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Notes and Comments

The Role of Predators in Maintaining the Geographic Organization of Aposematic Signals

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ABSTRACT: Selective predation of aposematic signals is expected to promote phenotypic uniformity. But while these signals may be uniform within a population, numerous species display impressive variations in warning signals among adjacent populations. Predators from different localities who learn to avoid distinct signals while performing intense selection on others are thus expected to maintain such a geographic organization. We tested this assumption by placing clay frog models, representing distinct color morphs of the Peruvian poison dart frog *Ranitomeya imitator* and a nonconspicuous frog, reciprocally between adjacent localities. In each locality, avian predators were able to discriminate between warning signals; the adjacent exotic morph experienced up to four times more attacks than the local one and two times more than the nonconspicuous phenotype. Moreover, predation attempts on the exotic morph quickly decreased to almost nil, suggesting rapid learning. This experiment offers direct evidence for the existence of different predator communities performing localized homogenizing selection on distinct aposematic signals.

Keywords: aposematism, predation, polymorphism, poison dart frog, spatial structure.

Introduction

Aposematism occurs when defended prey advertise their unpalatability to predators by displaying conspicuous colors and patterns (i.e., warning signals; Ruxton et al. 2004). This evolutionary strategy has been documented in a variety of animal taxa, including gastropods, millipedes, insects, amphibians, fishes, snakes, and birds (Ruxton et al. 2004).

Theory predicts that the effectiveness of a warning signal is dependent on the ability of predators to associate the prey's conspicuousness with its unprofitability (Mappes et

al. 2005). Hence, by providing predators with an indicator that defenses are present, the education of potential predators in recognizing and avoiding the warning signal is facilitated (Ruxton et al. 2004; Mappes et al. 2005).

While in most cases predators learn to avoid the most abundant warning signal, rare and novel phenotypes are not recognized as unpalatable and are therefore quickly counterselected, thereby maintaining the uniformity of the warning signals (Benson 1972; Mallet and Barton 1989; Kapan 2001; Pinheiro 2003). Although many organisms display monomorphic warning signals locally, impressive geographic variations of aposematic signals have been documented, sometimes at a scale of only a few kilometers. For instance, the Neotropical butterflies *Heliconius melpomene* and *Heliconius erato*, which are Müllerian mimics, exhibit up to 30 different combinations of color and pattern throughout their range (Jiggins and McMillan 1997). Similar mosaics have also been documented in other mimetic communities such as millipedes (Marek and Bond 2009), burnet moths (Turner 1971), cotton stainer bugs (Zrzavy and Nedved 1999), net-winged beetles (Bocak and Yagi 2009), and frogs (Symula et al. 2001), as well as in nonmimetic species (Noonan and Gaucher 2006; Wang and Shaffer 2008).

Although the mechanisms remain uncertain, theoretical models (Joron and Iwasa 2005; Sherratt 2006) suggest that localized positive frequency-dependent predation, if strong enough, could explain the maintenance of geographic mosaics characterized by the aposematic signals being locally monomorphic but displaying differences between localities. Such selection would lead to situations where predators from different localities recognize and avoid distinct warning signals. Previous studies, principally performed within a single aposematic signal's distribution or under laboratory conditions, have reported a higher predation rate of the exotic or novel warning signals compared with that of the local warning display, suggesting that predators

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have the ability to discriminate between distinct warning signals (Benson 1972; Mallet and Barton 1989; Kapan 2001; Pinheiro 2003; Harper and Pfennig 2007; Noonan and Comeault 2009; Borer et al. 2010; Kikuchi and Pfennig 2010).

A few studies have also investigated the differences in the discriminative behavior of predators from different localities. For instance, it has been shown in *Heliconius* butterflies (Mallet and Barton 1989) and alpine leaf beetles (Borer et al. 2010) that, when reciprocally transplanted in an adjacent locality dominated by another aposematic signal, the exotic signal experiences more predation attempts than the local aposematic signal. However, even if the exotic aposematic signal is more frequently attacked, it is not known whether it loses or retains its aposematic advantage over nonconspicuous sympatric taxa. Including a nonconspicuous signal in these studies would provide a means to weigh the selection pressure and help explain why uniformity of warning signals is observed instead of a nonequilibrium polymorphism. Despite having been tested in only a single locality, Noonan and Comeault (2009) did present empirical evidence that an exotic aposematic signal originating from a remote and isolated locality loses its aposematic advantage. However, little is known about the strength of the discriminative behavior of predators between adjacent localities, where predators may encounter the exotic aposematic signals more often due to the possible passage of both the predator and the prey between localities.

Interestingly, some of these experiments have demonstrated that predation of the novel aposematic morphs mostly occurred shortly after these individuals were released into the habitat, thus suggesting rapid avoidance learning by predators (Mallet and Barton 1989; Kapan 2001). Laboratory experiments have confirmed the capacity of predators (i.e., birds) to learn to recognize and subsequently avoid the novel aposematic signals on which they were trained (Alatalo and Mappes 1996; Mappes and Alatalo 1997; Riipi et al. 2001; Pinheiro 2003; Rowland et al. 2007). However, whether the spatial structure of aposematic signals is the result of the differential learning experiences of the natural predator communities has not yet been confirmed.

This study focuses on the ability of predators from adjacent localities to discriminate between distinct warning signals. To ascertain the discriminative behavior of the predator, predation on artificial prey models corresponding to either the local or the exotic aposematic signal will be compared within and between two sites harboring different aposematic signals. In contrast to previous studies, we will use nonconspicuous models to weigh selection on both aposematic phenotypes (in order to determine whether they retain their aposematic advantage when

transplanted). The learning capacity of predators will be ascertained according to changes in the predation rate over time.

At the edge of the Andes and the Amazonian lowlands in Northern Peru resides the small poison dart frog *Ranitomeya imitator*. This frog, while monomorphic within a given locality, displays highly variable and distinct aposematic signals among different localities. In the higher elevations of the Caimarachi Valley, *R. imitator* possesses a green reticulated pattern on a black background on the head, dorsum, and flanks, and the legs and ventral area have smaller blue-green reticulations on a black background. Ten kilometers to the East, in the lowland near the city of Yurimaguas, *R. imitator* displays a head, dorsal, and flank pattern consisting of thin longitudinal yellow stripes on a black background, while the legs and ventral area have a blue-green reticulation on a black background. Such systems, possessing adjacent phenotypically fixed aposematic signals, appear ideal for ascertaining the role of predators in the maintenance of geographically structured aposematic signals.

Material and Methods

The field experiments were conducted in the Department of San Martín (Peru) just before the start of the rainy season (December 2009). Two sites separated by ~15 km were chosen for this study. At the first site, a high-elevation valley (06°25'17.0"S, 076°17'28.4"W; altitude, 514 m), *Ranitomeya imitator* displays a vivid green reticulated dorsal pattern on a black background. The second site is situated in the lowland (06°17'23.0"S, 076°13'43.9"W; altitude, 192 m), and here *R. imitator* displays a dorsal gold striped pattern on a black background.

To test whether the observed geographic structure in aposematic signals is the result of the discriminative behavior of predators and whether this behavior is the result of the natural predators' ability to learn to recognize aposematic signals, clay frog models were placed in the habitat (Saporito et al. 2007; Noonan and Comeault 2009). These models, measuring 18 mm in length (i.e., snout-vent length), were made of colored Funstuff Plastimodal modeling clay molded with a plaster mold, and portions of toothpicks were used to make the front legs in order for the models to have a more natural posture. These models were hand-painted with Delta Ceramcoat acrylic paint to mimic the two distinct combinations of colors and patterns found among the two mimetic populations of *R. imitator*. A model of a nonaposematic brown frog with an appearance similar to the daytime coloration of some species of frogs in the genus *Eleutherodactylus* was used as a control to weight selection (fig. 1). At both sites, 300 models of each color and pattern combination (i.e., 900 models) were



Figure 1: The two aposematic phenotypes of *Ranitomeya imitator* (upper row) and their respective clay models below (lower row, left and right), as well as a nonconspicuous frog model (lower row, middle) used to measure predation rates.

randomly placed along trails, with a minimum distance of 5 m between them. To mimic the habitat use of *R. imitator*, the models were positioned on living understory leaves ranging from 0.5 to 2 m in elevation and were secured using a toothpick so they would not fall in the event of wind, rain, or predation attempts. The models were checked for predation attempts at 24-h intervals during the 72 h for which they were left at the sites. In order to standardize, between days, the disturbance to predators that was caused by our visits to the sites, each daily visit occurred at the same time that we had initially placed the models (11 a.m.) and we always followed the same route, taking approximately the same amount of time to do so every day (i.e., ~6 h). At each visit, attacked and destroyed models were removed and missing models of each phenotype were counted.

Predation marks on malleable models were analyzed in respect to the color and pattern combination and the nature of the predator (Brodie 1993; Kuchta 2005; Saporito et al. 2007; Noonan and Comeault 2009). For each site, variation in predation pressure between the different phenotypic models was compared globally and after each of the 24 h observation, using a global χ^2 test of independence on global or novel attack frequencies. When significant, the Freeman-Tukey (FT) deviates were compared with a

$\alpha = 0.05$ criterion corrected for multiple comparisons using the Bonferroni method in order to identify which model phenotype experienced significantly more or fewer predation attempts than expected under the null hypothesis of equal attack probabilities. The same statistical approach was used to ascertain the learning capacity of predators; variation in the frequency of new attacks for each of the three daily intervals and for a given model phenotype was analyzed using a global χ^2 test of independence followed by a Bonferroni-corrected Freeman-Tukey deviates test. A file containing these data has been deposited at Dryad (<http://dx.doi.org/10.5061/dryad.kr812>).

Results

Of the 900 models placed at each site, 94 models (10.4%) at site 1 and 126 at site 2 (14.0%) were missing or had been partly destroyed by ants or roaches and were excluded from the analyses. Ant bite marks are characterized by two symmetrical incisions and vary greatly in size and number on an individual model, while roach bite marks, although tiny, usually completely destroy a model due to their large numbers (the resulting model has a porous appearance). Of the remaining clay replicas, 127 models (15.8%) at site 1 and 102 models (13.2%) at site 2 displayed marks of

attacks by predators. Attacks by avian predators were recognizable by the pair of U-shaped marks left on opposite sides of the models (e.g., Brodie 1993) or by stab marks on the dorsum of the model (e.g., Kuchta 2005). Because of the small size of these models, many models bearing the marks of bird attacks were torn in half. Other forms of attack included variably deep puncture marks or missing body parts without any recognizable marks on the remaining body; these were categorized as unknown predator attacks.

At both sites, attack rates of avian predators for the different phenotypic clay models were significantly different ($\chi^2_2 \geq 15.662$; $P \leq .001$; fig. 2a). However, the attacks made by unknown predators did not appear to significantly differ between model phenotypes ($\chi^2_2 \leq 2.411$; $P \geq .299$; fig. 2a), although this might be a result of low sta-

tistical power due to the low number of unknown predator attacks that were observed.

Avian predation pressure appears geographically structured, as at both sites the distinct local aposematic signal ($FT \leq -2.791$; $P < .05$; fig. 2a) experienced nearly one-fourth of the predation attempts that the geographically adjacent and exotic warning signals did ($FT \geq 2.496$; $P < .05$; fig. 2a). The observed frequency of attacks on the brown model is intermediate between the local and exotic aposematic signals and does not deviate from expected values ($FT_{\text{glob}} = -0.363$ at site 1; $FT_{\text{glob}} = -0.155$ at site 2; $P > .05$ at both sites; fig. 2a). As such, at the first site (fig. 2a), the frequency of avian predation attempts was highest on the yellow-striped (i.e., exotic) models (26.6%), followed by the brown models (14.2%), and the green-reticulated phenotype (i.e., local) was the least-frequently

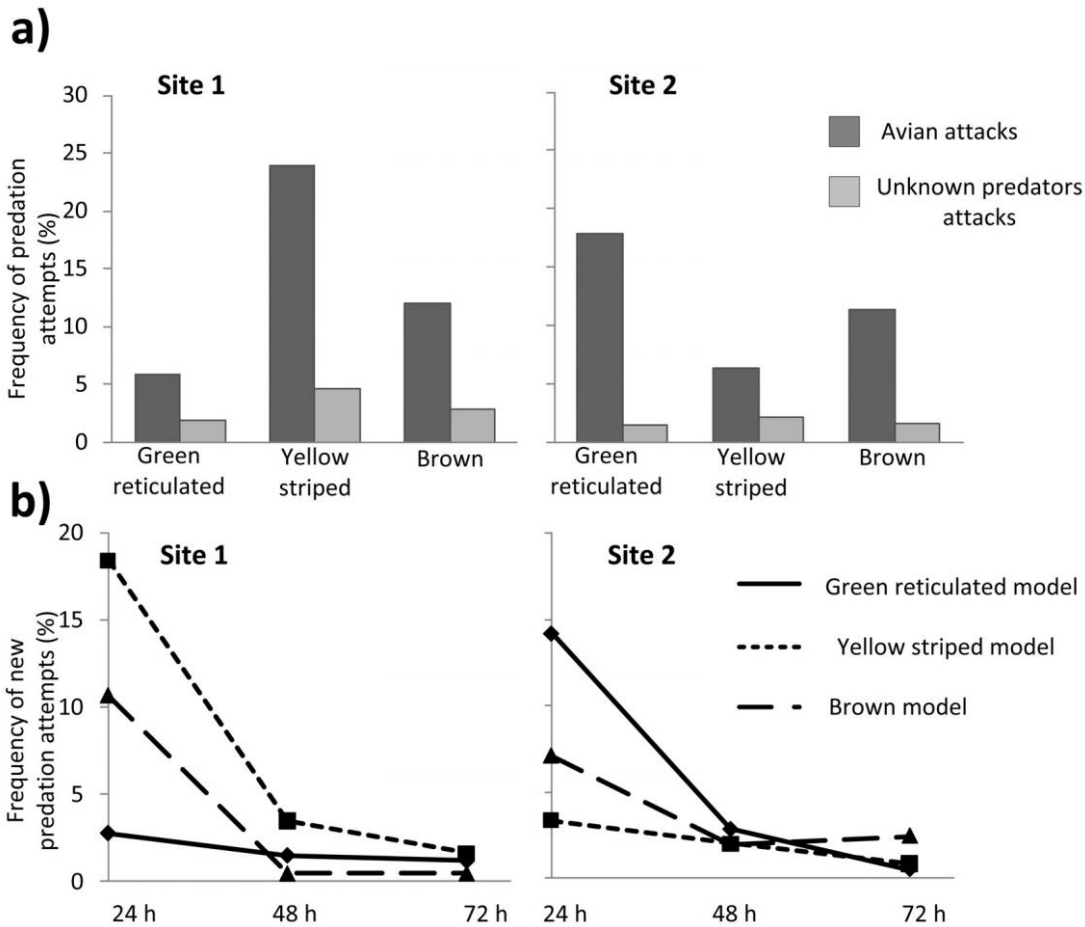


Figure 2: Predation frequency on clay models representing a nonconspicuous phenotype (brown) and two aposematic phenotypes (green reticulated and yellow striped) of *Ranitomeya imitator* at two sites characterized by distinct aposematic signals. *a*, Frequency of predation attempts by avian (dark gray) and unknown (light gray) predators on the different models. *b*, Frequency of avian predation attempts, as a function of time for each clay model phenotype.

attacked (7.2%). At the second site (fig. 2a), the green-reticulated models (i.e., exotic) were the most frequently attacked (18.9%), followed by the brown (12.7%) and the yellow-striped (i.e., local; 8.2%) models.

The changes in attack frequency on the different models over time are illustrated in figure 2b. At both sites, the attack rate on the local aposematic signal was low and did not significantly change during the 72-h trial ($\chi^2 \leq 3.828$; $P \geq .148$). However, for both the exotic aposematic signal and the brown model, attack frequency significantly varied ($\chi^2 \geq 11.493$; $P \leq .003$); at both sites, the majority of attacks occurred during the first 24 h of the trial (FT ≥ 2.302 ; $P < .05$ at both sites) and quickly decreased, before stabilizing between 24 and 72 h (fig. 2b; table 1). As such, while the difference in predation rates between the three types of clay model is highly significant after 24

h ($\chi^2 \geq 21.261$; $P < .001$), it decreases to a similar level after 72 h ($\chi^2 \leq 3.742$; $P > .154$; table 1).

Discussion

Our results demonstrate the ability of adjacent but distinct predator communities to discriminate between different conspicuous signals. The clay models displaying the local combination of color and pattern experienced fewer predation attempts in each habitat. Since the local aposematic signal present at the first site is exotic at the second site and vice versa, our results both validate that the strong homogenizing selection performed by predators can be geographically localized and emphasize the selective advantage of carrying the right conspicuous signal.

Clay models with the exotic aposematic phenotype, on

Table 1: Test of Freeman-Tukey deviates in individual cells of contingency tables with the number of avian attacks for each site over time for each model phenotype and for each model phenotype at every 24-h observation

	Site 1		Site 2	
	Attacked	Unattacked	Attacked	Unattacked
By model phenotype:				
Green-reticulated model:				
24 h	a	a	3.92	-1.28
48 h	a	a	-2.39	.56
72 h	a	a	-4.82	.87
Yellow-striped model:				
24 h	4.24	-1.635	a	a
48 h	-3.08	.82	a	a
72 h	-4.52	1.05	a	a
Brown model:				
24 h	4.12	-1.11	2.30	-.52
48 h	-4.06	-.61	-1.74	.34
72 h	-3.99	-.60	-1.23	.26
By observation time:				
After 24 h:				
Green-reticulated model	-5.19	1.35	2.97	-1.02
Yellow-striped model	3.52	-1.39	-3.21	.81
Brown model	.23	-.04	-.55	.19
After 48 h:				
Green-reticulated model	-.14	.05	a	a
Yellow-striped model	1.67	-.24	a	a
Brown model	-1.75	.21	a	a
After 72 h:				
Green-reticulated model	a	a	a	a
Yellow-striped model	a	a	a	a
Brown model	a	a	a	a

Note: Absolute values larger than the criterion with Bonferroni correction for six simultaneous tests (1.52) are in bold. These values identify the cells for which the number of observations significantly ($P < .05$) differs (is either higher or lower, as shown by the sign) from the corresponding expected frequencies.

^a Contingency tables for which the overall null hypothesis of complete independence of observations was not rejected.

the other hand, experienced more attacks than those displaying the brown phenotype and up to four times more attacks than those harboring the local warning signal. These differences in predation rates are most likely explained by the geographically adjacent exotic combination of vivid colors and patterns being easily detected by predators but not initially recognized as being aposematic. As such, these unrecognized phenotypes are at a great selective disadvantage, as they lack the protection conferred by crypsis (Mallet and Singer 1987; Mallet and Joron 1999) and, due to their conspicuousness, are more easily detected by naïve predators. A similar selection against exotic warning coloration has been demonstrated in *Heliconius* butterflies (Benson 1971; Mallet and Barton 1989; Mallet et al. 1990; Kapan 2001).

Avian predators have been shown to possess the relevant memory pattern to perform such a strong and directed selection (Langham 2004; Ihalainen et al. 2008). Indeed, marks left on clay models indicate that selection pressure on the aposematic signals was mostly performed by avian predators, which are known to be common predators of frogs in the tropics (Stiles and Skutch 1989; Poulin et al. 2001; Saporito et al. 2007; Noonan and Comeault 2008). Moreover, a difference in the predation rate according to phenotype was apparent only on models attacked by birds. Birds, which are known for their ability to differentiate colors (Poulin et al. 2001), appear to be the main predators performing selection on visual aposematic signals. This confirms that the inferior number of attacks on the local conspicuous signal is the result of avoidance (Saporito et al. 2007; Noonan and Comeault 2009).

Unknown assailants accounted for the rest of the attacks on the models. While it is possible that some of these attacks were caused by birds, we also documented puncture marks likely left by snakes or spiders (Saporito et al. 2007). In other similar studies, attacks by rodents (i.e., incisor bite marks) usually accounted for a significant proportion of the marks left on the models (Brodie 1993; Kuchta 2005; Saporito et al. 2007; Noonan and Comeault 2009). The absence of attacks in this study by rodents, which usually leave easily recognizable marks, is most likely the result of placing the clay models on understory leaves, which made them less accessible to roaming terrestrial rodents and more easily detected by avian predators.

While the clay models used in our experiments lacked the toxicity and natural behavior of live *Ranitomeya imitator*, the changes in predation rate over time appear to be consistent with the expectations that the discriminative behavior of predators is the result of learned avoidance. At both sites, the majority of attacks recorded on the non-profitable models harboring the exotic aposematic signal occurred during the first 24 h and quickly decreased to

nearly nil after 48–72 h. Similar observations have been reported for live aposematic *Heliconius* butterflies, whereby predators were less likely to attack individuals after having sampled a few unpalatable prey of the same phenotype (Langham 2004; Rowland et al. 2007; Mallet 2010). A similar trend was found with the brown models being attacked significantly more often during the first 24 h of this experiment. Although these models were built to resemble nontoxic frogs that are normally well camouflaged in leaf litter or on tree bark, they did not benefit from their usual cryptic appearance since they were placed on green understory leaves; this explains the high number of attacks observed. The decrease in attack rate is consistent with avian predators having the ability to learn to recognize and subsequently avoid novel nonprofitable prey items, as is expected for aposematism (Ruxton et al. 2004; Sherratt 2008).

It is interesting to note that the rate of attack on the local aposematic signal, while low, did not significantly change over time and is consistent with the expectation that the predator community has already learned to recognize that signal (Pinheiro 2003; Langham 2004; Ihalainen et al. 2008). However, despite being low, models with the local aposematic signal did experience predation attempts. In the absence of innate avoidance, many hypotheses have been suggested to explain this incomplete avoidance such as predator error (Lynn 2005), the presence of naïve predators (Saporito et al. 2007), forgetting (Speed 2000), ongoing learning (Noonan and Comeault 2009), and continued testing (Beatty et al. 2004; Noonan and Comeault 2009).

Regardless of an apparent rapid learning, selection on unrecognized (i.e., exotic or novel) signals by predators can be intense. Mathematical models and empirical data have shown that predators sample a fixed number of unpalatable prey that is independent of the prey's density before the predators learn to reject them (Müller 1878; Ruxton et al. 2004; Sherratt 2006; Rowland et al. 2007; Mallet 2010). Consequently, the more abundant a signal, the lower the per capita mortality will be; hence, the rare aposematic signals will experience greater mortality (Greenwood et al. 1989; Kapan 2001; Lindstrom et al. 2001; Ihalainen et al. 2008). As such, if individuals with novel aposematic signals appear in small numbers in a population, either because of migration or due to mutations, the rapid selection performed by predators will most likely prevent the spread of the exotic alleles underlying these phenotypic novelties within the population. Under this scenario, phenotypically distinct populations experiencing purifying selection pressures are expected to be highly isolated from each other. These conclusions are in accordance with research on mimetic *Heliconius* butterflies, which has demonstrated that selection across pop-

ulations in the context of aposematism and Müllerian mimicry can promote population divergence and even speciation (Jiggins et al. 2001).

Ranitomeya imitator is known to be involved in Müllerian mimicry with up to four species of *Ranitomeya*, and it displays a similar level of phenotypic variability among populations. While the directionality of the mimetic relationship is unknown (Chouteau et al. 2011), the intense selection performed by predators appears to explain the homogenization of warning signals at a local scale as well as the maintenance of the geographic organization of aposematic signals between localities. Such selection contradicts early views on mimicry, suggesting that convergence of conspicuous coloration is an adaptation to the nonbiotic environment (Grobman 1978).

In conclusion, we have empirically confirmed that avian predators can recognize and avoid distinct aposematic signals at different sites while performing intense selection on the novel phenotypes, possibly as a result of learning experience. This selective predation between close geographical populations is consistent with theoretical models explaining the maintenance of a geographic organization of aposematic signals, as any migrant or offspring deviating from the predators' recognized warning signal will most certainly experience an increased risk of mortality.

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Cloud forests of the Cordillera Escalera, Peru, home to many poison dart frogs. Photograph by Mathieu Chouteau.