

Sexual dimorphism and intra-population colour pattern variation in the aposematic frog *Dendrobates tinctorius*

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Abstract Despite the predicted purifying role of stabilising selection against variation in warning signals, many aposematic species exhibit high variation in their colour patterns. The maintenance of such variation is not well understood, but it has been suggested to be the result of an interaction between sexual and natural selection. This interaction could also facilitate the evolution of sexual dichromatism. Here we analyse in detail the colour patterns of the poison frog *Dendrobates tinctorius* and evaluate the possible correlates of the variability in aposematic signals in a natural population. Against the theoretical predictions of aposematism, we found that there is enormous intra-population variation in colour patterns and that these also differ between the sexes: males have a yellower dorsum and bluer limbs than females. We discuss the possible roles of natural and sexual selection in the maintenance of this sexual dimorphism in coloration and argue that parental care could work synergistically with aposematism to select for yellower males.

Keywords Aposematism · Polymorphism · Sexual dimorphism · Parental care · Poison frog

Introduction

Aposematism is an anti-predator strategy by which some animals warn their predators about their unprofitability with conspicuous colours or patterns (Poulton 1890; Ruxton et al. 2004). Because variation in aposematic signals makes it difficult for predators to learn and retain the association between colour patterns and distastefulness, warning signals are expected to be simple and uniform (Endler 1988; Joron and Mallet 1998; Endler and

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Mappes 2004; Darst et al. 2006). However, variation in aposematic species occurs in many different taxa such as moths (Nokelainen et al. 2012), ladybirds (O'Donald and Majerus 1984; Ueno et al. 1998), butterflies (Mallet and Joron 1999) and frogs (Myers and Daly 1983), suggesting that signal variation may serve other purposes or respond to additional selective pressures.

Recent studies have suggested that an interaction between natural and sexual selection might be responsible for colour pattern variation in some aposematic species. Different components of sexual selection (intra-sexual competition, female choice, etc.) might select for individuals with certain patterns to become more attractive to conspecifics (Ueno et al. 1998; Maan and Cummings 2009; Nokelainen et al. 2012), or to be better competitors during intra-sexual encounters (Crothers et al. 2011), possibly leading to sexual dimorphism in the aposematic signals (Maan and Cummings 2009). Natural selection, on the other hand, may give individuals with certain other patterns an advantage in avoiding predation, leading to the maintenance of such variation (Nokelainen et al. 2012).

Here we evaluate some of the factors that may allow for intra-population variability in aposematic signals in the wild. We studied a natural population of the aposematic, highly polymorphic poison frog *Dendrobates tinctorius* in order to (1) document in detail the main characteristics of their variable colour patterns and (2) test for the occurrence of sexual dimorphism in colouration. We predict that, if there were such dimorphism, males would be more conspicuous given their prolonged exposure to predators due to parental duties.

Methods

Study species and study site

Dendrobates tinctorius is one of the largest species of the Neotropical family Dendrobatidae (Silverstone 1975), with a body length (from snout to vent; hereon referred to as SVL) that ranges between 37 and 53 mm in adult individuals at the study site (this study).

This species is distributed along the Eastern Guiana Shield and is associated with canopy gaps in primary forests at elevations between 0 and 600 m (Noonan and Gaucher 2006; Born et al. 2010). This study was done at a lowland forest next to Camp Pararé, Les Nouragues Reserve, French Guiana (3°59'N, 52°35'W, at an elevation of approximately 120 m), over three field seasons between January and February 2009, January and March 2010, and January and June 2011. These months of the year correspond to part of the breeding season of the species. The population density at the study site is about 4.3 individuals/100 m² (Devillechabrolle 2011).

Like most dendrobatid species, *D. tinctorius* is diurnal and exhibits an elaborated paternal care that consists of clutch attendance and tadpole transport, both performed exclusively by males (Lötters et al. 2007; Rojas, personal observation). In contrast to all other dendrobatids, males of this species lack a regular advertisement call and seldom vocalise during courtship. When they do produce calls, they are very soft (Lescure and Marty 2000) and difficult for a human to hear (Rojas, personal observation); calls usually occur when the courting female is out of their sight (Rojas, unpublished data). Calls are also emitted during physical agonistic encounters, especially by the male being attacked (Rojas, personal observation).

Dendrobates tinctorius has alkaloid-based chemical defenses (Summers and Clough 2001) and bright colour patterns that, according to field experiments with clay models, seem to signal unprofitability to potential aerial predators (Noonan and Comeault 2009;

Comeault and Noonan 2011). These colour patterns vary significantly within (personal observation; Fig. 1) and among populations (Wollenberg et al. 2008).

Sexual dimorphism in colour patterns

At the beginning of the study, sex was identified on the basis of behaviour during courtship (i.e. individuals vocalising were males). Both courting individuals were caught when possible and their snout-vent lengths and disc widths (third finger of left hand) were measured. These data (from 36 males and 36 females) were used to construct a sex index from a discriminant function analysis so that all subsequent individuals could be assigned to male or female on the basis of their measurements. 100 % of individuals in the training set were classified correctly, indicating that this is a very reliable indicator of sex. Males are smaller than females (Table 1) and can be reliably distinguished from the latter on the basis of a combination of body size and the size of their finger discs (Fig. 2). Males have wider discs in proportion to their body size than females (Ancova: SVL: $F_{(1,310)} = 75.57$, $p < 0.001$; SVL*Sex: $F_{(1,310)} = 4.84$, $p = 0.029$, Sex: $F_{(1,310)} = 0.014$, NS; Fig. 2a). According to the discriminant analyses, based on SVL (discriminant function coefficient = -0.884) and disc size (discriminant function coefficient = 0.985), 100 % of the total number of individuals included in the study were classified correctly for sex (Canonical correlation = 0.932 , Wilks' Lambda = 0.132 , $\chi^2 = 621.28$, $df = 2$, $p < 0.001$; Fig. 2b), indicating that sex can be identified reliably from morphometrics.

Frogs (including those used to obtain the sex index) were found during daily surveys along the full length of a 1.5 km transect. Upon capture, every frog ($N = 321$) was photographed against graph paper for scale. Snout-vent length and disc size were measured on



Fig. 1 Colour pattern variation in *D. tinctorius* at the study site

Table 1 Descriptive statistics

Variable	Mean \pm SD (range)	
	Males	Females
Snout-vent length (mm)	43.32 \pm 1.97 (35.48–44.66) N = 311	46.19 \pm 2.55 (36.96–52.54) N = 141
Disc size (mm)	2.49 \pm 0.41 (1.52–3.35) N = 311	2.11 \pm 0.20 (1.52–2.61) N = 141
Proportion of arms covered with yellow	0.28 \pm 0.33 (0–1) N = 320	0.33 \pm 0.33 (0–1) N = 147
Proportion of arms covered with blue	0.37 \pm 0.38 (0–1) N = 320	0.30 \pm 0.36 (0–1) N = 147
Proportion of legs covered with yellow	0.02 \pm 0.08 (0–1) N = 320	0.02 \pm 0.07 (0–1) N = 147
Proportion of legs covered with blue	0.49 \pm 0.25 (0–1) N = 320	0.47 \pm 0.25 (0–1) N = 147
Number of yellow patches in the back	1.65 \pm 1.10 (1–7) N = 321	1.69 \pm 1.23 (1–7) N = 147
Number of dark patches within yellow	0.97 \pm 0.64 (0–3) N = 321	0.99 \pm 0.66 (0–3) N = 147
Number of interruptions of dorsal yellow	1.08–1.44 (0–7) N = 321	1.03 \pm 1.59 (0–7) N = 147
Proportion of dorsal yellow	0.30 \pm 0.09 (0.07–0.60) N = 321	0.29 \pm 0.09 (0.07–0.57) N = 147
Pattern elongation	2.46 \pm 0.37 (1.51–3.62) N = 321	2.45 \pm 0.36 (1.60–3.62) N = 147
Pattern complexity	0.07 \pm 0.02 (0.03–0.25) N = 321	0.07 \pm 0.03 (0.03–0.25) N = 147
Dorsal contrast	0.20 \pm 0.03 (0.06–0.25) N = 321	0.20 \pm 0.04 (0.06–0.25) N = 147
Proportion of ventral side coloured	0.46 \pm 0.22 (0–1) N = 115	0.42 \pm 0.24 (0–1) N = 55
Proportion of throat coloured	0.34 \pm 0.17 (0–0.81) N = 116	0.32 \pm 0.19 (0–0.81) N = 55
Throat contrast	0.19 \pm 0.06 (0–0.25) N = 116	0.18 \pm 0.07 (0–0.25) N = 55

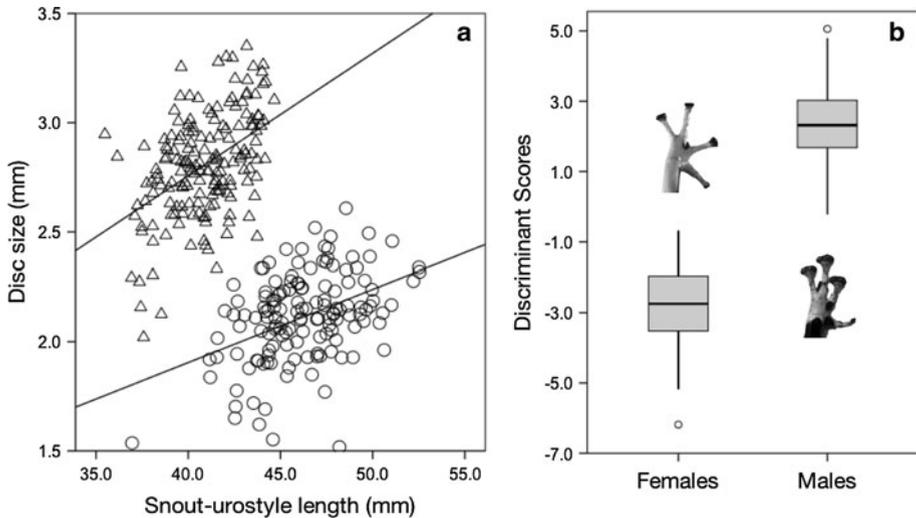


Fig. 2 **a** Scatterplot showing the relationship between snout-vent length and disc size in males (*triangles*; $r^2 = 0.21$) and females (*circles*; $r^2 = 0.18$) of *D. tinctorius*; **b** Box plots illustrating the distribution of discriminant scores for the two sexes (see “[Methods](#)” section for details on discriminant analysis)

the photos using the software ImageJ. The dorsal region of each frog was extracted from the photographs for subsequent analyses of colour patterns with a method (Endler 2012) that uses transects across colour patterns, and allows the estimation of parameters like pattern complexity, pattern elongation, and proportion of a particular colour based on the number of transitions between adjacent colours (in this case yellow and black). These analyses were done with MATLAB software. In addition to the parameters mentioned above, we also recorded the number of yellow patches and the number of interruptions of yellow in the back (modified from Wollenberg et al. 2008). We calculated a value of dorsal contrast by multiplying the proportion of yellow \times the proportion of black; a larger product means more contrast since if either colour is rarer the pattern has less contrast than if both are equally frequent. We estimated the rank proportion of blue and yellow covering both the arms and the hind limbs by choosing by eye one of five values between 0 (no blue or yellow at all) to 1 (either completely blue or completely yellow) representing the approximate proportion covered with each colour (0, 0.25, 0.5, 0.75, and 1). Ranks were used instead of direct measurements because arms and legs are difficult to photograph in a standard position in live frogs and therefore photographic measures of limb patterns would be unreliable. Because ventral patterns were not as variable as dorsal ones, we took ventral photographs of only a third (115) of the 321 individuals used for dorsal pattern analysis in order to estimate the coloured proportion of the ventral side (blue in most cases) and, more specifically, of the throat region. The presence of shadows and the variable position of the frogs in the ventral photos made it impossible to use the automated method for measuring ventral colour proportions. Therefore the rank proportion of ventral coloration was estimated in the same way as that of the limbs¹. The proportion of colour for the throat was estimated with the software ImageJ, and the throat contrast was calculated in the same way as dorsal contrast.

With the exception of pattern elongation (Endler 2012) none of the parameters of colour patterns were normally distributed even after transformations, so we used non-parametric analyses (Mann–Whitney) in order to test for differences in colour patterns characteristics between the sexes. Pattern elongation was compared between males and females by means

of a one-way Anova, p values were corrected for multiple comparisons using sequential Bonferroni tests. All statistical analyses were done with the software SPSS 19.0 for Mac.

Results

Intra-population variation in colour patterns

There is much variation in the characteristics of colour patterns studied in this population (Fig. 1; see Table 1 for descriptive statistics). In general, the background dorsal colour is black, with yellow dorsolateral lines that may fuse at the sacrum and extend to the vent. This often results in the appearance of a large ovoid black spot on the dorsum. The width of dorsolateral lines and completeness varies considerably covering between 7 and 60 % of total dorsum. The lines can be interrupted between one and six times forming, in some cases, discontinuous patches. As opposed to some other populations where individuals have a completely yellow dorsum (Lötters et al. 2007; Noonan and Comeault 2009), in the study population even the yellower individuals have a black patch within the yellow area, and some individuals have two or three. The limbs also have a black reticulated pattern with blue or a few scattered yellow patches. The ventral side has most often a reticulated pattern of black and blue, but can be almost entirely black. Aside from pattern complexity, none of the characteristics of the colour patterns measured was correlated with body size (Table 2). Table 2 provides a summary of the significant correlations among the colour pattern characteristics measured. Individuals with yellower arms have a larger proportion of dorsal yellow (Fig. 3a) distributed in fewer patches. Individuals with bluer arms have less yellow in their dorsum (Fig. 3b), more elongated patterns and a larger proportion of their ventral side coloured (Fig. 3c).

Pattern elongation is positively correlated with pattern complexity (Fig. 3d). Individuals with dark patches within the yellow area have higher contrast (Fig. 3f) and a higher pattern complexity (Fig. 3g), whereas those individuals with the largest number of interruptions of yellow had the lowest dorsal contrast (Fig. 3h).

Sexual dimorphism in relation to colour patterns

There are no differences between the sexes in pattern complexity, pattern elongation, number of interruptions of yellow patches, coloration of the hind limbs and the coloured (blue or yellow) proportion of the ventral side (Table 3). Males have a significantly larger proportion of dorsal yellow (Tables 1, 3; Fig. 4a) and a higher dorsal and throat contrast (Tables 1, 3). Both dorsal (Fig. 4b) and throat contrast (Fig. 4c) were, however, more variable in females than in males (Dorsal: Levene statistic_(1,320) = 10.071, p = 0.002; Throat: Levene statistic_(1,115) = 5.916, p = 0.016). The coloration of the arms also differs significantly between the sexes; females have yellower arms whereas males tend to have bluer arms (Tables 1, 3; Fig. 4d). The differences in throat contrast and proportion of arms covered with yellow do not hold after a sequential Bonferroni correction.

Discussion

Dendrobates tinctorius exhibits a remarkable variation in colour patterns in the population studied. Even though there seem to be discrete morphs given the little or no resemblance among some individuals, colour pattern variation in this population is continuous. In spite

Table 2 Non-parametric correlation matrix for body size and colour pattern characteristics

SUL	pYA	pBA	nY	nDP	nY	pVC	pDY	PC	PE	DC	pYL
SUL	1.000 (314)										
pYA	0.081 (314)	1.000									
pBA	-0.083 (314)	-0.854** (320)	1.000								
nY	0.010 (314)	-0.162** (320)	-0.002 (320)	1.000							
nDP	0.033 (314)	0.257** (320)	-0.125* (320)	-0.567** (320)	1.000						
nY	-0.059 (314)	-0.192** (320)	0.032 (320)	0.870** (320)	-0.564** (320)	1.000					
pVC	-0.101 (115)	-0.112 (115)	0.334** (115)	-0.273** (115)	0.238* (115)	-0.233* (115)	1.000				
pDY	-0.090 (314)	0.322** (320)	-0.124* (320)	-0.476** (320)	0.476** (320)	-0.515** (320)	0.280** (320)	1.000			
PC	-0.118* (314)	0.031 (320)	0.007 (320)	-0.052 (320)	0.216** (320)	-0.019 (320)	0.127 (320)	-0.080 (321)	1.000		
PE	-0.035 (314)	-0.100 (320)	0.138* (320)	-0.344** (320)	-0.018 (320)	-0.361** (320)	0.040 (320)	0.022 (321)	0.204** (321)	1.000	
DC	-0.089 (314)	0.322** (320)	-0.125* (320)	-0.477** (320)	0.477** (320)	-0.515** (320)	0.276** (320)	1.000** (321)	-0.081 (321)	0.024 (321)	1.000
pYL	-0.044 (314)	0.457** (320)	-0.286** (320)	-0.175** (320)	0.162** (320)	-0.172** (320)	-0.041 (320)	0.390** (320)	-0.021 (320)	-0.095 (320)	0.388** (320)
pBL	-0.079 (314)	-0.414** (320)	0.575** (320)	-0.144** (320)	0.081 (320)	-0.125* (320)	0.658** (320)	0.018 (320)	0.038 (320)	0.131* (320)	0.017 (320)
											-0.389** (320)

SVL snout-vent length, pYA proportion of arms covered with yellow, pYB proportion of arms covered with blue, nY number of yellow patches in the back, nDP number of dark patches within yellow, nY number of interruptions of yellow, pVC coloured proportion of the ventral side, pDY proportion of dorsal yellow, PC pattern complexity, PE pattern elongation, DC dorsal contrast, pYL proportion of legs covered with yellow and pBL proportion of legs covered with blue. Values given are Spearman rho and sample size (in brackets). Values in bold letters denote significant relationships at the 0.05 (*) or 0.01 (**) significance level

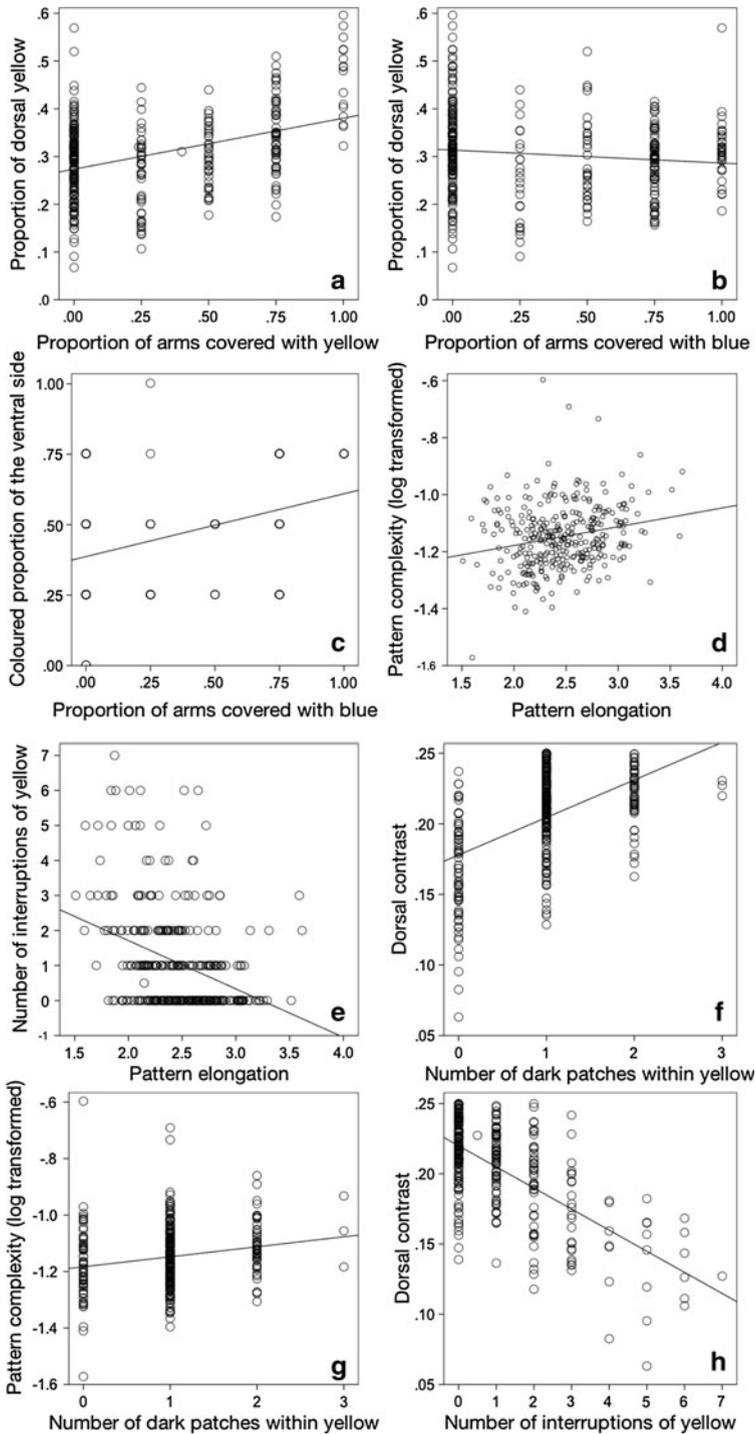


Fig. 3 Scatterplots showing the relationships among colour pattern characteristics. See Table 2 for details on statistics

Table 3 Differences between the sexes in colour pattern characteristics

Variable	U or F	N
Proportion of arms covered with yellow	10,623.0	320
Proportion of arms covered with blue	15,009.0**	320
Proportion of legs covered with yellow	13,097.0	320
Proportion of legs covered with blue	13,640.5	320
Number of yellow patches in the back	13,094.5	320
Number of dark patches within yellow	12,468.0	320
Number of interruptions of dorsal yellow	14,202.0	320
Proportion of dorsal yellow	15,723.5**	321
Pattern elongation	$F_{(1,321)} = 0.025$	321
Pattern complexity	13,134.0	321
Dorsal contrast	15,717.5**	321
Proportion of ventral side coloured	10,623.0	115
Proportion of throat coloured	$F_{(1,115)} = 1.865$	115
Throat contrast	2,166.0	115

Values given are Mann–Whitney U unless specified otherwise. Values in bold letters denote significant relationships at the 0.05 (*) or 0.01(**) significance level after the corresponding sequential Bonferroni correction (Rice 1989)

of this, there is sexual dimorphism in some characteristics of colour patterns: males have overall significantly yellower backs with a higher contrast and bluer arms than females, and show less variation in their coloration.

Understanding intra-populational variation in aposematic signals is challenging

As a result of stabilising selection, aposematic prey are expected to have uniform warning signals (Endler 1988; Joron and Mallet 1998; Endler and Mappes 2004; Darst et al. 2006). Signal variability should be selected against because it might reduce the ability of predators to learn and retain the association between colour patterns and unprofitability (Greenwood et al. 1981; Mallet and Joron 1999; Exnerová et al. 2006). In spite of this, aposematic polymorphisms do occur in nature in a variety of taxa (Myers and Daly 1983; O’Donald and Majerus 1984; Brakefield 1985; Ueno et al. 1998; Williams 2007; Nokelainen et al. 2012), making the selective pressures that lead to the origin and maintenance of variation in aposematic signals difficult to understand.

In species with known (or potential) aerial predators, dorsal coloration might be subject to natural selection. Ventral, throat, and limb coloration, on the other hand, could be the result of sexual selection if those parts are particularly exposed during mating (Siddiqi et al. 2004; Maan and Cummings 2008). A recent study on the geographic variation in colour patterns of *D. tinctorius* using neutral molecular markers suggests that dorsal colour patterns are under selection, whereas ventral colouration is not (Wollenberg et al. 2008). In support of this, studies with clay models have shown that dorsal patterns can indeed influence attacks by predators in *D. tinctorius* (Noonan and Comeault 2009; Comeault and Noonan 2011) as well as other species of poison frogs (Saporito et al. 2007; Chouteau and Angers 2011), and snakes (Brodie 1993; Valkonen et al. 2011), implying a possible role of natural selection in their evolution. Similarly, recent evidence has demonstrated that dorsal colour patterns might be related to differential attractiveness of some morphs over others in

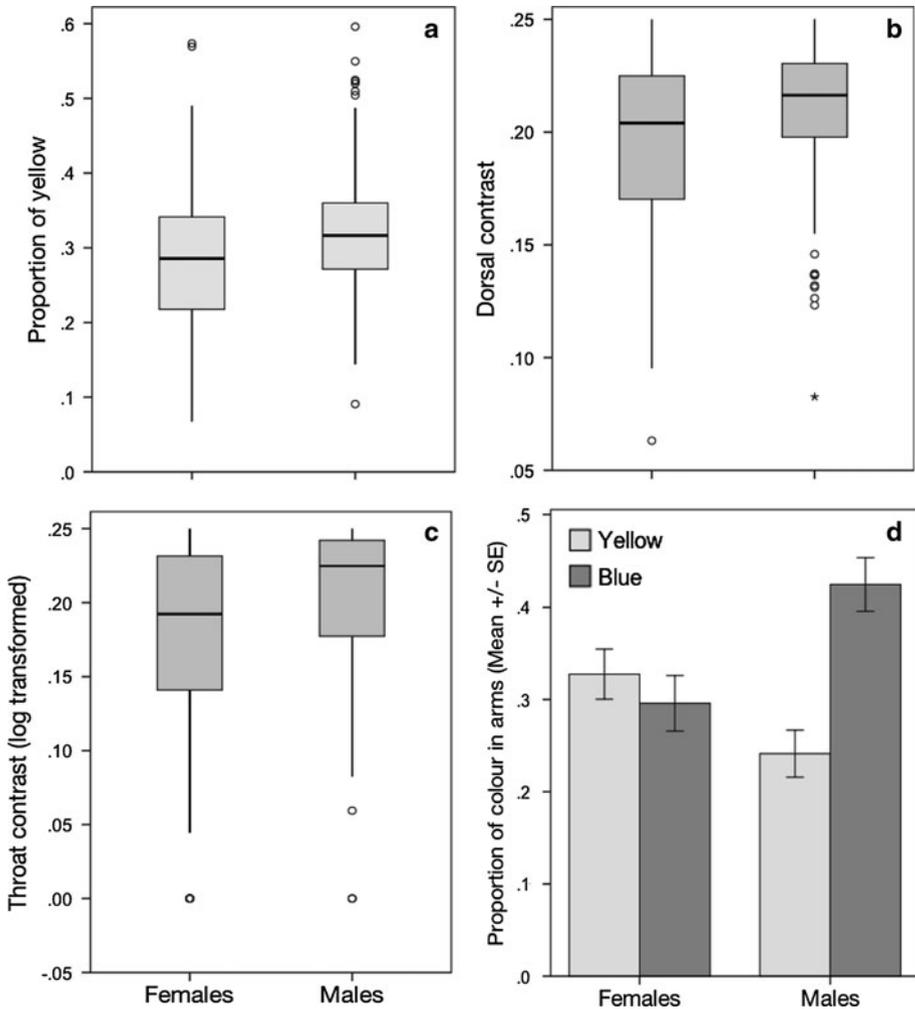


Fig. 4 Differences in colour pattern characteristics between males and females

the Ladybird *Harmonia axyridis* (Ueno et al. 1998) and the poison frog *Oophaga pumilio* (Maan and Cummings 2009), indicating a possible influence of sexual selection.

The interaction between natural and sexual selection has the potential to generate variation in phenotypes (Endler 2000). Thus, one possible explanation for the existence in intra-population variation in aposematic signals could come from interplay between these two forces. Recent approaches to the understanding of the origin and maintenance of aposematic polymorphisms seem to support this idea, for example white males of the wood tiger moth *Parasemia plantaginis* seem to have a selective mating advantage whereas yellow males are better protected from predators (Nokelainen et al. 2012).

Intra-population variation in aposematic colour patterns could also be possible because of ecological, physiological, or behavioural differences between/among the morphs. One possible explanation for the existence of these differences is correlational

selection, a type of selection that favours combinations of traits by generating linkage disequilibrium between them (Endler 1986; Brodie 1992; Sinervo and Svensson 2002). Correlational selection results mostly from frequency-dependent interactions like those between predators and prey or pathogens and hosts (Sinervo and Svensson 2002), and has been suggested to be the mechanism by which the color patterns and escape behavior of some non-aposomatic snakes are associated (Brodie 1992).

Because variation in aposomatic signals might imply differences in conspicuousness among the morphs, individuals could be subject to morph-specific attack rates (Endler 1988; Endler 1991). Therefore, aposematism as an anti-predator strategy might be less effective for individuals with some colour patterns than for others. These differences could also lead, for example, to differential microhabitat use. In such case, regardless of the availability of diverse niches for all types of colour patterns, only individuals with certain colour patterns would be favoured in one specific microhabitat (Gray and McKinnon 2007) either by increased conspicuousness or because it offers the best hiding or escaping opportunities. If an aposomatic species is variable, then it could be expected that each colour form should select the microhabitat or visual background that maximizes its conspicuousness, especially if a specific colour pattern can evoke different responses from predators depending on the surrounding background (Hegna et al. 2011). Males of the most conspicuous populations of *Oophaga pumilio*, for example, tend to choose more exposed perches for vocalisation than their less conspicuous counterparts (Pröhl and Ostrowski 2011; Rudh et al. 2011). The combination of colours exhibited by *D. tinctorius* at the studied population is especially suited for increased conspicuousness under the light conditions of gaps (Endler 1993), which are the most representative habitat of the species (Noonan and Gaucher 2006; Born et al. 2010). However, the specific hypothesis of microhabitat segregation in relation to colour patterns remains to be tested in the future.

Sexual dimorphism in colour patterns

Colour polymorphisms have been proposed to be a transitional state in the evolution of sexual dimorphism in colouration (Forsman and Appelqvist 1999). Sexual dichromatism may result from different selective pressures and is often associated with sex-bias in predation. Natural selection has favoured sexual dichromatism in viperid snakes, for example, because males' contrasting patterns seem to confuse visual predators when moving rapidly in search of mates (Shine and Madsen 1994). This was corroborated during a long-term field study on survival, which furthermore suggests that the higher survival of zig-zagged males is not caused only by their colour patterns but by an interaction between colour pattern and behaviour (Lindell and Forsman 1996). Sexual dimorphism in the bright coloration of *Papilio* butterflies, on the other hand, seems most likely to be the result of natural selection for the warning coloration of females (Kunte 2008) which, according to Wallace (1889; cited in Kunte 2008), are more vulnerable to predation because of the weight of their eggs and their less effective escape flight.

Sexual selection may also affect the sexes of aposomatic species differently. In the butterfly *Papilio polyxenes* sexual dimorphism on dorsal colour patterns seems to be the consequence of sexual selection favouring males that look as suitable mates or better competitors against other males (Lederhouse and Scriber 1987; Codella and Lederhouse 1989). In *Oophaga pumilio* sexual dimorphism in brightness could be a consequence of sexual selection either via female choice, given that females prefer brighter males (Maan and Cummings 2009), or via male–male competition because of its role in conflict resolution (Crothers et al. 2011). There is no evidence that yellower *D. tinctorius* males have a

mating advantage over duller ones, which makes female choice unlikely to be the mechanism explaining male-biased yellowness. In fact, there seems to be a mating advantage for yellower females (Rojas and Endler, in preparation). Intra-sexual selection is also unlikely to play a role in the *D. tinctorius* sexual dichromatism. Field data showed that both males and females engaged in agonistic interactions; we recorded 47 male–female, 6 male–male and 11 female–female interactions. On the basis of the sex ratio of 320 individuals and a null hypothesis of random encounters and interactions, there was a highly significant excess of male–female interactions, a significant deficiency of male–male interactions, and female–female interactions similar to expected from chance encounters ($\chi^2 = 16.374$, $df = 2$, $p < 0.001$). Altogether this suggests not only that intra-sexual selection is not responsible for the male-biased sexual dichromatism in *D. tinctorius*, but also that the colouration of males and females could indeed be subject to different selective pressures.

Males are likely to experience more predation in several taxa (Christe et al. 2006; Boukal et al. 2008). Animals with parental care often exhibit differences in behaviour between males and females, being the sex that performs the parental duties and remains in the nest less vulnerable to predation than the sex that, for example, travels looking for food (Stokes et al. 2011). In the case of *D. tinctorius*, parental duties involve moving for prolonged periods of time and long distances during tadpole transport, which could make males more detectable by predators. There is evidence that an increase in aposematic brightness enhances predator learning (Prudic et al. 2007), and that changes in colour (hue) may cause concomitant changes in brightness (Maan and Cummings 2009), so males could benefit from being yellower in order to quickly educate their predators and protect not only themselves, but also their offspring. We have weak evidence for this given that males are less variable than females, and stronger selection reduces variation more than weaker selection. Thus, males may have yellower backs and higher dorsal contrast than females as a result of a synergy between sexual selection in the form of parental care and natural selection in the form of enhanced aposematism. To our knowledge, this is the first study to consider the role of parental care as a selective force affecting the way in which aposematism works in a polymorphic species.

Additional evidence in support of this idea comes from the propensity of individuals with simpler colour patterns to invade fresh tree-fall gaps (which implies increased predation risk) earlier than individuals with complex patterns (Rojas and Endler, in preparation). This differential arrival in relation to colour patterns is more pronounced in females than in males, who are responsible for the transport of tadpoles to suitable rearing sites. The availability of new tadpole deposition sites is a key factor in tree-fall gap invasion by males (Rojas, in preparation). Since ensuring good rearing site increases the probability of offspring survival, especially given the high rates of larval cannibalism (Rojas, unpublished data), males that arrive early to a tree-fall gap increase the likelihood of their offspring being predators rather than prey. Hence, males might face a trade-off between the future survival of their offspring and their own, which odds could be improved by being yellower.

We must not assume that aposematism functions the same way for individuals with different colour patterns in both sexes. This study suggests that future attempts to understand the maintenance of aposematic signal variability must consider selective forces other than predation and mate choice as the only active component of sexual selection. Parental care, as a component of sexual selection, could work in synergy with aposematism to select for differences in colour patterns between the sexes. Additionally, colour-pattern mediated differences in aspects of the behaviour and ecology of polymorphic aposematic species are

worth exploring as forces that might work jointly to allow for the existence and maintenance of intra-population variation in aposematic colour patterns.

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