* 281: 20141761.
- Saporito, R.A., M.A. Donnelly, H.M. Garraffo, T.F. Spande and J.W. Daly. 2006. Geographic and seasonal variation in alkaloid-based chemical defenses of *Dendrobates pumilio* from Bocas del Toro, Panama. *J. Chem. Ecol.* 32: 795–814.
- Saporito, R.A., R. Zuercher, M. Roberts, K.G. Gerow and M.A. Donnelly. 2007. Experimental evidence for aposematism in the dendrobatid poison frog *Oophaga pumilio*. *Copeia* 2007: 1006–1011.
- Saunders, L.M., A.K. Mishra, A.J. Aman, V.M. Lewis, M.B. Toomey, J.S. Packer et al. 2019. Thyroid hormone regulates distinct paths to maturation in pigment cell lineages. *eLife* 8: e45181.
- Schiötz, A. 1967. The treefrogs (Rhacophoridae) of West Africa. *Spolia Zool. Musei Haunienses* 25: 1–346.
- Secondi, J., V. Lepetz and M. Théry. 2012. Male attractiveness is influenced by UV wavelengths in a newt species but not in its close relative. *PloS One* 7: e30391.
- Sherratt, T.N. and C.D. Beatty. 2003. The evolution of warning signals as reliable indicators of prey defense. *Am. Nat.* 162: 377–389.
- Shure, D.J., L.A. Wilson and C. Hochwender. 1989. Predation on aposematic efts of *Notophthalmus viridescens*. *J. Herpetol.* 23: 437–439.
- Silverstone, P.A. 1976. A revision of the poison-arrow frogs of the genus *Phylllobates* Bibron in Sagra (Family Dendrobatidae). *Nat. Hist. Mus. Los Angeles County Sci. Bull.* 27: 1–53.
- Skellhorn, J., H.M. Rowland, M.P. Speed and G.D. Ruxton. 2010. Masquerade: camouflage without crypsis. *Science* 327: 51–51.
- Sköld, H.N., S. Aspöngren and M. Wallin. 2012. Rapid color change in fish and amphibians—function, regulation, and emerging applications. *Pigm. Cell Mel. Res.* 26: 29–38.

- Smith, B.P., M.J. Tyler, T. Kaneko, H.M. Garraffo, T.F. Spande and J.W. Daly. 2002. Evidence for biosynthesis of pseudophrynamine alkaloids by an Australian myobatrachid frog (*Pseudophryne*) and for sequestration of dietary pumiliotoxins. *J. Nat. Prod.* 65: 439–447.
- Smith, P.E. 1916. Experimental ablation of the hypophysis in the frog embryo. *Science* 44: 280–282.
- Speed, M.P. 1999. Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evol. Ecol.* 13: 755–776.
- Speed, M.P., M.A. Brockhurst and G.D. Ruxton. 2010. The dual benefits of aposematism: predator avoidance and enhanced resource collection. *Evolution* 64: 1622–1633.
- Stackhouse, H.L. 1966. Some aspects of pteridine biosynthesis in amphibians. *Comp. Biochem. Physiol.* 17: 219–226.
- Stearner, S.P. 1946. Pigmentation studies in salamanders, with special reference to the changes at metamorphosis. *Physiol. Zool.* 19: 375–404.
- Stevens, M. 2005. The role of eyespots as anti-predator mechanisms, principally demonstrated in the Lepidoptera. *Biol. Rev.* 80: 573–588.
- Stevens, M., W.T.L. Searle, J.E. Seymour, K.L. Marshall and G.D. Ruxton. 2011. Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biol.* 9: 1–11.
- Stuckert, A.M.M., P.J. Venegas and K. Summers. 2014. Experimental evidence for predator learning and Müllerian mimicry in Peruvian poison frogs (*Ranitomeya*, Dendrobatidae). *Evol. Ecol.* 28: 413–426.
- Stuckert, A.M.M., E. Moore, K.P. Coyle, I. Davison, M.D. MacManes, R. Roberts et al. 2019. Variation in pigmentation gene expression is associated with distinct aposematic color morphs in the poison frog *Dendrobates auratus*. *BMC Evol. Biol.* 19: 1–15.
- Stuckert, A.M.M., M. Chouteau, M. McClure, T.M. LaPolice, T. Linderoth, R. Nielsen et al. 2021. The genomics of mimicry: gene expression throughout development provides insights into convergent and divergent phenotypes in a Müllerian mimicry system. *Mol. Ecol.* 30: 4039–4061.
- Sturm, R.A. 2009. Molecular genetics of human pigmentation diversity. *Hum. Mol. Genet.* 18: R9–R17.
- Stynoski, J.L., Y. Torres-Mendoza, M. Sasa-Marin and R.A. Saporito. 2014. Evidence of maternal provisioning of alkaloid-based chemical defenses in the strawberry poison frog *Oophaga pumilio*. *Ecology* 95: 587–593.
- Summers, K., R. Symula, M. Clough and T. Cronin. 1999. Visual mate choice in poison frogs. *Proc. R. Soc. B* 266: 2141–2145.
- Summers, K. and M.E. Clough. 2001. The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). *PNAS* 98: 6227–6232.
- Summers, K., T.W. Cronin and T. Kennedy. 2003. Variation in spectral reflectance among populations of *Dendrobates pumilio*, the strawberry poison frog, in the Bocas del Toro Archipelago, Panama. *J. Biogeogr.* 30: 35–53.
- Summers, K., T.W. Cronin and T. Kennedy. 2004. Cross-breeding of distinct color morphs of the strawberry poison frog (*Dendrobates pumilio*) from the Bocas del Toro Archipelago, Panama. *J. Herpetol.* 38: 1–8.
- Summers, K., M.P. Speed, J.D. Blount and A.M.M. Stuckert. 2015. Are aposematic signals honest? A review. *J. Evol. Biol.* 28: 1583–1599.
- Sun, Y.B., Y. Zhang and K. Wang. 2020. Perspectives on studying molecular adaptations of amphibians in the genomic era. *Zool. Res.* 41: 351–364.
- Sztatecsny, M., D. Preininger, A. Freudmann, M.-C. Loretto, F. Maier and W. Hödl. 2012. Don't get the blues: conspicuous nuptial colouration of male moor frogs (*Rana arvalis*) supports visual mate recognition during scramble competition in large breeding aggregations. *Behav. Ecol. Sociobiol.* 66: 1587–1593.
- Taboada, C., A.E. Brunetti, F.N. Pedron, F. Carnevale Neto, D.A. Estrin, S.E. Bari et al. 2017a. Naturally occurring fluorescence in frogs. *PNAS* 114: 3672–3677.
- Taboada, C., A.E. Brunetti, C. Alexandre, M.G. Lagorio and J. Faivovich. 2017b. Fluorescent frogs: a herpetological perspective. *South Am. J. Herpetol.* 12: 1–13.
- Taboada, C., A.E. Brunetti, M.L. Lyra, R.R. Fitak, A.F. Soverna, S.R. Ron et al. 2020. Multiple origins of green coloration in frogs mediated by a novel biliverdin-binding serpin. *PNAS* 117: 18574–18581.
- Taylor, R.C., B.W. Buchanan and J.L. Doherty. 2007. Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. *Anim. Behav.* 74: 1753–1763.

- Teyssier, J., S.V. Saenko, D. Van Der Marel and M.C. Milinkovitch. 2015. Photonic crystals cause active colour change in chameleons. *Nat. Comm.* 6: 1–7.
- Thibaudeau, G. and R. Altig. 2012. Coloration of anuran tadpoles (Amphibia): development, dynamics, function, and hypotheses. *Internat. Schol. Res. Notices* 2012: 725203.
- Tilley, S.G., R.B. Merritt, B. Wu and R. Highton. 1978. Genetic differentiation in salamanders of the *Desmognathus ochrophaeus* complex (Plethodontidae). *Evolution* 32: 3–115.
- Tilley, S.G., B.L. Lundrigan and L.P. Brower. 1982. Erythrism and mimicry in the salamander *Plethodon cinereus*. *Herpetologica* 38: 409–417.
- Titcomb, G.C., D.W. Kikuchi and D.W. Pfennig. 2014. More than mimicry? Evaluating scope for flicker-fusion as a defensive strategy in coral snake mimics. *Curr. Zool.* 60: 123–130.
- Thorogood, R., H. Kokko and J. Mappes. 2018. Social transmission of avoidance among predators facilitates the spread of novel prey. *Nat. Ecol. Evol.* 2: 254–261.
- Todd, B.D. and A.K. Davis. 2007. Sexual dichromatism in the marbled salamander, *Ambystoma opacum*. *Can. J. Zool.* 85: 1008–1013.
- Toews, D.P.L., N.R. Hofmeister and S.A. Taylor. 2017. The evolution and genetics of carotenoid processing in animals. *Trends Genet.* 3: 171–182.
- Toledo, L.F. and C.F.B. Haddad. 2009. Colors and some morphological traits as defensive mechanisms in anurans. *Int. J. Zool.* 2009: 910892.
- Tuma, M.C. and V.I. Gelfand. 1999. Molecular mechanisms of pigment transport in melanophores. *Pigm. Cell Res.* 12: 283–294.
- Twomey, E., J.S. Vestergaard, P.J. Venegas and K. Summers. 2016. Mimetic divergence and the speciation continuum in the mimic poison frog *Ranitomeya imitator*. *Am. Nat.* 187: 205–224.
- Twomey, E., J.D. Johnson, S. Castroviejo-Fisher and I. Van Bocxlaer. 2020. A ketocarotenoid-based colour polymorphism in the Sira poison frog *Ranitomeya sirensis* indicates novel gene interactions underlying aposematic signal variation. *Mol. Ecol.* 29: 2004–2015.
- Twomey, E., M. Kain, M. Claeys, K. Summers, S. Castroviejo-Fisher and I. Van Bocxlaer. 2020. Mechanisms for color convergence in a mimetic radiation of poison frogs. *Am. Nat.* 195: E132–E149.
- Twyman, H., M. Prager, N.I. Mundy and S. Andersson. 2018. Expression of a carotenoid-modifying gene and evolution of red coloration in weaverbirds (Ploceidae). *Mol. Ecol.* 27: 449–458.
- Umbers, K.D., J. Lehtonen and J. Mappes. 2015. Deimatic displays. *Curr. Biol.* 25: R58–R59.
- Umbers, K.D. and J. Mappes. 2015. Postattack deimatic display in the mountain katydid, *Acripeza reticulata*. *Anim. Behav.* 100: 68–73.
- Umbers, K.D., S. De Bona, T.E. White, J. Lehtonen, J. Mappes and J.A. Endler. 2017. Deimatism: a neglected component of antipredator defence. *Biol. Lett.* 13: 20160936.
- Umbers, K.D., J.L. Riley, M.B. Kelly, G. Taylor-Dalton, J.P. Lawrence and P.G. Byrne. 2020. Educating the enemy: Harnessing learned avoidance behavior in wild predators to increase survival of reintroduced southern corroboree frogs. *Cons. Sci. Pract.* 2: e139.
- Vaissi, S., P. Parto and M. Sharifi. 2018. Ontogenetic changes in spot configuration (numbers, circularity, size and asymmetry) and lateral line in *Neurergus microspilotus* (Caudata: Salamandridae). *Acta Zool.* 99: 9–19.
- Valkonen, J.K. and J. Mappes. 2014. Resembling a viper: implications of mimicry for conservation of the endangered smooth snake. *Cons. Biol.* 28: 1568–1574.
- Vásquez, T. and K.S. Pfennig. 2007. Looking on the bright side: females prefer coloration indicative of male size and condition in the sexually dichromatic spadefoot toad, *Scaphiopus couchii*. *Behav. Ecol. Sociobiol.* 62: 127–135.
- Vences, M., J. Kosuch, R. Boistel, C.F.B. Haddad, E. La Marca, S. Lötters et al. 2003. Convergent evolution of aposematic coloration in Neotropical poison frogs: a molecular phylogenetic perspective. *Org. Div. Evol.* 3: 215–226.
- Vestergaard, J.S., E. Twomey, R. Larsen, K. Summers and R. Nielsen. 2015. Number of genes controlling a quantitative trait in a hybrid zone of the aposematic frog *Ranitomeya imitator*. *Proc. R. Soc. B* 282: 20141950.
- Wang, I.J. and H.B. Shaffer. 2008. Rapid color evolution in an aposematic species: a phylogenetic analysis of color variation in the strikingly polymorphic strawberry poison-dart frog. *Evolution* 62: 2742–2759.

- Wang, I.J. 2011. Inversely related aposematic traits: reduced conspicuousness evolves with increased toxicity in a polymorphic poison-dart frog. *Evolution* 65: 1637–1649.
- Watanabe, M., M. Iwashita, M. Ishii, Y. Kurachi, A. Kawakami, S. Kondo et al. 2006. Spot pattern of leopard *Danio* is caused by mutation in the zebrafish connexin41.8 gene. *EMBO Reports* 7: 893–897.
- Weiner, L., R. Han, B.M. Scicchitano, J. Li, K. Hasegawa, M. Grossi et al. 2007. Dedicated epithelial recipient cells determine pigmentation patterns. *Cell* 130: 932–942.
- Wells, K.D. 1980. Social behavior and communication of a dendrobatid frog (*Colostethus trinitatis*). *Herpetologica* 36: 189–199.
- White, T.E. and K.D.L. Umbers. 2021. Meta-analytic evidence for quantitative honesty in aposematic signals. *Proc. R. Soc. B* 288: 20210679.
- Whiting, M.J., D.M. Stuart-Fox, D. O'Connor, D. Firth, N.C. Bennett and S.P. Blomberg. 2006. Ultraviolet signals ultra-aggression in a lizard. *Anim. Behav.* 72: 353–363.
- Williams, C.R., E.D. Brodie Jr., M.J. Tyler and S.J. Walker. 2000. Antipredator mechanisms of Australian frogs. *J. Herpetol.* 34: 431–443.
- Winters, A.E., N.G. Wilson, C.P. van den Berg, M.J. How, J.A. Endler, N.J. Marshall et al. 2018. Toxicity and taste: unequal chemical defences in a mimicry ring. *Proc. R. Soc. B* 285: 20180457.
- Wollenberg, K.C. and C.J. Measey. 2009. Why colour in subterranean vertebrates? Exploring the evolution of colour patterns in caecilian amphibians. *J. Evol. Biol.* 22: 1046–1056.
- Wolnicka-Glubisz, A., A. Pecio, D. Podkowa, L.M. Kolodziejczyk and P.M. Plonka. 2012. Pheomelanin in the skin of *Hymenochirus boettgeri* (Amphibia: Anura: Pipidae). *Exp. Dermatol.* 21: 537–540.
- Xiao, N., H. Li, L. Shafique, S. Zhao, X. Su, Y. Zhang et al. 2019. A novel pale-yellow coat color of rabbits generated via MC1R mutation with CRISPR/Cas9 system. *Front. Genet.* 10: 875.
- Yang, Y., C.L. Richards-Zawacki, A. Devar and M.B. Dugas. 2016. Poison frog color morphs express assortative mate preferences in allopatry but not sympatry. *Evolution* 70: 2778–2788.
- Yang, Y., M.R. Servedio and C.L. Richards-Zawacki. 2019. Imprinting sets the stage for speciation. *Nature* 574: 99–102.
- Yang, Y., S. Blomenkamp, M.B. Dugas, C.L. Richards-Zawacki and H. Pröhl. 2019. Mate choice versus mate preference: inferences about color-assortative mating differ between field and lab assays of poison frog behavior. *Am. Nat.* 193: 598–607.
- Yang, Y., V. Prémel and C.L. Richards-Zawacki. 2020. Prior residence effect determines success of male-male territorial competition in a color polymorphic poison frog. *Ethology* 126: 1131–1140.
- Yasutomi, M. 1987. Migration of epidermal melanophores to the dermis through the basement membrane during metamorphosis in the frog, *Rana japonica*. *Pigm. Cell Res.* 1: 181–187.
- Yovanovich, C.A., S.M. Koskela, N. Nevala, S.L. Kondrashev, A. Kelber and K. Donner. 2017. The dual rod system of amphibians supports colour discrimination at the absolute visual threshold. *Phil. Trans. R. Soc. Lond. B* 372: 20160066.
- Zamora-Camacho, F.J. and M. Comas. 2019. Beyond sexual dimorphism and habitat boundaries: coloration correlates with morphology, age, and locomotor performance in a toad. *Evol. Biol.* 46: 60–70.
- Zimova, M., K. Hackländer, J.M. Good, J. Melo-Ferreira, P.C. Alves and L.S. Mills. 2018. Function and underlying mechanisms of seasonal colour moulting in mammals and birds: what keeps them changing in a warming world? *Biol. Rev.* 93: 1478–1498.
- Zuasti, A. 2002. Melanization stimulating factor (MSF) and melanization inhibiting factor (MIF) in the integument of fish. *Microsc. Res. Tech.* 58: 488–495.