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ORIGINAL PAPER

Interacting selection diversifies warning signals in a polytypic frog: an examination with the strawberry poison frog

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Abstract Aposematic signals represent one of the most accessible traits to evaluate the interaction of natural and sexual selection on signal evolution. Here we investigate the contributions of these two selective forces on the aposematic signal evolution of the highly polytypic strawberry poison frog, *Oophaga pumilio*, of Bocas del Toro, Panama. Previous research has shown that the brightness of *O. pumilio* warning coloration can inform predators of the toxicity levels associated with different populations of the archipelago. Other studies suggest that sexual selection may be influencing warning signal brightness within populations via female mate choice (Isla Solarte, Isla Bastimentos, and Aquacate Peninsula populations) and male–male competition (Isla Solarte). Here we present two non-exclusive scenarios for how natural and sexual selection interact to drive phenotypic variation across this archipelago: (1) predators impose a selective regime whereby populations above a toxicity-brightness threshold are at liberty to diversify via sexual selection and below which populations are constrained to maintain a stricter resemblance to a more cryptic population mean, and (2) synergistic/additive effects of inter- and intrasexual selection drive the evolution of brighter males within populations above this toxicity threshold. We investigate whether aposematic patterns of divergence across the archipelago relative to the common mainland phenotype meet these predictions using existing data on *O. pumilio* morph toxicity measures and overall conspicuousness estimates to an avian predator. Using standardized z-scores to evaluate the range of trait values, we find that indeed the population representative of the common mainland phenotype (Almirante) represents an intermediate level of both toxicity and conspicuousness, and that derived Bocas del Toro populations vary in each of those components in directions predicted by the proposed scenarios. Furthermore, we find greater divergence towards conspicuousness than crypsis,

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a pattern suggestive of sexual and natural selection acting synergistically in morphs with high toxicity.

Keywords Aposematism · Brightness · Conspicuousness · Natural selection · Sexual selection · Phenotypic variation

Introduction

How do natural and sexual selection contribute to the origin and maintenance of phenotypic variation in nature? These are classic questions in evolutionary biology, and yet the answers are still evolving. When Darwin introduced the two main forces of evolution, he isolated each in separate tomes: natural selection (1859), and sexual selection (1871). As a (perhaps unintentional) result, evolutionary biologists often study these processes as if they are mutually independent. However, organisms are subject to natural and sexual selection simultaneously and the distribution of phenotypes in nature reflects a compromise. Theory suggests that interactions between natural and sexual selection can lead to multidimensional fitness landscapes that support several distinct, equally adaptive phenotypes (Schluter and Price 1993; Lorch et al. 2003; Reinhold 2004), thereby increasing the potential for evolutionary change and diversification. Theory is ahead of empiricism here; experimental studies demonstrating the interactive roles of natural and sexual selection in wild populations are rare (e.g. Endler 1983; Jiggins et al. 2001; Bernal et al. 2006; Nokelainen et al. 2011; Sharma et al. 2012). Yet, such studies are essential if we are to understand the mechanisms underlying the evolution and maintenance of phenotypic variation in nature.

Aposematic species comprise exceptional systems to investigate the interplay between the processes of natural and sexual selection. In such species, bright ornamentation has evolved through the process of natural selection to communicate some form of unprofitability to predators (Wallace 1867; Mallet and Joron 1999; Ruxton et al. 2004; Mappes et al. 2005). Though predators have historically been believed to be the primary agents shaping the evolution of aposematic signals (Müller 1879), recent research suggests that predator constraints on aposematic trait evolution can be relaxed (Darst and Cummings 2006), that aposematic signals can function in the context of conspecific communication (Jiggins et al. 2001), and even that sexual selection may influence the direction of aposematic trait evolution (Maan and Cummings 2009). Because aposematic species are highly conspicuous and can simultaneously signal to both predators and conspecifics with the same trait (Jiggins et al. 2001; Maan and Cummings 2008; Nokelainen et al. 2011), investigating how these viewers select on these signals can help clarify the underlying constraints governing the evolution of signals.

Importantly, studies of signal evolution in aposematic species can be seen as complementary to studies in non-aposematic organisms. Investigations of trait evolution in non-aposematic species typically focus on how natural selection may limit the evolution of a sexually selected signal (see Endler 1983 for a classic example). Studies of trait evolution in aposematic species can instead focus on the reverse phenomenon as they explore how sexual selection impacts signals that have arisen through natural selection (e.g., Jiggins et al. 2001). Such empirical investigations, working in tandem, can elucidate how Darwin's two processes of selection impact the diversification of signals in general, and even drive speciation (see Maan and Seehausen 2011 for a recent review on this topic). Here, we review a case study of signal diversification in one of the most polytypic vertebrates on earth: the aposematic strawberry poison dart frog (*Oophaga pumilio,* formerly

Dendrobates pumilio). Our investigations of this animal, combined with genetic and behavioral research by other laboratories, are beginning to shed light on the complex interaction between natural and sexual selection in the evolution of conspicuous aposematic signals.

The study species

Many frogs of the family Dendrobatidae are aposematic, exhibiting bright coloration and sequestering toxins acquired from their diet (Daly and Myers 1967; Daly et al. 1978). This family of poison frogs is found throughout the Neotropics (Grant et al. 2006), and many species exhibit great phenotypic variation in terms of aposematic coloration. Some of these species' phenotypic variants are evidently the results of extensive Müllerian mimicry rings (e.g., Symula et al. 2001). However, mimicry does not appear to account for aposematic variation in an extremely well studied dendrobatid (Summers et al. 1997; Siddiqi et al. 2004). The strawberry poison frog, *O. pumilio*, is perhaps the most polytypic of the poison frog species. *O. pumilio* is monomorphic in coloration across most of its geographic range from Nicaragua to Panama, with a reddish body and blue legs. However, in the Bocas del Toro archipelago, located in the Caribbean on the western end of Panama, the species exhibits dramatic variation in hue and brightness. Across island populations and throughout the mainland of this region, this species is estimated to exhibit >15 unique color patterns (Daly and Myers 1967; Siddiqi et al. 2004).

At first glance, the geographical isolation of the populations of Bocas del Toro seems to implicate neutral vicariance mechanisms in the diversification of *O. pumilio*'s aposematic coloration. However, the islands of the archipelago formed recently as sea levels rose during the Holocene. It has thus been estimated that these *O. pumilio* populations only became isolated over the course of the last 9,000 years (Anderson and Handley 2001) and strict divergence by vicariance models have since been rejected (Wang and Shaffer 2008). A number of investigations have found no evidence that genetic drift accounts for the divergence of color patterns in the species, and strong support for the role of selection in causing this diversification (Summers et al. 1997; Hagemann and Prohl 2007; Rudh et al. 2007; Brown et al. 2010; Wang and Summers 2010). However, while genetic drift has largely been ruled out as a major source of this remarkable variation, the specific selective forces that have produced it remain unclear. Here, we review recent evidence for both sexual and natural selection in the color evolution of *O. pumilio*, attempt to synthesize this data into a more holistic assessment of the causes and consequences of warning color diversification in the species, and finally test these emerging hypotheses with existing data of *O. pumilio* aposematic trait divergence.

Materials and methods

We used the toxicity and conspicuousness data from Maan and Cummings (2012) to test whether *O. pumilio* populations across the Bocas del Toro archipelago exhibit a pattern of divergence from the mainland morph in directions that promoted signal evolution towards both crypsis and conspicuousness and that reflected both honesty in warning signal toxicity and possible synergistic effects between natural and sexual selection. We collected *O. pumilio* individuals from 10 different color morphs in 9 locations in the Bocas del Toro Archipelago, Panama. Because the defense alkaloids of poison frogs target voltage-gated

Fig. 1 Proposed interactions between natural and sexual selection on signal diversification in *O. pumilio*. ▶ **a** Predicted extent of influence for each component of natural and sexual selection across the populations of the archipelago. **b** Proposed change in conspicuousness from the common mainland phenotype expected by the different sources of selection for populations exhibiting varying conspicuousness and toxicity (NS line = natural selection; SS line = sexual selection in the presence of natural selection). *Circles* on plot delineate the major mechanisms promoting the diversification away from the common mainland morph (*gray* = mechanisms of natural selection; *red* = mechanisms of sexual selection; *purple* = mechanisms of both natural selection and sexual selection). **c** Relationship between standardized measures of the log of morph toxicity and overall conspicuousness to an avian predator for different *O. pumilio* populations. *Color* contours outline populations that represent proposed deviations from the common mainland phenotype (*green* = "cryptic" populations; *orange* = "exceptionally conspicuous" populations). Z-scores calculated from data from Maan and Cummings (2012). (Color figure online)

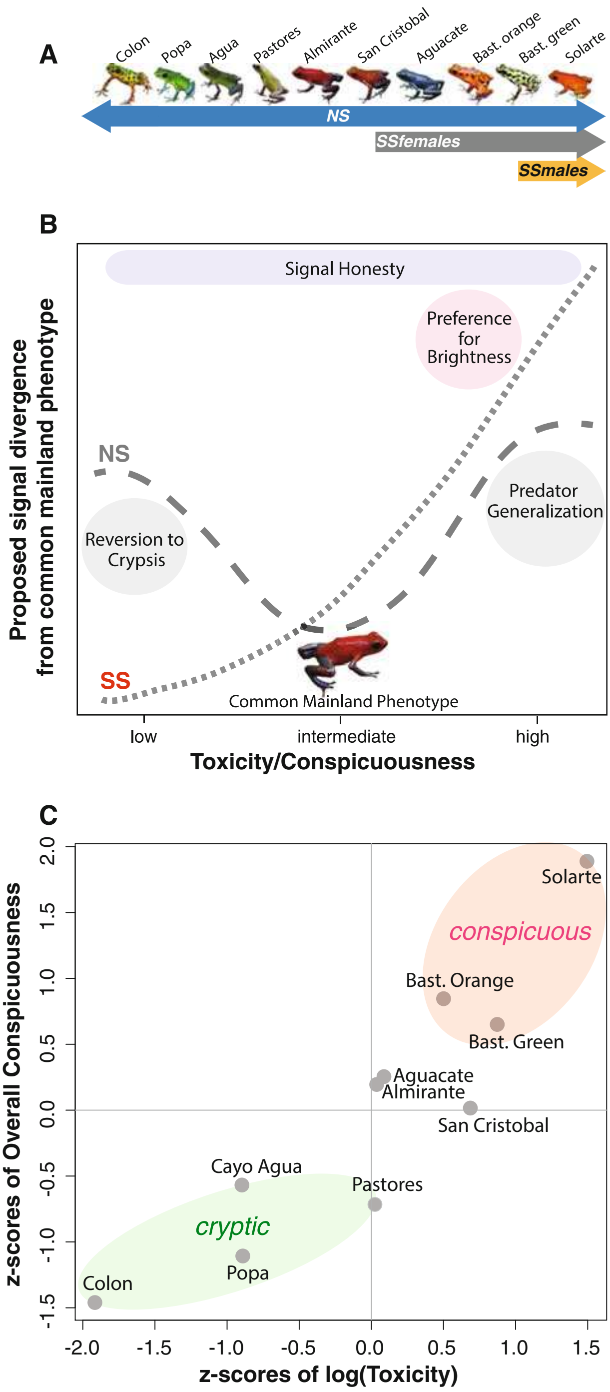
ion channels (Daly et al. 1980; Daly 1998; Bosmans et al. 2007), which are central components of nervous system function in both invertebrates and vertebrates, we used a toxicity/irritant assay for one vertebrate group (mice) as a general proxy for the response of natural predators. We injected frog skin extracts subcutaneously into sleeping laboratory mice and subsequently recorded the time, in minutes, it took the mice to return to sleep as a measure of toxicity, where longer latency is assumed to reflect increased toxicity (as in Darst and Cummings 2006; Darst et al. 2006).

We also evaluated the overall conspicuousness of the morphs of these different populations using spectral reflectances of frog dorsal body regions and avian visual models (developed in Siddiqi et al. 2004; Maan and Cummings 2009). We estimated the overall conspicuousness of a frog's dorsum when viewed against a natural background (green *Heliconia* sp. leaf) with irradiance measurements collected in an *O. pumilio* habitat with an avian-specific visual model that evaluates conspicuousness as an estimate of luminance ($\sim$brightness, ΔL) and spectral ($\sim$color, ΔS) differences with the background. Specifically, we evaluated overall conspicuousness as the Euclidean distance of these two detection parameters in an avian color space (overall conspicuousness $= OC = \sqrt{\Delta L^2 + \Delta S^2}$).

We used z-scores of the overall conspicuousness of the morphs and the log(toxicity) values to evaluate whether the data meet the predictions that (a) the mainland morph (Almirante) represents intermediate levels of both signal conspicuousness and toxicity, (b) that morphs diverged from this mainland phenotype in directions reflecting warning signal honesty, with more toxic morphs developing more conspicuous appearances to predators and less toxic morphs developing more cryptic appearances, and (c) divergence towards conspicuousness exceeded that of crypsis, possibly reflecting additive/synergistic effects of multiple selective forces (Fig. 1a, b).

Results

The standardized z-scores of morph toxicity and overall conspicuousness exhibited a linear pattern between the two aposematic trait variables ($r^2 = 0.816$; Fig. 1c). The relative pattern of divergence between the common mainland morph population (Almirante) and the other derived populations met the predictions of two proposed scenarios suggesting how natural and sexual selection interact to drive divergence. Almirante exhibited the least divergence from the mean ($\sim$intermediate) trait value with near zero z-scores for toxicity and conspicuousness (0.037 and 0.195, respectively). Derived populations diverged in conspicuousness from the standardized mean in a direction predicted by their standardized toxicity values, with more toxic morphs having more positive conspicuousness z-scores


A
Colon
Popa
Agua
Pastores
Almirante
San Cristobal
Aguacate
Bast. orange
Bast. green
Solarte
NS
SSfemales
SSmales
B
Signal Honesty
Preference for Brightness
NS
Reversion to Crypsis
Predator Generalization
SS
Common Mainland Phenotype
Proposed signal divergence from common mainland phenotype
low
intermediate
high
Toxicity/Conspicuousness
C
Solarte
conspicuous
Bast. Orange
Bast. Green
Aguacate
Almirante
San Cristobal
Cayo Agua
Pastores
cryptic
Popa
Colon
z-scores of Overall Conspicuousness
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
z-scores of log(Toxicity)

and less toxic morphs exhibiting negative conspicuous z scores (Fig. 1c). Lastly, the population with the greatest magnitude z-score for conspicuousness, Solarte, is also the morph with the greatest mean toxicity.

Discussion

The role(s) of sexual selection

As Darwin predicted (1871), strong sexual selection has been shown to correlate with species diversity within clades (e.g. cichlids: Seehausen et al. 1999a; insects: Arnqvist et al. 2000; lizards: Stuart-Fox and Owens 2003). Researchers have also found that sexual selection contributes to polymorphisms within species (e.g. cichlids: Seehausen et al. 1999b; Sato et al. 2004; and side-blotched lizards: Sinervo and Lively 1996). *O. pumilio* is characterized by strong sexual selection due to the intensity of the species' maternal care (Summers et al. 1997) and its great variance in male mating success (Prohl and Hodl 1999). Furthermore, males of the species are highly territorial, exhibiting territory site fidelity (McVey et al. 1981), and guarding areas that contain sites for foraging, tadpole rearing, and perches for calling to females (Donnelly 1989; Prohl 1997). Males are known to vigorously defend their sites against conspecific males through vocalizations and close-range aggressive encounters (Bunnell 1973; Forester et al. 1993; Baugh and Forester 1994; Prohl 2005; Gardner and Graves 2005). Hence, sexual selection in this species is likely to have significant intersexual and intrasexual components. Previous researchers (Summers et al. 1999; Siddiqi et al. 2004) have suggested that female choice is the driving force behind the color variation across this species. Here, we discuss the evidence for sexual selection in *O. pumilio*, focusing separately on the roles that female mate choice and male–male competition may play in signal diversification.

Female mate choice

There is ample behavioral evidence for sexual selection by female preference on male coloration and brightness in this species. Summers et al. (1999) first tested the possibility of assortative mating according to warning phenotype in *O. pumilio* through a series of dichotomous choice behavior tests, and found that females preferred to associate with individuals from their own population to individuals from other islands. However, in the absence of color information (through the use of different illumination techniques), females did not exhibit such a preference. This represented the first indication that females use visual information, and particularly coloration, in assessing potential mates. Follow-up studies in the laboratory (Reynolds and Fitzpatrick 2007; Maan and Cummings 2008) and in the field (Richards-Zawacki et al. 2012) provided further evidence for female preference based on male dorsal coloration (Reynolds and Fitzpatrick 2007; Maan and Cummings 2008), and some indication that females may also attend to males' patterning in a mate choice paradigm (Reynolds and Fitzpatrick 2007; though see Maan and Cummings 2008 for contradictory results). Importantly, our laboratory's detailed investigations of several populations' responses to subtle variation in dorsal and ventral color and dorsal patterning indicated that male dorsal coloration appears to be most important in female choice, and that females may be permissive to or even prefer male phenotypes that deviate from the average phenotype of their population (Maan and Cummings 2008). Thus, though previous behavioral work had indicated only that sexual selection by female mate choice was reinforcing the isolation of color patterns across the isolated Bocas del Toro populations (see also Richards-Zawacki and Cummings 2011), these experiments provided some evidence for directional sexual selection on warning coloration.

Summers and colleagues hypothesized that pre-existing mate preferences might drive rapid divergence in color across this group (Summers et al. 1997; Siddiqi et al. 2004) and Tazzyman and Iwasa (2010) theorized that this could be achieved through a process of "coupled drift," in which selection causes coloration to follow the trajectory of female preference, which largely evolves via drift. Recent research examining a simple preference for brighter males across populations of the archipelago suggests that directional selection for brighter phenotypes may contribute to the variation in color observed across populations (Maan and Cummings 2009). In order to determine whether female mate choice may have driven the diversification of warning coloration in the populations of Bocas del Toro, our lab performed a series of dichotomous choice laboratory experiments to see if females prefer novel variation in male phenotypes. We studied four geographically distinct populations of *O. pumilio* that represent a broad range of hues and brightness levels: the common red/blue mainland Almirante morph and three derived populations (Solarte and Bastimentos—orange; Bastimentos—green; Aguacate—blue). To remove any potential confound of behavioral or physiological correlates with male brightness, we paired males from each population matched for size, weight and dorsal reflectance flux to within one standard deviation of the population mean. The perception of male brightness was then altered using neutral density filters placed above one of the male tanks (the 'dark illumination'), with males alternatively being the 'brightly illuminated' male (full UV and Halogen light with forest filters, see Maan and Cummings, 2009) or 'dark illuminant' male (same set of lights with neutral density filters added that reduced the male brightness by 66 %) for each 15 min trial. Using a two-way choice paradigm that allowed us to manipulate female perception of male brightness by alternating illumination conditions for each male, we measured approaches and amount of time in close proximity that females directed towards each male. Field observations suggest that physical proximity and female approach behavior are good correlates of mating probability. Successful courtship involves prolonged behavioral interactions that consist of repeated approaches and turning away of the female, followed by repeated attempts of the male to lead her to an egg deposition site (Limerick 1980; Cummings and Crothers, *pers. obs.*).

Our results showed that in the three island/peninsular populations (Solarte, Bastimentos, and Aquacate) females exhibited significant preferences for brighter male phenotypes (Fig. 2; Maan and Cummings 2009), while females from the mainland population with a common mainland phenotype (Almirante) showed only weak preferences for brighter males. Importantly, spectrophotometric analyses revealed a case of sexual dimorphism in one of the derived island populations. Males of Isla Solarte, one of the exceptionally bright populations (Maan and Cummings 2012), were significantly brighter in dorsal brightness than females (Maan and Cummings 2009). The results of this study are coincident with sexual selection theory: females from many *O. pumilio* populations show preferences for brighter males, and this directional sexual selection can evidently lead to sexual dimorphism in aposematic brightness.

Male-male competition

Research into the contribution of intrasexual competition to signal divergence in this system suggests that male–male competition may have an additive or synergistic effect on the directional selection imposed by females in some populations. Our initial research with

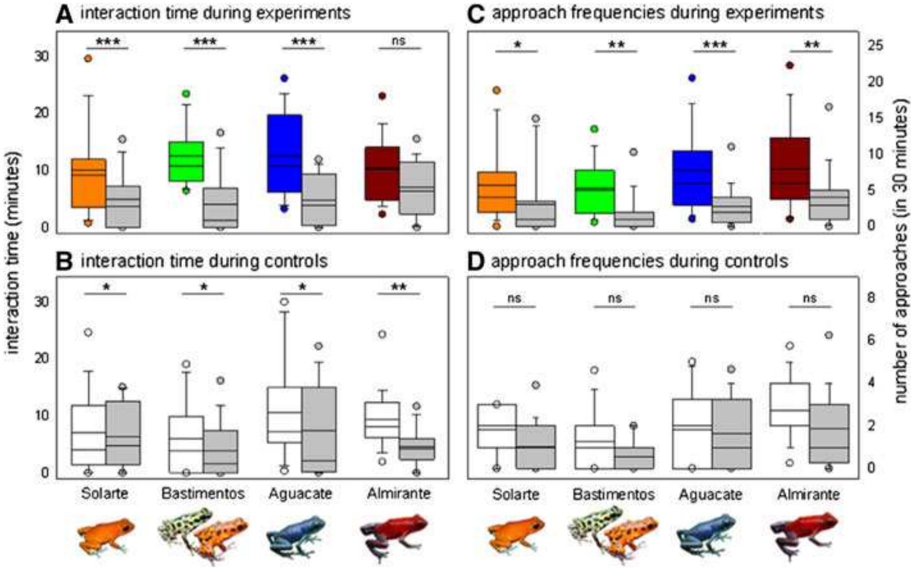


Fig. 2 Directional selection for brighter male phenotypes by female preference from Maan and Cummings (2009). Female interaction time (within 4 cm of plexiglass divider in front of focal male) with **a** males brightly illuminated (UV + Halogen + forest floor spectral filters; *colored boxes*) and darkly illuminated (UV + Halogen + forest floor spectral filters with neutral density filters in front; *grey boxes*), and with **b** empty control chambers brightly illuminated (*open boxes*) and empty control chambers darkly illuminated (*grey boxes*). Female approach frequencies **c** towards males brightly illuminated (UV + Halogen + forest floor spectral filters; colored boxes) and dark illuminated (UV + Halogen + forest floor spectral filters with neutral density filters in front; *grey boxes*), and approach frequencies with **d** empty control chambers brightly illuminated (*open boxes*) and empty control chambers darkly illuminated (*grey boxes*). Boxes indicate 25–75 percentiles intercepted by the median (*thin line*) and mean (*thick line*); *error bars* indicate 10–90 percentiles, symbols are 5–95 percentiles. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. (Color figure online)

the bright orange Isla Solarte morph demonstrated that Solarte males distinguish between rivals of differing brightness, with males directing more aggressive behaviors (calls and approaches) towards brighter stimulus frogs than duller ones (Crothers et al. 2011; Fig. 3). Interestingly, Solarte, potentially impacted by two sexual selective agents, is also the only population exhibiting sexual dimorphism. Males of this population have significantly brighter dorsal reflectances than females (Maan and Cummings 2009), and this population exhibits one of the brightest aposematic signals across the archipelago (2nd out of 10 morphs sampled; Maan and Cummings 2012). The emerging pattern suggests that when both intrasexual and intersexual selective pressures are operating on the same signal component, they may have a synergistic/additive effect on signal evolution.

Though sexual selection by female mate choice might be widespread in both monomorphic and sexually dimorphic populations of variable brightness (as evidenced by Maan and Cummings 2009), male–male competition may be playing a more limited role in the evolution of *O. pumilio*, perhaps constrained to only populations where warning signal brightness is a potentially informative cue for body condition, behavior or sex. In the Solarte population, in addition to male brightness affecting the behavior of male competitors, we also found that focal male brightness predicted a focal male's behavior (Crothers et al. 2011). Brighter males approached stimulus frogs faster than duller males

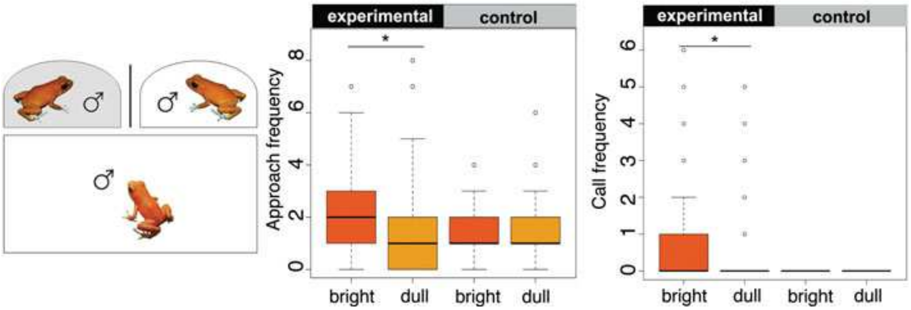


Fig. 3 Differential response of Solarte males towards 'brighter' rivals from Crothers et al. (2011). Schematic represents the agonistic choice experimental setup showing two stimulus males (small compartments) and the focal male (large compartment). Box-and-whisker plots depict approach and call frequencies towards brightly-("bright") and darkly-("dull") illuminated chambers in experimental trials and controls (empty stimulus chambers, lighting details same as in Fig. 2). Boxes span the first and third quartile of the data, and *horizontal black lines* represent the median. Whiskers span the range of the data, excepting outliers (*open circles*)

and directed more of their calls to bright stimulus frogs. Our laboratory is currently investigating this phenomenon further, as well as other mechanisms by which males may be selecting on warning coloration in this species.

The role(s) of natural selection

There are a number of ways that natural selection may have contributed to the diversification of *O. pumilio*'s signals: by interacting additively/synergistically with sexually-selected evolution, by being largely permissive to sexually-selected evolution, or by countering any sexually-selected evolution. Traditionally, natural selection is predicted to favor convergence across aposematic systems (Müller 1879); color pattern convergence reduces the number of color-toxicity combinations for predators to learn, and therefore decreases predation pressure by lowering the number of sacrificial individuals necessary to 'train' predators. However, recent research suggests that there are a number of abiotic and biotic processes that may relax selection for convergence. Researchers have begun to study how ecological factors (such as signaling environment, predator community, and alkaloid availability) and predator-specific interactions may contribute to variation in aposematic signal design (Speed 1999; Mallet and Joron 1999; Endler and Mappes 2004; Ruxton et al. 2004; Mappes et al. 2005; Speed and Ruxton 2007). Here we will review how some of these processes may be contributing to the signal divergence across *O. pumilio* populations.

Ecological constraints may contribute to the divergence of aposematic signals by imparting selection for crypsis. As derived populations inhabit new environments that are limited in chemical defense resources, aposematic signal diversification may be driven away from conspicuousness and towards cryptic forms if predators impose selection for honest aposematic signaling (Sherratt 2002; Blount et al. 2009; Speed et al. 2010; Lee et al. 2011). Poison frogs derive their toxicity from alkaloids sequestered from their diet (Daly et al. 1994; Saporito et al. 2004, 2007a, 2012), hence variation between sites in arthropod communities may lead to changes in toxicity levels between *O. pumilio* populations (Saporito et al. 2006, 2007b). If a population's mean toxicity level drops below a critical level for effective defense, then selection for more cryptic forms may be imposed on some populations. Furthermore, the predator community composition may also favor more cryptic aposematic forms. Endler and Mappes (2004) noted that if less than half of the predators are able to detect and learn to avoid noxious prey, then crypsis is favored over conspicuousness for aposematic organisms. Hence, as populations of *O. pumilio* become isolated on islands with potentially different predator communities, the selection pressure along the crypsis-conspicuous continuum may vary.

For predators that are able to learn to avoid aposematic prey, their learning biases may favor increases in conspicuousness of aposematic signals. Several studies have shown that increases in conspicuousness of aposematic signals can lead to more rapid predator learning (Gittleman and Harvey 1980; Sillen-Tullberg 1985; Endler and Mappes 2004; Darst et al. 2006; Gamberale-Stille et al. 2009). Furthermore, brightness contrast alone has been shown to serve as an effective warning signal, and can be important in the initial stages of aposematic learning (Prudic et al. 2007; Sandre et al. 2010). Hence, natural selection may act synergistically with sexual selection by favoring brighter, more conspicuous phenotypes in some *O. pumilio* populations.

Natural selection may be largely permissive of signal diversification by sexual selection due to psychological or sensory constraints of the predator. Variations in aposematic signals that are driven by sexual selection may not experience purifying selection by predators due to neophobia (Marples et al. 1998) or because predators generalize their learned avoidance to novel forms (Pavlov 1927; Exnerova et al. 2006; Darst and Cummings 2006). Experimental studies with bird predators and other poison frog species (*Epipedobates* sp.) have shown that predators respond to novel forms of aposematic prey in a toxicity-dependent manner. Specifically, predators familiar with more toxic prey species avoid novel prey forms, whereas predators familiar with less toxic prey do not avoid novel morphs (Darst and Cummings 2006). Hence, new variants of *O. pumilio* may be protected through a process of relaxed purifying selection on variants due to stimulus generalization. Another means by which predators may be permissive to sexually selected aposematic variation is if their sensory systems are unable to detect it. This appears to be the case with one population of *O. pumilio* (Solarte), where visual modeling investigations indicate brightness variation in male dorsal reflectance is detectable to conspecifics but not to avian predators (Crothers and Cummings 2013). The inability of birds to detect the extensive brightness variation found within a population where sexual selection appears to influence this trait hints at a permissiveness of predators to ongoing signal evolution promoted by conspecifics.

The potential role for natural selection in the divergence and/or maintenance of phenotypic variation across *O. pumilio* populations remains the least explored area of investigation in the species' color evolution. Though the main predators of *O. pumilio* in the Bocas del Toro region are still unknown, clay frog predation experiments have implicated birds as the major predator of several poison frog species (Noonan and Comeault 2009; Chouteau and Angers 2011; Comeault and Noonan 2011) as well as *O. pumilio* in other parts of the species' range (Saporito et al. 2007c; Hegna et al. 2011). It is has been suggested that predators were not a strong diversifying force in the species' color diversification, as two syntopic species of poison frog are not polytypic (Summers et al. 1997) and there is no evidence that *O. pumilio* is part of a Müllerian mimicry ring (Siddiqi et al. 2004). Yet, we find strong correlative evidence that brightness variation between morphs across the archipelago is more informative (=correlates with toxicity) to specific predators (birds) than to conspecifics (Maan and Cummings 2012; Fig. 4). Clearly, rigorous empirical work must be conducted to address the role of predation on signal evolution in this system.

In *O. pumilio*, a pioneering study by Daly and Myers (1967) found no correlation between conspicuousness and the substantial variation in toxicity between island

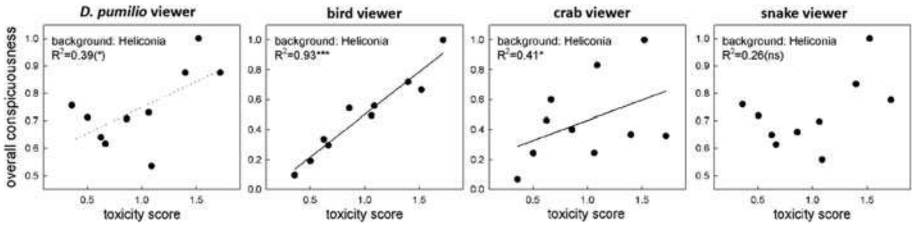


Fig. 4 *O. pumilio* morph toxicity and conspicuousness of dorsal coloration from Maan and Cummings (2012). Relative toxicity and overall conspicuousness of 10 different morphs from 9 populations across the Bocas del Toro archipelago (populations identified in Fig. 1) for four different viewers (conspecifics, birds, crabs and snakes). *Solid lines* are statistically significant relationships ($P < 0.05$); *broken lines* indicate statistical trends

populations. Our lab returned to this question recently, employing a different toxicity assay and more quantitative estimates of frog conspicuousness using spectrophotometry-based visual modeling techniques (Maan and Cummings 2012). Daly and Myers (1967) employed a lethality-based assay (LD_{50}) as a measure of toxicity, however, some researchers have resorted to irritant-based measures of toxicity (mouse recovery time post-injection of single skin extracts) in an effort to minimize sacrifice (Darst and Cummings 2006; Darst et al. 2006). Using this irritant-based toxicity assay along with taxon-specific visual models including conspecifics and potential predators such as birds, crabs, and diurnal snakes, we evaluated the relationship between morph toxicity and conspicuousness. Our results showed that the extreme color and brightness diversity of *O. pumilio* across the Bocas del Toro archipelago (both at inherent (dorsal reflectance flux) and apparent (visual model-specific) levels) covaries with the variation in morph toxicity ($r^2 = 0.61$ with dorsal flux; $r^2 = 0.94$ overall conspicuousness to avian predator), with more toxic frogs displaying more conspicuous coloration. The modeling results also implicated birds as potentially important poison frog predators because they show the strongest predictive relationship between toxicity and viewer-specific conspicuousness estimates (Fig. 4), even more so than that exhibited by conspecifics. Recent empirical evidence suggests that avian predators in Bocas del Toro respond to signal honesty in *O. pumilio* morphs. Using clay model replicas, Hegna et al. (2012) showed that birds attack a less toxic/less conspicuous morph (Colon) more often than a more toxic/more conspicuous morph (Almirante). Taken together, these results suggest that variation in conspicuousness observed across *O. pumilio* populations of the Bocas del Toro archipelago is not random with respect to natural selection.

A complex story of signal evolution

Taken together with our previous research, we present two non-exclusive scenarios for how natural and sexual selection interact to drive phenotypic variation across this archipelago. We propose that all three potential viewers (predators, females, and males) impart selective influences that may contribute to the diversification of color morphs in the derived populations of the Bocas del Toro archipelago relative to the mainland morph (Fig. 1). These scenarios are: (1) predators impose a selective regime whereby populations above a toxicity-brightness threshold are at liberty to diversify via sexual selection and below which populations are constrained to maintain a stricter resemblance to a more cryptic population mean, and (2) synergistic/additive effects of inter- and intrasexual selection drive the evolution of brighter males within populations above the toxicity threshold.

Natural selection: diversifying for crypsis and conspicuousness

The correlation that our laboratory identified between toxicity and conspicuousness in *O. pumilio* hints at the potential for multiple strategies being utilized in the species (Fig. 1c). These results suggest that natural selection is providing some constraint on aposematic signal evolution across the archipelago, and that perhaps only populations that are defended by high levels of toxicity/noxiousness can afford to be bright and conspicuous. Previous investigations in other laboratories have speculated that some of the less conspicuous archipelago populations represent evolutionary reversals to crypsis (Wang and Shaffer 2008; Prohl and Ostrowski 2011; Rudh et al. 2011). Our recent finding that many of these populations are also low-ranking in toxicity supports this assumption (Fig. 4, Maan and Cummings 2012). This possibility is further bolstered by several studies that have found a relationship between conspicuousness and “boldness” across populations (Breed 2008; Prohl and Ostrowski 2011; Rudh et al. 2011).

If predators are imposing a selective regime for honesty in aposematic signals (more conspicuous signals = greater chemical defense) in the Bocas del Toro archipelago, then we may predict that aposematic signals will diverge from the common mainland phenotype as they increase in toxicity (becoming more conspicuous) or decrease in toxicity (becoming more cryptic; Fig. 1b, c). Furthermore, we expect natural selection to operate differentially as populations become more or less toxic. Specifically, we predict that predators may exhibit purifying selection in populations that are weakly defended and exhibit greater tolerance of signal variation in populations that are strongly defended (Fig. 1b). Purifying selection against rare aposematic phenotypes has been observed in polymorphic insects (*Heliconius* butterflies: Kapan 2001; alpine leaf beetles: Borer et al. 2010) and other geographically variable poison frog species (Noonan and Comeault 2009; Chouteau and Angers 2011; Comeault and Noonan 2011), suggesting that such forces could also be at play in *O. pumilio*. We would expect that as populations lose their toxicity and develop more cryptic color patterns, individuals exhibiting aposematic signal deviations would be more vulnerable to detection by predators. Thus in these less toxic, more cryptic populations, sexual selection for brightness should be constrained by purifying selection by predators. In populations that are strongly defended, however, predators may largely be tolerant to signal variation due to predator generalization (Darst and Cummings 2006). Hence, diversification via sexual selection in populations that are more toxic than the common mainland morph is less likely to be subject to purifying selection and more likely to be tolerated by predators via processes such as predator generalization (Fig. 1b).

Our examination of the relative toxicity and conspicuousness of 10 different morphs in the Bocas del Toro archipelago shows an agreement with the above predictions (Fig. 1c). Firstly, we find that the population representing the most common mainland phenotype exhibits trait values that are closest to the mean (or intermediate level) for both toxicity and conspicuousness (Almirante z-scores lie closest to the origin in Fig. 1c). Secondly, populations that have deviated from the Almirante population by exhibiting greater toxicity are also more conspicuousness to a bird predator’s visual system, whereas those that have deviated from the Almirante population towards being less toxic are also more cryptic (Fig. 1c). Finally, the relative degree of divergence from the common mainland phenotype is greater for the conspicuous morphs than the cryptic morphs (with z-scores being further away from the origin for the conspicuous morphs than the cryptic ones), possibly due to the synergistic/additive effects of both natural and sexual selection.

Sexual selection: diversifying for more conspicuous morphs above toxicity threshold

If natural selection is imposing a constraint on diversification of morphs in populations below some defense (toxicity) threshold, we may expect the role of sexual selection on aposematic signal evolution to be greatest in populations that exceed some critical defense threshold (Fig. 1b). Sexual selection has been a potent force of signal divergence in other species (West-Eberhard 1983; Zamudio and Sinervo 2000; Seehausen and Schluter 2004; Dijkstra et al. 2005; Pryke and Griffith 2006), and there are several scenarios in which it could have been a major driver of *O. pumilio*'s phenotypic divergence, such as drift in the female preference trait, or directional selection driven by female preference and/or or male–male interactions paired with interdependence between aposematic signal components (brightness and hue).

Directional sexual selection for brighter phenotypes by female preference or male–male interactions, in the absence of drift, may have driven diversification of color patterns in the archipelago populations due to the interdependence of brightness and color (Maan and Cummings 2009). Brightness and hue (color) are interdependent features of a visual signal, and changes in signal brightness may lead to changes in signal hue. In general, creating a brighter visual signal can be achieved via two non-mutually exclusive design principles: increasing the peak reflectance (reflecting more light at a given wavelength), or increasing the spectral width of reflectance (reflecting light over a broader wavelength range). The increased brightness of the most exceptionally bright derived populations (Solarte and Bastimentos) exemplifies both principles: greater peak reflectances and shorter cut-on wavelengths (wavelength at which reflectance begins to exceed baseline), as compared with the common mainland morph (Almirante). The implication of this interdependence between brightness and hue is that directional selection on one aspect of the aposematic trait (brightness) may cause a concomitant change in the other (hue), leading to the brighter colors observed on the islands of Bocas del Toro (orange, yellow, and green). Many of the *O. pumilio* morphs inhabiting the islands of the Bocas del Toro region are brighter than the mainland morph, suggesting that female-mediated selection on brightness may have been a potent force in the signal evolution of populations of the archipelago (Maan and Cummings 2009).

Additionally, there is ample evidence that bright ornamentation can function as an indicator of body condition or territorial status in animals (reviewed in Andersson 1994 and Whiting et al. 2003). Such status-signals are widespread across the animal kingdom (arthropods, fish, birds, amphibians, reptiles, mammals; reviewed in Whiting et al. 2003). Orange and red coloration, as exhibited by many *O. pumilio* populations, is also well documented as a common signal of dominance/aggression across the animal kingdom (Pryke 2009). Thus, brightness of coloration may reveal information to conspecifics, functioning as an indicator of body condition, competitive ability, or survivorship. Our research provides some tantalizing evidence that male brightness may be a conditional trait in the exceptionally bright Solarte population (Crothers et al. 2011). If both males and females are assessing potential mates and rivals along the same trait axis (e.g., brightness) that provides both sexes with important information, the effect of intra- and intersexual selection is likely to be additive or synergistic, resulting in stronger directional selection (Fig. 1a, b). The fact that Solarte exhibits the greatest degree of divergence from the mean morph detectability to an avian predator (Fig. 1c; overall avian conspicuousness z-score

~2) is consistent with this hypothesis. Our ongoing investigations into the roles of male–male competition in this species also provide some indications that brightness asymmetries impact the outcomes of male aggressive interactions (L. Crothers, unpublished data). These investigations will allow us to determine whether male–male competition typically works synergistically/additively with female-mediated sexual selection in this species.

Conclusion

A benefit of investigating signal evolution in this species is that it is evident that the processes of selection are all impacting a single, quantifiable trait: aposematic coloration/brightness. The aposematic signal diversification of *O. pumilio* represents a complex interplay between natural and sexual selection. Natural selection appears to play a role in keeping the aposematic signal variation of *O. pumilio* across the Bocas del Toro archipelago region largely 'honest' in terms of chemical defense. However, our laboratory's investigations also indicate that predators may be largely permissive to the sexually selected variation in warning coloration in some populations of the species. The agent of diversification that appears most influential at the within population level for more toxic populations is sexual selection, either by female preference alone or in conjunction with male–male interactions. The variation in color patterns across the archipelago populations may therefore be "ecologically neutral," as long as each of the color patterns is sufficiently conspicuous to function as an aposematic signal to potential predators (Broom et al. 2006; Ruxton et al. 2007), or sufficiently cryptic in populations where the defense has weakened from the mainland condition. Future investigations by our laboratory and others will further clarify how natural and sexual selection interacted in the course of warning color evolution in this species.

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