

Aposematic coloration, luminance contrast, and the benefits of conspicuousness

Kathleen L. Prudic,^{a,b} Ana K. Skemp,^a and Daniel R. Papaj^a

^aEcology and Evolutionary Biology, University of Arizona, P.O. Box 210088, Tucson, AZ 5721, USA and

^bBio5: Institute for Collaborative Bioresearch, University of Arizona, P.O. Box 210036, Tucson, AZ 85721, USA

Many organisms use warning, or aposematic, coloration to signal their unprofitability to potential predators. Aposematically colored prey are highly visually conspicuous. There is considerable empirical support that conspicuousness promotes the effectiveness of the aposematic signal. From these experiments, it is well documented that conspicuous, unprofitable prey are detected sooner and aversion learned faster by the predator as compared with cryptic, unprofitable prey. Predators also retain memory of the aversion longer when prey is conspicuous. The present study focused on the elements of conspicuousness that confer these benefits of aposematic coloration. Drawing on current understanding of animal vision, we distinguish 2 features of warning coloration: high chromatic contrast and high brightness, or luminance, contrast. Previous investigations on aposematic signal efficacy have focused mainly on the role of high chromatic contrast between prey and background, whereas little research has investigated the role of high luminance contrast. Using the Chinese mantid as a model predator and gray-painted milkweed bugs as model prey, we found that increased prey luminance contrast increased detection of prey, facilitated predator aversion learning, and increased predator memory retention of the aversive response. Our results suggest that the luminance contrast component of aposematic coloration can be an effective warning signal between the prey and predator. Thus, warning coloration can even evolve as an effective signal to color blind predators. *Key words:* insect vision, mantid, predation, *Tenodera aridifolia sinensis*, warning display. [*Behav Ecol* 18:41–46 (2007)]

Signals must be detectable against background noise in order to be effective. Under certain circumstances, natural selection favors visual signals that contrast markedly with their background. A classic example is aposematic coloration. Aposematic, or warning, coloration is used by noxious organisms to signal their unprofitability to potential predators (Cott 1940; Guilford 1990). Such coloration is typically highly conspicuous. Not only is a conspicuously colored pattern by definition easier for the predator to detect against its background but it has also been shown to be easier to learn and less likely to be forgotten (Gittleman and Harvey 1980; Roper and Redstone 1987; Roper 1990; Alatalo and Mappes 1996). These multiple benefits to both predator and prey are believed to have facilitated the evolution of aposematic coloration from ancestrally cryptic patterns (Fisher 1930; Sherratt and Beatty 2003).

Less well understood are the specific features of the aposematic color signal that promote predator detection, learning, and memory retention. Aposematic color patterns could differ from cryptic ones in any of a suite of characteristics, including chromatic contrast and luminance contrast. Chromatic contrast, sometimes called color contrast, refers to differences in hue or chroma between an object and its background (Wyszecki and Stiles 1982; Adelson 2000). Luminance contrast refers to differences in amount of light reflected from an object and the background on which it occurs (Wyszecki and Stiles 1982; Adelson 2000). The perceptual equivalent of luminance contrast is brightness contrast (Adelson 2000). Both types of contrast have been shown to

be important in visual communication such as mating displays and seed dispersal by frugivores (e.g., Uy and Endler 2004; Schmidt et al. 2004, respectively).

Both contrast types also seem important for aposematic coloration signals. For instance, the definition of aposematic coloration often includes references to both chromatic and luminance contrast (e.g., colorful and bright) as key characteristics (Ruxton et al. 2004). Aposematic patterns typically show strong color contrast with background, as compared with cryptic patterns, and the predominant hues in aposematic patterns are red, yellow, or orange, which are distinct from the green or brown hues common in terrestrial environments (Joron 2003). Aposematic patterns often appear to show significant brightness, or luminance contrast with their background, as compared with cryptic patterns such as the golden poison dart frog or the pipevine swallowtail (Ruxton et al. 2004). Additionally, aposematic color patterns frequently show strong luminance contrast among elements of the pattern such as black and yellow striping of bees and wasps or the black and white patterning of skunks. Such patterning is thought to increase aversion learning of an aposematic signal relative to solid bright colors alone (Bowdish and Bultman 1993). Thus, luminance contrast is conceivably a viable signal between aposematic prey and predator and may confer the functional benefits of aposematic coloration.

Color contrast is considered more critical to the effectiveness of aposematic coloration signals based on experiments with avian predators. However, these results may not extend generally to all predator species detecting aposematic signals. Predators vary widely in terms of their color discrimination capabilities, ranging from dichromatic (most mammals and insects) (Goldsmith 1990; Briscoe and Chittka 2001, respectively) to tetrachromatic (butterflies and birds) (Briscoe and Chittka 2001; Goldsmith 1990, respectively) and even to dodecachromatic (mantis shrimp) (Marshall and Oberwinkle 1999). Color-blind predators can learn to avoid aposematic

Address correspondence to K.L. Prudic. E-mail: klprudic@email.arizona.edu.

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prey (Berenbaum and Miliczky 1984; Bowdish and Bultman 1993), and for these predators, luminance contrast may be very important in assessing warning coloration displays. Thus, prey luminance contrast might readily evolve as an aposematic signal between unpalatable prey and color-blind predator.

In this study, we examined if luminance contrast alone can function as an aposematic signal from the standpoint of praying mantids, cosmopolitan predatory insects that co-occur with a variety of aposematically colored prey. Praying mantids are generalist ambush predators relying heavily on visual cues to locate and capture prey (Hurd 1999; Prete 1999), and they can learn to avoid aposematic prey (Berenbaum and Miliczky 1984). However, existing physiological and molecular data suggest that praying mantids have very limited or no color vision (Sontag 1971; Rossel 1979; Towner and Gärtner 1994). These observations raise the possibility that aposematic signals, and the associated benefits of rapid learning and stronger retention, might not be mediated by color contrast per se but by luminance contrast. Using the Chinese mantid as a model predator and the milkweed bug as model prey in controlled laboratory experiments, we sought to determine if luminance contrast alone could function as an aposematic signal and, if so, whether it conferred the predicted benefits of aposematism in terms of rapid learning and improved memory retention of the learned aversion.

METHODS

Experimental arena

All experiments were conducted in a laboratory arena consisting of 3 components: a rectangular ramp, a square floor, and a cylindrical wall (Figure 1). The ramp began outside of the cylindrical wall, continued through a port in the wall, and continued upward inside the wall at a 30° angle. Both ramp and floor were constructed of wood and covered in poster board paper, whereas the cylindrical wall was constructed of just the paper. Ramp, floor, and wall were painted a dark uniform gray (see paint reflectance spectra in Figure 2A). The arena was illuminated by 3 full-spectrum halogen lamps (Solux-Eiko, Wiko Ltd., Tinley Park, IL, 50 W, 4700 K, 36° field of illumination) (see irradiance spectra in Figure 2B). Each lamp was positioned 23 cm above the highest point of the ramp and 20 cm from the other lamps.

Predators and prey

Laboratory-reared adult Chinese praying mantids (Mantidae: *Tenodera aridifolia sinensis*) served as the experimental predator. Egg cases were purchased from Carolina Biological Supply Company and reared to adults on 2 separate occasions: February 2003–May 2003 and February 2004–May 2004. On both occasions, mantids were reared in individual cages on a successive diet of fruit flies, houseflies, and crickets. Mantids did not have access to milkweed bug prey before the experimental feeding trials and therefore were not experienced with bug-shaped prey or distasteful prey. Each mantid was fed 2 adult crickets every night throughout the period of experimentation. Laboratory-reared milkweed bugs (Lygaeidae: *Oncopeltus fasciatus*) served as experimental prey. Milkweed bugs are known to sequester cardiac glycosides from milkweed seeds (Isman et al. 1977) and to be unpalatable to mantids (Berenbaum and Miliczky 1984). Milkweed bugs reared on sunflower seeds do not sequester cardiac glycosides (Duffey and Scudder 1972) and are palatable to mantids (Berenbaum and Miliczky 1984). Thus, prey palatability was manipulated in vivo by rearing bugs for 2 generations on either sunflower seeds (*Helianthus annuus*: palatable) or milkweed seeds (*Asclepias curassavica*: unpalatable).

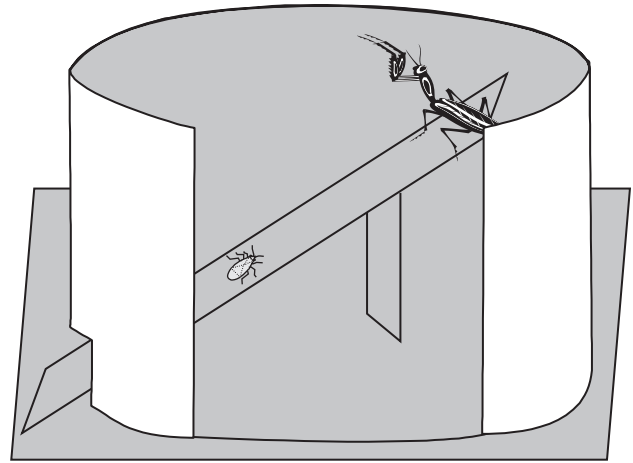


Figure 1

A cutaway diagram of test arena, shown approximately to scale.

Manipulation of prey contrast

Prey contrast against background was manipulated by painting milkweed bugs in either of 2 shades of gray and presenting bugs to mantids against a gray-painted background. Prior to being painted, each milkweed bug was chilled in the refrigerator until it was temporarily immobilized. All milkweed bug surfaces except the eyes were then painted with an artist's brush with 3 coats of the desired paint mixture. The paint was a mixture of black and white nontoxic tempera paint (Prang, Fila Company, Heathrow, FL). Painting did not affect

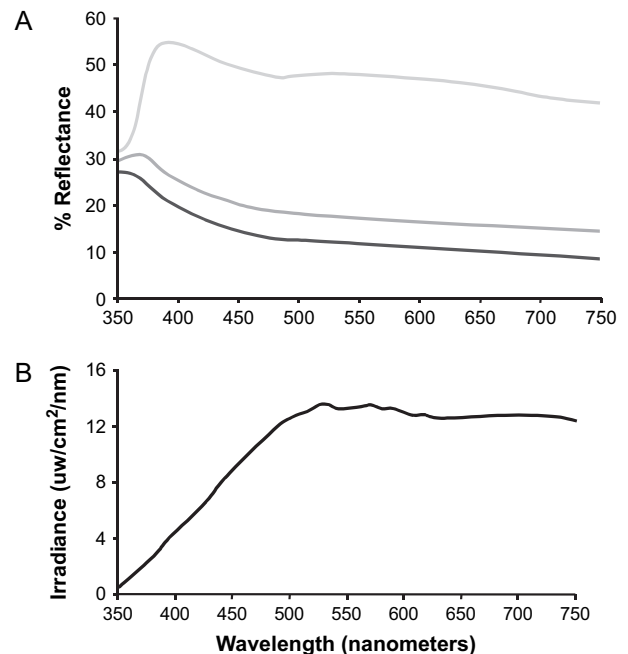


Figure 2

Percent reflectance spectra (A) of experimental gray paints. Background spectrum is indicated by dark-gray line (lowest reflectance), low-luminance contrast prey spectrum by medium-gray line (medium reflectance), and high-luminance contrast prey spectrum by light-gray line (highest reflectance). Irradiance spectrum (B) of the 50-W SoLux-Eiko lamps used in experiments (spectrum supplied by Eiko Ltd.).

the ability of the bug to move up the ramp or did it affect the prey palatability (Prudic KL, Skemp AK, and Papaj DR, unpublished data).

In preparing shades of gray for low-contrast prey, high-contrast prey, and prey background, we used a USB2000 spectrometer with tungsten-halogen light source (Ocean Optics Inc., Halma Group, Dunedin, FL) to obtain reflectance spectra of sample paint chips. Readings were made with an optical fiber probe directed at the surface at an angle of 45°, and percent reflectance was measured relative to a white Spectralon standard (Labsphere Inc., North Sutton, NH). We endeavored to use paint mixtures that were achromatic, that is, grays showing relatively flat reflectance, from 350 to 750 nm (Figure 2A). This range encompasses, at its low end, the minimum wavelength of illumination by experimental lamps (Figure 2B) and, at its high end, the maximum wavelength that insect visual systems are known to detect. In principle, if mantids cannot resolve color, as existing data suggest, use of achromatic paints with flat spectra is unnecessary. For a monochromatic animal, contrast can be assessed simply as the area under the reflectance curve over the range of wavelengths to which the animal is sensitive. However, in the event that mantids do perceive color, use of achromatic paints with flat spectra ensures that we were manipulating prey luminance contrast but not color contrast. The grays used were reasonably flat in the range from 380 to 750 nm (Figure 2A). There was a modest degree color contrast in the portion of the spectrum from 350 to 380 nm. However, the light sources in our experiments provided relatively little illumination in that range (Figure 2B), so it is unlikely the mantids were able to perceive the chromatic differences between the paints even if they are able to discriminate colors.

We quantified luminance contrast between background and prey using a relative luminance contrast index (Endler and Théry 1996; Uy and Endler 2004):

$$\int_{350\text{nm}}^{750\text{nm}} (IR_{\text{prey}} - IR_{\text{background}}) / (IR_{\text{prey}} + IR_{\text{background}})$$

where IR_{prey} = irradiance \times percent reflectance of the prey and $IR_{\text{background}}$ = irradiance \times percent reflectance of the background. This index varies from 0 to 1 where higher values represent a brighter signal. Low-contrast-painted milkweed bugs had a 0.19 contrast index, whereas high-contrast-painted bugs had a 0.57 contrast index.

Initiation of trials

In all experiments, a trial began by placing a single mantid at the top of the ramp inside the arena wall, such that the mantid's longitudinal axis was perpendicular to the long axis of the ramp. Each mantid was allowed to acclimate for 5 min before the trials began. All mantids remained at the top of the ramp for all experiments and trials. A single, painted milkweed bug was placed at the ramp base outside the arena wall, out of view of the mantid. Milkweed bugs consistently walked directly up the ramp at a steady pace through the port in the arena wall and into the mantid's field of view. The milkweed bug invariably continued up the ramp whereupon the mantid's response to the bug was recorded.

In numerous respects, we tried to make our experiment as "natural" as possible based on field observations of mantids and their prey. We used live prey, and the prey was presented to the mantid in a manner similar to how prey and mantid encounter each other in the field. The mantid was perched above the prey, and the prey moved toward the mantid from below the perch without intervention from a human observer

(Prete 1999). Our lighting regime was within the range of natural conditions. The lamps (Solus-Eiko 50 W each, 150 W total) emitted a continuous spectrum in the visible range, which resembled daylight (Figure 2B). This resulted in an overall irradiance that was moderate relative to the range of field conditions in which we have observed mantids hunting.

Conspicuousness assay

To determine if low-contrast milkweed bugs (0.19 contrast index) were less conspicuous to mantids than high-contrast bugs (0.57 contrast index), we measured latency to orientation and latency to attack for mantids in relation to prey contrast treatment. We compared both first-trial treatment differences between mantids and multiple-trial treatment differences within mantids. The bugs were reared on sunflower seeds and palatable. Mantids did not display any behavioral responses, such as refusal of prey or regurgitation, suggesting that either paints or sunflower-reared bugs were unpalatable. Each mantid ($n = 8$) was tested with 4 bugs from each contrast treatment (total = 8 milkweed bugs per mantid). The bugs were presented in a random order, and mantids had no prior experience with milkweed bugs. Two trials per mantid per day were conducted, with the successive trials separated by 4 h. Mantids are voracious predators (Prete 1999), and our satiation experiment indicated that the average mantid attacked and consumed 10 palatable, painted milkweed bugs in 30 min before refusing prey (Prudic et al. unpublished data). Thus, we assumed mantids had similar hunger levels between the morning and afternoon trials.

Prey detection was inferred when the mantid turned its head from a position perpendicular to the ramp to a position parallel to it, orienting toward the bug and tracking its movement up the ramp. Such orientation movements are striking and unambiguous in mantids. Latency to orientation was recorded as the time between the bug's appearance in the arena and the mantid's adoption of the orientation posture. Latency to attack was recorded as the time between orientation and the mantid's strike with its raptorial forelegs. We also measured the rate at which the prey moved up the ramp and the time spent feeding by the mantid. Data were log transformed for normalization and then checked for normality and homoscedasticity. Transformed data were analyzed using one-way or repeated measures ANOVA (JMP-In Statistical Exploration Software 2002). Means and standard error are reported for significant results ($P < 0.05$).

Learning assay

This experiment compared predator aversion learning rates for low-contrast (0.19 contrast index) versus high-contrast prey (0.57 contrast index). Milkweed bugs were reared on milkweed seeds and unpalatable. Mantids behaved in 2 ways suggesting that milkweed bugs reared on milkweed seeds were noxious. First, all mantids regurgitated at least once after eating part of the milkweed-reared bugs; regurgitation was never observed in mantids-eating bugs reared on sunflower seeds. Second, all mantids engaged in high rates of grooming behavior after eating milkweed-reared bugs as compared with sunflower-reared bugs (Prudic et al. unpublished data).

Naive mantids ($n = 14$, 7 per treatment) were assigned randomly either to low-contrast or high-contrast treatment. The experimental protocol was the same as described above except that a single mantid experienced only one prey contrast type. A trial ended either 5 min after a mantid attacked and ate the bug, or, if the mantid did not attack the bug, 5 min after the bug entered the arena. After the trial ended, the bug or its remains were removed. If the mantid attacked the bug, it

was returned to its holding cage after 2.5 min. If the mantid did not attack the bug, it was moved to a second arena after 2.5 min, which bore white surfaces instead of gray, and the mantid was allowed to acclimate for another 2.5 min. The mantid was then presented with a live, tethered cricket in order to evaluate its hunger status; if the mantid attacked the cricket, it was evaluated as hungry. The mantid was not allowed to feed on the cricket, the cricket being yanked away during the attack sequence. This protocol prevented the mantid from associating its response to the milkweed bug with a cricket reward. A mantid was considered to show an aversion to the bug when it oriented to a bug, failed to attack, but subsequently attacked a tethered cricket, in 3 consecutive trials. To evaluate if an increase in prey contrast was associated with an increase in aversion learning rate, the number of trials until mantids reached aversion criteria was compared between prey contrast treatments. Data were log transformed for normalization and then checked for normality and homoscedasticity. Transformed data were analyzed using one-way ANOVA (JMP-In Statistical Exploration Software 2002). Means and their standard error are reported for significant results ($P < 0.05$).

Retention assay

This experiment evaluated the number of days until the mantid reattacked a milkweed bug after reaching aversion criteria. We used palatable, sunflower-reared bugs in this experiment for 2 reasons. First, we wanted to determine if the aversive response required that bugs had fed on milkweed. We predicted that if this was true, the mantids would reattack the palatable milkweed bugs on the first trial. Such a response would suggest that cues other than the luminance contrast cue were involved in mediating the aversion, for example, an odor of the prey derived from feeding on milkweed. Second, and also important, sunflower-reared bugs were much more plentiful in culture than milkweed-reared bugs. Thus, we were guaranteed to have enough bugs of a singular toxicity to last through numerous retention trials. We have no reason to believe that any observed difference in memory retention between the 2 contrast treatments would depend on the change in the milkweed bug diet and corresponding palatability.

The same mantids ($n = 14$) used in the learning experiment were tested 2 days after the day they met aversion criteria (see above) and retested every second day thereafter. One mantid in the low-contrast treatment died over the course of this experiment and was excluded from the analysis. A trial ended either when the mantid attacked and consumed a bug or when the mantid oriented to a bug, failed to attack, but subsequently attacked a tethered cricket. A mantid was considered to have lost its aversive response when it attacked and consumed a bug. Data were log transformed for normalization and then checked for normality and homoscedasticity. Transformed data were analyzed using one-way ANOVA (JMP-In Statistical Exploration Software 2002). Means and their standard error are reported for significant results ($P < 0.05$).

RESULTS

Conspicuousness assay

Mantids attacked all milkweed bugs regardless of prey contrast treatment. In their first encounter with milkweed bugs, mantids oriented sooner to palatable bugs of high contrast (0.57 luminance contrast index) than to palatable bugs of low contrast (0.19 luminance contrast index) (one-way ANOVA, 7.05 ± 3.84 s vs. 22.68 ± 3.77 s, $F_{1,7} = 8.03$, $P = 0.019$, Figure 3A). Contrast also affected latency to attack, mantids took less time to attack high-contrast bugs during their first encounter (one-

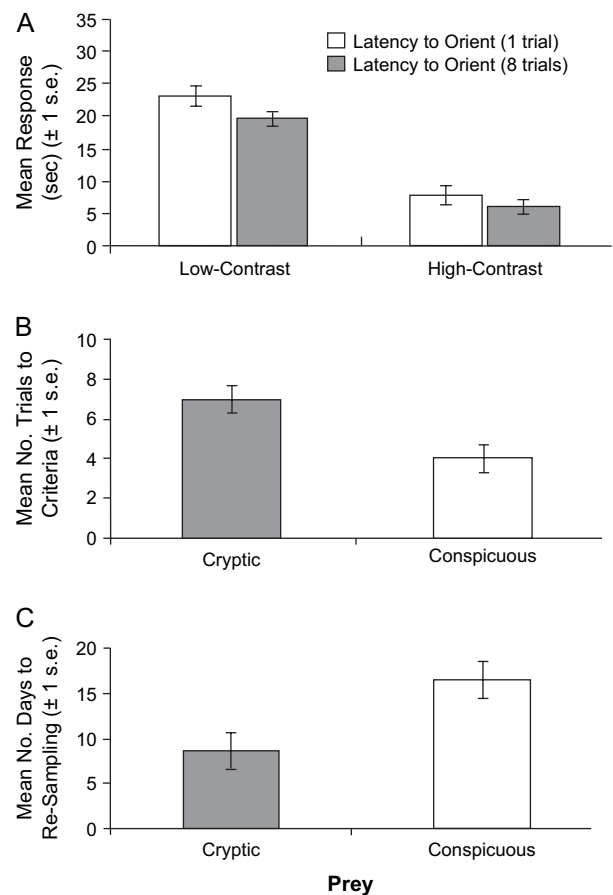


Figure 3

Detectability of low-luminance contrast and high-luminance contrast milkweed bugs (A), as measured by mantids' mean latency to orient in the first trial and over multiple trials. Learning performance by mantids exposed to low-contrast or high-contrast bugs (B), estimated as mean number of trials to reach aversion criteria. Retention of aversive response to low-contrast or high-contrast bugs (C), estimated as mean number of days until a bug is attacked again by the mantid.

way ANOVA, 3.75 ± 1.88 s vs. 16.77 ± 6.50 s, $F_{1,7} = 7.46$, $P = 0.034$, Figure 3A).

Data analyzed over multiple trials yielded similar patterns. Over multiple trials, mantids oriented sooner to palatable bugs of high contrast relative to palatable bugs of low contrast (repeated measures ANOVA, 5.04 ± 1.19 s vs. 18.33 ± 1.58 s, $F_{1,7} = 9.18$, $P = 0.018$). Contrast also affected latency to attack, with mantids taking less time to attack high-contrast bugs during over multiple trials (repeated measures ANOVA, 7.33 ± 4.15 s vs. 18.03 ± 5.72 s, $F_{1,7} = 4.13$, $P = 0.034$). For individual mantids, trial number did not affect attack rate (repeated-measures ANOVA, $n = 8$, $F_{1,7} = 0.80$, $P = 0.56$). Finally, paint treatment did not affect the movement rate of the milkweed bugs (one-way ANOVA, $F_{1,63} = 0.170$, $P = 0.682$) or the feeding rate by the mantids (repeated-measures ANOVA, $n = 8$, $F_{1,7} = 1.60$, $P = 0.213$).

Learning assay

Mantids learned to avoid high-contrast unpalatable milkweed bugs more rapidly than low-contrast unpalatable bugs (one-way ANOVA, 4.00 ± 0.71 encounters vs. 6.86 ± 0.71 encounters, $F_{1,13} = 9.14$, $P = 0.011$, Figure 3B). Two out of seven mantids in the high-contrast treatment demonstrated

single-trial aversion learning, whereas single-trial learning was never recorded in the low-contrast treatment.

In our learning assays, 2 trials were conducted per day, which resulted in a short interprey interval within days, followed by a long interprey interval between days. Because interprey interval could conceivably affect mantid motivation and learning rate, we conducted a test of time between prey consumption (cricket or bug) on mantid attack rate. Time since last cricket or milkweed bug consumption did not affect mantid attack rate (one-way ANOVA, $F_{1,13} = 1.93$, $P = 0.110$), so variation in the intertrial interval did not lead to the observed treatment differences.

Retention assay

All mantids in both treatments ($N = 7$ and 6) initially avoided the sunflower-reared, palatable bugs. This result suggests that mantids had not learned a cue acquired by bugs raised on milkweed; it seems most likely that they learned the luminance-contrast visual cue, although it is possible that other diet-independent cues such as odors were learned as well. All mantids eventually sampled the painted milkweed bugs. Collapsing the data across treatments, aversive responses lasted from 4 to 32 days. Mantids trained on high-contrast bugs retained their aversion almost twice as long as mantids trained on low-contrast bugs (one-way ANOVA, 16.60 ± 2.03 days vs. 8.57 ± 1.88 days, $F_{1,12} = 6.67$, $P = 0.026$, Figure 3C).

DISCUSSION

Aposematic coloration advertises prey unprofitability to a diversity of predator species. Given the prominent role of hue, it is natural to presume that the benefits of aposematic coloration are due primarily to the distinctive hues typical of warning displays. However, many predator species such as mammals and insects are less sensitive to hue and chromatic contrast (Goldsmith 1990; Briscoe and Chittka 2001, respectively). Given the diverse visual capabilities among predators, natural selection may often favor aposematic coloration with generalized signal applicability such as high luminance contrast with background as well as high luminance contrast among components of the coloration pattern.

In order for luminance contrast to be important in the evolution of warning coloration, it should provide the same benefits that have been documented with chromatic contrast. A conspicuous pattern can be costly in the sense that naive predators can readily detect and attack conspicuous prey. However, benefits of conspicuousness are presumed to offset this disadvantage when prey is unpalatable (Ruxton et al. 2004). Two functional benefits of conspicuousness in aposematic coloration have been identified: increased rate of predator aversion learning (Gittleman and Harvey 1980; Roper and Redstone 1987; Lindström et al. 1999) and improved predator memory retention (Roper and Redstone 1987; Roper 1994). In this study, we demonstrated for the first time that both benefits pertain to an invertebrate predator with limited or no color vision. When Chinese mantids were offered high-contrast prey, they detected the prey sooner. The mantids also learned to avoid high-contrast, noxious prey faster and retained the aversive response longer than mantids trained to avoid low-contrast, noxious prey (Figure 3). Once the aversion was learned, avoidance did not require that bugs had been reared on milkweed, a result consistent with the idea that the mantids learned to avoid bugs on the basis of the luminance contrast cue alone. Our results suggest that warning coloration, specifically the luminance contrast component, could evolve as an effective signal even if a predator lacks sophisticated color vision.

The broader implications of our work depend on the nature of mantid vision. If mantids do not discriminate color, our results imply that the functional benefits of conspicuousness in aposematic displays do not require color vision. This inference might seem particularly surprising given the weight that we humans attach to color vision. If mantids do discriminate colors, then our results imply that luminance contrast alone is sufficient to promote the faster learning and greater memory retention associated with aposematic coloration. This inference has a broad taxonomic context because color vision is probably the norm among potential predators of aposematically colored prey. The 2 inferences are subtly different but both are meaningful. They both suggest aposematic coloration, and its benefits do not depend entirely on prey color contrast.

At present, there is no clear consensus on whether mantids have color vision. Color vision requires at least 2 photoreceptor types with different spectral sensitivities (Kelber et al. 2003). In general, this is achieved with the use of 2 or more opsins that differ in wavelength sensitivity. A molecular study found that mantids possess only a single opsin (Towner and Gärtner 1994). Similarly, 2 electrophysiological studies using different techniques found evidence in mantids for a single visual pigment with maximum sensitivity at human green wavelengths (Sontag 1971; Rossel 1979). These findings suggest that mantids do not discriminate colors; however, a single-opsin pattern is extremely unusual in insects (Briscoe and Chittka 2001). Even close relatives of mantids, such as cockroaches, have been shown to possess dichromatic vision (Briscoe and Chittka 2001). Moreover, color vision does not in principle require more than one opsin; it can be achieved in conjunction with a filtering pigment that alters the photic environment of an opsin. The occurrence of such pigments has not been explored in sufficient detail to rule out the possibility of color vision in this group.

Luminance contrast may also enhance communication between prey and predators with color vision. Aposematic displays are generally multimodal (Ruxton et al. 2004), meaning multiple signals are transmitted to the receiver in more than one sensory modality. The deployment of signals in multiple modalities such as olfaction and vision increase the efficacy in aposematic displays (Rowe 1999). Within a modality, there are usually multiple components. Our results suggest that warning coloration is best regarded and investigated as a visual signal with multiple components. Chinese mantids use luminance contrast information both in learning to avoid unpalatable prey and retaining the aversive response. In a predator with color vision, the simultaneous use of color contrast and luminance contrast might increase the potency of aposematic coloration. Our results indicate that prey luminance contrast with background can confer the benefits of a warning visual signal under carefully controlled laboratory conditions. Future research in aposematic coloration can now address whether prey in nature differ in luminance and chromatic contrast, how the effectiveness of those 2 components change with predator guilds and environmental conditions, and the extent of which any differences relate to prey palatability.

Our results, although novel in the realm of aposematic coloration, are consistent with other visual signal studies. Luminance contrast is an important visual signal in sexual signaling such as mating displays and mate preference in various bird species (e.g., Uy and Endler 2004; Woodcock et al. 2005, respectively). Luminance contrast is also consequential in food selection by foragers. Insect frugivores attend to luminance contrast in foraging decisions especially when the fruit is red, whereas avian frugivores attend to chromatic contrast (Schmidt et al. 2004). Primates locate fruit using information from both luminance and chromatic contrast with

background (Dominy and Lucas 2001). Predatory reef fish attack prey with higher luminance contrast more frequently than prey with lower luminance contrast (Losey 2003). Our results and other examples from the foraging literature attest to a general need to consider how color elements might be tuned to details of a predator–prey interaction, not only in terms of the sensory and cognitive profiles of the predator but also in the contexts where the encounters occur. Future studies of aposematic coloration are now poised to focus on explicit considerations of a visual ecology perspective and the relative roles of chromatic and luminance in aposematic signal evolution.

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