

SHORT COMMUNICATION

Spatial variation in the fitness of divergent aposematic phenotypes of the poison frog, *Dendrobates tinctorius*

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Keywords:

adaptive landscape;
 aposematic polymorphisms;
Dendrobates tinctorius;
 frequency-dependent selection;
 predation.

Abstract

Aposematic species use brightly coloured signals to warn potential predators of their unpalatability. The function of these signals is largely believed to be frequency-dependent. All else being equal, stabilizing selection is expected to constrain the evolution of novel signals. However, despite the expected frequency-dependant function of aposematic signals, interpopulation variation in aposematic signals is ubiquitous in nature. Here, we used clay models of the poison frog *Dendrobates tinctorius* to test the nature of selection in regions containing varying frequencies of frogs possessing the local aposematic signal. Our findings support a role for stabilizing selection in maintaining the local signal type in a region of high signal frequency; however, we observe a lack of stabilizing selection at one site coincident with a decrease in the density of frogs possessing the local signal. Spatial variation in local aposematic signal frequencies may facilitate the evolution of novel signal types by altering the adaptive landscape for divergent aposematic phenotypes. Our results provide evidence for spatial variation in the selective regime acting on aposematic signals within an established aposematic system and highlight the need for further study of the nature of selection acting across different spatial scales in diverse aposematic systems.

Introduction

Aposematic signals are employed throughout the animal kingdom as a means of conveying an individual's unprofitable nature to prospective predators. The efficiency of aposematic signals in eliciting the desired response from predators (i.e. avoidance) is largely believed to be frequency-dependent (Harvey *et al.*, 1982; Leimar *et al.*, 1986; Endler & Rojas, 2009). That is, when the signal occurs above the threshold frequency required for predators to learn, and maintain, an association between the signal and unprofitability, positive frequency-dependent selection is predicted to stabilize the local signal. While this stabilizing selection is

expected to constrain the evolution of novel aposematic signals, intraspecific aposematic polymorphisms are frequently observed in nature (Santos *et al.*, 2003; Kronforst & Gilbert, 2008). Therefore, the evolution of novel aposematic signals is somewhat paradoxical: How do novel signals evolve when selection acts against novel phenotypes (Lindstrom *et al.*, 2001)?

Multiple processes have been proposed to explain the evolution of novel aposematic signals. Under predator-foraging-based models, the evolution of novel aposematic signals is facilitated by predators either not recognizing novel phenotypes as potential prey items (i.e. dietary conservatism) or actively avoiding novel phenotypes (i.e. neophobia) (Marples *et al.*, 1998; Thomas *et al.*, 2003; Marples *et al.*, 2005). As a result of aposematic individuals not being in the search image of potential predators, novel phenotypes do not suffer a selective disadvantage and are able to increase in frequency above the threshold for which stabilizing

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selection should act to maintain the aposematic signal. All else being equal (e.g. similar signal efficacy), as long as an aposematic signal falls outside of the search image of potential predators, predator-foraging models predict 'flat' fitness functions for divergent aposematic phenotypes independent of the local aposematic signal density. While both theoretical (Sillen-Tullberg & Bryant, 1983) and empirical (Marples *et al.*, 1998) studies have found support for predator-foraging models of aposematic evolution, others have shown that novel aposematic phenotypes are in fact selected against, indicating a selective constraint on novelty (Langham, 2004; Noonan & Comeault, 2009). Therefore, neophobia or dietary conservatism may facilitate the initial evolution and diversification of aposematic signals under certain conditions (for example, where unprotected prey are readily available and novel prey are costly to sample, e.g. Smith, 1975); however, when costs associated with sampling protected prey is low, novel phenotypes may be selected against due to predators either experiencing ongoing learning or constantly 'testing' potential prey items (Noonan & Comeault, 2009).

Recently, theoretical studies have proposed spatial variation in selection regimes as an alternative mechanism that can facilitate the evolution of novel signal types (Sherratt, 2006; Endler & Rojas, 2009). Namely, stabilizing selection is expected to breakdown in regions where the local density of a signal (x) falls below the learning threshold (T) of local predators (Sherratt, 2006; Endler & Rojas, 2009). Both Endler & Rojas (2009) and Sherratt (2006) show that this breakdown in stabilizing selection can facilitate the evolution of novel aposematic phenotypes because of the 'flat' adaptive landscape associated with regions of low signal frequency. Therefore, spatial or temporal variation in the local density of aposematic phenotypes may facilitate the evolution of novel signals as a result of coincident fluctuations in adaptive landscapes (Sherratt, 2006; Endler & Rojas, 2009); however, this process lacks empirical support (however, see Pfennig & Mullen, 2010 for an example related to Batesian mimicry).

The poison frog *Dendrobates tinctorius* is an aposematic species endemic to the Guiana Shield that exhibits a patchy distribution throughout its range (Noonan & Gaucher, 2006; Wollenberg *et al.*, 2008). In certain areas, these patches (i.e. populations) are frequently found along elevated ridges or plateaus and are isolated by adjacent lowland areas (A.A.C. & B.P.N, personal observations). Variation in the aposematic signal among these patches is typically large (Noonan & Gaucher, 2006), and there is evidence that within a given patch novel aposematic phenotypes are at a selective disadvantage relative to the local phenotype (Noonan & Comeault, 2009).

The aposematic signals of poison frogs have been shown to be subject to both natural and sexual selection (Summers *et al.*, 1999; Darst & Cummings, 2006; Saporito *et al.*, 2007; Reynolds & Fitzpatrick, 2007; Maan & Cummings, 2008, 2009; Noonan & Comeault, 2009).

Avian predators are believed to be the predominant predators of many aposematic species, including dendrobatid frogs (Master, 1999) because of the fact that aposematic signals are visual signals usually consisting of bright, contrasting colours, and avian predators are visual foragers possessing colour vision (Kelber *et al.*, 2003). Studies testing the mode of selection exerted on aposematic species by avian predators frequently find that predators avoid individuals possessing the aposematic signal for which the birds have learned a negative association while they frequently attack novel aposematic phenotypes (e.g. Brodie, 1993; Langham, 2004; Darst & Cummings, 2006; Noonan & Comeault, 2009). Therefore, there is strong evidence that the aposematic signal of poison frogs is subject to predator-mediated stabilizing selection as a result of avian predation (Noonan & Comeault, 2009).

While natural selection can be viewed as a powerful force acting to *maintain* local aposematic phenotypes, studies of natural selection acting on aposematic phenotypes fail to explain how novel signals may initially *evolve*. Here, we test whether spatial variation in the fitness of divergent aposematic phenotypes follows a pattern predicted by predator-foraging or density-dependent selection models of aposematic signal evolution by monitoring predation attempts made on clay models representing both the local and a novel aposematic phenotype of the poison frog *D. tinctorius* in regions where the density of the local signal varies.

Materials and methods

To quantify the effects of predation on different aposematic phenotypes, models were placed along transects within the Nouragues Natural Reserve, French Guiana (4.09°N, 52.68°W). *Dendrobates tinctorius* found within Nouragues Natural Reserve typically possess an aposematic signal consisting of yellow dorsolateral striping with occasional horizontal branches and blue limbs (Fig. 1). Clay models possessing the local phenotype ('pin-stripe'), a novel aposematic phenotype ('yellow') and a cryptic phenotype ('brown') were constructed as previously described (Fig. 1; Noonan & Comeault, 2009) and placed directly on the forest floor at five-metre intervals. The novel aposematic phenotype was selected because a population of *D. tinctorius* found approximately 10 km to the south of that presented here are known to possess either the pin-stripe phenotype or a divergent signal composed of reduced blue coloration and an increase in the amount of dorsal yellow (unpublished). We have also conducted reciprocal transects at a southern site where the yellow signal is the local type (Noonan & Comeault, 2009). Cryptic models were included to compare the evolutionary strategies of crypsis vs. aposematism. Equal numbers of each phenotype (35) were placed along transects with 5 m between each model. The sequence of phenotypes along each transect was

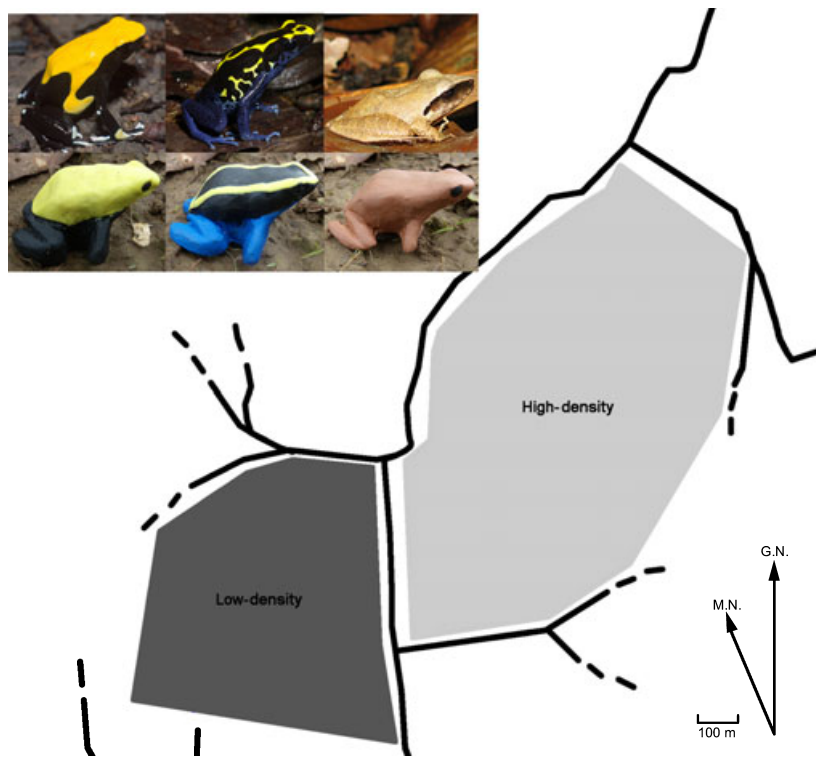


Fig. 1 Location of *Dendrobates tinctorius* population found near Nouragues Scientific Station, French Guiana that was the basis of this study. Polygons represent locations where model transects were run (dark grey: *D. tinctorius* present at low density; light grey: *D. tinctorius* present at high density). Black lines represent streams found in low-lying areas of the topography (see Methods for further description). Images in top left show (from left to right) *D. tinctorius* possessing an aposematic phenotype novel to this location ('yellow'), *D. tinctorius* possessing the local aposematic signal ('pin-stripe') and a cryptic species found at this site, *Pristimantis chiastonotus* (top row: actual frogs, bottom row: models used to represent each phenotype in this study).

determined randomly. Transects were placed on the forest floor during the morning (between 9:00 AM and 11:00 AM) and left for 72 h. Models were then collected, examined for evidence of predation attempts by visual predators (i.e. birds) and photographed. The characteristic 'U' shape left by a bird's beak denoted an avian predation attempt. While we recorded attacks made by rodents and insects for a subset of our transects (16 transects total), here we are solely concerned with avian predation attempts, as birds are believed to be the primary visual predators of species possessing aposematic signals (e.g. Brodie, 1993; Langham, 2004; Darst & Cummings, 2006; Noonan & Comeault, 2009; Pfennig & Mullen, 2010). For transects where nonavian attacks were recorded, there was no effect of model phenotype on the likelihood of being attacked by a nonavian predator ($G_2 = 0.002$, $P = 0.999$). Nonavian attacks other than rodents (which we infer to be the result of insects) were independent of phenotype when both high- and low-density sites were considered together ($G_2 = 0.742$, $P = 0.69$) and separately (high density: $G_2 = 1.895$, $P = 0.388$; low density: $G_2 = 0.085$, $P = 0.958$).

We took advantage of the local topography of the Nouragues Scientific Station (4.09°N, 52.68°W) and the patchy distribution of *D. tinctorius* in this area to explore how attack rates on aposematic phenotypes varied across the landscape. Transects of frog models were placed in two areas, one having a relatively large population of *D. tinctorius* ('high-density' site) and another where only

a few accounts of *D. tinctorius* have been reported over 3 years of observation (P. Gaucher, 'low-density' site). In over 60 days in the forest, we never encountered *D. tinctorius* in the low-density site. High- and low-density sites were located 100 m apart and within-site elevations ranged from 65 to 110 m above sea level. The areas of these sites were approximately 0.6 km² and 0.2 km², respectively, and are separated by natural variation in the topography (i.e. a shallow valley with a base elevation of ~40 m above sea level containing semipermanent creeks divided the study sites; Fig. 1). The close proximity and marked differences in local density of *D. tinctorius* found between our study sites provide a conservative test of the spatial scale for which variation in natural selection may be observed acting on aposematic signals. The G -test of independence was used to explore whether the proportion of predation attempts differed between phenotypes in areas of high and low density.

Results

A total of 1059 model frogs were recovered from 11 transects placed in the high-density site representing 311, 379 and 369 individuals of the local, novel and cryptic phenotypes, respectively. From the low-density site, a total of 832 models were recovered from eight transects representing 276, 280 and 276 individuals possessing the local, novel and cryptic phenotypes, respectively. A small proportion of models (17 total: five local, three novel and

nine cryptic) were not recovered following the 72-h exposure time. As we could not estimate the number of missing models that were the result of avian predation attempts, these models were not included in any of the analyses (inclusion of lost models did not significantly influence the results). The discrepancy between the number of local, novel and cryptic models recovered for the high-density site is because of the exclusion of models for which dorsolateral stripes were painted-on for the first four transects (stripes were placed on models using clay during all subsequent transects). While this did not affect the yellow or brown models, for two of these transects, the dorsolateral stripes were washed off the pin-stripe morph by rain, and these individuals are excluded from the totals presented as well as all subsequent analyses. We observed one instance where avian attacks were made on consecutive models (three yellow models at the high-density site). Following the methods of Brodie (1993), these three events were treated as a single attack to minimize the likelihood of nonindependent attacks influencing our results.

Of the 1891 models recovered, avian predators unambiguously attacked 49. Of these 49 predation attempts, 11, 26 and 10 were made on the local aposematic, novel aposematic and cryptic phenotypes, respectively. A marginal difference in the proportion of predation attempts made on the local vs. novel aposematic phenotype was found when all models were considered together ($G_1 = 3.904$, $P = 0.048$). Interestingly, there was no significant difference in the proportion of attacks made on any of the three phenotypes when comparisons were made between sites (low vs. high-density: pin-stripe, $G_1 = 1.918$, $P = 0.166$; yellow, $G_1 = 1.573$, $P = 0.21$; brown, $G_1 = 1.965$, $P = 0.161$). However, when predation attempts were considered in the context of local *D. tinctorius* population density, avian predators were found to attack models independent of their aposematic phenotype where population density was low ($G_2 = 0.082$, $P = 0.96$; Fig. 2), but were more likely to attack models possessing the novel aposematic phenotype where *D. tinctorius* population density was high ($G_2 = 12.362$, $P < 0.01$; Fig. 2). The overall number of avian predation attempts was found to be independent of location ($G_1 = 0.176$, $P = 0.675$), indicating that total predation pressure was constant between sites.

Discussion

Recent theoretical studies have shown that when selection is frequency-dependent and acts on a signal that varies in density across the landscape, a breakdown of stabilizing selection in regions of low signal frequency can facilitate the evolution of novel aposematic phenotypes (Sherratt, 2006; Endler & Rojas, 2009). Here, we provide empirical evidence that predators perceive aposematic signals differently across a small spatial scale (Fig. 2). Specifically, we show that the selective advantage

afforded to individuals possessing the local aposematic signal is not found in a region where the local signal is present at a very low frequency. While shifts in the proportion of attacks on the aposematic models occurred in the predicted direction between the high and low-density site, the proportion of attacks made on the cryptic phenotype did not differ from those made on either of the aposematic phenotypes at the low-density site. This result may be explained by spectral differences existing between our two sites, and future experiments of spatial differences in attack rates would benefit from the inclusion of spectral data collected from the models used, the frogs they are modelled after and the environments they are placed in. Here, we focus on interpreting results obtained for the two aposematic phenotypes because without spectral data, we cannot say that the cryptic morph was indeed cryptic at the low-density site.

The results presented here should be interpreted with caution as they are based on a single paired replicate. However, the shift in attack rates we observed on aposematic phenotypes at the low-density site occurred in the predicted direction. Also, a companion study using similar methods employed here found evidence for stabilizing selection acting on the yellow phenotype in a region where that signal was locally abundant (Noonan & Comeault, 2009). Evidence for the breakdown in stabilizing selection acting on the local aposematic phenotype provided in this study results in a 'flat' adaptive landscape lacking the fitness valleys expected to constrain the evolution of novel aposematic signals under stabilizing selection and provides the first empirical support for spatially variable selection on an aposematic signal coincident with variation in that signal's local frequency. Under a flat adaptive landscape, individuals possessing the local signal are no longer at a selective advantage and divergent signals may be able to evolve through processes such as drift or sexual selection (Uyeda *et al.*, 2009; Tazzyman & Iwasa, 2010).

With data presented here, we are unable to directly show the underlying mechanism responsible for the variation in attack rates between our two sites. However, inferring the increased proportion of attacks on the local signal at the low-density site is because of local predators not encountering the signal above the threshold frequency required for them to maintain an association between the signal and toxicity requires a discontinuity in predators, either species or individuals, between the two sites. Given their close proximity, the likelihood of there being no overlap in predators between sites seems low; however, many species of tropical birds show remarkably limited home ranges. In one study of an Amazonian bird community, 85 of 111 species for which territory size was measured had territories less than or equal to 0.16 km², an area of comparable size to either of our two study locations (Terborgh *et al.*, 1990). Another study of mixed species flocks led by antshrikes found that flocks had a mean territory size of 0.085 km² and that

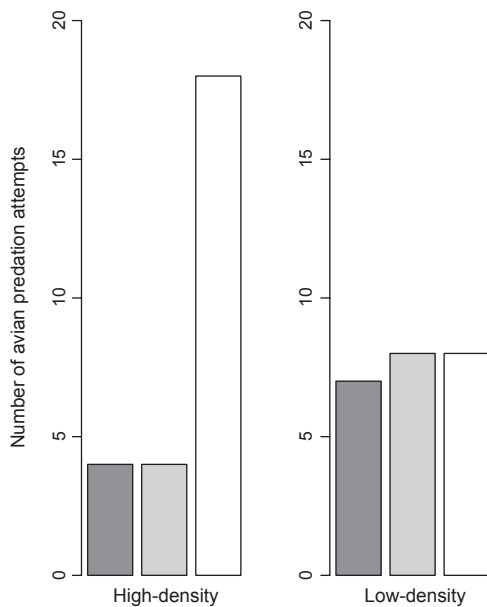


Fig. 2 Avian predation attempts on *Dendrobates tinctorius* phenotypes under conditions of varying local densities. Data are number of attacks on the cryptic (dark grey bar), local aposematic (light grey bar) and novel aposematic (white bar) phenotypes at both high and low-density sites ('high-density' and 'low-density', respectively). Attack rates were dependent on phenotype where *D. tinctorius* was found at high densities ($P < 0.01$) and independent of phenotype where *D. tinctorius* was found at low densities ($P = 0.96$).

these flocks were unlikely to cross canopy gaps (Develey & Stouffer, 2001). The streams that divide our two study sites result in a notable change in the local topography and forest structure that may form natural boundaries that limit dispersal and help to define individual territories. If this is the case, a significant discontinuity in predators may exist between our two sites.

Alternatively, if the same individual predators are foraging at both sites, how can the apparent loss of avoidance of the local phenotype at our low-density site be explained? One possibility is that birds found across our study areas have a learned foraging pattern that precludes them from attacking *D. tinctorius* possessing the local aposematic signal in areas where these frogs occur (i.e. the high-density site), but lack this association in regions where the frogs are absent (i.e. low-density site). Studies of the caching habits of jays have shown that certain birds are capable of both situational and contextual memory (Clayton *et al.*, 2003; Dally *et al.*, 2006). Future studies exploring the mechanism underlying variation in predator's perception of aposematic signals are needed to enhance our understanding of how variation in adaptive landscapes may arise.

Another mechanism that may underlie spatial variation in the adaptive landscape of aposematic signals is whether local predators learn that there is among-site variation in the toxicity of aposematic species. Many

toxins employed by protected species taste bitter and bitterness may be an honest signal of the potency of the toxin, or toxins, possessed by protected individuals (Skelhorn & Rowe, 2010). Toxins possessed by poison frogs belonging to the family Dendrobatidae are sequestered from their diet (Daly *et al.*, 1987, 1994); therefore, differences in the frog's diet may lead to local variation in their toxin profiles. While studies specifically exploring the toxicity of compounds possessed by *D. tinctorius* are lacking, studies of other species of dendrobatid frogs indicate that predators are able to sample individual frogs and reject them with little or no adverse effects to either the predator or the frog (Szelistowski, 1985; Darst & Cummings, 2006; Darst *et al.*, 2006). Therefore, variation in both signal type (conspicuousness) and toxicity may influence the adaptive landscape of divergent aposematic signals.

Conclusions

Empirical examples of the processes driving the evolution of novel aposematic signals remain largely lacking (however, see Jiggins *et al.*, 2008; Melo *et al.*, 2009; Salazar *et al.*, 2010 for an interesting example of hybridization resulting in the production of a novel aposematic signal). Here, we present preliminary evidence that the adaptive landscape for aposematic phenotypes can vary across a fine spatial scale coincident with a change in the frequency of the local signal. Our results demonstrate a lack of neophobia or dietary conservatism within the community of avian predators exposed to *D. tinctorius* at Nouragues Natural Reserve, French Guiana. Furthermore, we provide evidence that a breakdown in stabilizing selection acting on an established aposematic signal occurs in a region of low signal frequency. We argue that spatial variation in selection regimes, coincident with variation in signal frequency, is an important process that may facilitate signal diversification in this system. Generalization of our conclusions to diverse aposematic systems should be made with caution as replicated studies are needed. Future studies exploring the interaction between aposematic species and their predators in systems across varying spatial scales and where the rules of the interaction vary (e.g. deadly snakes, toxic frogs, noxious butterflies) will add valuable insight into the nature of selection acting on aposematic signals.

Acknowledgments

We thank Justin Yeager for thoughtful discussions of these experiments and Andrew Martin, Patrik Nosil and two anonymous reviewers for comments on earlier versions of this manuscript. Philippe Gaucher and the staff of Nouragues Scientific Station were indispensable during field seasons in French Guiana. Fieldwork in French Guiana was supported in part by a Nouragues grant from CNRS.

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Received 23 November 2010; revised 15 February 2011; accepted 16 February 2011