



# Teasing apart crypsis and aposematism – evidence that disruptive coloration reduces predation on a noxious toad

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Both cryptic and aposematic colour patterns can reduce predation risk to prey. These distinct strategies may not be mutually exclusive, because the impact of prey coloration depends on a predator's sensory system and cognition and on the environmental background. Determining whether prey signals are cryptic or aposematic is a prerequisite for understanding the ecological and evolutionary implications of predator–prey interactions. This study investigates whether coloration and pattern in an exceptionally polymorphic toad, *Rhinella alata*, from Barro Colorado Island, Panama reduces predation via background matching, disruptive coloration, and/or aposematic signaling. When clay model replicas of *R. alata* were placed on leaf litter, the model's dorsal pattern – but not its colour – affected attack rates by birds. When models were placed on white paper, patterned and un-patterned replicas had similar attack rates by birds. These results indicate that dorsal patterns in *R. alata* are functionally cryptic and emphasize the potential effectiveness of disruptive coloration in a vertebrate taxon. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, 00, 000–000.

**ADDITIONAL KEYWORDS:** aposematic – background matching – Barro Colorado Island – *Bufo typhonius* – camouflage – cryptic coloration – predation – predator – prey – *Rhinella margaritifera*.

## INTRODUCTION

Coloration of cryptic organisms prevents or reduces their exposure to predators by a variety of mechanisms (Ruxton, Sherratt & Speed, 2004), but two main strategies are background matching and disruptive coloration. In background matching, dorsal markings that match the colour and pattern of substrates reduce detection of prey by predators, whereas in disruptive coloration, contrasting patterns and false edges break up the outline of the prey's body shape and hinder recognition by predators (Stevens & Merilaita, 2009). In some instances, disruptive coloration may affect recognition but not detection, such that predators may be able to distinguish prey from the background but are unable to recognize prey for what they actually are (Stevens *et al.*, 2006). Therefore, disruptive coloration may provide cryptic protection even when prey are appar-

ently conspicuous. For instance, prey may benefit from disruptive coloration in scenarios where they are unable to background match (Schaefer & Stobbe, 2006; Stevens *et al.*, 2006). Alternatively, bright colour patterns may represent sexual signals for conspecifics but disruptive signals for predators (Toledo & Haddad, 2009). Finally, conspicuous colour patterns may represent aposematic signals for predators with colour vision, but disruptive coloration for colour blind predators (Brodie & Tumbarello, 1978; Brodie, 1993a; Brodie & Janzen, 1995; Wüster *et al.*, 2004; Toledo & Haddad, 2009). Distinguishing between background matching and disruptive coloration can be challenging, especially since both processes can occur synergistically to maximize crypsis (Stevens & Cuthill, 2006). However, background matching predicts that both colour and pattern are important for reducing predation, while disruptive coloration predicts that pattern but not necessarily colour is important. Although the concept of disruptive coloration has been considered a widespread

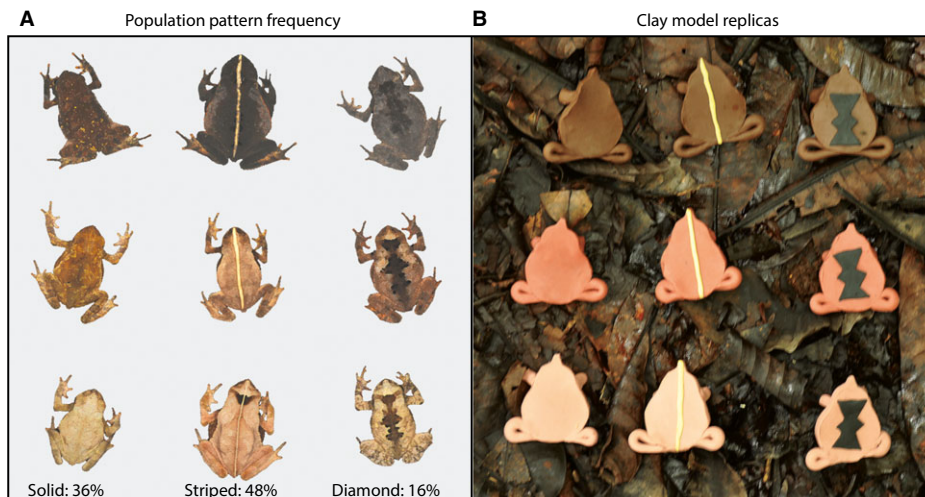
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anti-predator defence for over a century (Thayer, 1909; Cott, 1940; Ruxton *et al.*, 2004), its effectiveness has been demonstrated experimentally only within the last decade (Cuthill *et al.*, 2005; Stevens & Cuthill, 2006; Fraser *et al.*, 2007; Cuthill & Székely, 2009).

In contrast to crypsis, aposematism involves a conspicuous appearance that advertises chemical or structural defences of prey, leading to innate or learned predator avoidance (Ruxton *et al.*, 2004; Fraser *et al.*, 2007). Although bright and conspicuous coloration may promote the evolution of aposematic signals (Saporito *et al.*, 2007; Noonan & Comeault, 2009), it is not necessarily required. Aposematism may occur if predators can associate dull but characteristic prey phenotypes with a prey's defence (Sheratt & Beatty, 2003; Wüster *et al.*, 2004; Niskanen & Mappes, 2005). Although aposematism and crypsis appear to represent opposite strategies for reducing predation, they may not be mutually exclusive – presumed cryptic patterns may function as aposematic signals (Wüster *et al.*, 2004; Niskanen & Mappes, 2005), and vice versa (Brodie & Tumbarello, 1978), depending on the predator sensory system and on the background (Stevens, 2007). For instance, bright patterning may represent an aposematic signal towards avian predators with colour vision, but function as cryptic coloration towards colour-blind predators. Furthermore, colour patterns may combine crypsis and aposematism in a distance-dependent fashion, such that animals are cryptic from a distance but aposematic at close proximities (Tullberg, Merilaita & Wiklund, 2005).

The goal of this study is to determine whether specific dorsal colours and/or patterns reduce predation on a leaf litter toad, *Rhinella alata* (formally

*Bufo typhonius*; *Rhinella margaritifera*). This species is a diurnal, sit-and-wait forager and has a remarkable polymorphism in colour and pattern that is generally assumed to represent cryptic coloration (Fig. 1A). When attacked, *Rhinella* toads excrete parotoid secretions containing steroids such as bufogenines and bufotoxins (Toledo & Jared, 1995; Jared *et al.*, 2009). These steroids can affect vertebrates such as snakes and mammals and may cause cardiac abnormalities, localized paralysis, convulsions, and even death (Sciani *et al.*, 2013). Little information is known about the predators of *R. alata*, but snakes likely represent a primary predator (e.g. *Liophis* sp.; Kollartis *et al.*, 2013). White-nosed coatis (*Nasua narica*) occasionally eat cane toads (*R. marinus*; Gomppert, 1996) and are able to remove toxic secretions from prey by rolling them in the dirt (Sazima & Caramaschi, 1986; Jared *et al.*, 2009), and therefore may be able to consume *R. alata* despite its chemical defence. *Rhinella alata* is unpalatable to bats (Page *et al.*, 2012), and despite being an abundant leaf litter anuran in Panama it is not eaten by birds (Poulin *et al.*, 2001). It is unclear whether birds avoid attacking *R. alata* entirely, or whether attacks are abandoned following exposure to secondary chemical defences. In order to understand the evolutionary ecology of predator–prey dynamics in this system it is necessary to determine whether *R. alata* coloration functions as a cryptic signal, an aposematic signal, or both. Here I manipulate the colour and pattern of clay model replicas of *R. alata* and then determine whether and how different colours and patterns affect attack rates of visually oriented avian predators. Next, I tease apart three competing, but not mutually exclusive, hypotheses – that predation is reduced via: (1) background



**Figure 1.** A, Representative *R. margaritifera* phenotypes. Population frequencies grouped by pattern based on samples of 153 wild-caught individuals. B, Clay model replicas used in the study.

matching, (2) disruptive coloration, and/or (3) aposematic signaling.

## MATERIAL AND METHODS

### CLAY MODEL REPLICAS

*Rhinella alata* is represented by a variety of colour/pattern phenotypes that are found on Barro Colorado Island (BCI), Panama. I made models from non-hardening clay (Sargent Art) that represent the range of toad colours ('light', 'medium', and 'dark' brown) and each of three dorsal patterns ('solid', 'striped', and 'diamond') (Fig. 1). Clay model replicas provide an attack record in the plasticine body and have been widely used in a variety of field studies to model snakes (Brodie, 1993a), frogs (Saporito *et al.*, 2007), mice (Vignieri, Larson & Hoekstra, 2010), and butterflies (Ihalainen & Lindstedt, 2012). Clay models were not designed to match all toad phenotypes perfectly, but instead were designed to mimic a subset of the most common phenotypes (e.g. one rare *R. alata* phenotype has both a 'stripe' and a 'diamond', but was not represented in this study).

I matched clay colours by eye with the goal of representing the extremes and middle of the *R. alata* colour continuum. I estimated reflectance spectra from standardized photographs (Stevens *et al.*, 2007) of wild-caught toads and from clay models using the software program ColourWorker (v2.0). ColourWorker uses a reference library of real reflectance spectra to estimate reflectance spectra (400–700 nm) from digital photographs. To create the reference library I used a photospectrometer (OceanOptics USB4000) and measured reflectance spectra for ten toads and the three clay colours. Neither *R. alata* nor the toads reflected in the UV range. Reflection estimates from ColourWorker between the wavelengths 400–450 nm were highly variable, so these estimates were removed.

### MODELING AVIAN PERCEPTION

To determine how well clay colour matched toad colour and to determine the variation in toad coloration, I quantified colour differences in avian perception. I implemented the blue-tit model of avian vision using the R-package 'pavo' to model avian perception of both clay and toads (Maia, Eliason & Bitton, 2013b; Maia *et al.*, 2013a). To determine degree of variation in colour and degree of overlap between toads and clay I projected the clay and toad reflectance spectra into avian UV tetrahedral colour space (Maia *et al.*, 2013a). To determine whether or not different colours of clay and toads are perceived differently, I calculated achromatic colour contrasts between all

types of clay and all toads. Achromatic colour contrast is thought to be important for avian discrimination of objects (Kelber, Vorobyev & Osorio, 2003). Colour contrasts are reports in 'just-noticeable-differences' (JND). Two stimuli with  $JND < 1$  are considered indistinguishable, with stimuli becoming increasingly distinguishable as JND increases above 1 (Siddiqi *et al.*, 2004; Stoddard & Stevens, 2011). Here I use the following interpretations for JND of two stimuli: indistinguishable when  $JND < 1$ ; barely distinguishable when  $1 \leq JND < 2$ ; and easily distinguishable when  $2 \leq JND$ .

### LEAF LITTER EXPERIMENT

In the first experiment, 36 clay models (four each of nine morphs) were randomly ordered and placed on the leaf litter 5 m apart along 45 transects. Transects were placed perpendicular to trails and were separated from each other by 200 m. Models were retrieved after 72 h, scored for attack incident, and then repaired or replaced before re-deployment. Attack incidence was determined for 1620 models deployed on natural leaf litter. Reduced attack rates on one morph relative to another morph indicate whether the dorsal colour or pattern represents an anti-predator strategy, but do not differentiate between cryptic or aposematic mechanisms.

### WHITE PAPER EXPERIMENT

In the second experiment, models were deployed following the same protocol but were placed on  $8.5 \times 11.0$ " white paper along 28 transects. Attack incidence was determined for 1,008 models deployed on white paper. On white paper, all morphs should be equally visible to predators. Following Brodie (1993a), crypsis is suggested when models have low attack rates on leaf litter but high attack rates on paper, whereas aposematism is suggested when models have low attack rates on both backgrounds (also see Brodie & Janzen, 1995; Niskanen & Mappes, 2005; Noonan & Comeault, 2009). An assumption of this method is that any effect of the white paper treatment (e.g. predator neophobia) is consistent across cryptic and aposematic strategies.

### PHENOTYPE ABUNDANCE OF *R. ALATA*

Predator search image and density-dependent predation rates may account for fluctuations in the abundances of *R. alata* colour/pattern phenotypes in nature and influence attack rates on clay models (Endler, 1988; Ruxton *et al.*, 2004). To verify that attack rates on different models were not related to predator search image for abundant *R. alata*



phenotypes, I collected toads opportunistically along the experimental transects and along BCI trails. Toads were detected after they hopped away from my walking path, making it unlikely that sampling was biased towards more conspicuous phenotypes. Individuals were photographed in standardized light conditions with a colour standard (MacBeth Colour Checker) and scored for pattern phenotype and released. ‘Solid’ toads were those without dark triangular marking (i.e. no diamonds) or strong mid-dorsolateral stripes. ‘Striped’ toads were those with easily distinguishable mid-dorsolateral line, and ‘diamond’ toads were those with dark triangular shapes on their backs.

#### STATISTICAL ANALYSIS

Recovered models were assessed for ‘bird’, ‘mammal’, and ‘unknown’ attacks; unrecovered models (< 2%) were eliminated from analysis. Models with deep U- or V-shaped marks were attributed to birds, whereas those with incisor marks were attributed to mammals (Brodie, 1993a). To determine whether ‘colour’ and/or ‘pattern’ were predictors of attack rates, I used a general linear mixed model (GLMM; *glmer* from the *lme4* package in R; Bates *et al.*, 2014) with a binomial error distribution and *logit* link term. ‘Colour’, ‘pattern’, and the interaction between ‘colour’/‘pattern’ were treated as fixed effects with ‘transect’ and treated as a random effect in all models. Model selection was conducted using AIC values. I calculated *P*-values for GLMMs using a log-likelihood ratio test to indicate whether a statistical model was significantly better than a null model where attack incidence is constant among morphs. After selecting the best-fit model, I used a modified Tukey test using *glht* in the R-package *multcomp* (Torsten, Bretz & Westfall, 2008; Torsten *et al.*, 2015) to compare attack rate among patterns and among colours. Leaf litter and white paper experiments were analyzed separately and then compared to each other. Direct comparisons of attack rates between the two experiments may not be realistic because white paper background may elicit a predator response on its own such that ‘suspicious’ predators avoid the experiment all together (Saporito *et al.*, 2007). While absolute attack rates may differ between ‘leaf litter’ and ‘white paper’ experiments, the relative attack rates should remain the same between experiments for aposematic signals but not for cryptic signals (Brodie, 1993a; Saporito *et al.*, 2007). Finally, I compared the proportion of pattern phenotypes observed in nature to the proportion of morphs attacked in the leaf litter experiment with a chi-squared test. All statistical analyses were performed in R version 2.12.

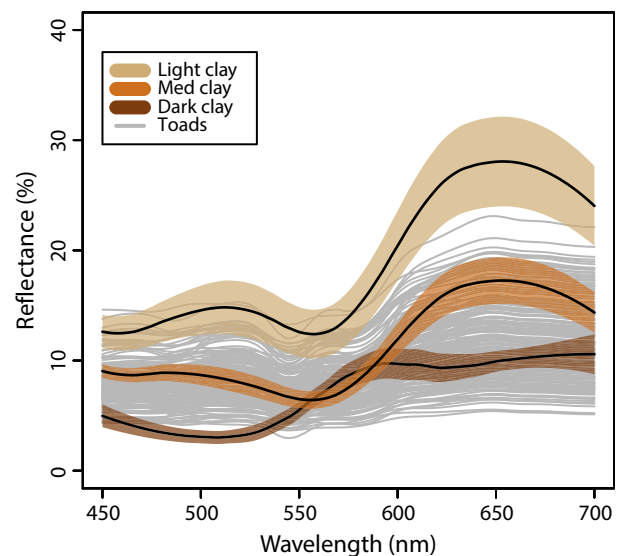
## RESULTS

### AVIAN PERCEPTION

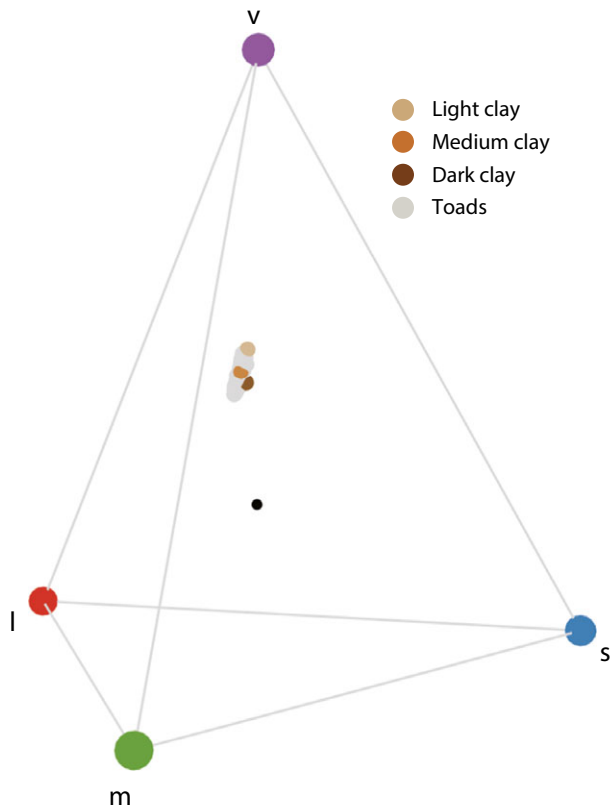
Even though toad coloration was best represented by a colour continuum (Figs 2, 3), there was substantial variation in avian perception of real toads. No toad was found indistinguishable from all other toads (Fig. 4A). Instead, any given toad was considered indistinguishable, barely, or easily distinguishable from its conspecifics depending on the individual comparison, indicating that there are perceivable differences in wild toads on which selection may act. Birds were able to easily distinguish between clay colours as well (Fig. 4B), indicating that ‘light’, ‘medium’, and ‘dark’ clay models were perceived differently by avian predators. ‘Medium’ and ‘dark’ clay overlapped with toad reflectance spectra (Fig. 2) and was indistinguishable from many real toads (Fig. 4C). ‘Light’ clay was substantially brighter than most spectra for real toads (Fig. 2) and was only indistinguishable and barely indistinguishable from just two real toads (Fig. 4C), indicating that ‘light’ clay represented an extreme (but still realistic) coloration.

### ATTACK RATES ON CLAY MODELS

Out of 1620 models deployed in the leaf litter experiment, 333 (20%) were attacked and 29 (< 2%) were not recovered. More of the attacks were attributable to birds (185 attacks, 56% of total attacked) than to



**Figure 2.** Estimated median reflectance spectra for light, medium, and dark clay models (bold lines  $\pm$  SE), and for wild-caught individuals (thin grey lines,  $N = 153$ ). The 95% confidence intervals for 400–450 nm varied widely so these wavelengths were removed.



**Figure 3.** Colour loci in the tetrahedral model for avian VS vision. Vertices represent maximal excitation of the violet (v), blue (s), green (m), and red (l) photoreceptors of VS vision. The black point represents equal excitation of each photoreceptor.

mammals (73 attacks, 22%) or to unknown predators (75 attacks, 22%). For predicting avian attack rates, the statistical model with ‘pattern’ had the best AIC value, and the models with ‘pattern’ ( $P < 0.01$ ) and ‘pattern and colour’ ( $P = 0.02$ ) outperformed the null model for predation, while the models with ‘colour’ ( $P = 0.35$ ) and the interaction between ‘colour’ and ‘pattern’ ( $P = 0.08$ ) were not significantly better than the null model (Table 1). When placed on leaf litter, ‘solid’ morphs had higher avian attack rates than did ‘diamond’ ( $P = 0.015$ ) or ‘striped’ morphs ( $P = 0.032$ ) and there was no significant difference in avian attack rate between ‘diamond’ and ‘striped’ morphs ( $P < 1.0$ ) (Fig. 5A). ‘Colour’ and/or ‘pattern’ were not associated with mammal or unknown predator attack rate, indicating that these predators attacked all models equally regardless of colour or pattern (Supporting Information, Tables S1, S2). In the second experiment (1008 models on white paper), 164 (16%) models were attacked and 30 (3%) were not recovered. Neither ‘colour’ nor ‘pattern’ nor their interaction predicted attack rate from birds (Table 1

and Fig. 5B,D), mammals (Supporting Information, Table S1), or unknown attackers (Supporting Information, Table S2).

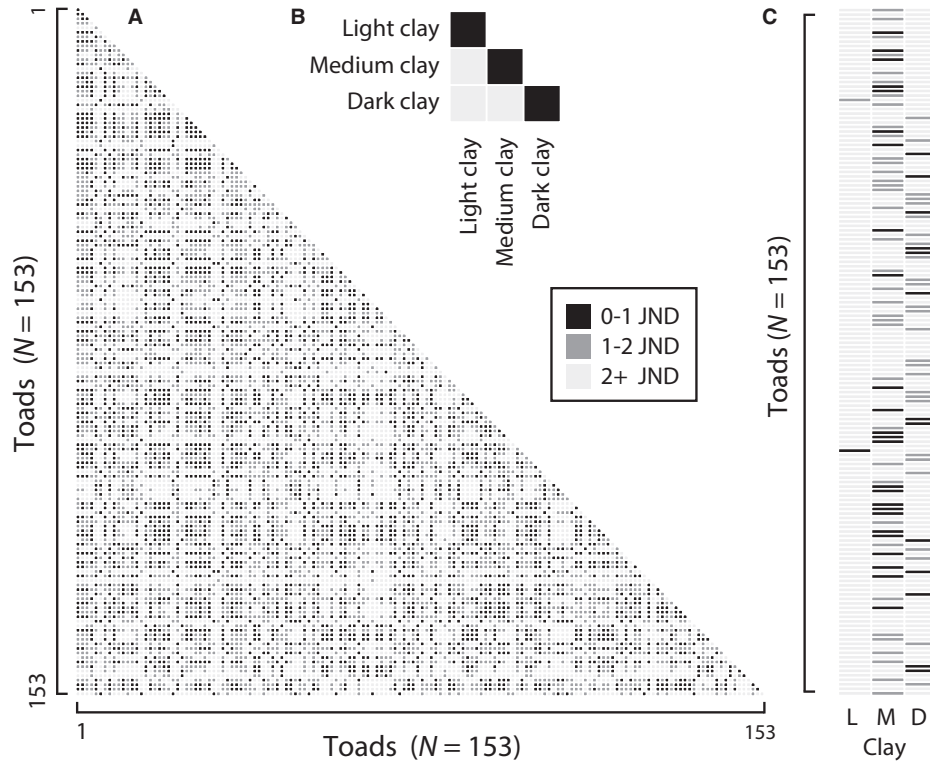
#### PHENOTYPE ABUNDANCE OF *R. ALATA*

When grouped by pattern, the proportion of wild-caught pattern phenotypes (Fig. 1A) differed from the proportion of clay models that were attacked by birds on leaf litter (Fig. 5A) ( $\chi^2$ : 9.92, d.f.: 2,  $P < 0.001$ ).

#### DISCUSSION

These data support the hypothesis that dorsal patterns in *R. alata* represent a cryptic anti-predator strategy that is best characterized by disruptive coloration. When placed on leaf litter, ‘striped’ and ‘diamond’ patterned models receive fewer avian attacks than do ‘solid’ models, and this trend disappears when clay models are placed on white paper. Following Brodie (1993a) and others (Brodie & Janzen, 1995; Niskanen & Mappes, 2005; Noonan & Comeault, 2009), this result indicates that reduced avian attacks on patterned models is due to a cryptic strategy, and not aposematic signaling. Furthermore, patterns function as disruptive coloration and not background matching because patterned models experienced fewer avian attacks regardless of clay colour. If background colour matching were a significant factor for reducing avian attacks in this system, then inconspicuous models should experience fewer attacks than conspicuous models. Conspicuousness depends on both the colour of the model and the substrate. While the colour of leaf litter substrate can be highly heterogeneous, ‘dark brown’ clay models were inconspicuous and ‘light brown’ clay models were conspicuous against the leaf litter because this study took place during the wet season when the substrate was predominantly dark, muddy, and decomposing (Fig. 1B). Despite being perceived differently (Fig. 4) and having varying degrees of conspicuousness against the leaf litter (Fig. 1B), birds attacked all colours equally (Fig. 5), indicating that birds were able to find models regardless of the degree to which a model matched the substrate. Therefore, these results best fit a model of disruptive coloration, and are consistent with previous findings that disruptive coloration can reduce predation even when prey colours are conspicuous against their background (Schaefer & Stobbe, 2006; Stevens *et al.*, 2006).

Although these results demonstrate the colours used herein (and therefore degree of matching) do not predict bird attack rates, they cannot rule out a potential role of background matching in real toads.



**Figure 4.** Just noticeable differences (JNDs) in achromatic avian vision for (A) toads and toads; (B) clay and clay; and (C) toads and clay. Two objects with  $JND < 1$  are considered indistinguishable in colour. JNDs between 1 and 2 are considered barely distinguishable, and JNDs  $> 2$  are easily distinguishable.

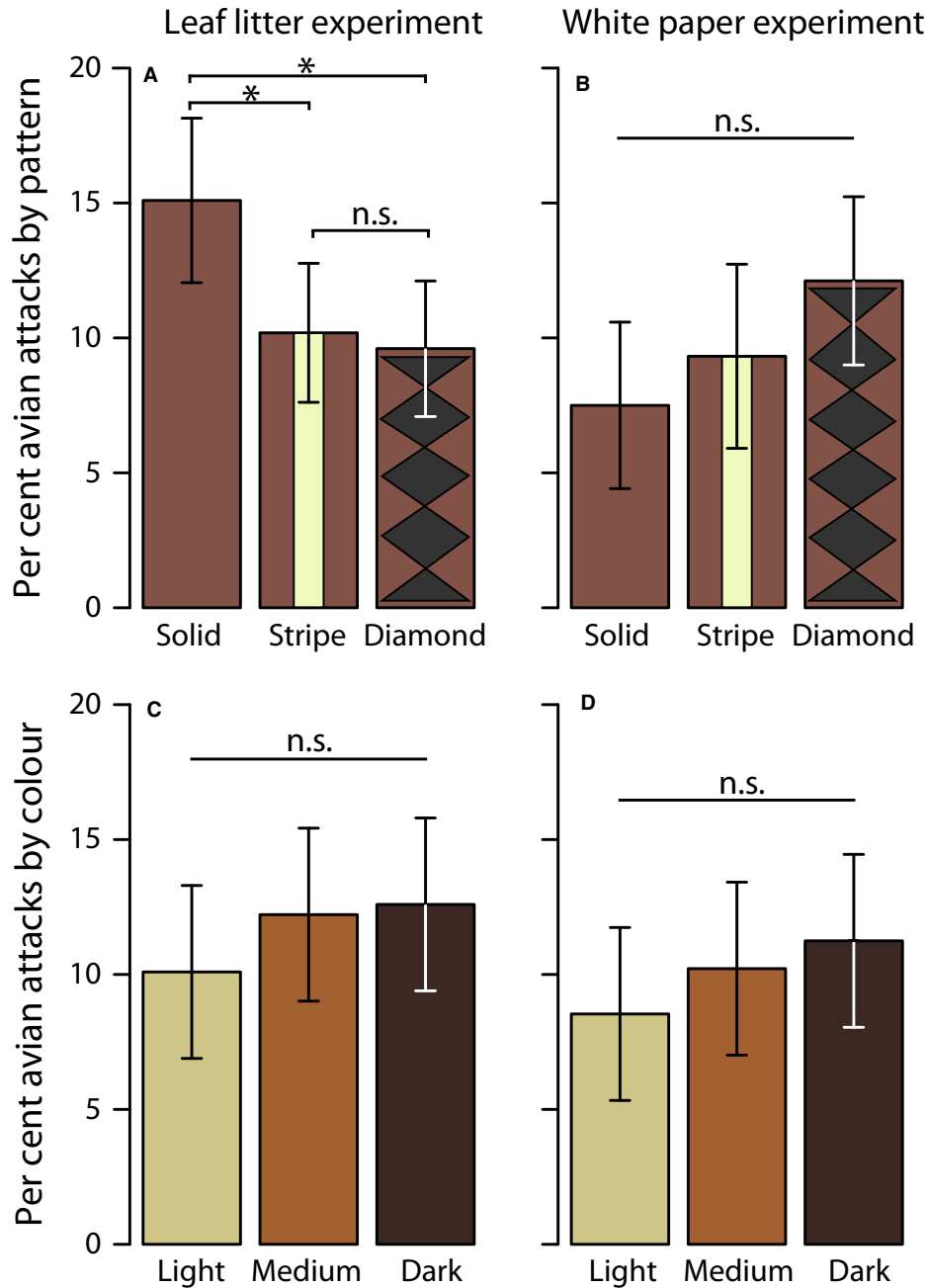
It is difficult to construct clay models that perfectly mimic the subtle texturing and blending that may be necessary for effective background matching in real toads. For real toads, subtle dorsal patterning on ‘solid’ morphs may enable successful background matching, leading to decreased predation on ‘solid’ phenotypes as well. While this experiment shows that coloration (and by extension conspicuousness) does not predict avian attack rates, we cannot reject the hypothesis that background matching may function in real toads to reduce avian attacks in the wild. Furthermore, in real toads, background matching would likely work synergistically with disruptive coloration to further reduce bird predation on patterned phenotypes (Fraser *et al.*, 2007). Since background matching depends on the characteristics of the substrate where the prey is located, its effectiveness may be compromised by spatial or seasonal habitat heterogeneity. Therefore, one advantage of disruptive coloration over background matching may be that patterned individuals can utilize habitats where crypsis via background matching is compromised (Ruxton *et al.*, 2004).

Apostatic selection, a type of negative frequency-dependent selection on colour pattern due to predators,

**Table 1.** Model selection for avian attacks on clay models during leaf litter and white paper experiments

Model terms	AIC	$\Delta_i$	$w_i$	$P$
Leaf litter experiment				
Pattern	<b>1115.0</b>	<b>0</b>	<b>0.66</b>	<b>&lt; 0.01</b>
Pattern + colour	1116.8	1.8	0.26	0.02
Null	1120.6	5.6	0.04	–
Pattern $\times$ colour	1122.5	7.5	0.01	0.08
Colour	1122.5	7.5	0.01	0.35
White paper experiment				
Null	<b>869.45</b>	<b>0</b>	<b>0.56</b>	–
Pattern	871.07	1.62	0.25	0.30
Colour	872.44	2.99	0.13	0.60
Pattern + colour	874.05	4.6	0.06	0.49
Pattern $\times$ colour	881.14	11.69	< 0.01	0.82

For each model I report the AIC, differential AIC ( $\Delta_i$ ), and the Akaike weight ( $w_i$ ). The Akaike weight can be interpreted as the likelihood for a particular model. The  $P$ -values ( $\alpha < 0.05$ ) indicate which models are significantly better than the null model where pattern and/or colour does not affect attacks on clay models. Bold value indicates best/significant model.



**Figure 5.** Avian attack rates in leaf litter experiment analyzed by (A) pattern and (C) colour. Avian attack rates in white paper experiment analyzed by (B) pattern and (D) colour. Horizontal bars indicate significant differences, where  $P$ -values of  $\alpha < 0.05$  are indicated by ‘\*’, and  $P$ -values of  $\alpha > 0.05$  are indicated by ‘n.s.’ Error bars represent 95% confidence intervals.

has long been considered an important mechanism for maintaining exuberant prey polymorphisms (Endler, 1988). When prey phenotypes vary in their degree of crypsis, apostatic selection alone may not promote prey polymorphism because selection should favor the most cryptic phenotypes (Franks & Oxford, 2011). However, dietary wariness – where predators

are unlikely to eat novel or uncommon prey phenotype – is an important and often unrecognized factor that can generate and maintain prey polymorphisms even when novel prey phenotypes are more conspicuous (Franks & Oxford, 2009, 2011). If ‘solid’ phenotypes are heavily predated and become rare, predators should switch their search image to more



abundant ‘striped’ or ‘diamond’ morphs. Under strict apostatic selection, ‘solid’ phenotypes would still be predated and potentially eliminated because they are more conspicuous. Therefore, dietary wariness may be an important factor in generating the observed polymorphism in *R. alata* because dietary wariness would enable the more conspicuous phenotype (i.e. ‘solid’) to bounce back from low abundances, which would be unlikely under a scenario of strict apostatic selection (Franks & Oxford, 2011). While a rigorous test of apostatic selection and dietary wariness is beyond the scope of this paper, as such a test would require repeated sampling over time (e.g. Ihalainen & Lindstedt, 2012) and space (e.g. Comeault & Noonan, 2011) to capture fluctuations in predation rates, it is unlikely to explain the differences in attack rate seen here. If the attack rates were simply due to predator search image and not variation in crypsis, then attack rates on different clay model morphs should be roughly proportional to the abundance of real toad phenotypes in the field. Instead, attacks were highest on ‘solid’ models even though ‘striped’ toads were the most abundant phenotype found in nature. The proportion of attacked models was significantly different than the proportion of toads observed in nature ( $P < 0.0001$ ), indicating that the elevated attack rate on ‘solid’ clay models was unlikely to be related to predator search image for real ‘solid’ toad phenotypes. However, correlational selection on prey coloration and escape behaviour can lead to intraspecific differences in anti-predator behaviour (Brodie, 1992, 1993b; Forsman & Appelqvist, 1998). Cryptic phenotypes may perceive predators as less threatening than more conspicuous phenotypes, and therefore be less likely to flee (Stankowich & Blumstein, 2005). In this study, I captured toads along transects as they hopped away from me. Therefore, field sampling for ‘striped’ and ‘diamond’ toads may have been underrepresented if those phenotypes are less likely to flee from potential predators than ‘solid’ phenotypes. Despite this potential sampling bias I found more ‘striped’ phenotypes than I did ‘solid’ phenotypes, which is not consistent with the elevated attack rate on ‘solid’ morphs due to a predator search image for ‘solid’ phenotypes.

Prior field experiments used clay models to evaluate aposematic warning coloration in frogs (Saporito *et al.*, 2007; Noonan & Comeault, 2009) and snakes (Brodie, 1993a; Wüster *et al.*, 2004; Niskanen & Mappes, 2005), but this present study uses clay models to evaluate the effectiveness of disruptive coloration for reducing predation by free-ranging predators in the field. That *R. alata* has disruptive coloration and chemical defence may be explained in a few ways. First, *R. alata* may depend on crypsis as a primary defence for avoiding detection by visual

predators (e.g. birds) and chemical defence as a secondary deterrent following detection. Since *R. alata* coloration is apparently not conducive for aposematic signaling, individuals should maximize crypsis because Panamanian birds eat a significant amount of leaf litter anurans (Poulin *et al.*, 2001). Following detection, secondary chemical defences could cause avian predators to reject *R. alata* as a prey item. Second, *R. alata* may use disruptive coloration to reduce detection from visual predators and chemical defence to protect from non-visual predators (e.g. snakes, bats, other mammals). Many mammals rely primarily on olfactory cues and secondarily on visual cues to find prey (e.g. coati – Hirsch, 2010). While this hypothesis is technically supported by the data – attack rates from mammalian and ‘other’ predators were not predicted by colour and pattern (Supporting Information, Tables S1, S2) – the result is likely misleading because predators using olfactory or chemical cues were sensing novel clay scent and not on actual prey items. Finally, coloration and defensive strategy may be under correlational selection (Brodie, 1992, 1993b; Forsman & Appelqvist, 1998), highlighting the complex nature of predator–prey interactions. Despite an apparent selective disadvantage of being a ‘solid’ toad, these phenotypes could be maintained in the system if correlational selection alters escape behaviour or leads to an increased level of chemical defence in the more conspicuous phenotypes.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Table S1.** Model selection for rodent attacks on clay models during leaf litter and white paper experiments.

**Table S2.** Model selection for unknown attacks on clay models during leaf litter and white paper experiments.