Environment-dependent attack rates of cryptic and aposematic butterflies

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Abstract

Many organisms have evolved adaptive coloration that reduces their risk of predation. Cryptic coloration reduces the likelihood of detection/recognition by potential predators, while warning or aposematic coloration advertises unprofitability and thereby reduces the likelihood of attack. Although some studies show that aposematic coloration functions better at decreasing attack rate than crypsis, recent work has suggested and demonstrated that crypsis and aposematism are both successful strategies for avoiding predation. Furthermore, the visual environment (e.g., ambient lighting, background) affects the ability for predators to detect prey. We investigated these 2 related hypotheses using 2 well-known visually aposematic species of Heliconius butterflies, which occupy different habitats (open-canopy vs. closed-canopy), and one palatable, cryptic, generalist species Junonia coenia. We tested if the differently colored butterflies differ in attack rates by placing plasticine models of each of the 3 species in 2 different tropical habitats where the butterflies naturally occur: disturbed, open-canopy habitat and forested, closed-canopy habitat. The cryptic model had fewer attacks than one of the aposematic models. Predation rates differed between the 2 habitats, with the open habitat having much higher predation. However, we did not find an interaction between species and habitat type, which is perplexing due to the different aposematic phenotypes naturally occurring in different habitats. Our findings suggest that during the Panamanian dry season avian predation on perched butterflies is not a leading cause in habitat segregation between the 2 aposematic species and demonstrate that cryptically colored animals at rest may be better than aposematic prey at avoiding avian attacks in certain environments.

Key words: avian attacks, camouflage, Heliconius, Junonia, light environment, plasticine models, predation, warning coloration.

Many animals face high rates of predation in the wild and have evolved a diverse array of defenses to increase survival (Poulton 1890; Cott 1940; Ruxton et al. 2004; Stevens and Merilaita 2009). One adaptation to avoid predation is camouflage, in which a prey’s color pattern blends with that of the visual background (i.e., crypsis), rendering that individual difficult for potential predators to detect (Edmunds 1974; Endler 1984; Cuthill et al. 2005; Stevens and Merilaita 2011; Seymoure and Aiello 2015). Another common defensive adaptation is aposematism, in which the characteristics of potential prey animals that are potentially damaging to predators (e.g., stings, toxins, armor, etc.) are coupled with conspicuous signals to facilitate predator recognition of unprofitable prey (Wallace 1867; Poulton 1890; Ruxton et al. 2004). The functional benefits of both crypsis and aposematism are well documented (Endler 1981; Heiling et al. 2005; Mappes et al. 2005; Speed et al. 2010; Summers et al. 2015); however, comparisons between the 2 visual strategies are lacking (but see Carroll and Sherratt 2013).

Little is known about the differential fitness benefits between these 2 types of defensive coloration, crypsis and aposematism. Does aposematic coloration reduce predation better than crypsis due to

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mutual benefits to both the prey (i.e., survival) and predator (i.e., avoiding noxious characteristics; Papageorgis 1975; Guilford 1990; Guilford and Dawkins 1993; Mappes et al. 2005; Saporito et al. 2007)? Until recently there was no direct comparison of attack rates on cryptic and aposematic prey by wild predators in the field. Carroll and Sherratt (2013) used pastry baits with paper model wings and found that aposematic prey and cryptic prey had the same overall attack rates, but that aposematic prey were less fully consumed than cryptic prey. In other words, although the attack rate on aposematic prey and cryptic prey is similar, cryptic prey are more likely to be fully consumed, rather than bitten and released. Hence, there appear to be opportunities for aposematic, but not cryptic, prey to be taste-rejected by predators, leading to higher survival of aposematic prey (Wiklund and Jarvi 1982; Pinheiro 1996; Nokelainen et al. 2014).

The intensity of selection from visually hunting predators will not only be a function of unpalatability and predator cognition, but also how coloration and backgrounds are perceived by the visually hunting predators. Perception of prey depends upon several factors including the reflectance of the prey’s surface, the behavior of both prey and predator, the ambient lighting, transmission properties of the environment, and predator visual sensitivity (Endler 1990, 1993; Stevens 2013; Hutton et al. 2015). These various determinants of trait perception have led to the hypothesis that the nature of selection on cryptic and warning coloration will be different in disparate environments (Endler 1990, 1992; Stevens and Merilaita 2011). Camouflage depends on the ambient illumination and visual background; therefore, 1 phenotype may be cryptic in 1 set of conditions and very conspicuous in another (Endler and Greenwood 1988; Rojas 2014). Also, Douglas (2013) demonstrated that aposematic butterflies differ in coloration depending on the habitat in which they are found, with tropical understory butterflies exhibiting high achromatic contrast (i.e., black and white), while butterflies that occupy open habitats exhibited highly chromatic contrasts (e.g., yellow and red). However, no study to date has tested attack rates of naturally cryptic individuals and of aposematic species in different habitats. Different habitats should affect predation rates due to visibility of prey (e.g., dense forest vs. open fields), local abundance of predators, environmental effects on conspicuousness (i.e., lighting and visual background), as well as differences in prey abundance and predator experience with specific warning color patterns. Therefore, the environmental context must be considered when assessing the survival advantages of particular “conspicuous” aposematic and “inconspicuous” cryptic phenotypes.

Lepidoptera offer excellent opportunities to comparatively test the environmental factors that affect the adaptive value of crypsis and aposematism (Endler 1984; Nokelainen et al. 2014). Many Lepidoptera, such as the common buckeye butterfly Junonia coenia, are profitably prey with inconspicuous coloration when perched (Silbergled et al. 1979; Devries 1987; Pinheiro 1996; Camara 1997), whereas other species such as Heliconius butterflies sequester host plant toxins and display a conspicuous warning coloration (Chai 1986; Devries 1987). Both J. coenia and Heliconius butterflies occur in Panama (Brown 1981; Kozak et al. 2015). Unlike the palatable J. coenia, Heliconius butterflies contain cyanogenic glycoside toxins (Cardoso and Gilbert 2013), which combined with their conspicuous color patterns leads avian predators to avoid consuming them (Chai 1986; Finkbeiner et al. 2014; Langham 2005). Furthermore, Heliconius butterflies exhibit immense color diversity both within and between species and may have up to 5 different aposematic color patterns that are segregated by habitat in 1 forest (Papageorgis 1975; Devries 1987; Mallet and Gilbert 1995; Thurman and Seymour 2016). In the lowland rainforest of Panama, 2 aposematic coloration patterns are segregated by habitat, the Postman (yellow, red, and black; comprised of Heliconius mel- pompome and Heliconius erato) occurs in open-canopy, disturbed habitats and the Blue–white (blue, white, and black; comprised of Heliconius cydno and Heliconius sapho) occurs in closed-canopy, undisturbed forest (Estrada and Jiggins 2002). Therefore, these 2 different aposematic groups live in areas with different ambient illumination (brighter and broad spectrum in open-canopy, while darker and rich in green light in closed-canopy), as well as with different avian predators (Endler 1993). Due to the habitat segregation of these aposematic patterns, tests of environmental effects on the effectiveness of aposematic coloration are possible (Endler 1992).

Here, we utilized plasticine models of a cryptic species J. coenia, and the 2 species with aposematic color patterns (H. melpomene for the Postman mimicry ring and H. cydno for the Blue–white mimicry ring) to test 3 sets of hypotheses and predictions where both butterflies and educated predators naturally occur: 1) cryptic and aposematic individuals have evolved coloration to reduce predation and therefore will have similar attack rates; 2) the cryptic species has evolved to be undetected at rest and therefore the cryptic species will have similar attack rates across both habitats; and 3) the aposematic species’ warning signals are most effective in their respective habitats and therefore we predict that the Postman will be attacked less in open-canopy while Blue–white will be attacked less in closed-canopy habitats.

Materials and Methods

Model construction

We collected 3 males each of H. melpomene (Postman pattern), H. cydno (Blue–white pattern), and J. coenia in lowland rainforest habitats of central Panama in July 2012 using aerial nets. We then used these males to develop artificial models following the methods of Finkbeiner et al. (2012) and Seymour and Aiello (2015). The models were constructed using scanned images (Brother MFC-4510DN Scanner, Brother Industries, Nagoya, Japan) of ventral wing surfaces of each species because individuals of Heliconius and Junonia perch with their wings closed unless they are thermoregulating or involved in courtship (Brown 1981; Devries 1987). High resolution models were printed onto Whatman filter paper (GE Healthcare Life Sciences, Pittsburgh, PA, USA) with a Brother MFC-4510DN printer (Brother Industries, Nagoya, Japan) of ventral wing surfaces of each species because individuals of Heliconius and Junonia perch with their wings closed unless they are thermoregulating or involved in courtship (Brown 1981; Devries 1987). High resolution models were printed onto Whatman filter paper (GE Healthcare Life Sciences, Pittsburgh, PA, USA) with a Brother MFC-4510DN printer (Brother Industries, Nagoya, Japan) of ventral wing surfaces of each species because individuals of Heliconius and Junonia perch with their wings closed unless they are thermoregulating or involved in courtship (Brown 1981; Devries 1987).

Model color measurements

To confirm that each model type was visually indistinguishable from the natural butterfly wings, we quantified full-spectrum reflectance and incorporated the data into avian visual threshold models (Vorobyev and Osorio 1998; Maia et al. 2013). We measured the ventral reflectance of the main color patches for each species using 3 male individuals and then measured the same color patches of 3 of each printed model type using a USB2000 Spectroradiometer (Ocean Optics, Dunedin, FL, USA) and Xenon standardized light source (Ocean Optics). Wing color reflectance was measured as the
proportion of a white reference standard (WS-1-SL, Ocean Optics) using a coaxial fiber cable (QR400-7, Ocean Optics). We used avian
visual thresholds using the PAVO program within R (Maia et al.
2013; R Core Team 2014) to determine if the artificial wing models accurately represented the coloration of natural wings, as seen
through the eyes of birds with both ultraviolet-sensitive (UVS) and
ultraviolet-sensitive (UV) visual systems (Vorobyev and Osorio
1998; Osorio and Vorobyev 2005). Although the main predators of
Heliconius are jacamars and tyrant flycatchers (Pinheiro 2011),
which have the UV visual system, the predators of J. coenia may
include predators with either the VS or UVS visual system (Dervi-
ves 1987). We applied von Kries transformation to account for receptor
adaptation and used the default parameters for Weber's fraction
(0.05), illumination (D65 irradiance spectrum for standard day-
light), background, and cone ratios of N1 = 1, N2 = 2, N3 = 2,
N4 = 4 (Hart 2001: Maia et al. 2013). We calculated both achro-
matic and chromatic just noticeable differences (JNDs) for each
main color patch of each model compared with its respective natural
butterfly: Postman red, Postman yellow, Postman black, Blue–white
white, Blue–white black, Blue–white red, Junonia brown, and
Junonia orange, see Supplementary Figure S1. We did not run JND
tests for the blue of the Blue–white mimicry ring because the blue is
iridescent and in most cases will be seen as black. It is only at certain
angles that a blue hue is reflected from the wing. As we were not
able to replicate the iridescence in these paper models, we focused
on replicating the black, as this is most likely what predators will see
when butterflies are roosting. JNDs represent the ability of a visual
system to perceive 2 colors differently, with a JND value of < 1 being
indistinguishable in ideal conditions (Siddiqi et al. 2004). All com-
parisons had JNDs of < 1 for achromatic and chromatic compar-
sions for both the V/Vis and UV/Vis visual systems, see
Supplementary Figures S2 and S3. Therefore, we inferred that in the
eyes of birds the difference in coloration between the models and
real butterflies would be minimal if not imperceptible. Furthermore,
spectral reflectance curves for each model fit within the natural
color variation of each species, see Supplementary Figure S1.

Attack rate experiments
We tested the attack rates of our model types in 2 different habitats
in Soberania National Park in Central Panama (9.1° N, 79.7° W).
Models were set out in blocks of 3 that included one of each color
pattern (i.e., Postman, Blue–white, and Junonia). Within each block,
models were arranged randomly 1–3 m apart at heights ranging
from 0.2 m to 2 m. We tied each model with black string to leaves
and branches of rainforest plants. Although we did not specifically
control for background, there is no evidence that Heliconius individ-
uals or J. coenia choose a particular type of vegetation or back-
ground for resting (Devries 1987; Mallet and Gilbert 1995).
Furthermore, due to the heterogeneity of the vegetation at each site,
it is unlikely that a predator would see all 3 models instantaneously.
Each block was placed 100 m from the nearest block to reduce the
risk of the same bird attacking models as most avian predators of
butterflies have home ranges of < 1 ha (Buskirk et al. 1972; Karr
1977). Furthermore, it is unlikely that predators learned that the
plasticine body was unprofitable due to the few exposures of the
plasticine bodies. Learning experiments indicate that birds need
more than 3 experiences to learn unpalatability and thus develop
avoidance (Skelhorn et al. 2016). As we were testing the efficacy of
the coloration of the 3 species of butterflies, we did not manipulate
secondary defenses to control for any chemical cue that predators
may rely upon. Blocks of models were placed in each habitat type,
analysis regardless of whether the model was attacked first in the block or after an initial attack on another model in the same block; and 2) with only the models in a block that were attacked first and other sequential attacks were censored. Both statistical approaches resulted in the same test statistics and thus we conclude that although the methods may have violated a statistical assumption of the OR test, our findings are rigorous.

**Results**

Over the 8 different trials, all of which lasted 3 days, 12.1% (54/447) of the models showed evidence of attack by birds. Avian attack rates in the open habitat were 14.8% (44/297) and in the closed habitat were 6.7% (10/150). Attacks by non-avian predators (e.g., rodents and insects) contributed another 2.2% (10/447), while 7.6% (34/447) of the models were missing (Table 1). Lastly, the open habitat had 10.8% (32/297) of the models missing while the closed only had 1.3% (2/150). The high rates of missing models in the open habitat are due to areas of forest being clear cut and removing 15 models, 5 of each model type. We included these missing models into our analysis because the clear cutting occurred after day 1, thus allowing for the use of attack data from these models for at least 1 day.

Model survivorship curves differed significantly by model type (Cox regression, $F = 2.049$, $P = 0.040$; Figure 2A) and habitat (Cox regression, $F = 2.536$, $P = 0.011$; Figure 2B), but not with placement date (Cox regression, $F = 1.784$, $P = 0.074$), nor the random factor of block (Cox regression, $F = 0.07$, $P = 0.53$). Also, the model statistic was the same regardless if only the first model attacked was included in the model when compared with having all attacks in each block included. Furthermore, there was not an interaction between model type and habitat (Cox regression, $F = 0.533$, $P = 0.594$). Pairwise comparisons revealed that independent of habitat, aposematically colored *Heliconius melpomene* models were attacked more often than cryptically colored *J. coenia* models (Wald = 10.18, df = 2, $P = 0.006$, OR = 2.29), but aposematically colored *H. melpomene* had similar attack rates to aposematically colored *H. cydno* models (Wald = 5.26, df = 2, $P = 0.061$, OR = 1.177). *Heliconius cydno* and *J. coenia* models also had similar attack rates (Wald = 4.73, df = 2, $P = 0.094$, OR = 1.945). Also, the number of attacks on *H. melpomene* differed between habitat types with much higher predation in the respective, open habitat of *H. melpomene* (Wald = 4.48, df = 1, $P = 0.034$, OR = 3.966; Supplementary Figure S4), while the number of attacks on the other 2 species did not differ between habitats (*H. cydno*: Wald = 0.840, df = 1, $P = 0.358$, OR = 1.607; *J. coenia*: Wald = 1.38, df = 1, $P = 0.240$, OR = 2.4; Supplementary Figure S4).

**Figure 2.** Survival curves for the 3 different models. Red represents postman *H. melpomene*, blue represents Blue–white *H. cydno*, and brown represents the cryptic model *J. coenia*. (A) Combined habitat survival curves for each morph. (B) Individual survival curves for each morph in each habitat. Long dashes represent survival in the open habitat while dots represent survival in the closed habitat.

**Discussion**

Previous research has shown that both cryptic individuals and aposematic individuals have similar attack rates in artificial prey (Carroll and Sherratt 2013). Here, we demonstrate that attack rates on 2 different aposematic species (*Heliconius*) and cryptic (*Junonia*) individuals depend on coloration as well as the environment. We found that the aposematic Postman models were attacked more than the cryptic model, yet the 2 aposematic color patterns had similar attack rates. Furthermore, the attack rates differed among habitats with more attacks occurring in the open habitat than in closed habitat. Our results, along with Carroll and Sherratt’s (2013) results, indicate that aposematic theory needs to include factors other than just conspicuousness and unpalatability.

*Heliconius* butterflies are aposematic and several studies have demonstrated that avian predators recognize the visual warning signals of *Heliconius* to avoid attacking individuals (Chai 1986, 1996;...
Chai and Syrjälä 1990; Langham 2004, 2005). Previous research on the avian community in central Panama has revealed that the closed habitat has different insectivorous bird species compared with open and edge habitats (Karr 1977; Samuel et al. 1985; Poulin and Lefebvre 1996; Robinson et al. 2000). However, at the family level, the composition is similar with the main Lepidoptera predators being non-migratory flycatchers, jacamars, and warblers (see Poulin and Lefebvre 1996; Robinson et al. 2000). The likely avian predators of Heliconius and other tropical butterflies are flycatchers and jacamars (Pinheiro 1996), which often aerially attack prey at the thorax and then either consume palatable prey or taste reject chemically defended prey (Pinheiro 2011). Thus, our study is complicated at 2 levels: 1) our models were sedentary and may not be the best surrogate for naturally occurring attack rates and 2) our models did not differ in palatability and we could not assay taste rejection by avian predators. Taste rejection is likely an adaptation to find palatable mimics of aposematic prey and the act of taste rejection has been shown to leave butterflies intact and capable of flight (Wiklund and Jarvi 1982; Sillén-Tullberg 1985; Pinheiro 1996, 2011). Therefore, although we found that the cryptic species had fewer attacks than the aposematic Postman species, we were not able to determine whether the aposematic species would have been taste rejected since the bodies were plasticine. It is likely that the survival rates of all 3 species are similar in wild butterflies due to taste rejection by birds. In fact, Carroll and Sherratt (2013) demonstrated that artificial models made to be unpalatable with quinine pastry baits, were attacked at the same rate as palatable, cryptic pastry bait models, but that the unpalatable pastry baits were taste rejected more often. Further studies to test taste rejection in these species of butterflies in the wild are needed to better understand the role of predator behavior in selecting for aposematic and cryptic phenotypes.

Our study replicated components of the study by Merrill et al. (2012) in that we used plasticine models of Postman and Blue–white butterflies in Panama to determine if predation rates differed between aposematic morphs in different habitats. Although we found similar results as Merrill et al. (2012) for the overall study in that butterflies were not less likely to be attacked in their respective environment, we found that overall attack rate did differ between forest edge and forest habitats, whereas Merrill et al. (2012) did not find differences in attack rates dependent upon habitat. Our findings may differ from Merrill et al. (2012) because we tested predation during the dry season instead of the wet season. Avian predation has been reported to increase during the dry season due to lower availability of prey, which may mean that aposematic prey are attacked more during the dry season than in the wet season (Kricher 2011). In fact, we observed an attack rate that was 3 times that recorded by Merrill et al. (2012, 12% compared with 4%), even though the overall methods were very similar. Seasonal differences in attack rates have also been reported by Mappes et al. (2014), who found that the attack rates of cryptic and aposematic larvae in Finland varied with season. Specifically, Mappes et al. (2014) attributed the seasonal attack differences between cryptic and aposematic larvae to seasonal differences in the prior experiences of avian predators. Naive fledglings attacked more aposematic prey than cryptic prey, but later in the year when all birds were experienced, the cryptic prey were attacked more than aposematic prey. In our study, it is possible that differences in predation rates between aposematic and cryptic morphologies were due to bird age and experience. Both tyrant flycatchers and jacamars have breeding seasons that begin at the transition from wet season to dry season and thus naive fledglings begin foraging during the dry season and may have not learned to avoid aposematic species (Skutch 1968; Hoyo et al. 2004).

There were more overall attacks for each species in the open habitat, although there was only a significant difference for H. melpomene. This finding is most likely due to visibility and predator composition. The closed, forested site where models were placed was thick with vegetation and therefore it may have been harder for birds to detect even the conspicuous models. Also, predator composition varies between the 2 habitats and the forest edge habitat has high abundance of insectivorous birds such as tyrant flycatchers (del Hoyo et al. 2004). The Postman coloration was attacked more in its respective habitat than in the habitat where it does not reside. This is contrary to our predictions as we predicted that predation on aposematic models would be lower where the aposematic model is common due to experienced predators as has been supported by previous research (Mallet and Barton 1989; Merrill et al. 2012). As stated previously, this suggests that avian predators are likely attacking aposematic individuals and then deciding whether to consume or reject the prey dependent upon chemical defenses (Wiklund and Jarvi 1982; Sillén-Tullberg 1985; Pinheiro 1996; Pinheiro 2011; Carroll and Sherratt 2013). Heliconius species have many palatable mimics that may be rewarding avian predators that test the palatability of prey items (Pinheiro 1996, 2007, 2011). And if the palatable mimics are segregated by habitat like their aposematic model (i.e., Postman butterflies), then predators may be searching for individuals with the Postman coloration. Furthermore, the Postman has high chromatic contrast (red, yellow, and black color pattern) and thus is highly noticeable in well-lit environments like edge habitats and may be easier to detect by avian predators in the edge habitat (Douglas 2013). Further research into the rates of taste rejection in aposematic species is needed to understand the evolutionary processes behind warning coloration and mimicry.

Plasticine models have been used to test many hypotheses explaining differences in morphology, as well as hypotheses relative to the ecology and evolution of predator–prey interactions (Papageorgis 1975; Cuthill et al. 2003; Finkbeiner et al. 2012; Seymoure and Aiello 2015). However, in several such studies, the plasticine model manipulations done to address the questions they proposed are artificial and do not resemble any natural prey item (see Cuthill et al. 2003; Carroll and Sherratt 2013) or are drastically different from the natural coloration (see Finkbeiner et al. 2014; Seymoure and Aiello 2015). It is conceivable that this may lead to attack rates that are higher than would occur with natural coloration. Hence, the comparatively low predator attack rates that we observed might be due to the relatively natural appearance of the plasticine models that we used.

Our findings here suggest that both aposematism and cryptic coloration have low attack rates in the wild. However, the plasticine models are a surrogate for wild butterflies and may not be equally representative of the attack rates for living cryptic and aposematic individuals. Most prey items move, especially butterflies, and the models used in this study were static, so perhaps predation rates between cryptic and aposematic animals differ when movement is included. In fact, cryptic organisms are hypothesized to move less than conspicuous organisms because predators can use movement to detect prey (Stevens and Merilä 2011).

In conclusion, our study suggests that both aposematic coloration and cryptic coloration can be adaptive strategies for avoiding predation at rest as all models had low attack rates. The findings...
suggested that the form of aposematic coloration and the habitat (i.e., open-canopy vs. closed-canopy) in which an organism resides affects the predation rate. All 3 color forms were attacked more in the open habitat, which is most likely due to visibility and perhaps greater abundance of predators. Furthermore, the more chromatic aposematic species was attacked more than the cryptic species. Lastly, this study highlights the need for further research into the tradeoffs of crypsis and aposematism including using avian visual models to determine how different habitats (open vs. closed) affect the conspicuousness of color patterns. Why do some animals evolve crypsis while others evolve aposematism, if both have similar rates in survival? Future work studying the role of life history (e.g., dispersal, mobility, and host plants) and predation risk in the context of crypsis and aposematism is needed to understand the selection pressures leading to crypsis or aposematism.

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Supplementary Material
Supplementary material can be found at https://academic.oup.com/cz.

References


