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Experimental Evidence for Aposematism in the Dendrobatid Poison Frog *Oophaga pumilio*

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Brightly colored poison frogs of the family Dendrobatidae contain an alkaloid-based chemical defense against predation. The bright coloration of these frogs is generally considered an aposematic signal to potential predators; however, relatively few studies have specifically tested this hypothesis. Herein we report the results of a field-based experiment designed to test the hypothesis of aposematism in the dendrobatid frog, *Oophaga* (= *Dendrobates*) *pumilio* from the La Selva Biological Station, Costa Rica. We used plasticine frog models to evaluate natural predation rates as a function of color. Predation rates on brown models were almost twice that of red models, suggesting that predators avoid brightly colored frog models. Birds accounted for the majority of attacks on the models. The results of this study provide experimental evidence in support of the hypothesis that bright coloration in dendrobatids functions as an aposematic signal to predators.

IN chemically defended organisms, conspicuous coloration and/or patterns generally function as an advertisement of unpalatability or noxiousness to potential predators (aposematism; Poulton, 1890; Cott, 1940). The use of aposematic (or warning) signals is well documented among animal taxa, including invertebrates, fishes, amphibians, snakes, and birds (Edmunds, 1974; Ruxton et al., 2004). The effectiveness of aposematic signals is dependent on the ability of predators to form an association between conspicuous coloration and unprofitability, which results in prey avoidance (Ruxton et al., 2004; Mappes et al., 2005). Avoidance is generally a learned response based on previous experiences, but in some instances prey avoidance is an innate response (Smith, 1975; Pough, 1988; Ruxton et al., 2004).

Certain members of the family Dendrobatidae are well known for their conspicuous colorations/patterns and presence of skin alkaloids, which appear to act as a chemical defense against predation (Daly et al., 2005). Some dendrobatid species are unpalatable, and in certain cases toxic (Daly and Myers, 1967), to various potential invertebrates and vertebrates (Brodie and Tumbarello, 1978; Fritz et al., 1981; Szelistowski, 1985). On the basis of this information, the conspicuous coloration of alkaloid-containing dendrobatids is generally believed to function as an aposematic signal (Myers and Daly, 1983; Pough et al., 2001; Summers and Clough, 2001), but little experimental evidence exists in support of this hypothesis.

In recent years, the evolution of conspicuous coloration in dendrobatid frogs has received a great deal of attention (Summers and Clough, 2001; Hagman and Forsman, 2003; Santos et al., 2003). Using a variety of comparative approaches, both single and multiple origins of aposematism have been proposed for dendrobatids (Summers and Clough, 2001; Santos et al., 2003; Vences et al., 2003). Organisms that are aposematically colored are often mimicked by other species (Cott, 1940; Edmunds, 1974), and accordingly, both Batesian and Müllerian mimicry have been suggested to explain the striking coloration of certain species of dendrobatids (Nelson and Miller, 1971; Symula et al., 2001; Darst and Cummings, 2006). Recently, Darst et al. (2006) and Darst and Cummings (2006) experimentally demonstrated that naïve domestic chickens could learn to associate conspicuous coloration with unpalatability and avoid certain species of dendrobatids (*Ameerega* [= *Epipedobates*; Grant et al., 2006] *parvulus*, *A. bilineatus*, and *A. hahneli*), which suggests that coloration may function as an aposematic signal to natural predators.

To test experimentally the hypothesis that conspicuous coloration in dendrobatids functions as an aposematic signal to natural predators, we conducted a field-based predation experiment using plasticine model replicas of the dendrobatid frog, *Oophaga* (= *Dendrobates*; Grant et al., 2006) *pumilio*, and brown leaf-litter frogs that resemble members of the genus *Craugastor* (= *Eleutherodactylus*; Frost et al., 2006) at La Selva Biological Station in northeastern

Costa Rica. Plasticine models have been used successfully as an experimental approach to study aposematism and mimicry in millipedes, snakes, and salamanders (Brodie, 1993; Brodie and Moore, 1995; Kuchta, 2005). *Oophaga pumilio* is a common leaf-litter frog at La Selva Biological Station, characterized by the presence of alkaloids, conspicuous reddish-orange dorsal color, and blue-black appendages (Guyer and Donnelly, 2005). *Oophaga pumilio* occurs microsympatrically with several brown (or cryptic; Savage and Emerson, 1970) colored leaf-litter frogs of similar size (mainly of the genus *Craugastor*). If bright coloration functions as an aposematic signal to predators, we expected to find a reduced number of attacks (a measure of predator avoidance) on red colored models of *O. pumilio* as compared to brown models of other leaf-litter frogs.

MATERIALS AND METHODS

Model design.—Our methods largely follow those of Brodie (1993). We constructed frog models by hand using precolored, non-toxic plasticine modeling clay (Sculpey III®). Previous studies have demonstrated that soft modeling clay will retain impressions from predation attempts and is an ideal medium from which to construct experimental models (Madsen, 1987; Brodie, 1993). We constructed two types of models: models with red bodies and blue appendages, representing the dendrobatid frog *O. pumilio*, and models with brown bodies and appendages, representing the common brown leaf-litter frogs present in the area (e.g., *Craugastor* species; Fig. 1). *Oophaga pumilio* does not exhibit appreciable levels of UV reflectance (Summers et al., 2003), and therefore model colors were chosen by eye, on the basis of comparisons with live animals. To ensure that UV reflectance did not influence the results of this study, we measured the reflectance of each model type using a portable spectrometer (Ocean Optics S2000) and found no UV reflectance for Sculpey III®. We used a black permanent marker to place eyes on each of the models. Each model was approximately 20 mm in snout-to-vent length (the average size of *O. pumilio* in the region).

Experimental design.—To assess predation under natural conditions, we placed 800 frog models along 40 transects throughout La Selva Biological Station, Costa Rica between 14 June and 20 July 2006. To ensure that we represented the diversity of habitats present at La Selva, we placed 12 transects in non-overlapping areas of old-growth, secondary, and agro-forestry sites (for a total of 36 transects) and four transects in the arbore-

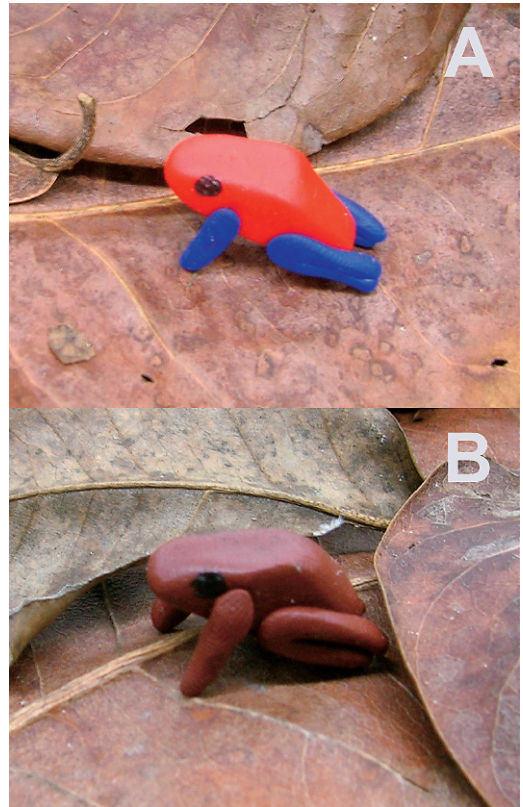


Fig. 1. Plasticine model of *Oophaga pumilio* (A) and brown colored frog (B) placed on leaf-litter.

tum. Each transect was 100 m long and contained ten models of each color type (20 models per transect). We placed individual models in random order every five meters along the transect line. To prevent clumping of color types, we ensured that every 50 m along a transect contained a random assortment of five red and five brown colored models (Kuchta, 2005). Transects were separated by at least 100 m. One-half of the transects contained models that were placed directly on the forest floor, representing a natural setting (20 transects). To account for the possibility that cryptic coloration affected attack rates of models placed on the forest floor (i.e., reduced attack rates on brown models), models for the other half of the transects were placed on 9.5 × 10.5 cm sheets of white “Rite in the Rain®” paper (20 transects). Models of either color placed on a white background should be equally visible to potential predators, resulting in a measure of predator avoidance versus an effect of cryptic coloration (Brodie, 1993). After 48 hours, we collected all models from each transect and recorded the number of attacks.

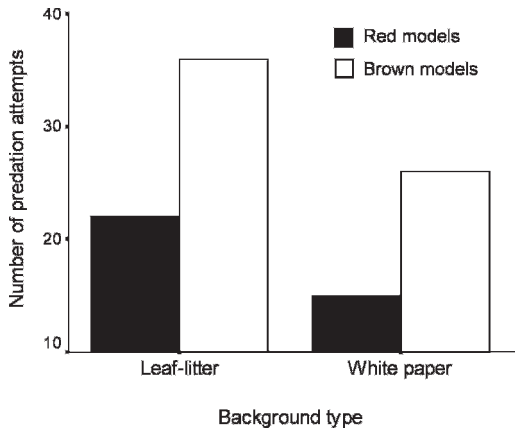


Fig. 2. Total number of predation attempts on red and brown models for each background type.

Quantifying predation and statistical design.—We assessed each model for the presence/absence of attacks and assigned each attack mark to a predator type, which included birds, mammals, ants, and unidentified predators. We considered multiple marks on a single model as a single predation attempt. We recorded models that could not be found after 48 hours as missing, and performed statistical tests including missing models as both “predation events” and “non-predation events.” Brodie (1993) suggested that consecutive attacks on models along a transect may be due to the same individual predator. To ensure that this did not influence our results, we analyzed attack data “including” and “not including” models that were attacked consecutively along a transect. We used binary logistic regression to determine if ‘frog model color’ and ‘background type’ were significant predictors of predation (rates). All statistical analyses were performed using SPSS v. 11.5 for Windows.

RESULTS

Of the 800 models placed on our transects, predators attacked 99 models (12.4%) and 24 models were missing (3.0%). ‘Frog model color’ was a significant predictor of predation, and brown models were attacked at almost twice the rate of red models ($P = 0.007$; odds ratio = 1.83; $CI_{0.95} = 1.19, 2.84$; Fig. 2). These data were analyzed assuming that missing models were not preyed upon; however, the results are essentially unchanged when we include missing models as being preyed upon (data not shown). There was no difference in predation rates when consecutive models were included and excluded from the analysis (data not shown). Models placed directly on leaf-litter were attacked more fre-

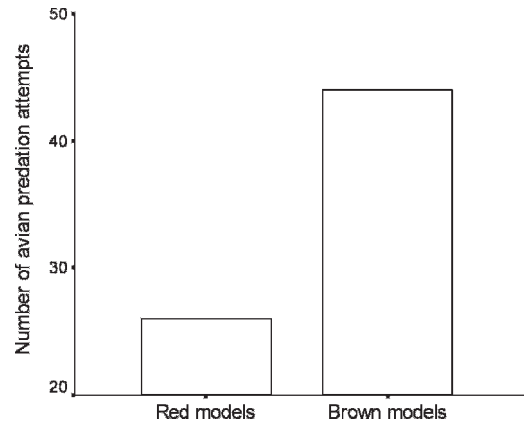


Fig. 3. Total number of avian predation attempts on red and brown models.

quently than models placed on white backgrounds (Fig. 2); however, ‘background type’ was not a predictor of predation ($P = 0.063$; odds ratio = 1.51; $CI_{0.95} = 0.99, 2.34$).

Birds made the majority of predation attempts on models, accounting for 72% of the attack marks, and were recognizable by distinctive U-shaped or V-shaped marks on the models (Brodie, 1993). In many cases, multiple predation attempts by the same bird were apparent on a single frog model. Birds attacked brown models at almost twice the rate of red models, and ‘frog model color’ was a significant predictor of bird predation ($P = 0.018$; odds ratio = 1.84; $CI_{0.95} = 1.11, 3.06$; Fig. 3). Mammals accounted for 5% of the attacks on models and were characterized by teeth marks. The shapes of the teeth imprints on the models suggest that the majority of mammal attacks were from small rodents. Unknown predators accounted for 23% of the marks on models. The majority of these marks appeared bird-like; however, they lacked some component of the characteristic U- or V-shape. Other marks included small symmetric holes that resembled fang imprints, deep slits, and a variety of non-descript holes. Some of the models contained marks from ant mandibles (likely *Atta* spp.); however, these were not recorded as predation attempts.

DISCUSSION

Aposematism and predation.—The results of our study experimentally demonstrate that natural attacks on red frog models occur at a lower rate than attacks on brown frog models. Furthermore, these differences in attacks are the same for models placed on natural backgrounds as well as white backgrounds, suggesting that the lower

number of attacks on models of *O. pumilio* is the result of predator avoidance. Therefore, our findings are consistent with the hypothesis that conspicuous coloration in *O. pumilio* functions as an aposematic signal to potential predators.

Although it appears clear that predators are avoiding the conspicuously colored models of *O. pumilio*, it should be noted that the number of colors differed between model types: models of *O. pumilio* had two colors (red and blue), whereas models of brown frogs had one color (brown). Therefore, we cannot rule out the possibility that differences in predator avoidance were due to predator's abilities to distinguish two colors (and potentially avoid them) as opposed to avoiding conspicuous coloration in general. However, it is most likely that both of these colors account for the aposematic signal in *O. pumilio*, and the difference in the number of colors on the models themselves did not influence the results of this study.

The total number of frog models attacked on white backgrounds was lower than the number attacked on the forest floor. Although background type was not a significant predictor of predation in our model, the marginal *P*-value (0.063) suggests that background type may influence the response of predators. It appears that some predators may have been 'suspicious' of white paper and avoided attacking models placed on this background type. Avoidance of white paper does not appear to have influenced the results of our experiment, but is something that should be considered in future experiments.

Birds are common predators of frogs in the Neotropics (Stiles and Skutch, 1989; Poulin et al., 2001) and represent the largest group of predators on frog models in our study. Color vision is well known among birds, and it is likely that they are able to detect the conspicuous coloration of *O. pumilio* (as well as other dendrobatid frogs; Hart, 2001; Siddiqi et al., 2004). The lower number of attacks by birds on conspicuously colored models suggests that birds are able to discriminate between colors and avoid preying on chemically defended prey. Although generally avoided, birds did attack a small number of red models, suggesting that some birds are not deterred by conspicuous coloration. These results may be due to the presence of naïve bird predators and/or the possibility that some birds are able to successfully prey on *O. pumilio*. The latter assumption is supported by predation on other dendrobatids, namely *Dendrobates auratus*, by adult rufous motmots (*Baryphthengus marhi*; Master, 1998).

Unknown predators accounted for the majority of the remaining predation attempts on *O.*

pumilio models. Although most of these predation attempts were likely from birds, it is interesting to note the presence of puncture marks that are consistent with fangs on some of the models, which suggests that snakes and possibly spiders attacked models. Both snakes and spiders are common predators of small frogs (Poulin et al., 2001), and snakes have cones in their retina and may be able to detect color (Repérant et al., 1992). The snake *Liophis epinephelus* has been reported to prey on *Phyllobates terribilis* (Myers et al., 1978) and *O. pumilio* (J. W. Daly, pers. comm.), and the snake *Coniophanes fissidens* has been observed to attack *O. pumilio* (M. A. Donnelly, pers. obs.). Both of these snakes occur at La Selva (Guyer and Donnelly, 2005) and may be natural predators of *O. pumilio*. In addition, the tarantula *Sericopelma rubronitens* is known to prey on *D. auratus* (Summers, 1999), and tarantulas may also prey on *O. pumilio* at La Selva.

Color variation in Oophaga pumilio.—Although populations of *O. pumilio* in Costa Rica are generally red or reddish orange with black to bright blue appendages, populations in the Bocas del Toro region of Panama exhibit extreme variation in color, spanning the spectrum from blue to red, including black and white (Myers and Daly, 1983; Summers et al., 2003). This extreme color diversity among populations does not appear to be explained by Müllerian mimicry (Summers et al., 1997), suggesting that factors other than predation may also be important in explaining color variation. Summers et al. (1999) suggest that color variation is the result of sexual selection, particularly the use of visual cues in mate selection, and Siddiqi et al. (2004) suggest that color in *O. pumilio* is an effective signal to conspecifics and potential avian predators. It is therefore possible that conspicuous coloration in *O. pumilio* functions as both an aposematic and mating signal.

The tremendous variation in color of *O. pumilio* over a relatively small geographic area is especially intriguing with respect to its function and effectiveness as an aposematic signal. Siddiqi et al. (2004) suggest that conspicuous coloration in *O. pumilio*, regardless of specific colors (and patterns), is likely effective as a warning signal to potential predators. However, there is also evidence that differences in coloration play a role in the vulnerability of certain prey to visually orientated predators (e.g., Forsman and Shine, 1995; Kingsolver, 1996; Forsman and Appelqvist, 1999). Further studies are necessary to provide additional information regarding predator responses to different color morphs of *O. pumilio*.

The association between conspicuous coloration and chemical defense in dendrobatids has generally been accepted as an example of aposematism. The findings of our study experimentally demonstrated that conspicuous coloration in *O. pumilio* from northeastern Costa Rica functions as an aposematic signal to potential predators. These results suggest that conspicuous coloration in other dendrobatids may also be aposematic.

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