

A Study On The Variations In Timing, Physiology And Function Of Colour Change In Amphibians

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Abstract

Amphibians have the incredible ability to change colour, yet the hormonal drivers and evolutionary functions are poorly known in most species. Herein we review the variations in timing, physiology and function of colour change in amphibians. Additionally, we investigate how sexual selection may drive colour change in anuran amphibians by examining breeding pattern and reproductive behaviour of sexually dichromatic species and relating these to function.

We identify three patterns of colour change based on speed, hormonal mechanisms and ecological function. 1. Ontogenetic colour change is a unidirectional, permanent change from a juvenile to an adult colour phase. The function of this change is mostly unknown but is driven by natural and sexual selection processes. 2. Seasonal colour change is a temporary colour change that occurs over weeks or months. It commonly occurs in sexually dichromatic, explosive breeding species, where it functions as an intrasexual signal for sex recognition. 3. Rapid colour change occurs in just minutes or hours and is also reversible. It is commonly used as for camouflage or thermoregulation (78%). In some species (22%) only males change colour and this predominantly occurs in prolonged breeders where it functions as an intrasexual signal.

Keywords: Colour change, sexual selection, natural selection, sexual dichromatism, amphibian reproduction, sexual signalling.

1. Introduction

Colour change is widespread in the animal kingdom. It occurs in many species from the well-known fascinating displays seen in chameleons and cephalopods to lesser-known ectothermic animals including crustaceans, insects, fish, reptiles, and amphibians. In many species, the color change is an essential warning sign and camouflage mechanism allows better capacity for thermoregulation and an integral part of mating and reproductive behavior (Stuart-Fox & Moussalli, 2009). Coloration in lower vertebrates is produced by the absorption and reflection of light by specialized pigment-containing cells called chromatophores (Bagnara, Fernandez & Fujii, 2007). In amphibians skin colour is predominantly based on the number and organization of three types of chromatophores: melanophores (contain light-absorbing pigments), xanthophores (contain bright colored pigments such as pteridines or carotenoids), and iridophores (contain reflecting platelets). The arrangement, presence, and location in the dermis vary among species (Ali & Naaz, 2014; Bagnara et al., 1968) and the location on the body of the individual.

Colour change is either achieved through a change in pigment cell organization and number (morphological colour change), or by rapid pigment migration within chromatophores [physiological colour change] (Bagnara & Hadley, 1973). The lightning and darkening seen in many amphibians is a physiological colour change in which colour change is the result of pigment movement from the center of the melanophore to the cell periphery where it covers theiridophores and/or xanthophores, increasing light absorption (Bagnara, 1964). A change in colour from a juvenile to adult color phase is usually the product of morphological colour change as it involves the destruction and creation of new pigment or chromatophore types.

In amphibians, colour change is mainly controlled by hormones or neuro-hormones in response to external triggers such as temperature, light intensity, and behavioral cues. The types of hormones that control pigment movement have been well studied (Nery & Castrucci, 1997; Sköld, Aspengren & Wallin, 2013). Determining these physiological processes and causal mechanisms provides a conceptual framework for evolutionary studies, and therefore physiological processes were included where possible in this review. Physiological mechanisms are subject to selection just as much as the phenotypic expression and function, and one cannot fully understand one without the other. Although there is increasing knowledge in both physiology and function of colour change in amphibians a disconnection between them still exists, with studies often studying one component without relating it to the other.

Herein we examine the physiological structure and hormonal mechanisms of colour change, current knowledge on variations in colour change patterns (speed and duration), and review the ecological and evolutionary drivers of colour change in amphibians. Our literature search spanned across disciplines and includes past reviews, experimental studies, natural history notes, field guides and accounts from other researchers. We firstly compiled a list of all amphibians (anurans and urodela, excluding tadpoles) known to undergo colour change and where possible identified the duration, function and possible physiological process. We identified 282 species that matched our criteria; however, this number is likely to be an underestimate as many mentions of colour change may be in short natural history notes or anecdotal comments which are difficult to pick up in literature searches. For sexually dichromatic species (where colour is thought to be controlled by sexual selection) we examined the relationships between breeding system (according to Wells 1977) and colour change pattern to further elucidate the potential evolutionary function. Our study confirms the high diversity of physiological processes and function that exists in amphibians and highlights disconnection between physiological and evolutionary or behavioural studies; in particular those changes driven by sexual selection.

2. Patterns of Colour Change

The timing of colour change in amphibians can vary greatly from slow unidirectional changes which occur throughout the life of an individual, usually a juvenile to adult colour phase to reversible changes that can take a few hours or minutes. In many descriptions of colour changing occurrences exact timings are left out, descriptions of ontogenetic colour changes usually just mention differences in juvenile and adult colouration (n=130 species) or in the case of reversible colour changes only seasonal (n=56 species) or diurnal (n=48 species) changes are reported. Other studies just use general observations such as 'hours' without including exact time measurements (n=13 species).

Herein we distinguish between three forms of colour change, one unidirectional (ontogenetic) and two reversible changes (seasonal and rapid). It is important to note that individual species can exhibit more than one form of colour change driven by different functions. Ontogenetic colour

change (OCC) is a unidirectional change in colouration usually from a juvenile colour phase to an adult colour phase. OCC is a form of morphological colour change, whereby the change in skin colour is a result of pigment synthesis and/or change in chromophore distribution through the dermis. OCC has been documented to occur in approximately 132 species with roughly 50% displaying sexual dichromatism. OCC is common in species in the family Hyperoliidae where females and some males often develop different colours to juveniles (Richards, 1976). Seasonal colour change (SCC) has been recorded in at least 62 species (table 1). It is reversible and typically occurs during the breeding season where the male changes colour (82% brighten and 11% darken). In the remaining 7% seasonal variations in colour occur in both sexes. Due to the slower (days to months) development of pigment colouration, SCC is likely to be a form of morphological colour change. Rapid color change (RCC) is another reversible color change, lasting from minutes to several hours. Over 121 species (123 occurrences) have been recorded due to the ephemeral nature of this form of colour change this number is likely to be an underestimate, in particular more subtle lightening or darkening of skin tone which most amphibians are assumed to be capable of. Rapid colour change is a physiological change, where the movement of pigment within chromophores (predominantly the melanophores) creates colour change.

The degree individual species change colour can range from differences in shade (like the light to dark green in *Hyla crucifer* or *H. japonica*) to vivid dichromatic changes in colour (like in the brown to yellow in *Litoria wilcoxii*) depending on the evolutionary function. Males change colour in 22% of individuals (19% brighten and 3% darken). However, it is most common (78%) for both sexes to undergo colour change (both lighten and darken).

Table 1: Summary of colour changes associated for ontogenetic, seasonal and rapid colour change, showing the number of species documented to display each form of colour change and percentage of this for each pattern of colour change; note that some species exhibit more than one type of colour change or variation of change.

Pattern of colour change	Male brightens #species (%)	Male darkens #species (%)	Female brightens #species (%)	Female darkens #species (%)	Both sexes brighten #species (%)	Both sexes darken #species (%)	Both sexes change #species (%)
Ontogenetic (n=132)	20 (15%)	3 (3%)	34 (26%)	16 (12%)	31 (23%)	28 (21%)	0 (0%)
Seasonal (n=62)	51 (82%)	7 (11%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	4 (7%)
Rapid (n=121)	23 (19%)	4 (3%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	96 (78%)

3. Physiology of Colour Change

Colour change in amphibians is predominantly driven by hormones and is regulated by the pars intermedia of the brain. The hormonal drivers of colour change have been well researched in some species, mainly using in vitro studies such as skin bioassays without much reference to the natural pattern or function of colour change. Serotonin (5HT) receptors have been found to regulate physiological colour change in the Indian bullfrog *Hoplobatrachus tigerinus*, however whether this is related to the dynamic breeding colouration seen in males has not been determined. Experimental studies on whole organisms have primarily focused on background matching and only more recently

on other functions of colour change.

4. Evolutionary Functions

Colour change is driven by processes of natural and sexual selection. In species where both sexes change colour (especially those undergoing RCC) processes of natural selection such as camouflage and thermoregulation appear to be the main drivers of colour change. In sexually dichromatic species, where colour change occurs in one sex only (either rapidly or over a breeding season) it is most likely been driven by sexual selection. Some specific ecological drivers or functions mentioned in the literature thus far include camouflage, thermoregulation (including UV protection), aposematism, mimicry, male competition, sex recognition and female choice.

5. Sexual Selection and the Association between Dichromatism and Breeding Systems

We found that sexually dichromatic species displaying ontogenetic and rapid colour change had a greater proportion of prolonged breeding species whereas in species undergoing SCC there was no difference between numbers of explosive or prolonged breeders. Prolonged breeders spend a far greater investment into breeding, and female choice or male competition often play a role in mate selection. For species displaying OCC relationships between breeding system and colour change are difficult to determine due to the lack of data on current functions and breeding system (no breeding information was available for 40% of species). For species capable of RCC, the ability to switch colour on and off could allow signals to be utilised more effectively over a longer period. Bright colours could be effectively turned on if a prospective mate or conspecific was in sight and then turned off for predator avoidance or thermoregulatory requirements.

Males developed brighter colouration in 15% of ontogenetic amphibians, which traditionally suggests sexual selection is the driver of colour change. It is likely that female choice and aspects of sex recognition play a role for these types of colour change, but to date only a few studies have shown any conclusive results. A female preference for brighter males was shown in two species *Oophaga pumilio* and *Scaphiopus couchi*. Because colouration is maintained throughout adulthood it is likely that colour is an indicator of male quality.

6. Natural Selection

Ontogenetic colour changes from bright juveniles to dull adults may be driven by differing habitat or foraging requirements. In juvenile Eastern newts (*Notophthalmus viridescens*), the difference in light environments and predator visual systems between terrestrial and aquatic environments may drive the ontogenetic change from bright red to a dull brown-green. Another possible explanation is that the toxin (TTX) found in juvenile newts may not be as useful for aquatic adults because the toxin may disperse too quickly in water, making dull colouration more beneficial than aposematic colouration. There are also some species from the genus *Pseudotriton* which mimic the colouration of *N. viridescens*, the change in mimic species may be due to increased predation pressure. Juvenile *Oreophryne ezra* are black with golden spots and are active (and surprisingly conspicuous) during the day while the adults are light pink/peach and active at night, although there is currently no conclusive evidence of the function of this change, it may be related to the ambient light and vegetation type the individual uses or an aposematic function.

Interactions between Natural and Sexual Selection

Although it is easy to assume that there is only one selective pressure driving colour change evolution it is generally more complex. The development of bright breeding colouration conflicts with an

animal's ability to avoid predation and rapid dynamic colour change can be a solution to this, as breeding colours can be turned on or off when need. In the neo-tropical toad *Incilius luetkenii* yellow males (which undergo a seasonal change from brown to yellow) faded rapidly (within hours) to brown after amplexus with a female, as well as after capture, indicating that although turning yellow is an important aspect to their courtship (possibly for sex recognition) it is also a costly signal. Similar observations occurred in the Madagascan Mantellid, *Aglyptodactylus securifer* where a captured individual displaying yellow breeding colouration had lost much of its brightness overnight in a collection bag.

In contrast species, such as *L. wilcoxii* and *Amietophrynus lemairii* which both change colour in just a few minutes remain bright yellow during amplexus. Bright yellow *L. wilcoxii* can also rapidly change back to brown if handled, suggesting that rapid colour change allows for camouflage when needed. There is little evidence of disadvantage of attaining bright breeding colouration in *L. wilcoxii*. This suggests that either these species don't have natural predators that rely on colour to detect species or the gain of this colour change override the predation risks associated with bright colouration.

7. Conclusion

Colour change in amphibians is primarily the result of a change in pigment cell distribution and pigment movement within individual cell types. The distribution of these cell types can determine the capacity for colour change in species. Pigment movement is mainly driven by hormones and the timing can vary from just minutes to permanent changes that occur over months or years. The type of hormone driving the colour change is often related to the speed of change, reproductive hormones trigger seasonal or ontogenetic colour changes that often occur in one sex only whereas peptide and neuro-hormones stimulate rapid changes. The complexities and colours observed in amphibians are astonishing. The use of these colours demonstrates the importance of vision as a communication tool and colour changing species are excellent models for evolutionary studies.

OCC is driven by natural and sexual selection and has a variety of functions, yet these have only been confirmed in approximately 10% of species. Despite the small amount of studies there appears to be a large variation in function including female choice, camouflage (niche partitioning) and aposematism. SCC is primarily driven by sexual selection, especially sex recognition, commonly observed in explosively breeding species. RCC is driven by natural and sexual selection. Colour changes for camouflage and thermoregulation are widespread and commonly reported and are mainly associated with diurnal / nocturnal changes, thermoregulatory requirements or in response to a predator attack. Sexual encounter colour change (intra sexual signalling, male-competition and female choice) has been reported in 22% of RCC studies, and may be more common than previously thought.

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