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Ground Anoles (Anolis humilis) Discriminate between Aposematic and Cryptic Model Insects

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ABSTRACT.—Aposematic coloration allows predators to use visual cues to avoid eating potentially toxic or distasteful prey. Predators across many animal taxa actively avoid aposematically colored prey and remember distasteful brightly colored prey longer than cryptically colored prey. Lizards of many species are known to use aposematic coloration when foraging; however, most previous studies investigating the recognition of aposematic coloration by lizards have used live prey. This factor makes it difficult to determine whether lizards rely solely on visual cues or use a combination of sensory cues in prey selection. To determine whether anoles can select prey relying on only visual cues, we investigated the foraging response of Ground Anoles (Anolis humilis) to aposematic prey. By using clay models, we were able to remove any natural olfactory or behavioral cues that lizards may use in prey selection. We presented anoles with aposematically and cryptically colored insect models and found that lizards recognized and avoided aposematic models. This study demonstrates that A. humilis are able to use visual cues alone when selecting prey items. Our findings support previous work demonstrating that aposematic coloration is advantageous for prey, as it decreases the risk of attack by predators. The coloration also benefits predators, as they are able to recognize aposematic prey by sight alone, and avoid expending energy on an unpalatable meal.

RESUMEN.—La coloración aposemática permite a los depredadores utilizar señales visuales con el fin de evitar el consumo de presas potencialmente tóxicas o de sabor desagradable. En varias taxa, los depredadores de animales evitan presas con colores aposemáticos. Además, recuerdan las presas desagradables por más tiempo si estas son de colores brillantes a que si son de colores crípticos. Muchas especies de lagartijas son conocidas por utilizar coloración aposemática al escoger su presa. Sin embargo, la mayoría de los estudios previos que investigan el reconocimiento de coloración aposemática por lagartijas han utilizado presas vivas, lo cual dificulta determinar si las lagartijas se basan únicamente en señales visuales o si usan una combinación de señales sensoriales en la selección de la presa. Para determinar si los anolis pueden seleccionar su presa basados solamente en señales visuales, estudiamos la respuesta de forraje de la lagartija Anolis humilis con presas aposemáticas. Usamos modelos de plastilina para eliminar cualquier señal olfativa o de comportamiento natural que usan las lagartijas para la selección de presas. Se presentaron modelos de insectos de colores aposemáticos o crípticos a los anolis y encontramos que las lagartijas reconocieron y evitaron los modelos aposemáticos. Este estudio demuestra que A. humilis es capaz de utilizar exclusivamente señales visuales al seleccionar presas. Nuestros hallazgos apoyan el trabajo previo que demuestra que la coloración aposemática es ventajosa para la presa y disminuye el riesgo de ataque de los depredadores. La coloración también beneficia a los depredadores, ya que son capaces de reconocer la presa aposemática exclusivamente por la vista y evitar gastar energía en una comida desagradable.

PREDATORS rely on a wide variety of sensory cues to differentiate between potential prey items and unpalatable organisms. Many predators recognize aposematic coloration and patterns to avoid distasteful and potentially toxic prey (Prudic et al., 2007). Aposematic animals have bright coloration, are distasteful or unpalatable, and can be easily recognized by a visual predator (Harvey and Paxton, 1981). Aposematism has evolved multiple times in the animal kingdom and is advantageous to both prey and predator (Sillen-Tullberg and Bryant, 1983). Potential prey benefit from having bright coloration, because it acts as a pursuit-deterrent signal to dissuade predation by organisms that use visual cues in selecting prey (Hasson, 1991). Predators benefit from recognizing aposematic coloration in two ways. First, some prey have enough toxin or venom to cause serious illness or even death if consumed or attacked. For example, the easily recognizable bright colors and pattern of coral snakes deter predation by birds (Wiklund and Järvi, 1982). Second, it is unprofitable for a predator to expend energy in attacking, but not consuming, a distasteful prey item (Hasson, 1991).

Predators respond to aposematic prey via innate avoidance or learned avoidance mechanisms (Lindström et al., 1999), and these mechanisms vary among species. Wild-caught species of European tits preferentially consume cryptically colored prey items over aposematic prey; however, some tit species demonstrate learned avoidance of the prey, whereas others have an innate avoidance (Exnerová et al., 2006). Predators learn to avoid unpalatable prey items faster when they are aposematic than when they are cryptically colored (Sillen-Tullberg and Bryant, 1983). In addition, the more colorful and luminant a distasteful prey item, the longer a predator will remember the unpleasant experience and continue to avoid the prey (Prudic et al., 2007). Predators also will remember more toxic prey for longer and avoid such prey more deliberately than they will less toxic counterparts (Darst and Cummings, 2006).

Many species of lizards have demonstrated avoidance of aposematic insects and their associated characteristics, such as bitterness and distastefulness. Lizards are able to differentiate between colors to modify feeding behavior in the laboratory (Leal and Powell, 2011) and will reject bitter prey items (Stanger-Hall et al., 2001). Lizards are known to use a multimodal combination of cues, such as color, size, shape, and smell, to recognize and avoid unpalatable insects (Tseng et al., 2014). When foraging, Carolina anoles (Anolis carolinensis) use a variety of cues, such as color, size, shape, and smell, to determine whether to attack a prey item (Krall et al., 1999). Visual aposematic cues are important during foraging by...
whiptail lizards (Aspidoscelis inornata) in selecting prey (McGovern et al., 1984), whereas fringe-toed lizards (Acanthodactylus dumerillii) use both visual and olfactory cues in combination to differentiate between distasteful and nondistasteful aposematically colored grasshoppers (Sword et al., 2000). The extent, however, to which lizards are capable of recognizing aposematic insects solely on color-based cues has not yet been determined. Establishing whether lizards can discriminate against aposematic prey based on color alone will help to determine the importance of visual versus olfactory cues in lizard foraging behavior. Because tropical rain forests are filled with visual and olfactory stimuli, it is likely that the ability to perceive and make foraging decisions based on bright colors would be advantageous.

To control for cues elicited by other senses, clay models are a viable alternative to live insects. Clay models lack any familiar scents that organisms may utilize to determine what food is edible, and as a result, predators will be entirely dependent on color recognition. Previous studies have demonstrated clay models to be suitable replacements for live prey items in determining predation levels of aposematic prey, especially when the models move to simulate live organisms (Paluh et al., 2014).

In this study, we investigated whether Ground Anoles (Anolis humilis) would attack aposematic model prey items at a lower frequency than cryptically colored model prey items. We predicted that A. humilis would use color recognition for prey differentiation, because Kawamura and Yokoyama (1998) demonstrated that lizards can detect a wide range of color and Sexton et al. (1966) showed they avoid aposematically colored live organisms; but, the mechanism (e.g., olfactory, color recognition, movement pattern) is unknown. Furthermore, as sit-and-wait predators within the Iguania suborder, A. humilis are likely to rely more heavily on vision in prey selection than scleroglossans (Vitt et al., 2003), or active foraging lizards (Cooper, 1995).

MATERIALS AND METHODS

This study was conducted from 11 to 22 December 2013 at La Selva Biological Station, Heredia, Costa Rica. We collected specimens by walking along marked trails, either in the morning (0800–1130 h) or in the afternoon (1400–1600 h). Trails covered areas of both secondary and primary forest, and we did not collect from the same area twice.

Anolis (Norops) humilis is a small insectivorous species of lizard found from central Costa Rica to Panama (Lieberman, 1986). Anolis humilis Peters was first described in 1863 (Peters, 1863), and also has been defined with the specific epithet quagguclus based on hemipenis morphology (Köhler et al., 2003); however, humilis is still commonly used (Tulli, 2012), and because of overlaps in range and confusion in differentiation between hemipenis morphology in some cases (Köhler et al., 2006), we continue to use the specific epithet humilis. Anolis humilis are sit-and-wait foragers and usually perch on leaf litter and vegetation located near the ground, waiting to attack prey items that come near where they are sitting (Savage, 2002). They are generalized predators, but prefer dipterans, orthopterans, coleopterans, isopods, spiders, and lepidopteran larvae as well as the eggs and pupae of these and other arthropods (Andrews, 1979; Corn, 1981; Guyer, 1988; Vitt and Zani, 1998). There is a wide diversity of flying and crawling insects that A. humilis are likely to encounter at La Selva, including a collection of aposematically colored prey items such as lepidopteran larvae and hemipteran nymphs (McDade, 1994). Anolis humilis at La Selva are therefore a suitable species to test predator discrimination of aposematic prey by using a clay model experiment, because of their opportunistic feeding style and wide variety of natural prey items.

We captured 83 anoles by using either a noose attached to a collapsible fishing rod (Cabela’s, Inc., Sydney, Nebraska, USA) or by hand. We placed anoles in individual plastic bags and transported them to La Selva’s ambient laboratory. Each anole was placed in an individual mesh cage (36 × 36 × 58 cm) and provided water. We allowed the anoles to acclimate overnight without food and then tested their behavior the following morning if caught in the morning, or the following afternoon if caught in the afternoon. Although we were unable to control for how recently the anoles had eaten before capture, model color presented to each anole was random and therefore any variation in hunger levels was consistent across groups and was not a confounding factor.

We created insect models from nontoxic plasticine by using orange clay (product no. 140018, BACO, S.A., Mexico) for aposematic insect models and gray clay (product no. 140017, BACO, S.A.) for cryptic models. The orange models were based on orange and red insects at La Selva, including assassin bugs (Triatominae; McDade, 1994) that are aposematic.

We selected orange for our aposematic models, because even though Anolis aggasizi are attracted to orange and yellow, they also were shown to consume mostly cryptically colored food, and because no orange or yellow organisms were found on the island (Rand et al., 1975). At La Selva, there are many brightly colored aposematic insects, and A. humilis has not been shown to have a preference for orange. Therefore, we concluded that orange would still be an appropriate aposematic model for our experiment. The gray models were based on cryptic lepidopteran larvae and coleopterans that we had observed at the site. Models were designed to be reasonable representations of palatable and unpalatable prey that could be encountered at La Selva, but they were not exact replicas of any specific species. Insect models were 4 mm in length and 2.5 mm in width (Fig. 1). We drew circumferential black stripes on the models with a Sharpie® permanent marker to mimic common insect patterns. We then attached a model to the end of a 75-cm fishing line that was connected to a fishing rod.

During feeding trials, we first removed the mesh covering the top of the cage and allowed 1 min for the anole to acclimate to the change. After 1 min, the tester approached the cage and slowly lowered the model into the cage near the anole. We gently shook the model to simulate an insect flying approximately 4 cm from the anole’s head and slowly moved the model around. By shaking the model, we simulated a flying insect so the models could not be mistaken for fruit or seeds. In addition, moving clay models offer a better simulation of living organisms than do stationary models (Paluh et al., 2014). Trials started as soon as the tester lowered the model into the cage and lasted 90 sec or until the anole attacked the model. An attack was defined as an anole successfully biting, or attempting to bite and missing the model. We alternated trials with orange and gray models, and each anole was tested only once. If an attack occurred, we noted the time to attack as well as the color of the model.

After each trial, we determined the sex of each anole by checking dewlap size and coloration, with males exhibiting large red dewlaps, and females exhibiting small white, or
nonexistent dewlaps. In addition, we measured snout-to-vent length (SVL) of each individual to the nearest 0.01 cm. Before releasing anoles near their site of capture, we marked each anole’s ventral side with a Sharpie permanent marker to avoid resampling. We released all specimens the same day they were tested and no more than 28 h after initial capture.

We used a generalized linear model binomial logistic regression to determine which measured variables influenced A. humilis to attack. The predictor variables were model color, anole sex, anole SVL, and anole sex × SVL interaction. Anole sex, SVL, and sex × SVL were included in the model to ensure there were no confounding factors affecting color selection or attack rate. All statistical analyses were performed using RStudio (vers. 0.98.1091), with α = 0.05. Descriptive statistics are reported as means ± SD.

RESULTS

We captured and tested 56 male and 27 female A. humilis. The mean SVL was 30.2 ± 0.32 mm for males and 33.1 ± 0.35 mm for females. Of the 83 anoles tested, only 21 attacked the presented model. Neither the interaction between SVL and sex [P = 0.705, Exp(B) = 1.95], nor the additive factors of sex [P = 0.115, Exp(B) = 1.95] or SVL [P = 0.536, Exp(B) = 1.45] were significant in predicting the likelihood of attack. Color was the only variable that was significant and included in the final model. Of the anoles that attacked, 19 attacked the gray model and 2 attacked the orange model (Fig. 2). Anoles were more likely to attack gray models than orange models [P = 0.0004, Exp(B) = 16.1].

DISCUSSION

Our study demonstrates that A. humilis were much more likely to attack gray models than orange models. Another anole species, A. carolinensis, also use aposematic coloration when selecting prey items, being less likely to eat aposematic insects unless they have been starved (Seaston et al., 1996). Previous studies of predator recognition of aposematic prey in both birds (Sillen-Tullberg and Bryant, 1983; Exnerová et al., 2006) and lizards (Seaston et al., 1996; McGovern et al., 1984; Krall et al., 1999; Stanger-Hall et al., 2001) have used live insects, whereas we used clay models. Using live models is advantageous because the predator is more likely to attack during the trial; however, live models have confounding factors, including odor, insect behavior, and previous interactions with the prey. The clay models we used were visually identical except for color; emitted no natural chemical signals; and were similar to, but not exact replicas of, a specific insect. Therefore, we concluded that A. humilis avoid aposematic prey items based on color recognition without the aid of natural olfactory or behavioral cues.

In general, A. humilis were most likely to avoid attacking plasticine insect models of any color, suggesting that anoles exhibit neophobia, dietary conservatism, or both, as is known in some bird species (Jones, 1986; Marples et al., 1998). In this study, we presented anoles with insect models that were similar to, but not exact replicas of, prey at La Selva; for this reason, they could have treated the prey cautiously. Stress from capture and observer activity also could have contributed to low attack rates. Nevertheless, many anoles in our sample did attack and demonstrated marked and significant bias based on prey color.

The mechanism leading to avoidance of aposematic coloration, whether innate or learned, cannot be precisely determined from our study; but, lizards are able to taste bitterness (Stanger-Hall et al., 2001) and also able to change foraging behavior based on color recognition (Leal and Powell, 2011). Furthermore, tree lizard Japalura swinhonis that have previously encountered aposematic weevils are able to avoid these prey items at a much greater rate than naive tree lizards, suggesting learned avoidance (Tseng et al., 2014). In addition, a significantly higher percentage of experienced tree lizards attacked weevils that had been painted cryptic colors, indicating a strong reliance on coloration to avoid distasteful insects (Tseng et al., 2014). Future studies in aposematism recognition could aim to better understand the role of learning versus innate behaviors in prey selection in this species.

In conclusion, this study demonstrated that A. humilis recognizes and avoids attacking potential prey items with aposematic coloration. We demonstrated the value of clay model experiments with lizards to determine foraging behavior based on visual cues alone, rather than with live prey. Our findings complement previous work demonstrating the benefit
of aposematic coloration both for prey in avoiding predation, and for predators in avoiding energy expenditure for an unpalatable meal.

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LITERATURE CITED


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