

Predation on heliconia bugs, *Leptoscelis tricolor*: examining the influences of crypsis and predator color preferences

C.W. Miller and S.D. Hollander

Abstract: Individuals in natural populations commonly vary in color, and such color variation can be important for survival under predation pressure. Potential prey may be more likely to survive when they are cryptic against their backgrounds. Alternatively, individual coloration, regardless of background, may itself best predict predation events. Few studies have simultaneously tested the importance of crypsis and predator color preferences in explaining predation events. In this study we used objective measures of coloration to examine whether heliconia bugs, *Leptoscelis tricolor* Westwood, 1842 (Hemiptera: Coreidae), resembling their background were less likely to be eaten by avian predators (crypsis hypothesis). Next, we evaluated whether insect color, irrespective of background, best explains predation events (color preference hypothesis). We found the strongest evidence for the crypsis hypothesis; predators chose prey that differed most from their background in color saturation. Some evidence was also found for the color preference hypothesis; predators avoided brightly colored prey. These results suggest that crypsis can be effective in detouring predation. However, when potential prey are detected, predator color preferences may best explain predation events.

Résumé : Dans les populations naturelles, les individus diffèrent couramment de coloration. Une telle variation de couleur peut être importante pour la survie sous la pression de la prédation. Les proies potentielles peuvent être plus susceptibles de survivre lorsqu'elles sont bien camouflées dans leur arrière-plan. D'un autre côté, la coloration individuelle, quel que soit l'arrière-plan, peut en elle-même être la meilleure variable prédictive des événements de prédation. Peu d'études ont testé simultanément l'importance du camouflage et les préférences de couleur des prédateurs afin d'expliquer les événements de prédation. Notre étude utilise des mesures objectives de coloration afin de voir si les punaises du balisier, *Leptoscelis tricolor* Westwood, 1842 (Hemiptera : Coreidae), qui ressemblent à leur arrière-plan sont moins susceptibles d'être consommées par des oiseaux prédateurs (hypothèse du camouflage). Nous évaluons ensuite si la couleur de l'insecte, indépendamment de l'arrière-plan, explique le mieux les événements de prédation (hypothèse de la préférence de couleur). Nos données appuient plus fortement l'hypothèse du camouflage; les prédateurs choisissent les proies qui diffèrent le plus de leur arrière-plan en saturation des couleurs. Il y a aussi des données qui appuient l'hypothèse de préférence de couleur; les prédateurs évitent les proies de couleur vive. Nos résultats indiquent que le camouflage peut être efficace pour éviter la prédation. Cependant, une fois que les proies potentielles sont détectées, les préférences de couleur du prédateur peuvent mieux expliquer les événements de prédation.

[Traduit par la Rédaction]

Introduction

Animals express a dazzling array of colors, including the multicolored displays of guppies, the striking yellows and blacks of some wasps, the showy plumage of birds of paradise, and the remarkable background matching of lepidopteran pupae (Poulton 1890). Some colors and patterns are important for sexual selection (Darwin 1874; Andersson

1994), some for thermoregulation (Fields and McNeil 1988; Goulson 1994; Hazel 2002), and some may be aposematic and advertise distastefulness (Poulton 1890), while others may primarily serve to hide or disguise potential prey (Thayer 1909).

Variation in color does not only occur across species and populations. Even within natural populations individuals often differ to a remarkable extent in their expression of color (Holloway 1993; Hazel 2002; Hochkirch et al. 2008). Such dissimilarity can result in differential survival of prey (Sillén-Tullberg 1985a; Godin and McDonough 2003; Millar et al. 2006). While color certainly plays a role in determining predation events, few studies have simultaneously examined the influences of cryptic coloration and predator color preferences in predicting predation events.

Crypsis is defined as possessing colors and patterns that

Received 26 June 2009. Accepted 28 October 2009. Published on the NRC Research Press Web site at cjz.nrc.ca on 7 January 2010.

C.W. Miller¹ and S.D. Hollander. Entomology and Nematology Department, University of Florida, Gainesville, FL 32605-0620, USA.

¹Corresponding author (e-mail: cwmiller@ufl.edu).

lower the probability of detection by predators (Behrens 2009; Stevens and Merilaita 2009). Interest in crypsis has long linked biologists, artists, hunters, and the military (Thayer 1909; Behrens 2009). Given this history, the progression of research in this area has been surprisingly slow (Stevens and Merilaita 2009). One reason may be the lack of objective measures of crypsis; often human observers have been used to make subjective assessments. Over the past several years, there has been a growing appreciation of the use of objective assessments of color, and the number of studies of crypsis has increased dramatically (Endler 2006; Stevens and Merilaita 2009).

Here, we examine an insect species with substantial color variation as juveniles (Figs. 1*b*, 1*c*) to address the significance of color variation when under the risk of avian predation. Using objective measures of coloration, we first tested whether insects that are similar in color to a host-plant background (Figs. 1*a*–1*d*) will be less likely to be eaten by avian predators (crypsis hypothesis). Because predation events are likely not shaped by detection alone, we tested a competing, albeit nonexclusive, hypotheses for the significance of variable color expression: that insect color, irrespective of background, will predict predation events (color preference hypothesis).

We experimentally tested these hypotheses with the heliconia bug, *Leptoscelis tricolor* Westwood, 1842 (Hemiptera: Coreidae). Nymphs of this species grow and develop on a variety of different species of heliconia plants that vary widely in color, from yellow to deep red. Fourth- and fifth-stage nymphs often have regions of their body that resemble the colors of their natal host plants (Figs. 1*b*, 1*c*; C.W. Miller, unpublished data), suggesting crypsis through background matching may be an antipredator strategy in this species (Miller 2007).

Materials and methods

Research organisms

We collected heliconia bug nymphs from the inflorescences of various heliconia species growing wild near Gamboa, Panama. When the nymphs reached the fifth instar, we froze them individually in plastic tubes. We used only these dead nymphs in our experiment to control for potential effects of prey movement on the behavior of predators. Freezing these insects had no visual impact on their color. Our focal host-plant species for this study was the expanded lobsterclaw, *Heliconia latispatha* Benth. (Figs. 1*a*, 1*d*). This heliconia species is one of the most common host plants of heliconia bug nymphs in the study area, and inflorescences vary in color, from yellow to oranges and reds. Nymphs developing on *H. latispatha* vary similarly in color (C.W. Miller, unpublished data). Nymphs found on the other common host plants in the area, i.e., false bird of paradise (*Heliconia platystachys* Baker) and beef-steak heliconia (*Heliconia mariae* Hook. f.), are nearly always restricted to reds and black, closely matching these inflorescences (C.W. Miller, unpublished data). The coloration of insects in this family is likely due to pigments such as anthocyanin, carotenoids, and flavonones (Palmer and Knight 1924; Cromartie 1959).

We used four domestic chickens, *Gallus gallus domesticus* (L., 1758), as model avian predators, a species com-

monly used in studies of prey color and the associated implications (Roper and Marples 1997; Gamberale-Stille and Tullberg 2001; Darst and Cummings 2006). Chicks were raised together on a mixture of grains. Occasionally we supplemented their diet with mealworms placed upon heliconia inflorescences to acclimate them to the colors and shape of heliconia. The chickens were approximately 4 weeks old at the initiation of the study and 9 weeks old at the termination of the study.

Chicken vision is undoubtedly different from human vision in several ways. First, birds possess four cone cells, rendering their vision tetrachromatic as opposed to the human trichromatic visual system. Chicken vision has peak absorptions at approximately 415, 460, 507, and 565 nm (Govardovskii and Zueva 1977; Yoshizawa 1992). Their ability to discriminate hues is likely enhanced by colored oil droplets that change the peak sensitivity and dynamic range of cone cells (Partridge 1989). Also, fowls possess a double cone with photoreactive pigments, the function of which is unknown (Meyer 1986). For these reasons, reflectance spectrometry provides a useful, objective tool for color studies involving chickens and other birds.

Objective measurements of color

We used reflectance spectrometry to measure both nymph and heliconia inflorescence coloration (Fig. 2). Readings of nymphs and inflorescences, as well as all calibrations, were conducted in a dark room. We repeated each measurement three times in series, with the fiber-optic cable repositioned between each measurement. We then averaged these measurements for the analyses. Nymph reflectance was estimated by placing the bifurcated cable on the center of the dorsal side of the abdomen of a previously frozen individual. To measure background reflectance, we first haphazardly selected points located on the faces of two parallel bracts on heliconia inflorescences. We then marked the locations where nymphs would be placed and took reflectance readings at four points directly surrounding these marks.

We measured reflectance using an Ocean Optics USB2000 Fiber Optic Spectrometer, PX-2 Pulsed Xenon light source, and 00IBase32 software. We used a 45° probe pointer (Andersson and Prager 2006) to minimize glare, improve aiming, and control distance. We recalibrated the spectrometer at the beginning of each measurement period and between every 10 readings by taking a white reference reading of a WS-1 diffuse reflectance standard and a dark reading.

Reflectance spectrometry allows for objective measurements of color, but we did not specifically assess what a chicken sees. To estimate the photon catch of chicken cones would require measurements of the transmission properties of air and the bird's ocular media, as well as the spectral sensitivities of the birds' retinal cones. This technique is more involved and makes several key assumptions, but is currently the best approach in assessing what animals actually perceive (Montgomerie 2006).

Experimental design

We conducted 13 preference trials over a 5-week period. All trials took place in an enclosed arena with four sides, each 74 cm long and 60 cm high. The walls of the enclosure

Fig. 1. (a) Inflorescence of an expanded lobsterclaw (*Heliconia latispatha*) from our study area. (b) “Dark” and (c) “light” fifth instar heliconia bug (*Leptoscelis tricolor*) nymphs where sighted on their natal inflorescences in the wild. (d) The experimental arena. Domestic chickens (*Gallus gallus domesticus*) were given the opportunity to consume one of two nymphs placed on the inflorescence of a *H. latispatha* (photographs by C.W. Miller).

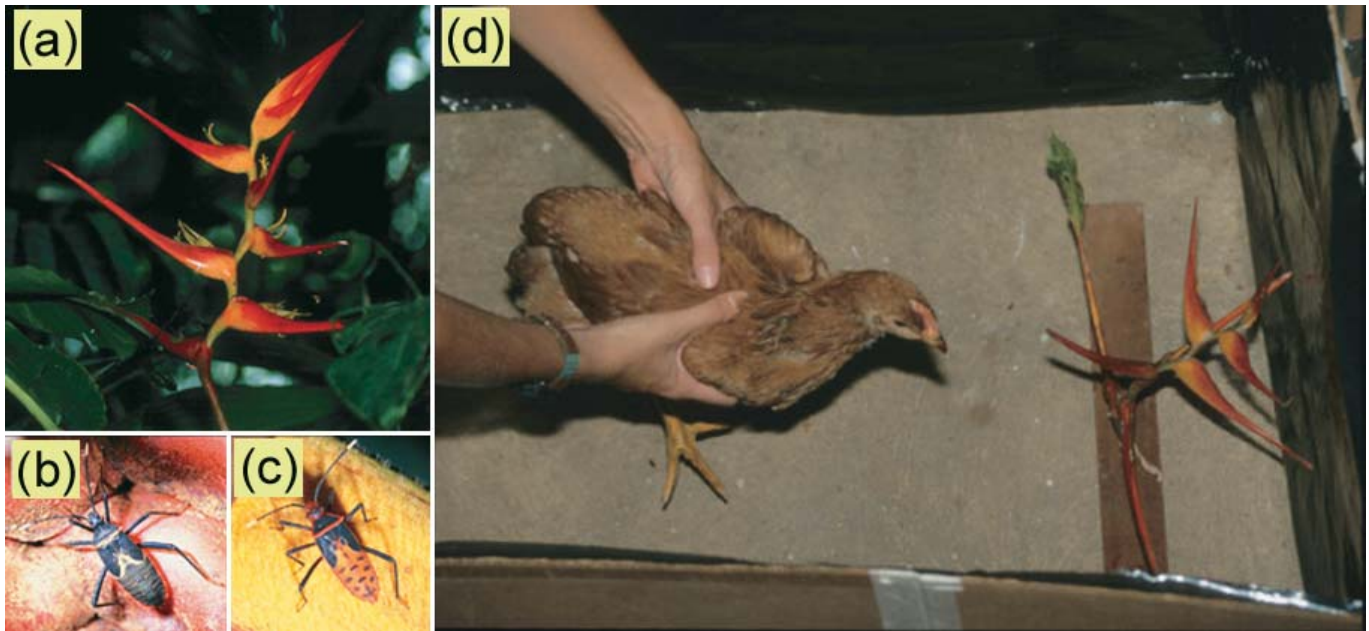
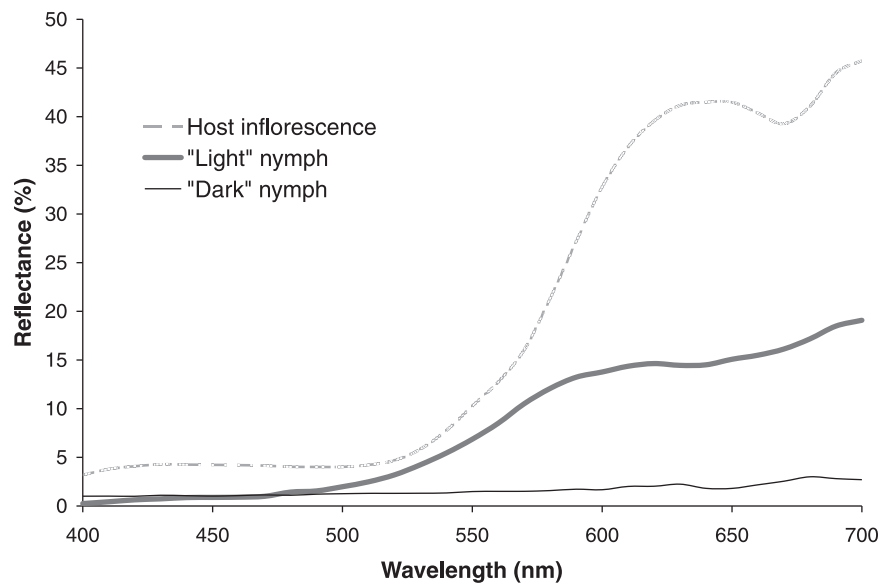


Fig. 2. Representative reflectance spectra for the inflorescence of an expanded lobsterclaw (*Heliconia latispatha*), as well as a “light” and “dark” nymph of a heliconia bug (*Leptoscelis tricolor*).



were covered in black plastic, the base was cement, and the top was open. An inflorescence mounted upright was placed against one wall of the enclosure (Fig. 1d).

One experimenter (S.D. Hollander) separated nymphs into “light” and “dark” groups based on visual estimation (Figs. 1b, 1c, 2) and chose nymphs of similar size from each group to be presented together. We secured these two nymphs with nontoxic glue onto parallel bracts of each inflorescence with their dorsal portion facing out. The chickens thus were given a choice between “light” and “dark” nymphs based on a qualitative separation without regard to

background coloration. We note, however, that all analyses were conducted based only on spectrometer readings and not based on the qualitative estimates.

In each set of trials, we presented a chicken with a different nymph pair on an inflorescence. Each inflorescence was presented to all four chickens, but a chicken was never presented the same nymph or the same inflorescence more than once. The chickens were familiarized with the environment prior to experimentation by placing them in the enclosure with live mealworms on an inflorescence and allowing them to each eat the same number of mealworms. Before each

trial, we left the chickens without food for at least 1 h to increase hunger. During the experiment, we placed a single chicken in the enclosure facing the inflorescence (Fig. 1d). The trial ended when one nymph was consumed, which usually only required a few seconds.

Statistical analysis

Color was expressed as percent reflectance per nanometre wavelength. We used principal component analysis (PCA) on the correlation matrix to generate orthogonal variables directly from the reflectance spectra data. PCA minimizes the inaccuracies and approximations common with the use of the tristimulus color variables: brightness, saturation, and hue (Cuthill et al. 1999; Montgomerie 2006). To allow discussion of the meaning of PCA values in terms of human perception, new variables produced through PCA can be categorized according to brightness, saturation, and hue by visual estimation and by correlating the PCA values with the standard tristimulus color variables (Montgomerie 2006).

We collapsed raw reflectance data into 10 nm bins using Color version 1.5 (R. Montgomerie, ©2002). Then we took the mean score for each individual or plant for each bin. We used wavelengths 400–700 nm for the analysis. Wavelengths up to 399 nm were disregarded because of high variability from wavelength to wavelength that suggested human sweat and fingerprints had accumulated on the WS-1 diffuse reflectance standard. Such marks can be invisible to researchers at the time measurements are made, but reflect strongly in the UV (Andersson and Prager 2006). Chickens do not appear to be able to detect wavelengths under 360 nm, and have little or no sensitivity to wavelengths 360–399 nm (Wortel et al. 1987; Prescott and Wathes 1999), thus the exclusion of wavelengths <399 nm is unlikely to qualitatively alter our findings.

We ran two types of PCAs. First, we used the absolute differences in reflectance for each bin between the nymphs and the *H. latispatha* for each trial. This PCA allowed us to examine whether crypsis influences the likelihood of predation. Second, we used color reflectance readings for only heliconia bugs, allowing us to test for potential color preferences of predators.

We used conditional logistic regression for matched-pairs data (i.e., case-control data) based on variation in color summarized by PCA to test for two hypotheses regarding the likelihood of predation. A matched-pairs logistic regression is most suitable for our experimental design, because it can handle case-control data sets, where for each pair (trial) the dependent variables necessarily differ in outcome (Allison 1999). Note that this design compares relative differences within a trial to interpret predation influences.

We simultaneously compared models that reflect the two hypotheses using an information-theoretic approach, based on Akaike's information criterion adjusted for sample size (AIC_c): (1) an intercept only model, (2) models based on differences in insect color and background heliconia color, and (3) models based on heliconia bug color. For our approach, we compared models that included both principal components (PCs) describing color and models that included each component separately, resulting in a total of seven models being compared. A model selection approach was used here because such an approach allows for simultane-

ously comparing different models that reflect biological hypotheses (Johnson and Omland 2004). We initially screened the data to determine if the placement of bugs (left or right side) on heliconia influenced predation rate. Because there was evidence for such effects ($P = 0.039$), we forced placement of bugs into subsequent modeling efforts to control for potential effects of placement on predation.

Results

For each PCA, two PCs explained most of the variation in reflectance (93.4%–97%; Fig. 3). Overall, the first PCs were summarized by coefficients with similar loadings across the entire wavelength gradient, which we interpret as an overall measure of brightness (Cuthill et al. 1999; Montgomerie 2006). We separately calculated standard brightness from the raw data (Montgomerie 2006) and found that brightness was indeed highly correlated with PC1 from our PCA, lending further support to our interpretation (insect value, $r = 0.95$; differences in insect and background value, $r = 0.86$). The second PCs were consistently reflecting a short-long wavelength gradient, with opposite loadings at the extremes of this continuum (Fig. 3). Thus, variation among spectra is due to the relative amount of red versus blue reflected light. Such a pattern can be seen as variation in red saturation (Cuthill et al. 1999; Montgomerie 2006). A separate estimate of saturation from the raw data (Montgomerie 2006) was highly correlated with PC2 from our analyses (insect value, $r = -0.67$; differences in insect and background value, $r = 0.80$).

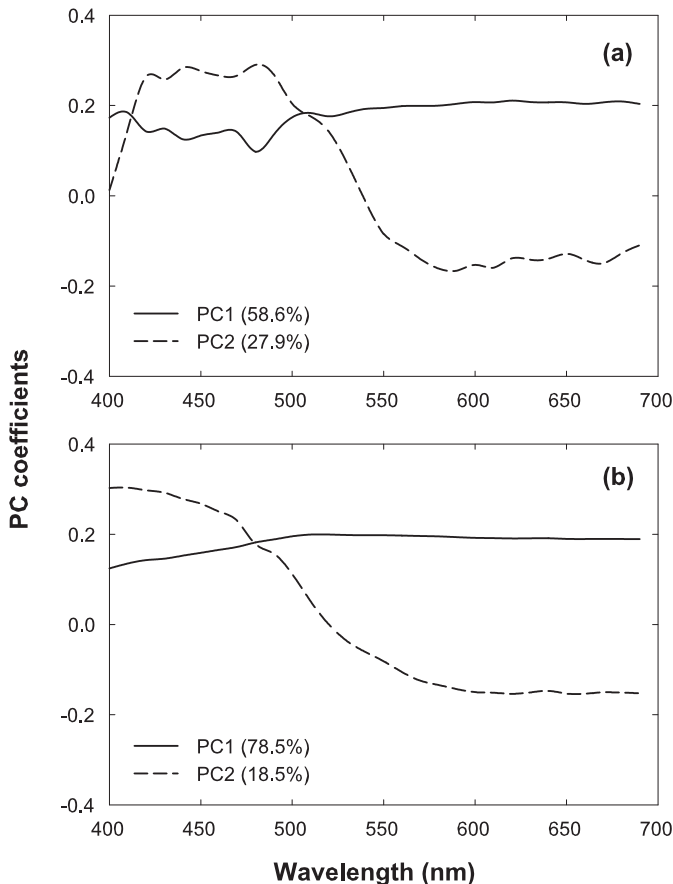
Based on the comparison among models, there was more support for the crypsis hypothesis, and in particular PC2_C ($P = 0.017$), explaining predation of heliconia bugs (Table 1). When controlling for placement, predation increased with increasing values of PC2_C (odds ratio = 1.279, 95% confidence interval (CI) = 1.046–1.564), which describe increasing differences between the nymphs and the *H. latispatha* across the short-long wavelength gradient (Fig. 3). In other words, heliconia bugs were most likely to be eaten when their saturation differed most from the saturation of their background.

The color preference hypothesis was also supported, although to a lesser extent (total AIC weight = 0.377 vs. 0.614 under the crypsis model; Table 1). In this color preference model, PC1_P best explained predation on heliconia bug nymphs ($P = 0.028$). Controlling for placement, predation increased with increasing values of PC1_P (odds ratio = 0.912, 95% CI = 0.840–0.990). Thus, the brighter nymphs had a lower probability of being eaten.

Discussion

Color variation is common among individuals in natural populations and may have a variety of fitness consequences. Here, we examined whether the extreme color variation in juvenile heliconia bugs may influence predation risk. Unlike many previous studies, we simultaneously tested two non-exclusive hypotheses on predation risk as related to color: (1) nymphs most closely matching their background will have a lower risk of predation (the crypsis hypothesis) and (2) nymph color will influence predation risk (the color preference hypothesis). We found support for both of these hy-

Fig. 3. Principal component (PC) scores for (a) the absolute difference in the reflectance of a heliconia bug (*Leptoscelis tricolor*) and an expanded lobsterclaw (*Heliconia latispatha*) and (b) heliconia bug alone. The percentage noted in parentheses reports the amount of variation of reflectance explained by each PC.



potheses; however, the crypsis model best explained the data.

The model avian predators (chickens) in this study were more likely to eat nymphs that differed the most from their background in saturation (Table 1). These results suggest that the color variation seen in immature heliconia bugs does function as a means of crypsis and can detour predation, at least by one model avian predator. During development, these nymphs may be using cues such as light reflectance or diet chemistry to match their level of pigment saturation to their backgrounds (Greene 1989, 1996; Miller 2007). The ability to use environmental cues to enable background matching occurs across taxa and includes the rapid and reversible color modifications in cephalopods (Mäthger et al. 2008), developmental shifts enabling butterfly larvae to mimic different plant structures (Greene 1989), and the accumulation of pigments in some species of tortoises (Woolley 1957).

The chickens used in this study showed a preference for the least cryptic prey. However, it seems that when the predators were able to see both nymphs, they preferentially selected their prey based upon its color, and in particular, its brightness (Table 1). Brightness can be defined as the level of “lightness” or the total amount of reflected light coming from a surface. Chickens preferred nymphs that were not

Table 1. Conditional logistic regression for three models explaining predation events (probability of being eaten) on an expanded lobsterclaw (*Heliconia latispatha*) based on principal component (PC) scores of color.

| Model* | AIC _c | ΔAIC _c | K [†] | AIC weight |
|-------------------------------------|------------------|-------------------|----------------|------------|
| Intercept model | 70.78 | 6.99 | 1 | 0.010 |
| Crypsis | | | | |
| PC1 _C + PC2 _C | 64.46 | 0.67 | 4 | 0.229 |
| PC1 _C | 66.95 | 3.16 | 3 | 0.066 |
| PC2 _C | 63.79 | 0.00 | 3 | 0.320 |
| Color preference | | | | |
| PC1 _P + PC2 _P | 65.78 | 1.99 | 4 | 0.118 |
| PC1 _P | 65.25 | 1.46 | 3 | 0.154 |
| PC2 _P | 66.02 | 2.23 | 3 | 0.105 |

Note: Models with the lowest Akaike’s information criterion adjusted for sample size (AIC_c) and the greatest AIC weight have the most support.

*Placement (left or right side) of heliconia bugs was included in all models.

[†]Number of parameters in model.

brightly colored, and these nymphs likely possess a higher concentration of pigment.

The coloration of potential food items is known to influence the feeding preferences of many species of birds (McPherson 1988; Puckey et al. 1996; Hartley et al. 2000; Schaefer et al. 2008), with heavily pigmented colors of orange or red often associated with benefits to immune response (Fenoglio et al. 2002; Blount et al. 2003; Chew and Park 2004; Schaefer et al. 2008) and to the expression of sexual ornaments (Hill 2006). Thus, these chickens may have preferred less bright nymphs for their salubrious pigments.

Another reason that the chickens in this study may have preferred more heavily pigmented nymphs may be due to the aposematic appearance of the brighter nymphs (Fig. 1c). Chickens originate from red jungle fowl, *Gallus gallus* (L., 1758), which naturally feed on a mixture of insects, seeds, fruits, and plant parts. Some evidence suggests that chickens show different color preferences depending upon whether the food item is a fruit or an insect (Gamberale-Stille and Tullberg 2001). One reason for such variable preference is that colors such as yellow, orange, and red, especially in a disruptive pattern with black, can be aposematic in insects and associated with defensive compounds (Gamberale-Stille and Tullberg 2001). The brighter nymphs of this species often express pigmented spots on their dorsal abdomen, a combination that may appear aposematic (Fig. 1c). The chickens used in this experiment likely lacked experience with aposematic insects; however, evidence exists that chickens and other birds may possess an innate aversion to aposematic insect prey (Sillén-Tullberg 1985a, 1985b; Gamberale-Stille and Tullberg 2001), although other evidence refutes this point (Roper and Cook 1989). Further studies are needed in this insect species to examine whether the detected nymphs chosen by avian predators reflect an aversion to aposematic-appearing individuals and (or) a preference for insects with more pigmentation.

Acknowledgements

We thank John Steffen and Jessica Stapley for helpful advice on the use of the spectrometer and in measuring color, and Bob Mongomerie for the color analysis software. We appreciate the assistance of Robert J. Fletcher in performing statistical analyses and providing useful comments on a previous version of the manuscript, as well as Enrique Espinosa for research assistance and Tom Martin for the use of the spectrometer. The Smithsonian Tropical Research Institute provided important logistical support. This material is based upon work supported under a National Science Foundation Graduate Research Fellowship and a Smithsonian Tropical Research Institute Short-Term Fellowship to C.W.M.

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