# Frog or Fruit? The Importance of Color and Shape to Bird Predators in Clay Model Experiments

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Clay model experiments are commonly used to measure natural rates of predation and have become an important method in studying predator avoidance of aposematic frogs. Previous clay model experiments have demonstrated that conspicuous coloration in dendrobatid frogs is an effective deterrent to avian predators. It is generally assumed that predators recognize clay models as frogs, but few studies have examined this hypothesis. Certain aposematic frogs are similar in color to fruits on the forest floor, and it is possible that frugivorous or omnivorous birds perceive clay models as fruit. In the present study, we further investigate aposematism in *Oophaga pumilio* and specifically examine the importance of model shape and color. We assessed natural avian predation rates using clay models, which were either red or brown in color, and frog or ball (fruit) shaped. Overall, avian predation was significantly higher on red ball-shaped models when compared to red frog-shaped models. Brown frogs were also more likely to be preyed upon than red frogs. The omnivorous Great Tinamou (*Tinamus major*), however, exhibited no preference for frog color. Feeding naturally on fruits and seeds, tinamous in our study preferred and attacked red ball models more frequently, suggesting that they recognized these models as fruits. Collectively, our results provide evidence that birds distinguish between shapes and colors when making decisions about predation and that these attacks are dependent on the dietary preference of the predator. Clay model studies should take into account both color and shape of models, and consider that predation rates are likely dependent on the species assemblages present at a location and their specific dietary preferences.

CHEMICALLY defended prey often display conspicuous colors as visual aposematic (or warning) signals of unpalatability or toxicity to natural predators (Poulton, 1890; Cott, 1940; Edmunds, 1974). This type of signaling is a relatively widespread defense adaptation and is found in a diversity of animal taxa, including mollusks, arthropods, fishes, amphibians, reptiles, birds, and mammals (see Ruxton et al., 2004 for review). Avoidance of aposematic prey is largely based on a predator's ability to detect and recognize specific color signals, and this can be a learned or innate behavioral response (Servedio, 2000; Endler and Mappes, 2004; Ruxton et al., 2004; Mappes et al., 2005).

Many frogs within Dendrobatidae exhibit conspicuous coloring that indicate to predators the unpalatability (and in some cases toxicity) associated with their alkaloid-based chemical defenses (Summers and Clough, 2001; Siddiqi et al., 2004; Saporito et al., 2007, 2012). Common predators of frogs in the Neotropics include birds (Stiles and Skutch, 1989; Poulin et al., 2001), which can utilize their color vision to detect and differentiate prey (Hart, 2001; Siddiqi et al., 2004; Aronsson and Gamberale-Stille, 2008). Recently, avian visual modeling has provided evidence that birds can detect specific color differences in dendrobatids (e.g., Siddiqi et al., 2004; Maan and Cummings, 2012; Richards-Zawacki et al., 2013; Willink et al., 2013; however, see Crothers and Cummings, 2013 for discussion on avian vision and frog brightness). Certain birds recognize and avoid aposematic dendrobatids (e.g., Comeault and Noonan, 2011; Chouteau and Angers, 2012; Amézquita et al., 2013; Paluh et al., 2014), and in some cases learn to avoid them (e.g., Darst and Cummings, 2006; Stuckert et al., 2014). Collectively, these findings suggest that coloration in dendrobatids is perceived as a warning signal to some avian predators, resulting in avoidance of these frogs as prey.

Clay model experiments are commonly used to quantify natural predation on prey (Brodie and Moore, 1995; Kuchta,

2005; Marek et al., 2011; Mochida, 2011; Valkonen et al., 2011), and have recently become an important tool for studying aposematism in dendrobatids (Saporito et al., 2007; Noonan and Comeault, 2009; Comeault and Noonan, 2011; Chouteau and Angers, 2011, 2012; Hegna et al., 2011, 2012; Stuart et al., 2012; Amézquita et al., 2013; Richards-Zawacki et al., 2013; Paluh et al., 2014; Rojas et al., 2014; Willink et al., 2014). Model replicas of dendrobatids have largely been made of clay (see Amézquita et al., 2013 and Rojas et al., 2014 for use of wax), which retains predator impressions (i.e., attack marks) and allows for an indirect measure of predation, and in some cases, specific predator identity. Most studies are conducted with stationary models (however, see Paluh et al., 2014) that are placed on the forest floor for a set period of time and then collected and assessed for predation. Based on these types of experiments, birds represent the major predator of frog models (e.g., Comeault and Noonan, 2011; Chouteau and Angers, 2012; Hegna et al., 2012). Clay models are constructed to appear similar in size, shape, and color to dendrobatids, and it is generally assumed that birds recognize them as frog prey, yet this has not been explicitly tested. Although some birds probably recognize models as dendrobatid frogs and avoid them, some aposematic colors (e.g., red, orange, blue) are similar in color to fruit and may act as an attractant to frugivorous or omnivorous birds (Willson et al., 1990; Puckey et al., 1996; Gamberale-Stille and Tullberg, 2001). Stationary frog models may superficially resemble fruits found on the forest floor, especially when experiments are conducted in locations with similarly sized and colored fruits. Model experiments are generally presented to free-ranging bird communities, which can include frugivores, omnivores, and carnivores, yet identifying bird species based on beak imprints alone is difficult (however, see Paluh et al., 2014 and Willink et al., 2014). In previous clay model experiments, all avian attacks on aposematic frog models have

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been considered predation events (e.g., Saporito et al., 2007; Hegna et al., 2011, 2012), but it is possible that some birds recognize and attack models expecting them to be fruits. If this were the case, then mistaken attacks would overestimate the presumed degree of predation on aposematic frogs. Therefore, understanding how natural bird communities respond to different colored and shaped clay models (e.g., those shaped like fruits vs. those shaped like frogs) may provide valuable information on how certain birds perceive clay frog models, especially in areas with fruit-colored frogs.

In northeastern Costa Rica, the strawberry poison frog *Oophaga pumilio* is characterized by its red-orange dorsal coloration (Guyer and Donnelly, 2005) and is commonly found on the forest floor alongside a number of similarly colored fruits. Numerous stationary model experiments have been conducted with *O. pumilio* in this region and have shown their coloration to be an effective deterrent to avian predators (Saporito et al., 2007; Hegna et al., 2011; Stuart et al., 2012); however, it is possible that some red frog models are perceived as fruits and attacked by frugivorous or omnivorous birds. To gain a better understanding of how avian predator communities perceive the shape and color of clay models at this location, a stationary clay model experiment similar to that of Saporito et al. (2007) was conducted. In particular, avian predation upon red frog-shaped models of *O. pumilio* and brown frog-shaped models (resembling palatable frogs) were compared to red and brown ball-shaped models of similar size, which were constructed to superficially resemble fruits.

## MATERIALS AND METHODS

This study took place at the La Selva Biological Research Station in northeastern Costa Rica. *Oophaga pumilio* is a common leaf-litter frog at this location characterized by its diurnal activity, alkaloid-based chemical defenses, and conspicuous reddish-orange dorsal coloration and blue-black appendages (Guyer and Donnelly, 2005). Many brown colored, diurnally active, leaf-litter frogs (e.g., members of genus *Craugastor* and *Pristimantis*) are also found in the same microhabitat as *O. pumilio* and are of similar size (Saporito et al., 2007), yet they lack defensive chemicals and are considered palatable to potential predators. There are a number of red fruits commonly found on the forest floor at La Selva that may superficially resemble red frog models and be attacked by frugivorous or omnivorous birds. Some of these include the fruits of *Anthurium flexile*, *Chamaedorea pinnatifrons*, *Chilone venosa*, *Marcgravia mexicana*, *Miconia barbinervis*, *Pouteria reticulate*, *Virola koschnyi*, and *Virola sebifera*.

*Model design.*—Frog models were constructed using a rubber mold following the methods of Hegna et al. (2011), and legs were constructed and attached to the body by hand. Precolored, non-toxic plasticine modeling clay (Sculpey III®) was used to make models. This soft clay has been shown to preserve impressions of predation attempts (e.g., Madsen, 1987; Brodie, 1993; Saporito et al., 2007) and has no UV reflectance (Saporito et al., 2007). Summers et al. (2003) found that *O. pumilio* has no UV reflectance, suggesting that avian predators are not utilizing reflected light in the UV range to detect these poison frogs. Four model types were constructed: (1) red-bodied frog models with blue appendages (representing *O. pumilio*); (2) completely brown frog models (representing common leaf-litter frogs in the genus *Craugastor* or *Pristimantis*); (3) red balls
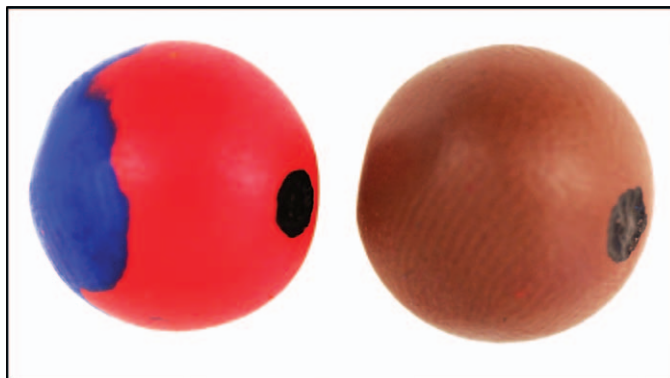


**Fig. 1.** Red ball-shaped model (left) and brown ball-shaped model (right). Models were given two eyes (only one shown here).

with a small blue region, to control for the blue appendages on models of *O. pumilio*; and (4) completely brown balls (see Saporito et al., 2007 for images of frog models; see Fig. 1 for images of ball models). To create more lifelike frogs, black eyes were drawn on the frog models with a permanent marker (Sharpie Fine Tip®). Ball models were rolled into a spherical shape by hand, and to control for the appearance and chemical cues of the permanent marker, black eyes were also drawn on the balls. All ball models were made with the same amount of clay as frog models, and were approximately the same size. Following Saporito et al. (2007), Red Hot Red (Sculpey III color 583) and Blue (Sculpey III color 063) clay were used to construct red models, and Chocolate Brown (Sculpey III color 053) clay was used to construct brown models.

*Experimental design.*—Eight hundred models (200 red frogs, 200 red balls, 200 brown frogs, and 200 brown balls) were placed along 40 100-meter transects. Models were placed throughout La Selva Biological Station, Costa Rica between 1 July and 12 July 2008. Transects were placed at least 100 m away from one another, each transect contained an equal number of red and brown models of the same shape, and every model was placed 5 m apart. Placement of models was randomized with a coin toss, but no more than two of either model type were placed consecutively along a single transect. Models were placed directly on leaf-litter, eyes facing forward (see Fig. 1), and 1 m away from the transect line (following Saporito et al., 2007). All models were collected after 48 hours in the field and were examined for predation attempts. In an attempt to identify specific predators, a Cuddeback EXcite (C-2000) digital game-trail camera was placed at a subset of the model locations. All cameras were placed at least 1 m in distance from a model, and the motion/heat detector sensitivity was set to high.

*Statistical analyses.*—Each model was assessed for predation attempts upon collection. On the basis of Saporito et al. (2007), each mark (i.e., impression) was assigned to one of four categories: (1) bird; (2) mammal; (3) arthropod; or (4) unidentified. Only marks left by birds were considered predation attempts, as mammals and arthropods rely largely on non-visual cues (olfaction and chemoreception) in detecting prey and are likely attracted to clay independent of its color, pattern, or shape (Bell and Cardé, 1984; Vander Wall, 1998; Valkonen and Mappes, 2012). Bird predation attempts were recognizable by distinctive U or V-shaped
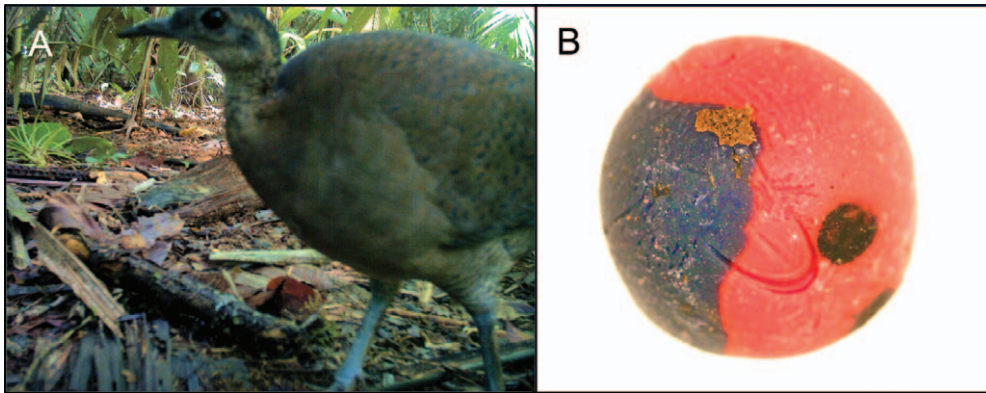
**Fig. 2.** (A) Image of Great Tinamou (*Tinamus major*) captured on game-trail camera trap; (B) red ball model with beak imprint from Great Tinamou.

marks and/or large indentations on the models (Brodie, 1993; Niskanen and Mappes, 2005; Paluh et al., 2014). In most cases, identifying specific beak impressions was not possible; however, one of the game-trail cameras captured a Great Tinamou (*Tinamus major*) preying upon a red ball-shaped model (Fig. 2). On the basis of its distinct beak imprint (see Fig. 2 and Willink et al., 2014), the Great Tinamou represented 35% of all avian predation upon models, and separate statistical analyses were conducted for this species. If multiple marks were found on a single model, they were counted as a single predation attempt. If consecutive attacks occurred within the same transect, they were assumed to have occurred by the same predator (Brodie, 1993; Saporito et al., 2007). Binary logistic regression was used to determine if model shape and color were significant predictors of predation. Statistical tests were run including and excluding consecutive attacks and missing models. All statistical analyses were performed using SPSS v. 18 for Mac.

## RESULTS

Of the 800 frog and ball models (400 red and 400 brown) placed on transects, 193 models (24%) contained identifiable imprints, 25 models (3%) were missing, and 22 models (<3%) had marks that could not be identified. Bird attacks represented the majority of identifiable imprints (111 models or 58%), which accounted for 14% of the overall marks on the 800 models.
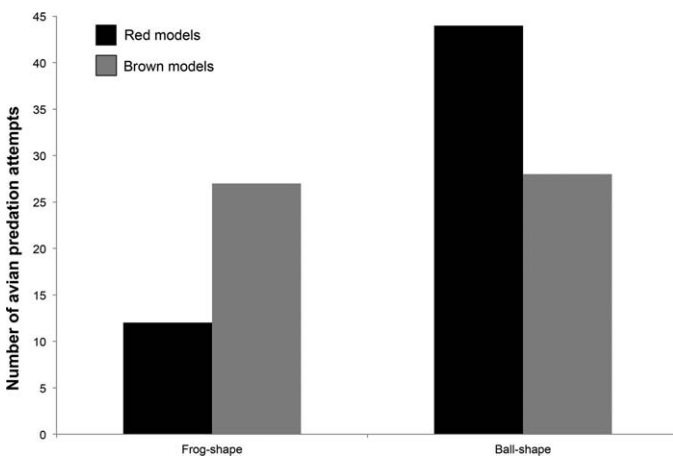
***Overall bird predation.***—Avian predators attacked a total of 12 red frog models (6%), 27 brown frog models (14%), 44 red balls (22%), and 28 brown balls (14%; Fig. 3). 'Frog model color' was a significant predictor of avian predation, and brown frog models were attacked at more than twice the rate of red frog models ($P = 0.014$; Exp(B) = 2.5; $CI_{0.95} = 1.2$, 4.9). 'Model shape' was a significant predictor of avian predation for red models ($P \leq 0.001$; Exp(B) = 4.4; $CI_{0.95} = 2.3$, 8.7), and red ball models were attacked at more than four times the rate of red frog models. However, 'model shape' was not a predictor of predation for brown models ($P = 0.885$). 'Ball model color' was also a significant predictor of predation ($P = 0.039$; Exp(B) = 0.6; $CI_{0.95} = 0.3$, 1.0), and red ball models were attacked by birds more often than brown ball models. No differences in predation rates were found when consecutive model attacks were included and excluded from the data analysis (data not shown).

***Great Tinamou predation.***—The Great Tinamou (*Tinamus major*) accounted for 35% of all bird predation, and attacked a total of five red frog models (3%), six brown frog models (3%), 19 red ball models (10%), and nine brown ball models (5%; Fig. 4). 'Frog model color' was not a significant predictor of predation by the Great Tinamou ($P = 0.760$), and there was no difference in predation between red frogs and brown frogs. 'Model shape' was a significant predictor of predation for red models ($P = 0.006$; Exp(B) = 4.4; $CI_{0.95} = 4.1$, 11.2), and red ball models were attacked at more than four times the rate of red frog models. However, 'model



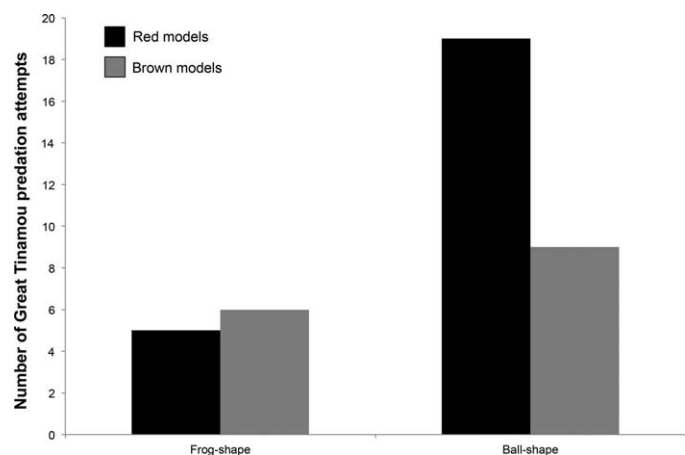**Fig. 3.** Total number of avian predation attempts upon different model types.



**Fig. 4.** Total number of predation attempts by the Great Tinamou upon different model types.

shape' was not a predictor of predation for brown models ($P$ = 0.433). 'Ball model color' was not a significant predictor of predation by the Great Tinamou ($P$ = 0.055), although there was a marginal trend for the Great Tinamou to attack red ball models more than brown ball models. No differences in predation rates were found when consecutive model attacks were included and excluded from the data analysis (data not shown).

*Other model imprints.*—Arthropods left imprints on 5.3% of all models and mammals left imprints on 2.3% of all models, but there was no difference in the number of impressions among model types ($P$ > 0.05 for all comparisons).

## DISCUSSION

Clay model experiments are commonly used to measure natural predation on prey and have become an important tool in studying predator avoidance of aposematic frogs. Most studies have found birds to be the major predators in model experiments (e.g., Saporito et al., 2007; Comeault and Noonan, 2011; Chouteau and Angers, 2012; Paluh et al., 2014), and the results of our study are consistent with this finding. In some cases, aposematic frogs can be similar in color to fruits on the forest floor, and it is possible that frugivorous or omnivorous birds perceive some clay model frogs as fruits. The results of our study demonstrate that natural free-ranging birds can differentiate between frog- and fruit-shaped models, and suggest that color and shape are important characteristics used by birds to identify different food types.

On the basis of our study, red ball-shaped models are four times more likely to be attacked by avian predators than red frog-shaped models. These findings suggest that birds recognize and prey upon different shaped models. It is likely that red ball-shaped models were considered edible fruits by certain frugivorous or omnivorous birds, whereas red frog-shaped models were recognized as the aposematic frog *Oophaga pumilio* and avoided. Avian predation was also greater on brown frog models when compared to red frog models, which is similar to Saporito et al. (2007) and Paluh et al. (2014), and provides additional evidence that birds recognize our models as frogs and most often avoid those that are similar in color and shape to *O. pumilio*. Interestingly, there was no difference in avian predation between brown frog-shaped models and brown ball-shaped models. It is possible that birds were not able to discriminate between brown shapes; however, it is more likely that both brown model shapes were considered palatable prey items and attacked equally by avian predators. Brown frog models were constructed to represent palatable frogs (members of *Craugastor* and *Pristimantis*), whereas brown ball models likely represented edible fruits or seeds. Birds attacked red ball-shaped models significantly more often than brown ball-shaped models, which could be due to a preference for red fruits by frugivorous or omnivorous birds present at La Selva. Some studies have found that frugivorous birds prefer red-colored fruits (Willson, 1994; Puckey et al., 1996; Hartley et al., 2000), whereas other studies have demonstrated that preferences for certain fruit colors are extremely variable (Willson et al., 1990; Willson and Comet, 1993). Red colored models may also appear more conspicuous and have a higher contrast with the forest floor (e.g., Siddiqi et al., 2004; Maan and Cummings, 2012; Willink et al., 2014); thus, higher predation on red ball-shaped models may

simply be associated with their being easier to locate by bird predators.

Birds are common predators of frogs, fruits, and seeds in the Neotropics (Stiles and Skutch, 1989; Loiselle and Blake, 1990; Poulin et al., 2001), and were the primary predator on both frog- and ball-shaped models in the present study. Model experiments are typically presented to free-ranging bird communities, which can include different assemblages of frugivores, omnivores, and carnivores. In most cases, however, identifying specific bird predators (or their feeding preference) is difficult, and therefore all beak imprints found on frog models are considered avian predation, regardless of whether or not they are truly predators of frogs (e.g., Saporito et al., 2007; Comeault and Noonan, 2011; Chouteau and Angers, 2012; Hegna et al., 2012). Recently, studies have begun to identify specific avian predators of frog models, which now include the Rufous Motmot (*Baryphthengus martii*), Blue-crowned Motmot (*Momotus momota*), Great Curassow (*Crax rubra*), and Great Tinamou (*Tinamus major*; Paluh et al., 2014; Willink et al., 2014, which also includes non-avian predators of frog models), all of which are present at La Selva. Rufous Motmots have been reported as preying upon live dendrobatid frogs (*Dendrobates auratus* and *Oophaga pumilio*) from Costa Rica (Master, 1998; Alvarado et al., 2013), and two red frog-shaped models in our study contained beak imprints consistent with predation by motmots. In a similar study at the same location, Paluh et al. (2014) reported that the majority of their moving red frog-shaped models were also attacked by motmots. Although the specific species responsible for most bird attacks in the present study could not be identified, the Great Tinamou was identified as attacking 35% of all clay models.

The Great Tinamou is an omnivorous, ground-dwelling predator that feeds primarily on fallen fruits and seeds, but also preys upon arthropods and small vertebrates, including frogs (Stiles and Skutch, 1989; Loiselle and Blake, 1991). Consistent with the tinamous dietary preference for fruit and seeds, the results of our study indicate that ball-shaped models were more likely to be attacked than frog-shaped models. Differences in attacks between red and brown ball-shaped models were marginal ($P$ = 0.055), but suggest that tinamous may prefer red ball-shaped models. Collectively, these findings indicate that tinamous can differentiate between model types, and appear to recognize red ball-shaped models as fruit.

In contrast to other non-identifiable bird attacks, tinamous equally attacked red and brown frog-shaped models. This could indicate that tinamous do not recognize the conspicuous colors of our frog models as aposematic, or that they are able to feed on chemically defended frogs, such as *O. pumilio*. Willink et al. (2014) recently reported that tinamous attacked some of their conspicuously colored clay frog models of *Oophaga granulifera* in Costa Rica, but they do not report the number of predation attempts between different colored frogs models. Given that tinamous feed primarily on fruits and seeds, however, it is likely that some of the attacks on red frog-shaped models in the present study were mistakes in identity, in which they considered the models to be fruits rather than frogs.

Brown frog-shaped models are commonly used as controls in aposematism experiments, where it is assumed that these models are considered palatable to avian predators and therefore attacked significantly more than aposematic models. Although this has been experimentally demonstrated

in some studies (e.g., Saporito et al., 2007; Stuart et al., 2012; Paluh et al., 2014), this is not always the case (e.g., Comeault and Noonan, 2011; Chouteau and Angers, 2012; Hegna et al., 2012). Although there are a variety of reasons for this discrepancy between studies, one possibility is that attacks on aposematic frog models are dependent on the specific bird community present at a location and whether or not frogs are fruit colored. Although bird communities in the tropics are variable (e.g., changing with habitat, season, etc.), frugivorous birds are most common in secondary forests, and their abundance is correlated with temporal changes in fruit abundance (Levey, 1988; Loiselle and Blake, 1990; Lumpkin and Boyle, 2009). If the majority of attacks upon aposematic models are the result of frugivorous or omnivorous birds (such as tinamous in the present study), then natural predation upon aposematic frogs could easily be overestimated and result in an incorrect interpretation of the experiment. This is particularly important given that overall avian predation on clay frog models is extremely low (e.g., Paluh et al., 2014:table 1). Therefore, continuing to gain a better understanding of the specific predators that are attacking clay models will undoubtedly be an important direction for future clay model experiments.

Our results illustrate the importance of color and shape for prey selection by bird predators in clay model experiments, and add to the experimental evidence that bright coloration of *O. pumilio* from northeastern Costa Rica functions as an aposematic signal to avian predators. Avian predation rates on red frogs were significantly different from red balls, suggesting that birds are able to distinguish model color as well as shape. Predation upon specific model shapes and colors are likely dependent on the bird assemblages present at a location and their specific dietary preferences. Given our results, we suggest that future studies consider the importance of clay shape and color in an attempt to provide a more realistic assessment of natural predator responses.

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