Mimicry's palette: widespread use of conserved pigments in the aposematic signals of snakes

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SUMMARY   Mimicry, where one species resembles another species because of the selective benefits of sharing a common signal, is especially common in snakes. Snakes might be particularly prone to evolving mimicry if all species share some of the same proximate mechanisms that can be used to produce aposematic/mimetic signals. We evaluated this possibility by examining color pigments in 11 species of snakes from four different families, three species of which participate in a coral snake mimicry complex involving convergence in coloration. We found that all 11 species used combinations of two pteridine pigments and melanin in their coloration, regardless of whether or not they were mimics. Furthermore, the presence or absence of red pteridines was strongly correlated with the relative excitation of medium- and long-wavelength photoreceptors in birds, thereby linking shared pigmentation to perception of those pigments by likely agents of selection. Thus, precise color mimicry might be relatively easy to evolve among snakes owing to symplesiomorphies in pigmentation.

INTRODUCTION

Convergent evolution—in which two or more species evolve similar phenotypes in response to similar selective pressures—may be the product of either different developmental pathways or developmental systems that are shared on some proximate level (Arendt and Reznick 2008; Manceau et al. 2010). Either route may underpin defensive mimicry, where a species converges on the aposematic signals of another species (the model) because resemblance is favored when predators cannot distinguish between the two (Ruxton et al. 2004). Because selection for mimicry can be strong (e.g., Pfennig et al. 2001), convergence between taxa in aposematic/mimetic signals might occur even when species possess novel ways of producing these signals. At the same time, because aposematism is often distinctive (Ruxton et al. 2004), shared developmental systems might expedite the evolution of mimicry. Despite the potential importance of proximate mechanisms in facilitating the evolution of mimicry, relatively little is known about how mimetic phenotypes are produced in most taxa; documenting this is a necessary step in answering the more general question of why some taxa produce so many mimics.

Most of what we do know regarding the proximate mechanisms underpinning aposematic/mimetic signals comes from studies of *Heliconius* butterflies (Beldade and Brakefield 2002; Papa et al. 2008). Mimicry among closely related, distasteful species of *Heliconius* is controlled by three major loci that appear to have allelic effects on color pattern across species (Joron et al. 2011; Reed et al. 2011; Martin et al. 2012). Furthermore, species appear to have exchanged alleles regularly throughout their evolutionary history via hybridization (Dasmahapatra et al. 2012). Thus, in *Heliconius*, shared proximate mechanisms have promoted convergence on a complex phenotypic adaptation. However, most other species involved in mimicry are more distantly related to each other than are different species of *Heliconius*. Moreover, introgression of genes via hybridization is not a likely general explanation for the evolution of mimicry.

Snakes are an excellent taxon for studying how mimetic phenotypes arise, but little is known about how aposematic/mimetic signals are produced. Mimicry appears to be particularly common among snakes—especially mimicry of brightly colored, venomous coral snakes (family Elapidae; Brodie and Brodie 2004). Indeed, one of the first reported cases of mimicry involved coral snake mimicry (Wallace 1867). At least 18% (115 species) of New World snakes are thought to mimic coral snakes (Savage and Slowinski 1992). Mimetic species have evolved with non-mimetic species in every subfamily of New World colubrid snakes. Within those groups of snakes where mimicry has been studied from a phylogenetic perspective, it has been found to have arisen independently (Pyron and Burbrink 2009; Kikuchi and Pfennig 2010a), suggesting multiple independent origins of the adaptation. Why so many species converge on the coral snakes' distinctive patterns of red, yellow (or white), and black (i.e., tricolor) rings remains one of herpetology's most enduring problems (reviewed in Brodie and Brodie 2004).

Here, we consider the possibility that snakes might share common developmental mechanisms for producing these tricolors.

Recent research supports this hypothesis. Eastern coral snakes, *Micrurus fulvius*, and their harmless mimics, scarlet kingsnakes, *Lampropeltis elapsoides*, share proximate mechanisms for producing phenotype (Kikuchi and Pfennig 2012). Specifically, the pigments used to produce coloration, and the organization of their color-producing cells (chromatophores), are the same for both species (Kikuchi and Pfennig 2012). Nonetheless, it is unclear whether the proximate similarity between these two species reflects a shared, inherited character (i.e., a symplesiomorphy) in color production systems in snakes generally or whether it represents a unique instance of convergence.

We specifically evaluated coloration across a diverse array of snakes to determine if similar pigments occur in different snake taxa, thereby helping to explain why coral snake mimicry is so widespread. Because coral snake mimicry involves distantly related taxa (i.e., species from different families), studying mimicry within this group could provide more general insight into the mechanisms behind the evolution of mimicry.

MATERIALS AND METHODS

We collected individuals of a coral snake mimicry complex from the southwestern United States. The venomous Arizona coral snake, *Micruroides euryxanthus* (family Elapidae; Fig. 1A) is the most basal taxon of the New World coral snakes (Pyron et al. 2011). Its potential mimics include Arizona mountain kingsnakes, *Lampropeltis pyromelana* (family Colubridae; Fig. 1B) and long-nosed snakes, *Rhinochelius lecontei* (family Colubridae; Fig. 1C). We also collected eight species found in sympatry with coral snakes that do not participate in this mimicry complex. Sampling the latter eight species allowed us to compare pigments and coloration across a wide taxonomic set of three families and seven genera. These species (and families) included: rosy boa, *Lichanura trivirgata* (Boidae); Yaqui black-headed snake, *Tantilla yaqui* (Colubridae; Fig. 1D); plains black-headed snake, *Tantilla nigriceps* (Colubridae); gopher snake, *Pituophis catenifer* (Colubridae; Fig. 1E); Western hognose snake, *Heterodon nasicus* (Colubridae); whip snake, *Masticophus flagellum* (Colubridae); green rat snake, *Senticolis triaspis* (Colubridae; Fig. 1F); and black-tailed rattlesnake, *Crotalus molossus* (Viperadae).

Reptiles and amphibians (including snakes) produce colors by selectively reflecting or absorbing certain wavelengths of light with specialized cells called chromatophores (reviewed in Cooper and Greenberg 1992; Olsson et al. 2013). There are three principle kinds of chromatophores: erythrophores, iridophores, and melanophores. Erythrophores (sometimes

Fig. 1. Representative taxa sampled for pigment analysis. (A) Arizona coral snake, *Micruroides euryxanthus*. (B) Arizona mountain kingsnake, *Lampropeltis pyromelana*. (C) Long-nosed snake, *Rhinochelius lecontei*. (D) Yaqui black-headed snake, *Tantilla yaqui*. (E) Gopher snake, *Pituophis catenifer*. (F) Green rat snake, *Senticolis triaspis*.

called xanthophores) can contain a variety of blue, green, and ultraviolet-absorbing pigments. Pteridines and carotenoids comprise the two groups of pigments that have been found in erythrophores. Animals produce pteridines endogenously, whereas they must acquire carotenoids from their environment (McGraw et al. 2005). Iridophores contain guanine crystals that reflect certain wavelengths of light (Nielsen and Dyck 1978; Gosner 1989; Morrison 1995; Morrison et al. 1995; Kuriyama et al. 2006). Melanophores in non-mammalian and avian taxa have thus far been found to contain only the black pigment eumelanin, which absorbs light evenly across the spectrum. Typically, chromatophores are arranged from the surface of the skin in the order erythrophores, iridophores, melanophores, and beneath them lies a basement membrane that is highly and evenly reflective (Cooper and Greenberg 1992). However, not all types of chromatophores have been found in all colors of tissue (e.g., Gosner 1989; Kikuchi and Pfennig 2012).

In this study, we focused on the pigments sequestered in erythrophores. We did so because previous experimental studies have shown that the amount of red coloration in a coral snake mimic's dorsum is crucial in protecting it from potential predators (Smith 1975, 1977; Harper and Pfennig 2007; Kikuchi and Pfennig 2010a). Moreover, the pigment responsible for one of the other tricolors—black—is eumelanin (Kikuchi and Pfennig 2012), which is highly conserved across animals (Ito and Wakamatsu 2003).

All snakes used in the procedures described below were collected in Cochise County, AZ. Live snakes were captured and held at the Southwestern Research Station (SWRS) in Portal, AZ until the reflectance of their colors could be measured with a spectrophotometer. They were then released where they were captured. Snakes found dead on roads were collected and frozen immediately. Their reflectance was measured a few days later (after the snakes were thawed). Then they were moved to $-80°C$ where they remained for several months until pigment analysis. We have found that snakes preserved at very low temperatures retain their colors much better than those preserved using other methods, and that qualitative analyses of pigments are not affected by such preservation. We sacrificed a live coral snake immediately before measuring its reflectance by anesthetizing it with chloroform and severing the cervical vertebrae. It was then frozen until pigment analysis could be performed.

To identify the pigments in each snake's color patches, we took small skin samples. We washed each sample and blotted it dry on Kimwipes to remove any pigments that might be present in the blood. We then finely diced the tissue sample before placing it in a microcentrifuge tube and homogenizing it in 1 ml 1 N NH_4OH. Next, we added 0.5 ml 1:1 hexanes:tert-butyl methyl ether, vortexed the sample, and centrifuged it at 8000 RPM for 5 min. The rationale behind this extraction was to isolate polar and organic pigments in two separate phases (pteridines and carotenoids are polar and organic, respectively; Steffen and McGraw 2009). Kikuchi and Pfennig (2012)

previously identified drosopterins as the principle pigment of red skin in *M. fulvius* and *L. elapsoides*, and proposed that a pigment that absorbed strongly in the ultraviolet was isoxanthopterin. We therefore used thin-layer chromatography (TLC) of our aqueous pigment extract of the coral snake's white tissue and an isoxanthopterin standard to confirm this. For TLC, we used cellulose on glass plate as the solid phase and a 1:1 isopropanol:2% ethyl acetate mixture as the mobile phase.

We then measured the absorbance of each phase of each sample between 200 and 800 nm. Carotenoid pigments can be identified by a characteristic triplet of absorbance peaks (Britton 1985). The red pteridine pigments known as drosopterins have a single broad absorbance maximum between 490 and 500 nm, while isoxanthopterin has an absorbance maximum around 340 nm (Albert and Wood 1953). We looked for these characteristic spectral peaks to identify pigments in our sample of snakes. We scored snake color patches as having the presence or absence of carotenoids, drosopterins, and isoxanthopterin.

In studying the mechanisms behind visual mimicry (e.g., the pigments involved), it is important to relate them to the way models and mimics are perceived by relevant agents of selection (e.g., predators). Color discrimination depends on the overlap between the spectral sensitivities of cone photoreceptors in animals' eyes (Kelber et al. 2003), so human evaluation of how a pigment impinges on a snake's color is not necessarily relevant. Stronger inference can be made by modeling color perception through the eyes of relevant predators (Stoddard 2012). It is also important to verify the effects of pigments on coloration: pigment concentration can be decoupled from color (Steffen and McGraw 2009), or pigments can produce different colors in vivo than they do in vitro (Wijnen et al. 2007). For these reasons, we sought to determine the effect that snake skin pigments have on the way that they are perceived by avian predators.

We characterized the reflectance spectra of a subset of the snakes we collected (because of transportation considerations, we were unable to measure reflectance of all snakes). We used a UV–Vis spectrophotometer (USB2000 with PX-2 pulsed xenon light source, Ocean Optics, Dunedin, FL, USA) to measure reflectance. Reflectance spectra were measured in a dark room with the reflectance probe positioned perpendicular to the desired patch and were measured relative to a Spectralon diffuse reflectance white standard (Labsphere, Inc., North Sutton, NH, USA) as used by Taylor et al. (2011). To capture the measured reflectance spectra, we used the program Spectrasuite (Ocean Optics) to collect reflectance from 300 to 700 nm. The spectra were then compiled into one nanometer bins using CLR files (Montgomerie 2008). We measured each color patch on the snakes twice and took the midpoint of these two measurements. When snakes had multiple patches of the same color, we measured up to three of them and averaged them to get a mean value of that color for the snake. Finally, for analysis, we averaged the spectra of each color for each species.

To relate a snake's pigmentation to the way that natural predators see it, we correlated the presence or absence of drosopterins with avian cone excitation. We used the program tetracolorspace to describe how the reflectance spectra of each color patch excite avian cones (Stoddard and Prum 2008). Tetracolorspace output includes the measures θ, ϕ, and r for all colors, which describe the position of a color in a three-dimensional space defined by the relative excitation of the four avian cone types. Of these variables, we were chiefly interested in θ, which indicates the relative stimulation of medium- and long-wavelength sensitive cones. Those cones are responsible for distinguishing between the reddish and greenish aspects of hues (those ranging from 500 to 700 nm), and should be most responsive to variation in drosopterins. We used the blue tit to represent avian vision, as its visual system is a well-established model (Hart et al. 2000; Hart 2001; Hart and Vorobyev 2005). Avian medium- and long-wavelength photoreceptors vary little across the avian phylogeny in their peak sensitivity (Hart 2001), so the blue tit is a good representative of all likely avian predators. We built a simple regression model to test the prediction that the presence of drosopterins causes the relative stimulation of medium:long cones decrease (meaning that heuristically, colors look "redder") by coding θ as a dependent variable and the presence or absence of drosopterins as an independent predictor (residuals did not differ significantly from normality; Shapiro–Wilks test, $P > 0.25$). Model selection criteria (AIC) indicated that model fit was not improved though the use of snake species as a random effect, so we omitted it from the final model.

RESULTS

We found no evidence of carotenoid pigments in any of the color patches that we sampled. In contrast, pteridine pigments were widespread—snake tissue that appeared reddish contained drosopterins, and almost all contained isoxanthopterin, which strongly absorbs ultraviolet and whose identity was confirmed in our TLC test (Table 1). Only the ventrum of both *Tantilla* and the gray neck of *Masticophus bilineatus* lacked isoxanthopterin. Among the sample of snakes for which we had both reflectance spectra and pigment data, we found that the presence of drosopterins was strongly correlated with the relative excitation of avian medium- to long-wavelength cones (df = 12, $P = 0.0004$; Fig. 2). This illustrates the importance of these shared pigments in creating a similar perceptual experience for snake predators.

DISCUSSION

Our results, together with those of an earlier study (Kikuchi and Pfennig 2012), reveal that snakes in general appear to share a pigment production system. Furthermore, we have shown that

red drosopterin pigments in snakes predict how their skin color appears to birds, which are key predators of snakes and therefore likely agents of selection on their coloration. Although we are at an early stage in deciphering the proximate mechanisms by which snakes produce coloration, it supports the hypothesis that mimetic convergence can be facilitated by conserved developmental systems.

The expression of coloration involved in mimicry is likely under predator-mediated selection. Strong selective forces are often detected in field studies of snake coloration (e.g., Brodie 1992, 1993; Pfennig et al. 2001; Wüster et al. 2004; Kikuchi and Pfennig 2010a; Valkonen et al. 2011; Cox and Davis Rabosky 2013), and (as noted earlier) the amount of red coloration on a snake's dorsum has been shown to play an important role in predators' response to aposematic signals on snakes (Smith 1975, 1977; Harper and Pfennig 2007; Kikuchi and Pfennig 2010b). Red drosopterin pigments produce an effect that is not only visible to humans, but also to relevant predators (i.e., birds). Thus, it appears that potential coral snake mimics have the ability to produce a vital component of the mimetic phenotype in common with their models, which we hypothesize might help to explain why so many serpents participate in mimicry. In an ideal scenario, we could use the comparative method to directly test the hypothesis that shared developmental systems between species foster the evolution of mimicry. This could be done by examining taxa with high proportions of mimics and those that do not, and seeing whether or not mimics were more likely to radiate if they share relevant developmental systems with their models. However, such an analysis awaits information from more taxonomic groups.

The study of mimetic signal production and convergence on the proximate level has not at present been extended to many taxa, but what is known is intriguing. For example, Vereecken and Schiestl (2008) have shown that deceptive orchids (i.e., species that do not provide nectar rewards to pollinators) mimic pheromone compounds that their bee pollinators prefer. The metabolic pathways that underlie the production of alkenes are not homologous between orchids and bees (Schlüter et al. 2011). Thus, although some taxa may be predisposed to evolving mimicry, convergence without homology between models and mimics can occur. Convergent coloration that does not result in mimicry has been extensively studied in phenotypes that rely on the relatively well-understood melanin pigments (e.g., Rosenblum 2005; Hoekstra 2006). However, complex mimetic patterns often depend on the regulation of pteridine and carotenoid pigmentation, which is less well understood. Application of approaches used in the study of melanin adaptations might be helpful in elucidating mechanisms of convergent coloration in general, but will require a more comprehensive understanding of how other pigments are incorporated into color patterns. Butterflies use both carotenoid and pteridine pigments (Ford 1953), and so genes involved in the formation of their color patterns may also be applicable to other

Table 1. Pigment presence and absence among a taxonomically diverse assemblage of snakes from the western United States

Species	Tissue	Pigment presence and absence		
		Carotenoids	Drosopterins	Isoxanthopterin
Micruroides euryxanthus	**Red dorsum**	Ø	+	+
	White dorsum	Ø	Ø	+
Tantilla nigriceps	**Dorsum**	Ø	Ø	+
	Ventrum	Ø	+	Ø
Tantilla yaqui	Dorsum	Ø	Ø	+
	Ventrum	Ø	Ø	Ø
Rhinocheilus lecontei	**Red dorsum**	Ø	+	+
	White dorsum	Ø	Ø	+
Lichanura trivirgata	Red dorsum	Ø	+	+
	White dorsum	Ø	Ø	+
Heterodon nasicus	Brown dorsum	Ø	Ø	+
Masticophus bilineatus	**Gray dorsum**	Ø	Ø	Ø
	Reddish dorsum	Ø	Ø	+
	Light stripe	Ø	Ø	+
Gonyosoma oxycephalum	**Light dorsum**	Ø	Ø	+
	Dark dorsum	Ø	Ø	+
Crotalus molossus	Light dorsum	Ø	Ø	+
	Dark dorsum	Ø	Ø	+
Lampropeltis pyromelana	**Red dorsum**	Ø	+	+
	White dorsum	Ø	Ø	+
Pituophis catenifer	**Light dorsum**	Ø	+	+
	Dark dorsum	Ø	+	+

The absence of a pigment is denoted by Ø and its presence by + for each type of skin tissue that we sampled. Tissues marked in **bold** are included in our reflectance spectra sampling.
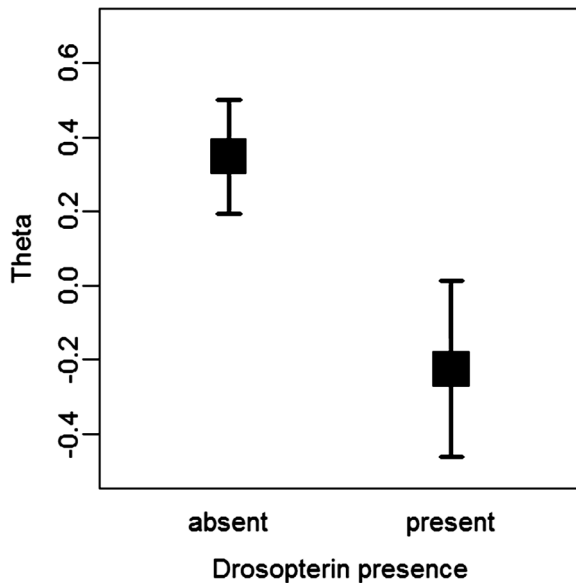
Fig. 2. The effect of the presence or absence of red drosopterin pigments on how birds perceive snake color. Theta describes the relative excitation of medium- and long-wavelength sensitive cones in the avian eye. More negative theta values indicate a higher relative excitement of long-wavelength cones. From the human perspective, this is analogous to red:green color vision, although humans are most sensitive at different wavelengths than are birds.

systems. Even if they are not, ongoing work in vertebrate systems may illuminate the developmental processes responsible for pteridine coloration in vertebrates (Ziegler 2003; Protas and Patel 2008). Either of these eventualities may greatly augment our ability to study these unique adaptations.

In addition to needing more information to discern the importance of developmental mechanisms for explaining why mimicry is so widespread in some taxonomic groups, we also do not yet know why particular species of snakes evolve mimicry and others do not. Our finding that diverse lineages of snakes share a common system for producing coloration may mean that, as a group, they are particularly prone to producing mimetic species. Nonetheless, although many snakes might be capable of producing tricolor patterns, not all do, even if their phenotypes include red and yellow colors (e.g., some species within *Masticophis*, *Farancia*, and *Thamnophis*). Coral snake mimics tend to be slender, fossorial, nocturnal, and (most importantly) syntopic with coral snakes. Thus, shared developmental systems may predispose snakes in general to evolving coral snake mimicry, but additional factors may be critical for predicting its precise occurrence. Explanations for why certain taxa are mimetic and others are not often invoke body plan and ecology (Ruxton et al. 2004). Indeed, phylogenetic analyses suggest that body size and diet type are important for explaining mimicry in the colubrid tribe Lampropeltini (Pyron and Burbrink 2009). A broader and more extensive taxonomic study within the group

Serpentes could shed more light on the factors that select for snake mimicry in general, and coral snake mimicry in particular.

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