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Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns

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ABSTRACT

The role of colours and colour patterns in behavioural ecology has been extensively studied in a variety of contexts and taxa, while almost overlooked in many others. For decades anurans have been the focus of research on acoustic signalling due to the prominence of vocalisations in their communication. Much less attention has been paid to the enormous diversity of colours, colour patterns, and other types of putative visual signals exhibited by frogs. With the exception of some anecdotal observations and studies, the link between colour patterns and the behavioural and evolutionary ecology of anurans had not been addressed until approximately two decades ago. Since then, there has been ever-increasing interest in studying how colouration is tied to different aspects of frog behaviour, ecology and evolution. Here I review the literature on three different contexts in which frog colouration has been recently studied: predator–prey interactions, intraspecific communication, and habitat use; and I highlight those aspects that make frogs an excellent, yet understudied, group to examine the role of colour in the evolution of anti-predation strategies and animal communication systems. Further, I argue that in addition to natural-history observations, more experiments are needed in order to elucidate the functions of anuran colouration and the selective pressures involved in its diversity. To conclude, I encourage researchers to strengthen current experimental approaches, and suggest future directions that may broaden our current understanding of the adaptive value of anuran colour pattern diversity.

Key words: colouration, predator–prey interactions, visual communication, sexual selection, conflict resolution, space use.

CONTENTS

I. INTRODUCTION

“An extensive survey of the organic world thus leads us to the conclusion that colour is by no means so unimportant or inconstant a character as at first sight it appears to be; and the more we examine it the more convinced we shall become that it must serve some purpose in nature, and that besides charming us by its diversity and beauty it must be well worthy of our attentive study, and have many secrets to unfold to us.” – A. R. Wallace (1877, p. 643)

Signals are supposed to evolve so that the signal-to-noise ratio (the contrast between the signal and the background noise) is maximised (Bradbury & Vehrencamp, 2011; Endler, 1992, 1993*a*), while signal degradation is minimised (Endler, 1992). Selection also tends to favour signals with a high efficacy not only in terms of their transmission and detection, but also in their ability to elicit a response in the receiver that increases the sender’s fitness (Guilford & Dawkins, 1991) while maintaining the receiver’s fitness unaffected. An exception to this is deceptive signals, which deliver incorrect information about the signaller and thus benefit the sender at the expense of the receiver (Mokkonen & Lindstedt, 2015; Wiley, 1983, 1994).

Different modalities of communication entail diverse advantages and constraints on the signals involved (Bradbury & Vehrencamp, 2011). Acoustic signals can be advantageous over long distances because sound waves can travel for longer through either air or water without degrading compared to, for example, light. This is particularly useful for nocturnal animals given the low or non-existent light levels at night (Bradbury

& Vehrencamp, 2011). Chemical or olfactory signals are also good in low-light scenarios, but they rely heavily on the characteristics of the medium in which they are transmitted (Bradbury & Vehrencamp, 2011). Visual signals, on the other hand, work well over short to medium distances provided there is a lack of physical obstacles between the sender and the receiver, suitable contrast with the background, and a minimum of environmental light (Endler, 1992, 1993*a*); they can have different shapes and sizes, and may convey information either on their own (static signals; e.g. diverse and conspicuous colour patterns in bird plumage; Andersson, 1994) or when accompanied or enhanced by repeated movements or displays (dynamic signals; e.g. the extension of a coloured dewlap in combination with head bobbing in *Anolis* lizards; Losos & Chu, 1998).

The role of colour patterns as visual signals in animal behaviour and ecology has been studied extensively in a variety of contexts and taxa, but has been neglected in others. For example, for decades anurans have been the focus of studies on acoustic signalling due to the prominence of vocalisations in their communication system. Not only has it been demonstrated that frogs emit calls with different functions (Gerhardt & Huber, 2002), but they have also been shown to have outstanding sensory abilities that allow them to be both physiologically (Capranica & Moffat, 1983) and behaviourally (Amézquita *et al*., 2011) tuned to the characteristics of their own species-specific acoustic signals. By contrast, the link between colouration and the behavioural and evolutionary ecology of anurans had not been properly addressed until approximately two decades ago. Previous studies focused mostly on the inheritance of colour patterns (Blouin, 1989; Davison, 1963; Fogleman, Corn & Pettus, 1980; Resnick & Jameson, 1963); but see Nevo, 1973, for an early study on the selective pressures involved in the maintenance of colour polymorphism in cricket frogs). Recently, more attention has been paid to the enormous diversity of colours, colour patterns, and other types of visual signals displayed by frogs (e.g. Hödl & Amézquita, 2001), and how those signals are tied to different aspects of frog ecology and behaviour. Here I aim to review the diversity of frog colouration in relation to behaviour and ecology. I do so whilst focusing on those cases in which colour patterns are visual signals on their own, describing how these signals are currently thought to function in the context of anti-predation strategies, intraspecific communication and habitat use. Lastly, I suggest future directions within each context that might fill some of the current gaps in frog colouration research; and highlight the need to strengthen and broaden the current experimental approaches in order to widen our understanding of the adaptive value of diversity in frog colouration, and to identify the candidate selective pressures that might be shaping such diversity.

II. PREDATOR–PREY INTERACTIONS

Colouration may have an enormous effect on animals' fitness because of its adaptive function as an interspecific signal in the context of predation, among others. While some animals gain protection from predators by blending with their surroundings (camouflage; Edmunds, 1974), many species also have conspicuous colour patterns that warn predators about their unprofitability (Ruxton, Sherratt & Speed, 2004). The latter strategy is referred to as aposematism (Poulton, 1890).

(1) Camouflage

Camouflage involves a series of strategies that prevent prey from being detected or recognised by predators (Edmunds, 1974; Stevens & Merilaita, 2009). Such strategies include, for instance, crypsis and masquerade. Common types of crypsis are background matching, whereby an animal resembles its background colouration and thus avoids detection (Endler, 1988), and disruptive colouration, which involves markings that make it difficult for the predator to distinguish the outline or shape of the prey (Cott, 1940; Thayer, 1909). Masquerade, whereby animals resemble an uninteresting object in their surroundings (i.e. a rock, a leaf, a stick, etc.), prevents prey recognition instead (Skelhorn *et al*., 2010). Both crypsis and masquerade ultimately deprive the predator of key information about the prey and, therefore, constitute a form of deception (Caro, 2014; Mokkonen & Lindstedt, 2015). Camouflage is a widespread anti-predator strategy among anurans, which is reflected in the prevalence of earthy colours such as different shades of green, brown and grey in many species (Wells, 2007). It can be effective on its own, as in young *Pristimantis zeuctotylus* whose colour patterns resemble those of the mossy substrate (Fig. 1A), or *Hyla japonica*, which changes its dorsal colour to match that of the background (Choi & Jang, 2014); but can also be enhanced with particular behaviours. Individuals of *Craugastor fitzingeri*, for example, become completely immobile after every jump and can also hide their head in the leaf litter; experiments with human observers who knew exactly where to search but still could not easily locate individuals have demonstrated that the detection of these frogs can be extremely difficult for predators (Cooper, Caldwell & Vitt, 2008).

Colour pattern polymorphisms [the simultaneous occurrence of two or more forms within a population with the rarest form occuring at frequencies higher than those expected by mutation pressure (Ford, 1945)] are very common among cryptically coloured species, and frogs are no exception (Hoffman & Blouin, 2000; Wells, 2007). For example, the frequencies of colour patterns (grey, green, and red) in two species of *Acris* (*A. gryllus* and *A. crepitans*) are correlated locally with variations in substrate colour (Nevo, 1973). Remarkably, these species show seasonal variation in the frequencies of each colour pattern, suggesting that a morph that is, for example, favoured in spring when everything is green, will not be favoured in the autumn, when the background vegetation will be more red. Likewise, in *Dendropsopus* (formerly *Hyla*) *labialis*, a frog species with an extensive latitudinal and altitudinal distribution, there are at least five distinct morphs whose frequency seems to be correlated with the predominant background at each location. For instance, individuals with spotted colour patterns are more common in populations at high elevations, where the background vegetation is dominated by mosses (Amézquita, 1999). This suggests that colour polymorphism in this species may have evolved as a form of crypsis (Amézquita, 1999). Interestingly, colour patterns also seem to be related to body size, so that green-dominated morphs are smaller than brown ones (Amézquita, 1999), pointing at a potential link between colouration and life-history traits that has been surprisingly understudied in anurans. A long-term study on *Eleutherodactylus coqui* in Puerto Rico revealed the existence of 21 distinct pattern morphs whose frequencies also differ among populations and are correlated with the background colouration (Woolbright & Stewart, 2008). Individuals with longitudinal dorsal stripes were most common in grassland areas, whereas individuals with spots and bars were more common in the forest (Woolbright & Stewart, 2008). Likewise, females of *Rhinoderma darwinii*, which are mostly brown, are found on brown substrates, whereas males, which can be either green or brown, are distributed across brown, green and brown–green backgrounds (Bourke, Busse & Bakker, 2011).

In general, the association between body and background colouration suggests that frogs try to reduce predation risk through crypsis. Cryptic polymorphic species may have an advantage over monomorphic ones if they are exposed to predators that prey disproportionately on the most common phenotypes (apostatic selection), because the fitness of each morph will be inversely related to its frequency in the population (Allen & Greenwood, 1988; Bond, 2007; Bond & Kamil, 1998; Endler, 1991*a*). Thus, by being polymorphic the *per capita* predation risk of a given species might be reduced, as the abundance of any of its morphs would be low compared to a monomorphic species (Endler, 1991*a*). Despite the prevalence of colour pattern polymorphisms among cryptically coloured anurans, the mechanisms that allow for their maintenance remain rather obscure. According to Hoffman & Blouin (2000), there is evidence that variation in colour patterns can be inherited and strong indications that predation could indeed be the selective pressure behind such diversity, but with a few exceptions (Morey, 1990; Tordoff, 1980; Wente & Phillips, 2005) most evidence to date remains merely correlational.

Although there are many frog examples illustrating the benefits of background matching, evidence describing the function of disruptive colouration or masquerade is very limited and mostly anecdotal. Indeed, despite the fact that it has been suggested to be common among anurans (Wells, 2007), disruptive colouration has not been purposely examined experimentally (Rudh & Qvarnström, 2013). Examples of what might be disruptive colouration are markings such as light dorsal stripes, and blotches or spots that hinder definition of the body shape or break up the limbs (Wells, 2007), as well as lateral lines that cross the eyes while confounding their shape (Amat, Wollenberg & Vences, 2013; Toledo & Haddad, 2009). The best-known illustration of masquerade, on the other hand, is probably found in species living in forests, which can presumably trick predators by looking like dead leaves (Duellman & Trueb, 1994), such as some species of the genus *Rhinella* (Fig. 1B–D).

Attempts to demonstrate the adaptive value of any of these forms of camouflage, or to test specifically for the role of predators as the selective pressure behind this diversity in protective colour patterns (i.e. through apostatic selection), could benefit from the use of well-established protocols employed in other systems. For example, experiments with both human and avian predators foraging on either artificial prey items, or virtual prey on computer screens have demonstrated that certain colour patterns increase prey survival, *via* background matching or disruptive colouration, implicating the role of visual predators as a selection agent on the evolution of diverse protective colouration (Allen & Clarke, 1968; Allen & Greenwood, 1988; Bond & Kamil, 2006; Fraser *et al*., 2007; Karpestam, Merilaita & Forsman, 2013, 2014). An alternative approach to tackle similar kinds of questions, which has been widely used for research on aposematism (see Section II.2), is to deploy artificial prey in the field and document and compare attack rates on different morphs by natural visual predators (Cuthill *et al*., 2005; Farallo & Forstner, 2012; Valkonen *et al*., 2011). Studies involving actual frogs would also be highly informative, as they can account for decisions made by the individual frogs themselves. For instance, in an elegant experiment investigating whether individuals of two different morphs of *Hyla regilla* expressed colour pattern-mediated microhabitat selection, chemical cues of a snake predator were used to evaluate how predator presence affected the frogs' choice (Wente & Phillips, 2005). The authors found that, in the presence of predator cues, both green and brown frogs preferred a substrate that matched their own colour. In the absence of predator cues, however, only green frogs exhibited a significant preference for a matching background, which suggests a possible genetically linked association between phenotype (i.e. dorsal colouration) and behaviour (i.e. preference for a matching background) (Wente & Phillips, 2005).

Finally, the combination of these kinds of experiments with methods that allow for detailed analyses of colour patterns while accounting for predator perception (Endler, 1978, 1984, 1990, 2012; Endler & Mielke, 2005; Kemp *et al*., 2015; Osorio & Srinivasan, 1991; Renoult, Kelber & Schaeffer, 2015; Voroyeb & Osorio, 1998; Voroyeb *et al*., 1998) opens a broad range of possibilities to study the evolution of camouflage strategies in anurans. For instance, a field experiment where dummies with different colour patterns are deployed on different backgrounds to evaluate how attack rates differ among groups could be complemented with a survey of the actual frogs in their natural habitat, recording information on the exact spot where each individual is found. If not only this information is collected, but also standardised photographs are taken of both the individual frog and its microhabitat, similarities between the frog colour patterns and its background could be measured, and the accuracy of camouflage quantified.

(2) Aposematism and mimicry

Aposematism is an anti-predator strategy through which prey warn predators about their unprofitability (presence of toxins or physical defences such as spines or irritant hairs) by means of specific colour patterns that act as warning signals (Cott, 1940; Poulton, 1890; Rojas, Valkonen & Nokelainen, 2015*b*; Ruxton *et al*., 2004). This strategy works in such a way that predators learn the association between the warning signals and the unprofitability of the prey, and subsequently avoid them (Endler, 1991*a*; Endler & Mappes, 2004; Ruxton *et al*., 2004).

Several species of frogs exhibit conspicuous colouration and have a wide array of skin toxins (Wells, 2007), such as various species of *Mantella* (Fig. 2A,B) and the 'Tomato frogs' (genus *Dyscophus,* Microhylidae; Fig. 2C) from Madagascar (Garraffo *et al*., 1993*a*); the Corroboree frogs (*Pseudophryne corroboree*; Fig. 2D) and other myobatrachids from Australia (Daly *et al*., 1990); *Brachycephalus ephippium* from

Brazil (Fig. 2E) (Sebben *et al*., 1986); and numerous species of Bufonids in the genera *Melanophryniscus* (Fig. 2F) (Garraffo *et al*., 1993*b*; Grant *et al*., 2012) and *Atelopus* (Fig. 3A,B; Kim, Kim & Yotsu-Yamashita, 2003) from South and Central America. However, probably the best-known example of aposematic frogs are the dart poison frogs (Dendrobatidae; Fig. 4) (Stynoski, Shelton & Stynoski, 2014). The varied toxins found in this Neotropical frog family (Daly *et al*., 2002, 1994; Daly & Myers, 1967; Myers & Daly, 1976, 1983) are sequestered from their specialised diet (Saporito *et al*., 2007*a*, 2004), which consists mainly of ants, termites, mites and other arthropods found in the leaf litter (Darst *et al*., 2005; Toft, 1995). Toxins vary noticeably within the family in composition, amount, and power, but most are lipophilic alkaloids (Saporito *et al*., 2012). One dendrobatid species, *Phyllobates terribilis* (Fig. 4D), has the most potent non-proteolytic (alkaloid) toxin among vertebrates, batrachotoxin (Myers, Daly & Malkin, 1978). Each of these golden yellow or metallic orange frogs can have up to 1.2 mg of toxin which, if it comes into contact with an open wound, could potentially be lethal to humans in a dose as low as 200 µg (Myers *et al*., 1978).

During the last 15 years, various studies have demonstrated an evolutionary link between colouration and toxicity in dendrobatid frogs (Darst *et al*., 2005; Santos, Coloma & Cannatella, 2003; Summers, 2003; Summers & Clough, 2001), suggesting that bright colouration has evolved independently at least three times. Diet specialisation, which is in turn linked with higher levels of toxicity (Darst *et al*., 2005), might have itself evolved independently at least two, but possibly three times (Santos *et al*., 2003; Vences *et al*., 2003). The combination of bright colours and high toxicity in these frogs has traditionally been put forward as an example of aposematism (Myers & Daly, 1983; Pough *et al*., 2001), even though the first experimental attempts to show predator aversion of colourful dendrobatids only took place a few years ago (Saporito *et* *al*., 2007*b*). While it has been suggested that some crabs, snakes, beetle larvae and spiders feed on dendrobatid tadpoles (Gray & Christy, 2000; Stynoski *et al*., 2014), and some seemingly toxin-resistant snakes might feed on juveniles (Myers *et al*., 1978), the major predators of adult poison frogs are still not known with certainty, presumably due to the frogs' success at deterring predators. As indicated by anecdotal observations and experiments in the field, ants, *Paraponera clavata* (Fritz, Rand & Depamphilis, 1981), and spiders, *Cupiennius coccineus* (Szelistowski, 1985) and *Sericopelma rubronitens* (Gray, Kaiser & Green, 2010), reject them as prey; but there are also some accounts of fish (Santos & Cannatella, 2011), snake (Fig. 5A) (Lenger, Berkey & Dugas, 2014; Ringler, Ursprung & Hödl, 2010), and spider (T. Larsen, personal communication; Fig. 5B) predators. Experiments with frog clay models (see below), suggest that poison frogs could be subject to attack by birds and crabs. These results are in agreement with at least one observation of a crab feeding on an individual of *Oophaga histrionica* in the Chocó region of Colombia (A. Vélez & S. Körting, personal communication; Fig. 5C), and two observations of adult rufous motmots (*Baryphthengus martii*) consuming one individual of *D. auratus* with no apparent negative effects (Master, 1999) or feeding individuals of *O. pumilio* to their offspring (Alvarado, Alvarez & Saporito, 2013) (Fig. 5D). Additional evidence obtained in studies incorporating taxon-specific vision modelling (Crothers & Cummings, 2013; Dreher, Cummings & Pröhl, 2015; Maan & Cummings, 2012) indicate that the colour patterns of poison frogs are indeed likely to be designed to signal primarily to birds and crabs. However, it is important to note that both these vision models and the experiments with clay models are unable to assess the importance of predators such as snakes, which do not rely predominantly on visual cues for prey detection, but use mostly olfactory, thermal or movement cues instead (Saviola, McKenzie & Chiszar, 2012).

Further support for the role of poison frog colour patterns as an anti-predator strategy has been obtained in recent studies. Various field experiments have shown that colourful models representing local frogs are usually less frequently attacked than dull models, models representing novel morphs, or familiar models placed on novel backgrounds, at least for colours resembling the morphs of *Oophaga pumilio* in Costa Rica (Hegna *et al*., 2011; Saporito *et al*., 2007*b*; Stuart, Dappen & Losin, 2012) and *Dendrobates tinctorius* in French Guiana (Noonan & Comeault, 2009; Rojas, Rautiala & Mappes, 2014*b*). Interestingly, an experiment carried out in Isla Colón (Panamá) showed that the local, green morph of *O. pumilio* was attacked at significantly higher frequency than the foreign, red morph from the mainland (Hegna, Saporito & Donnelly, 2013). According to the authors, this result suggests that red might be a more efficient predator-deterrent warning signal regardless of what the local signal is. Finally, movement has been shown to affect attack rates on clay models of different colours (Paluh, Hantak & Saporito, 2014). In a study comparing attack rates on stationary brown and red clay models to those on moving models of the same colours, Paluh *et al*. (2014) demonstrated that not only was bird predation significantly higher on moving brown frog models, but also significantly lower on moving red frog models. These findings provide evidence of the significance of prey movement for visual predators, and highlight the importance of incorporating elements that offer more representative measures of predation in the wild into clay model experiments.

In addition to aposematism *per se*, studies demonstrate that both Batesian (a palatable species mimicking the colouration of a defended one; Bates, 1862) and Müllerian (two defended species sharing similar colour patterns; Müller, 1878) mimicry exist among frog species. In Ecuador, the aposematic frogs *Ameerega* (*Epipedobates*) *bilinguis* (Fig. 4B) and *A. parvula* occur parapatrically and serve as models to their nondefended mimic, *Allobates zaparo*, which adopts the corresponding colouration of its model at each locality (Darst & Cummings, 2006; Darst, Cummings & Cannatella, 2006). Likewise, *Allobates femoralis* (Fig. 6A, right), an Amazonian species with a wide geographic distribution and great interpopulational variation in the colouration of both their inguinal and axillary patches, has been thought to be a Batesian mimic of *Ameerega hahneli* (Fig. 6A, left) (Amézquita *et al*., 2009). *Ranitomeya imitator* from Peru, on the other hand, is by far the best-known example of a Müllerian mimetic radiation in amphibians (Symula, Schulte & Summers, 2001; Twomey, Vestergaard & Summers, 2014; Twomey *et al*., 2013). This species (Fig. 6H–K) has diverged in both colour pattern and brightness among populations to resemble the colour patterns of its putative defended models: *R. variabilis* (Fig. 6D, highland morph; Fig. 6G, lowland morph), *R. summersi* (Fig. 6E), and *R. fantastica* (Fig. 6F) (Yeager *et al*., 2012; but see Chouteau *et al*., 2011). Recent experiments with chickens have demonstrated that models and mimics in this complex might indeed share the costs of predator learning (Stuckert, Venegas & Summers, 2014*b*). Furthermore, a comparison between the alkaloid profiles of mimics and models has confirmed that all co-mimics possess chemical defences (Stuckert *et al*., 2014*a*). Reciprocal learned avoidance by predators and possession of secondary defences by all the species in the mimetic complex are two fundamental assumptions of Müllerian mimicry (Müller, 1878). Among frogs, however, these assumptions have been tested and confirmed only for the *R. imitator* complex thus far. Another case of Müllerian mimicry was recently proposed, without further experimental support, where the leptodactylid *Leptodactylus lineatus* (Fig. 6C) previously thought not to be chemically defended, resembles the colouration of the dendrobatid *Ameerega picta* (Fig. 6B) (Prates *et al*., 2012). Also, phylogenetic analyses used to study the evolution of colour patterns in Malagassy poison frogs (genus

Mantella) suggest that the convergence in colouration between *M. madagascariensis* and *M. baroni* (Fig. 2A), which occur sympatrically, may represent another case of Müllerian mimicry (Schaefer, Vences & Veith, 2002). This hypothesis, however, has not been tested either. Therefore, given the great variability in toxicity and colour patterns within anurans, and the co-occurrence of toxic with nontoxic species in wide geographical ranges, it seems likely that even more examples of both types of mimicry are waiting to be uncovered.

(*a*) *The puzzle of polymorphic warning signals*

Warning signal variability may reduce the ability of predators to learn and retain the association between colour patterns and distastefulness (Exnerová *et al*., 2006; Greenwood, Wood & Batchelor, 1981; Mallet & Joron, 1999). As a result of stabilising selection, it is expected that aposematic prey will have little to no variation in their warning signals (Darst & Cummings, 2006; Endler, 1988; Endler & Mappes, 2004; Joron & Mallet, 1998). Hence, polymorphisms should be selected against in aposematic species (Endler & Mappes, 2004). However, there are several cases of aposematic species exhibiting colour polymorphisms in nature, for example ladybirds (O'Donald & Majerus, 1984; Ueno, Sato & Tsuchida, 1998), beetles (Borer et al., 2010) and moths (Hegna, Galarza & Mappes, 2015). In anurans, despite many aposematic species showing geographic variation in colouration (Amézquita *et al*., 2013; Brusa *et al*., 2013; Chouteau *et al*., 2011; Hoogmoed & Avila-Pires, 2012; Lötters *et al*., 1997; Myers & Daly, 1983; Noonan & Gaucher, 2006; Wollenberg *et al*., 2008), within-population variability in warning signals has been reported only for *Oophaga pumilio* (Fig. 7A–D) (Maan & Cummings, 2012), *O. histrionica* (Amézquita *et al*., 2013), *Dendrobates tinctorius* (Rojas & Endler, 2013) (Fig. 7E–H) and *Melanophryniscus rubriventris* (Fig.

3C) (Bonansea & Vaira, 2012). Nevertheless, given that levels of variation have not been investigated in many species, it is highly likely that more examples are yet to be discovered.

Although there are several instances of polymorphic aposematic populations, the mechanisms allowing warning signal polymorphisms to persist are not yet fully understood. Recent approaches suggest a number of possible explanations: (1) an interaction between natural and sexual selection (Crothers & Cummings, 2013; Cummings & Crothers, 2013; Nokelainen *et al*., 2012); for example, in the aposematic wood tiger moth (*Parasemia plantaginis*), where males can be either yellow or white, yellow individuals have been found to be better protected from predators, whereas under certain circumstances whites have a higher mating success (Gordon *et al*., 2015; Nokelainen *et al*., 2012). In *O. pumilio* from Solarte Island (in the Bocas del Toro archipelago), the stabilising selection exerted by predators to keep colour patterns uniform is most likely counteracted by directional sexual selection favouring brighter males, which are preferred by females (Maan & Cummings, 2009). (2) Spatio-temporal variation in selection (Endler & Rojas, 2009; Galarza *et al*., 2014; Nokelainen *et al*., 2014), for instance in the composition of local predator communities, which may generate a geographic mosaic of selection throughout the distribution range of a species. (3) A link between colour patterns and a fitness-related trait (or group of traits), either behavioural or physiological. Examples of this are differential activity patterns and investment in immune defences according to colour, as in wood tiger moths, or the association between movement type and colour patterns in the dyeing poison frog (*Dendrobates tinctorius*) (Nokelainen, Lindstedt & Mappes, 2013; Rojas, Devillechabrolle & Endler, 2014*a*; Rojas, Gordon & Mappes, 2015*a*). (4) Relaxed selection towards warning signals or predator generalisation, which involves predator avoidance of one signal and the expansion of this aversion towards other signals similar enough to the one learnt (Amézquita *et al*., 2013; Darst *et al*., 2006; Richards-Zawacki, Yeager & Bart, 2013). (5) Non-adaptive forces such as hybridisation among geographic variants or drift (Gray & McKinnon, 2007; Medina *et al*., 2013; Thompson, 1984). Whatever the mechanism, for polymorphisms to be maintained there should be no differences in fitness among the morphs.

(*b*) *Honesty in warning signals*

The 'handicap principle' (Zahavi, 1975) suggests that selection should favour signals that provide reliable information about an individual's quality. These signals must represent costs for the signaller, so that they are unaffordable for individuals whose quality is lower. Although suggested originally for sexual signals, honest signals have the potential to evolve in predator–prey relationships as well (Guilford & Dawkins, 1993).

For aposematic individuals, it is likely that warning signals are reliable indicators of prey's unprofitability (e.g. toxicity), as only well-defended prey can afford the costs of being easily detectable by predators (Sherratt, 2002). However, detectability is not necessarily the only cost aposematic species may incur. Theoretical studies have shown that simultaneous investment in pigments and chemical defences may trade off within the same individual (Blount *et al*., 2009). Thus, warning signals are likely to be honest signals of the quality (or quantity) of chemical defences, as only well-defended individuals could profitably tolerate the costs of strong warning signals.

A positive correlation between warning signals and toxicity has been found across species of dart poison frogs in a study where phylogenetic constraints were taken into account, and where both colouration and toxicity were considered 'either/or' traits

(Summers & Clough, 2001). However, quantitative approaches to whether poison frogs' warning signals are honest or not have yielded mixed evidence. For instance, among different populations of *Oophaga pumilio* colouration has been suggested to be an honest indicator of toxicity, such that the brightest populations are also the most toxic (Maan & Cummings, 2012). However, a negative correlation between these two traits has also been found, both between and within species. The conspicuous species *Ameerega* (*Epipedobates*) *bilinguis* has a lower toxicity level than its less-conspicuous counterpart, *Ameerega* (*Epipedobates*) *parvulus* (Darst *et al*., 2006). Notably, experiments with chicks revealed that both increased conspicuousness and increased toxicity are equally effective when it comes to predator deterrence (Darst *et al*., 2006). Likewise, in different populations of *Oophaga granulifera* conspicuous colouration and toxicity are inversely related, such that the most conspicuous populations show the lowest levels of toxicity. In fact, these populations, where individuals are bright red, lack four of the alkaloids present in populations with the less conspicuous yellow or green colouration (Wang, 2011). According to Blount *et al*. (2009), this scenario is plausible when resource availability is high, as suggested for the seven-spot ladybird, *Coccinella septempunctata* (Blount *et al*., 2012). However, a recent theoretical approach found that, at equilibrium, a negative correlation between conspicuousness and defence strength does not hold (Holen & Svennungsen, 2012). This is because, if a trade-off between the resources invested in warning signals and chemical defences is assumed, the benefit of more conspicuous signals is a low risk of prey being attacked after detection, whereas the cost is a reduced defence level, which will bring decreased probabilities of survival upon attack (Holen & Svennungsen, 2012). Toxins such as those found in dendrobatid, mantellid or bufonid frogs are believed to be mainly sequestered from their diet (Clark *et al*., 2005; Daly *et al*., 1997; Hantak *et al*., 2013), which consists primarily of leaf-litter arthropods. This means that, as suggested by previous studies (Maan & Cummings, 2012; Wang, 2011), variation in toxicity levels among populations of the same species might be due to variation in prey availability. However, this does not necessarily explain why some species (or individuals within the same population) are more toxic, or more conspicuous, than others.

Finding correlations, either positive or negative, between warning signals and the quality or quantity of chemical defences in the species mentioned above has been very informative on the dynamics of predator–prey relationships in anurans. However, empirical studies tend to miss one (or more) of the key elements about honesty, such as evidence that predators really pay attention to variation in toxicity and/or see (and care about) the difference among signals. Often only a correlation between toxicity and colouration is found, and the rest is assumed. Therefore, as Summers *et al*. (2015) state in a recent review, one key question is how to differentiate between quantitative honesty and other ways in which conspicuousness and toxicity may be correlated without involving honest signalling.

The next steps thus should also include observations and experiments leading to a better understanding of the costs associated both with toxin sequestration and storage, and with the production of warning signals (i.e. pigments). For example, in species with variable colour patterns, it could be tested whether in cohorts of individuals raised from larvae in the same conditions, juvenile colour patterns are correlated with life-history traits such as size and time to metamorphosis. Additionally, juveniles could be raised in semi-natural enclosures differing in diet restrictions to see whether resource availability affects colouration, or toxicity, or both. A primer on this is a recent study on *Dendrobates auratus*, where the effects of rearing tadpoles on either a high-food or low-food diet were tested on body size and luminance at metamorphosis (Flores *et al*., 2013).

The authors found that in metamorphs raised on a high-food diet body size and luminance were negatively correlated, whereas this correlation was positive in froglets reared on a low-food diet. According to Flores *et al*. (2013), these findings suggest either a trade-off in resource allocation, or developmental plasticity aimed at minimising predation risk at the most vulnerable (early) stages. Life-history trade-offs in relation to frog colouration may therefore be more common than usually thought, especially if the resource-allocation hypothesis holds.

(3) Conspicuous colouration revealed through movement or behaviour

Besides the very well-studied active visual displays that some frog species perform with their fore and hind limbs (i.e. arm waving, foot flagging, etc.), some of which expose coloured patches (reviewed in Hödl & Amézquita, 2001), several anuran species reveal coloured parts of their body through movement or specific positions (Hödl & Amézquita, 2001). Some species that use camouflage as their primary defence against predators have a secondary 'hidden' conspicuous colouration which is revealed under threat (i.e. deimatic displays; Edmunds, 1974; Umbers, Lehtonen & Mappes, 2015). Species in the genera *Phyllomedusa* and *Agalychnis*, for example, have this kind of colouration on their flanks (Fig. 8A). Their markings display combinations of yellow, orange, or purple with black stripes, and might serve as a warning signal to their irritating skin secretions (Wells, 2007, and references therein) and strong smell (B. Rojas, personal observations) when handled. The anti-predator function of these colour patterns warrants experimental testing. Species of the genera *Physalaemus*, *Pleurodema* and *Edalorhina* exhibit what resemble eyespots in the lower part of their dorsum (Fig. 8B). These markings are better seen when the frogs hide their head in the substrate, leaving visible only the posterior part of the body (Lenzi-Mattos *et al*., 2005; Martins, 1989). Fire toads of the genus *Bombina* expose their conspicuous ventral colouration by raising the legs and arching their body ('unken reflex') when threatened (Bajger, 1980). This behaviour is also common among South American frogs of the genus *Melanophryniscus* (Fig. 8C–E) (Caorsi *et al*., 2014; Grant *et al*., 2012; Santos & Grant, 2011). Finally, the conspicuous and very distinctive ventral colouration exhibited by some species of *Atelopus* (Fig. 3B) has also the potential to deter predators, especially given the highly toxic tetrodotoxins present in the genus (Fuhrman, Fuhrman & Mosher, 1969; Kim *et al*., 2003), but this hypothesis also requires in-depth examination.

III. INTRASPECIFIC COMMUNICATION

(1) Mate preferences and assortative mating

Bright colours can be important signals in mate choice (Andersson, 1994), particularly, but not exclusively, for diurnal species that use a wide range of visual signals during courtship (e.g. poison frogs: Hödl & Amézquita, 2001; Zimmermann & Zimmermann, 1988). For example, females of different taxa prefer to mate with more colourful or brighter individuals (Bajer *et al*., 2010; Gomez *et al*., 2009; Maan *et al*., 2004). In some cases, not only the colour but also a variety of different criteria such as the number, size or shape of patches or spots are important in mate choice (Petrie, Halliday & Sanders, 1991; Pincemy, Dobson & Jouventin, 2009). Although in many cases the explanations for mate preferences remain obscure, it has often been found that they are associated with the indirect benefits of 'good genes' (Cutrera, Fanjul & Zenuto, 2012; Hamilton & Zuk, 1982; Milinski & Bakker, 1990; Stange & Ronacher, 2012). Female preferences can exert directional selection on male traits that provide reliable information about their quality, because high-quality mates presumably lead to higher quality offspring, *via* increased fitness [through, for example, parasite resistance (Barber *et al*., 2001; Demuth, Naidu & Mydlarz, 2012; Horak *et al*., 2001; Milinski & Bakker, 1990) or protection from predators (Lancaster, Hipsley & Sinervo, 2009; Sheldon *et al*., 2003)]. In spite of this, there are hardly any studies either on the influence of colouration on mate choice or on the fitness consequences of such choices in anuran species.

Some nocturnal frog species are known to pay attention to colours when choosing a mate, given their ability to see some colour cues under low light (Gomez *et al*., 2010). Using video playbacks of frogs emitting identical calls but differing in the colour and brightness of their vocal sac, Gómez *et al*. (2009) demonstrated that female *Hyla arborea* are more attracted to males with a more colourful sac and prominent lateral stripe, which may together boost male conspicuousness. Furthermore, given that carotenoid production is costly, the authors hypothesised that carotenoid-based colours in the vocal sac might convey information about male quality (Gomez *et al*., 2009). Similarly, female *Scaphiopus couchii* prefer brighter males; in this species, both colour and patterning of males are reliable indicators of body size, which may in turn be an indicator of male quality (Vasquez & Pfennig, 2007). Finally, when presented with two models differing in colour pattern but emitting identical calls, female *Hyla squirrella* seem to be more attracted to males with large lateral stripes (Taylor *et al*., 2011).

Among diurnal frogs, the only species in which visual mate choice has been studied extensively to date is *Oophaga pumilio*. Females in this species have been shown to prefer males with higher dorsal brightness (Maan & Cummings, 2009). Although ventral colouration could be expected to be more important than dorsal patterns for intraspecific communication given that most interactions occur while frogs are facing each other (Siddiqi *et al*., 2004), this and other studies support the idea that male dorsal colouration is the most relevant trait on which females base their preferences (Maan & Cummings, 2008; Summers *et al*., 1999). *Oophaga pumilio* has also been the focus of several studies because of its extensive interpopulation variation in colour patterns, especially in the Bocas del Toro Archipelago in Panama (Fig. 7A–D). Here, at least 15 different morphs have been identified among different islands (Myers & Daly, 1983; Siddiqi *et al*., 2004), but, with the exception of one population at Isla Bastimentos, populations of this species are known to be monomorphic. Understanding the origin of such geographic diversity in colour pattern has proved challenging, although there are strong indications that, besides natural selection, sexual selection may play a role in its maintenance (Crothers & Cummings, 2013; Cummings & Crothers, 2013; Maan & Cummings, 2009; Summers *et al*., 1997).

A possible mechanism by which sexual selection can promote the maintenance of geographic variants is through assortative mating, the non-random pairing of two individuals on the basis of a shared trait (Kondrashov & Shpak, 1998); be it morphological, ecological, or behavioural. Assortative mating has been broadly documented in a wide variety of organisms, and can be either positive (matings between individuals with the same phenotype) or negative (matings between different phenotypes). Colours seem to play a prominent role in the occurrence of assortative mating in taxa such as fish (Maan & Seehausen, 2011; Seehausen & van Alphen, 1998; Terai & Okada, 2011), birds (Andersson, Ornborg & Andersson, 1998), butterflies (Melo *et al*., 2009), and frogs. In a set of choice experiments with *O. pumilio* in the laboratory, females presented with males from two different populations (i.e. two different colour morphs) were more likely to spend time with the male from their own population (Reynolds & Fitzpatrick, 2007; Summers *et al*., 1999). Another study, with four populations, found that female mating preferences are influenced by male colours in such a way that native males were favoured, but that this preference relies heavily on the phenotype of the second male that is presented in the experiment (Maan &

Cummings, 2008). Recent work inferring patterns of colour-based mating in *O. pumilio* from wild pedigrees indicates that the assortative mating found in the laboratory does not necessarily translate completely to the field, where choices are actually made (Richards-Zawacki, Wang & Summers, 2012). It would be interesting to determine whether these preference patterns apply to other dart poison frog species with comparable geographic variation in colour patterns (Hoogmoed & Avila-Pires, 2012; Lötters *et al.*, 2007; Silverstone, 1975). Likewise, it would be intriguing to determine whether colours play a role in mate choice in completely unrelated taxa such as species of the genus *Mantella*. This group of Malagassy frogs seems a striking example of evolutionary convergence with dendrobatids not only because of their conspicuous colouration (Schaefer *et al.*, 2002) and skin alkaloids (Garraffo *et al.*, 1993*a*), but also because of their complex social and reproductive behaviour (Heying, 2001). Other suitable candidates for this kind of investigation are species of the genus *Melanophryniscus*, such as *M. rubriventris* (Bonansea & Vaira, 2012).

(*a*) *Colours can attract both mates and predators*

One problem that animals face when they have conspicuous colour patterns is that they may be providing information about their presence and location to both wanted and unwanted receivers. While aposematic species have evolved distastefulness as a way to deter predators, unprotected organisms must find a way to efficiently attract conspecifics without attracting too much attention from predators or sneakers (Endler, 1978, 1980). This problem might be overcome by using ‘private communication channels’ so that conspicuousness is higher towards conspecifics than it is towards predators (Endler, 1978, 1980, 1991*b*; Schaefer, 2010), which would imply that the visual sensitivity of conspecifics is better ‘tuned’ to the characteristics of their visual signals than is the predators' sensitivity (Endler, 1991*b*). Alternatively, there could be spatio-temporal constraints on the use of conspicuous signals, for example in species with explosive breeding (i.e. breeding activity limited to only one or a few days, often following the first rains of the season; Wells, 2007, and references therein).

There are various examples of spatio-temporal niche partitioning in frogs, most of which relate to their acoustic signals in complex assemblages (Amézquita *et al*., 2011; Check, Bogart & Lougheed, 2003; Duellman & Pyles, 1983; Lüddecke *et al*., 2000). Recent studies, however, have shown that such partitioning could also be related to colouration, and occur at an intraspecific level. The toad *Bufo luetkeni* breeds at the very beginning of the rainy season in Costa Rica. Males of this species, which are otherwise dully coloured, become lemon yellow when they are ready to breed, and combine this conspicuous signal with distinct calls to create a multimodal display that attracts females. Females, as well as recently mated males, are dull brown, which suggests that this temporal change in colouration may be influenced by sexual selection, and restricted in time presumably due to increased risk of predation when conspicuous (Doucet & Mennill, 2010). In *Rana temporaria*, males in breeding aggregations display brighter throats (Fig. 9A), whereas male moor frogs (*Rana arvalis*) turn blue (Fig. 9B). Such colour changes have been suggested to function as a sex-recognition cue to prevent mismating attempts during the intense scramble competition common among explosive breeders (Sztatecsny *et al*., 2012, 2010).

(*b*) *Sexual dichromatism*

The changes in colouration described above occur in just one sex, and are therefore considered examples of sexual dichromatism. Also, because they occur only temporarily, during breeding, they are considered to be 'dynamic'. This type of colour change has been studied most thoroughly in the context of frog behaviour or ecology. However, due to its visibility for only a short period of time – ranging from a few hours to a few weeks – its occurrence is thought to be underestimated, i.e. it probably is more common than we are aware of in anuran taxa (Bell & Zamudio, 2012). There are also cases of ontogenetic colour change, where males differ from females in colouration from early life stages (Bell & Zamudio, 2012). For example, female African reed frogs of the genus *Hyperolius* change their colour patterns when attaining maturity, whereas males keep their juvenile colours (Veith *et al*., 2009).

In one of the populations of the Bocas del Toro archipelago, the aposematic frog *O. pumilio* is known to be sexually dimorphic in terms of brightness, a non-chromatic component of colour patterns, with adult males as the brighter sex (Maan & Cummings, 2009). This is most likely due to directional sexual selection (Maan & Cummings, 2009). Male *Dendrobates tinctorius* from a highly polymorphic population in French Guiana, on the other hand, are overall yellower than females. This has been suggested to be the product of a synergy between sexual selection in the form of parental care, and the potential increased predation risk for males during the prolonged exposure involved in tadpole transport (Rojas & Endler, 2013). Despite these examples, sexual dichromatism is still surprisingly understudied considering how widespread it seems to be among anurans (Bell & Zamudio, 2012).

(2) Intrasexual competition and conflict resolution

Intraspecific aggression has been widely documented and can occur in different contexts (Lorenz, 1966; Riechert, 1998). Individuals can behave aggressively against conspecifics when they threaten the survival of their offspring (Sommer, 1987), when they threaten access to potential mates (Andersson, 1994), or when they are defending a space that holds resources essential for their survival (i.e. food or shelter) or reproduction. The latter case is normally referred to as territoriality (Kaufmann, 1983; Maher & Lott, 1995). However, aggression *via* escalated conflict is costly in terms of energy and confers the risk of being injured (Maynard Smith & Harper, 2005). Therefore, under specific circumstances, the resolution of conflicts *via* the exchange of signals is expected to be favoured over physical aggression as an evolutionarily stable strategy (Maynard Smith, 1982; Maynard Smith & Harper, 2005). In fact, the mitigating effect of signalling during agonistic interactions has empirical support (Logue *et al.*, 2010).

During a conflict, contestants should assess the probability of defeat by comparing their own fighting abilities with those of their opponent (Riechert, 1998). This means that both individuals are at the same time senders and receivers, as they exchange information about status, relative fighting ability, and relative resource value. Such information could be given and obtained on the basis of behavioural traits such as the rate at which displays are repeated (Johnstone, 1997). For example male jacky dragons (*Amphibolurus muricatus*) respond to video playbacks of conspecifics displaying at varying time intervals with aggressive push-ups (Ord & Evans, 2003). Alternatively, information can be contained in intrinsic characteristics of an individual such as colours, size, condition, or the size or complexity of weaponry such as horns or antlers (Bradbury & Vehrencamp, 2011).

Colouration is a reliable signal of status and an important determinant of conflict resolution for several species of insects, fish, lizards, and birds (López, Martin & Cuadrado, 2004; Morimoto, Yamaguchi & Ueda, 2005; Pryke & Andersson, 2003*a*; Stuart-Fox & Johnston, 2005). Not only the colour, but also the size and shape of visual signals may provide information about fighting abilities during agonistic encounters.

There is much evidence that more colourful males, and sometimes females, tend to acquire and retain higher status within a group of individuals, whereas dull-coloured individuals are often subordinate. For example, redder male firemouth cichlids (*Cichlasoma meeki*) are more likely to win contests than duller ones (Evans & Norris, 1996); and sand lizards (*Lacerta agilis*) with more colourful badges are more likely to initiate and win fights (Olsson, 1994); Similar trends have been found in African red-shouldered widowbirds (*Euplectes axillaris*), where individuals with redder patches are more likely to acquire territories and outcompete rivals (Pryke & Andersson, 2003*b*).

If colour pattern is an honest signal of an individual's ability to defend its territory, one may also expect brighter or more colourful individuals to win contests more often than the dull ones, and thus be more successful in acquiring and maintaining high-quality territories. As predicted, we find many examples of this throughout different taxa. For instance, territorial Augrabies flat lizard (*Platysaurus broadleyi*) males have a lower ultraviolet reflectance than floaters (Whiting *et al*., 2006), and the size of the red spots in the wings of male rubyspot damselflies (*Hetaerina americana*) promotes successful defence of a territory (Grether, 1996).

Nearly all anurans defend small, short-term individual spaces during the breeding season, as they confer a particular advantage for the propagation of mating signals or better access to mates (Wells, 2007, and references therein). Dendrobatid frogs seem to be a remarkable exception to this generalisation, as all of the species studied to date exhibit some degree of long-term territoriality (Pröhl, 2005; but see Born *et al*., 2010). They defend multi-purpose territories that aid in mate attraction (Wells, 2007) and subsequent breeding. Defended resources within each territory vary from species to species (Pröhl, 2005), but are most often related to their elaborate parental care.

Even though most frogs rely on acoustic signals for communication, resident male dendrobatids generally advertise territory ownership to intruders with a combination of acoustic and visual signals (Hödl & Amézquita, 2001; Zimmermann & Zimmermann, 1988), and in some cases physical combats can occur until the intruder is chased away, or gains the territory over the resident. For example, according to Wells (1980), territorial male *Mannophryne* (= *Colostethus*) *trinitatis* turn black when calling while non-calling males remain brown. Most interestingly, black males seem to react aggressively only towards other black males, and often engage in wrestling. At the end of the encounters, one of the males changes his colour back to brown, which presumably decreases the probability of being attacked by a black male (Wells, 1980). A recent study in laboratory conditions showed that *O. pumilio* males call and approach brighter males more frequently than duller ones. Furthermore, a male's own brightness also predicts his own behaviour, such that brighter males approach stimulus frogs faster and call more towards other bright individuals (Crothers, Gering & Cummings, 2011). A field study on males of the same species showed that the most aggressive males from eight sampled populations were the ones with the most conspicuous colouration (Rudh, Breed & Qvarnstrom, 2013).

While these links between colouration and behaviour seem to be reported more frequently, the mechanisms explaining how they appear and persist warrant in-depth examination. Correlational selection, which may favour certain combinations of traits (such as behaviour and phenotype) expressed at the same time in an individual without affecting the expression of each trait on its own (Brodie, 1992; Endler, 1986; Sinervo & Svensson, 2002), may be one possibility. Pleiotropy and gene linkage have also been advocated as possible explanations for the higher levels of dominance of Gouldian finches (*Erythrura gouldiae*) bearing a red head, even when their head colour was manipulated to look like the subordinate morphs (Pryke & Griffith, 2006).

Some species need acoustic and visual signals together (like the inflation–deflation of the vocal sac) in order to trigger agonistic behaviour (de Luna, Hödl & Amézquita, 2010; Narins, Hödl & Grabul, 2003). Thus, the importance of visual signals and the potential role of colouration and colour patterns in the agonistic interactions of species that emit very soft sounds (*Dendrobates leucomelas*, *D. truncatus* and *D. auratus*; Erdtmann & Amézquita, 2009), or lack an acoustic advertisement call (*Dendrobates tinctorius*; Born *et al*., 2010; B. Rojas, personal observations) demands further investigation.

As shown above, both male territorial behaviour and male–male aggression have been well documented in dendrobatoids (Pröhl, 2005). Aggression between females, on the other hand, has been poorly studied. Wells (1980) reported aggression between females of *Mannophrynne trinitatis.* A resident female challenges an intruder by acquiring an upright posture, and pulsating her bright yellow throat. Female *Dendrobates auratus* behave aggressively by chasing each other or wrestling in the presence of calling males (Summers, 1989). Apart from these studies, no others have been conducted on the role of colours in the agonistic behaviour of female frogs, and reports of its occurrence remain mostly a matter of side observations in male mating behaviour studies (Summers, 1992; Wells, 1978). Female aggression occurs in at least four colourful species: *O. pumilio*, *D. auratus*, *D. leucomelas* (Meuche, Linsenmair & Proehl, 2011; Summers, 1989, 1992; Wells, 1978) and *D. tinctorius* (B. Rojas, personal observations). Given that females do not vocalise at all, their means of acquiring, defending, and maintaining resources are still obscure. Hence, species with territorial females constitute an excellent target for examining the importance of colour patterns during agonistic interactions.

IV. HABITAT SELECTION AND SPACE USE

The distribution of individuals of a species within a particular habitat might be explained by the location of resources or anti-predator refuges, the suitability of different microhabitats, or the preferences of conspecific individuals (Alcock, 2001). There are at least two ways in which colours or colour patterns can be associated with habitat selection and space use. First, animals might choose a habitat that provides the best blending opportunities in order to minimise detection by predators (Ruxton *et al.*, 2004). This can be achieved, for example, either by background matching (Endler, 1984; Pellissier *et al.*, 2011), or by mixing with groups of species with similar colouration (Munday, Eyre & Jones, 2003). Second, animals can select microhabitats that increase their own conspicuousness or the conspicuousness of their sexual displays (Endler, 1993*b*; Heindl & Winkler, 2003; Théry, 2001; Théry & Endler, 2001). Section II.1 discussed how some species with cryptic colouration may select the habitat that best matches their colours in order to avoid being detected by predators. By contrast, in this section I will address implications other than background matching of colour-mediated space use and habitat selection.

As discussed above, aposematic species rely on their conspicuousness to teach predators about their unprofitability which should lead to monomorphism of the warning signal. However, as explained previously there are many polymorphic (and polytypic) aposematic species. It is possible that these species benefit from colour pattern-mediated habitat selection as a mechanism to maintain colour pattern variability. In such cases, each morph could choose a habitat that maximises its conspicuousness. Alternatively, if conspicuousness differed among morphs, less-protected individuals could benefit from choosing microhabitats that provide extra protection from predators, for example hiding places. The former seems to be the case for males of *O. pumilio*, which seem to select vocalisation perches that maximise their conspicuousness (Pröhl & Ostrowski, 2011). Likewise, males from more conspicuously coloured populations of *O. granulifera* (Fig. 4G) tend to call from more exposed perches than populations with duller males (Willink *et al*., 2013).

Aposematic colour patterns may be associated with aspects of space use other than habitat selection. For aposematism to work, prey density must be high (Mappes, Marples & Endler, 2005; Ruxton *et al*., 2004; Speed, 2000), or at least above a certain threshold (Endler & Rojas, 2009), so that the frequency of encounters between the predator and the defended prey enhances predator learning. Therefore, aposematic organisms are assumed to benefit from spatial aggregations (Alatalo & Mappes, 1996; Lindström *et al*., 2001; Mappes & Alatalo, 1997; Riipi *et al*., 2001), and at least in some taxa it has been demonstrated that gregariousness appeared after warning colouration (Beltrán et al., 2007; Sillén-Tullberg, 1988). This does not necessarily occur in all aposematic species. While colourful dendrobatids are also highly toxic, their strong territorial behaviour makes them unlikely to be aggregated. However, one might predict that the territories of conspicuous species are more aggregated than those of dull-coloured species.

Another way to approach the same conceptual problem would be to conduct studies comparing populations of colourful species that differ in abundance. There is good theoretical and increasing experimental support in favour of the idea that spatial variation in selective pressures (i.e. predation) might be a relevant factor shaping the evolution of aposematic signals (Chouteau & Angers, 2011; Nokelainen *et al*., 2014; Valkonen *et al*., 2012), and that the emergence of novel signals can be a frequency-dependent process (e.g. Endler & Mappes, 2004; Endler & Rojas, 2009). To date, however, there is only one empirical study examining how the spatial variation in the frequency of different warning signals may enable the emergence of novel signal types (Comeault & Noonan, 2011). Using clay models Comeault & Noonan (2011) compared the attack rate on different morphs of *Dendrobates tinctorius* in two populations differing in the abundance of the local morph. This study provided evidence that selective pressures affecting the survival rate of a 'protected' morph vary in accordance with its relative abundance in the population. In other words, an aposematic signal that is successful at high densities might not be so when the densities are low.

V. FUTURE DIRECTIONS

Even though the diversity of colours seen in anurans has been documented for decades, only relatively recent studies have directly assessed its function and adaptive significance (reviewed in Rudh & Qvarnström, 2013). Specifically, greater emphasis has been placed on examining the role that colours and other visual signals play in frog behaviour and ecology, especially in relation to protection from predators and mating. Likewise, current research has increasingly explored the synergy between different sensory modalities during mate attraction and male–male competition. Altogether, this indicates that frogs are excellent subjects for research on the evolution of colour-related anti-predation strategies and intraspecific communication systems. Future research should focus on a variety of key issues listed below.

First, experimental approaches could be used to test the efficacy of eyespots and flash colours as signals addressed to potential predators. Among diurnal frogs, predation seems to be the selective pressure that stimulates the most interest among researchers studying colour pattern diversity, but most studies have been carried out in one taxon only (Neotropical dart poison frogs) even though there is a great array of anuran taxa that possess diverse colour patterns (i.e. Mantellidae, Myobatrachidae, Bufonidae, Brachycephalidae, etc.). Furthermore, many recent studies have used clay models; although these studies represent a significant step forward in the study of warning signals, they are biased towards an overestimation of deaths, i.e. ignoring the fact that an attacked individual may survive. Additionally, research with clay models does not account for predators like snakes, which most likely would not attack the models, or for any behavioural correlates that act in concert with the warning signal. Future research could thus benefit from complementary studies where the survival of individuals bearing different colour patterns is tracked, for example, using capture–mark–recapture methods in semi-natural or wild conditions. Also, given their dissimilar distribution ranges, it would be especially interesting to compare the role of natural and sexual selection in the colour diversification of dendrobatids to that of mantellids, which show remarkable signs of evolutionary convergence in other aspects of their biology.

Second, the role of colour patterns is relatively unexplored in mate choice and other aspects of sexual selection such as intrasexual competition, especially in highly territorial species. Studies on how nocturnal species use information conveyed in visual signals and why they may have retained colour vision and coloured traits whose expression may be costly, could refine our understanding of the function and importance of multimodal communication, which has proven increasingly prominent in anurans (Starnberger, Preininger & Hödl, 2014). Beyond the actual mate preferences, there is not much evidence to date supporting the function of colours as reliable indicators of good genes in frogs. It is unknown, for example, whether females obtain indirect benefits when mating with brighter males or males with certain colour patterns and whether that enhances the survival of their offspring.

Third, there is a surprisingly large gap in studies linking colour patterns and life history, especially in aposematic species. It would be very exciting to know what the costs and constraints are that compromise signal efficacy, and whether colours are honest signals for all receivers (i.e. both conspecifics and heterospecifics), or whether they are instead deceptive.

Finally, we must consider other selective pressures besides mate choice and predation in order to investigate how variation in colour patterns can originate and be maintained. Future research should thus focus on exploring more aspects of the behaviour and ecology of the studied species in order to have a better understanding of the function and evolution of the great diversity in colour patterns that exists among anurans today.

VI. CONCLUSIONS

(1) Animals use different modalities of communication depending on both intrinsic and extrinsic factors. Frogs are widely known for their acoustic signals, which are particularly useful for nocturnal animals. Recently, also the use of visual signals in frog communication has become a focus of research.

(2) The first approaches to studying variation in frog colouration dealt mostly with the inheritance of colour patterns. However, not many studies have addressed directly the selective pressures involved in the maintenance of such variation.

(3) Dorsal colour patterns can be directly related to predator avoidance. Some frogs blend with their surroundings in different ways such as matching the colouration of their background, exhibiting colour patterns that make it difficult to distinguish their outline the shape, or by resembling an inanimate object. By contrast, other species of frogs display conspicuous colour patterns which are often coupled with some form of unprofitability. Such colour patterns are thought to aid in predator education. Bright

colouration displayed in other parts of the body such as the flanks or ventral side have been much less studied, and their role in predator deterrence is yet to be tested.

(4) Cryptically coloured frogs are often polymorphic, which may be favourable as a strategy to reduce the *per capita* predation risk. The mechanisms that maintain such polymorphisms are still poorly understood, but predation seems to be a good candidate. Aposematic species, on the other hand, are not expected to be polymorphic because intrapopulational variation in warning signals might interfere with predator avoidance learning. Nonetheless, a few aposematic species exhibit colour pattern polymorphisms. Recent research suggests that such polymorphisms could be maintained *via* an interaction beteween predation and sexual selection, spatio-temporal variation in selection, an association between fitness-related traits and colour patterns, predator generalisation, hybridisation among variants or genetic drift.

(5) Experiments in the field with frog models displaying conspicuous colouration have shown the effectiveness of some colour patterns in predator deterrance. With a few exceptions, local morphs tend to be less attacked than novel ones, and moving models exhibiting conspicuous colouration receive fewer attacks than stationary ones.

(6) In natural frog populations some palatable species mimic the coloration of defended species, obtaining benefits against predation without investing in the production or sequestration of defensive chemicals (Batesian mimicry). Two (or more) chemically defended species can also share similar colour patterns, thus sharing the costs of predator education (Müllerian mimicry). Only a handful of studies have been able to demonstrate the occurrence of either type of mimicry in anurans, and they have focused only on one taxonomic group.

(7) Aposematic individuals are likely to display warning signals that are reliable indicators of their unprofitability, as only defended prey can afford the costs of being

detectable and of having the pigments required for strong warning signals. To demonstrate signal honesty, showing a positive correlation between warning signals and toxicity is not enough. It is necessary to differentiate between quantitative honesty and other ways in which colour patterns and chemical defences can be correlated without involving honest signalling.

(8) Colours can have an important role in mate choice, particularly for diurnal species. Interestingly, some species of nocturnal frogs have been shown to pay attention to different components of male colour patterns. This has also been studied extensively in one diurnal species. However, the fitness consequences of female preferences regarding male colouration remain poorly understood.

(9) In certain cases, colour patterns may provide information about the social status or fighting abilities of an individual during agonistic encounters. Although this has been shown for the males of some species, there is increasing evidence that colours might play a role in conflict resolution also among females.

(10) Besides background matching, habitat selection and space use may also be related to colouration such that different morphs of a species choose a habitat that boosts their conspicuousness. Alternatively, in accordance with the assumed benefits of aggregation of aposematic species, the territories of aposematic frogs might be clumped compared to those of cryptic species. This hypothesis warrants further examination.

(11) The detailed study of colour pattern variation, particularly with an experimental approach, should facilitate the formulation and testing of hypotheses on the evolution of predator–prey interactions, mating preferences and communication systems, and provide valuable knowledge on the mechanisms promoting and maintaining signal diversity.

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Figure legends

Fig. 1. An example of background matching in a young *Pristimantis zeuctotylus* (A); and examples of masquerading, where a female *Rhinella margaritifera* is shown to resemble a dead leaf (B–D). Images C and D are for the same individual photographed at different distances. Photo credits: Bibiana Rojas.

Fig. 2. Aposematic frogs (A) *Mantella baroni*; (B) *Mantella aurantiaca*; (C) *Dyscophus guineti*, known as the 'Tomato frog'; (D) *Pseudophryne corroboree*; (E) *Brachycephalus ephippium*; and (F) *Melanophryniscus rubriventris*. Photo credits: A–C, Gerardo García; D, J.P. Lawrence; E, Taran Grant; F, Marcos Vaira.

Fig. 3. *Atelopus* aff. *franciscus* (A) dorsal and (B) ventral colouration. (C) Geographic variation in the dorsal and ventral colouration of *Melanophryniscus rubriventris*. Photo credits: A,B, Bibiana Rojas; C, Marcos Vaira.

Fig. 4. Dart poison frogs represent the best-known example of aposematism among anurans. (A) *Adelphobates galactonotus*; (B) *Ameerega bilinguis*; (C) *Dendrobates truncatus*; (D) *Dendrobates tinctorius*; (E) *Phyllobates terribilis*; (F) *Dendrobates auratus*; (G) *Oophaga granulifera*; (H) *Phyllobates lugubris* and (I) *Ranitomeya imitator*. Photo credits: A,C, Taran Grant; B,F,H,I, J.P. Lawrence; D,G, Bibiana Rojas; E, Roberto Márquez.

Fig. 5. Known predators of dendrobatid frogs: (A) the snake *Rhadinaea decorata*, feeding on *Oophaga pumilio*; (B) wolf spider (Lycosidae) preying on *Ameerega trivittata*; (C) crab holding an individual *Oophaga histrionica*; (D) rufous motmot (*Baryphthengus martii*) taking an *O. pumilio* to its nest. Photo credits: A, Matthew Dugas; B, Trond Larsen; C, Alejandro Vélez; D, Ralph Saporito.

Fig. 6. Examples of mimicry among poison frog species. (A) *Ameerega hahneli* (left) is thought to be a model for *Allobates femoralis* (right); *Leptodactylus lineatus* (C) has been suggested to be a Müllerian mimic of *Ameerega picta* (B). The best-known case of a Müllerian mimicry system is that of *Ranitomeya imitator*. D–G are the model species: *Ranitomeya variabilis*, highland morph; *R. summersi*, *R. fantastica*, *R. variabilis* lowland morph. The different morphs of *R. imitator* are shown below: (H) spotted; (I) banded; (J) varadero; and (K) striped. Photo credits: A, Jason L. Brown; B, Mauricio Pacheco; C, Quentin Martínez; D–K Evan Twomey.

Fig. 7. Examples of geographic variation in the colour patterns of *Oophaga pumilio* (A–D); and intrapopulation variation in *Dendrobates tinctorius* (E–H). Photo credits: A–D, J.P. Lawrence; E–H, Bibiana Rojas.

Fig. 8. Flash colouration in the flanks of *Phyllomedusa tomopterna* (A); ‘eye spots’ in the lower dorsum of *Edalorhina perezi* (B); and (C–E) the ‘unken reflex’ performed by species of the genus *Melanophryniscus*, even in amplexus (D) . All have been suggested to function as deimatic displays. Photo credits: A,B, J.P. Lawrence; C,D, Marcos Vaira; E, Taran Grant.

Fig. 9. Breeding aggregation of *Rana temporaria* (A) and a pair of the moor frog (*Rana arvalis*) in amplexus (B). Note the bright throats and blue colouration of the males, which are thought to function as sex-recognition cues to prevent mismatings. Photo credits: Marc Sztatecsny.

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80x60mm (300 x 300 DPI)

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80x92mm (300 x 300 DPI)

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107x59mm (300 x 300 DPI)

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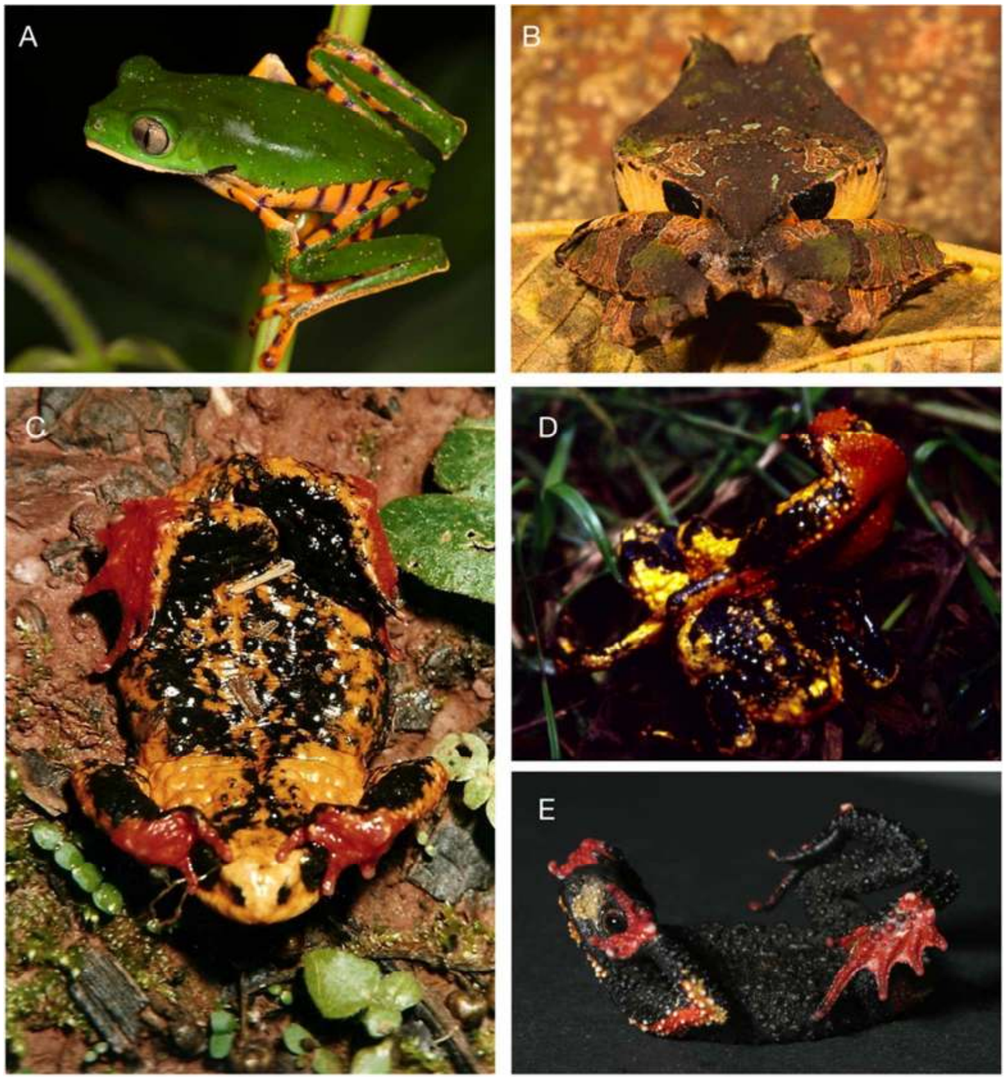
119x46mm (300 x 300 DPI)



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76x81mm (300 x 300 DPI)

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119x43mm (300 x 300 DPI)