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The fitness consequences of the autotomous blue tail in lizards: an empirical test of predator response using clay models

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ABSTRACT

Numerous vertebrates employ one or more autotomous body parts as an anti-predation mechanism. Many lizards possess an autotomous tail that is brightly colored blue, which has been suggested to either serve as a decoy mechanism to divert predator attention to the autotomous body part, as an interspecific signal, or as an aposematic signal to predators that it is distasteful or dangerous. While theoretical studies suggest that a conspicuous autotomous body part that increases the probability of escape while not increasing the rate of detection will be favorable over a completely cryptic form, there is little empirical evidence supporting the adaptive benefit of an autotomous blue tail. We used in situ clay models of a scincid lizard to test the fitness consequences of blue coloration. Lizard models with a dark base color and blue decoy coloration experienced no measurable difference in avian predation relative to an all-dark model, which suggests that blue coloration neither serves as an aposematic signal nor increases the conspicuousness of the lizard model. Despite statistically similar attack rates, avian attacks on models with blue coloration were indeed focused on body sections that were colored blue. Our results suggest that the blue tail in lizards serves as an effective decoy, and that avian predation has possibly played a role in the evolution of the blue tail.

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1. Introduction

Predators can exert strong influences on the phenotype of their prey, including prey coloration (Reznick and Endler, 1982; Losos et al., 2006; Rosenblum, 2006). Predator-mediated selection may lead to coloration in prey species that minimizes detection by predators (crypsis), a strategy employed by many animals, such as moths (Endler, 1985), frogs (Osorio and Sriaivasan, 1991), snakes (Wasco and Sasa, 2009), and fish (Willis and Anderson, 2003). Some cryptic animals possess body sections with bright color that can be displayed under threat as flash or startle coloration (Cott, 1940; Ruxton et al., 2004). Other animals are not cryptic and their bright coloration can be explained by one of two general mechanisms. First, bright coloration may be driven by intraspecific signaling and sexual selection (e.g., guppies: Endler, 1980, 1995; agamid lizards: Stuart-Fox et al., 2003) with the trade-off of increased predation (Godin and McDonough, 2002). Second, bright coloration may minimize lethal attacks after detection, either by signaling noxiousness

(e.g., poison dart frogs: Santos et al., 2003; Siddiqi et al., 2004; salamanders: Hensel and Brodie, 1976) or by serving as a decoy (Wilkinson, 2003) to divert attacks to less lethal areas of the body. If the fitness benefits of exhibiting bright coloration are greater than the costs, then such a phenotype would be favored over a cryptic form (Wilkinson, 2003).

Many lizards possess an autotomous tail that can be cast off and later regenerated if seized by a predator. This can be at a short-term fitness cost (e.g., metabolic or locomotor deficits) to the lizard (Dial and Fitzpatrick, 1983; Cooper et al., 2004; Bateman and Fleming, 2009). Some lizards have autotomous tails with bright coloration such as red, green or blue (Pianka and Vitt, 2003). Especially common is a phenotype with a bright blue tail, with the rest of the body dark in color (in most cases longitudinally striped). This trait is widespread among lizards and found in seven families on four continents (Fig. 1; see also Table S1 in Appendix A). The ubiquitous nature of this trait suggests that this may be an important anti-predation mechanism among lizards.

The adaptive significance of bright blue tail coloration in an otherwise cryptic lizard (such as five-lined skinks) has been the subject of some scientific interest (e.g., Clark and Hall, 1970; Arnold, 1984; Castilla et al., 1999). Although untested, it is assumed that the blue tail increases conspicuousness of the lizard to predators (Clark and

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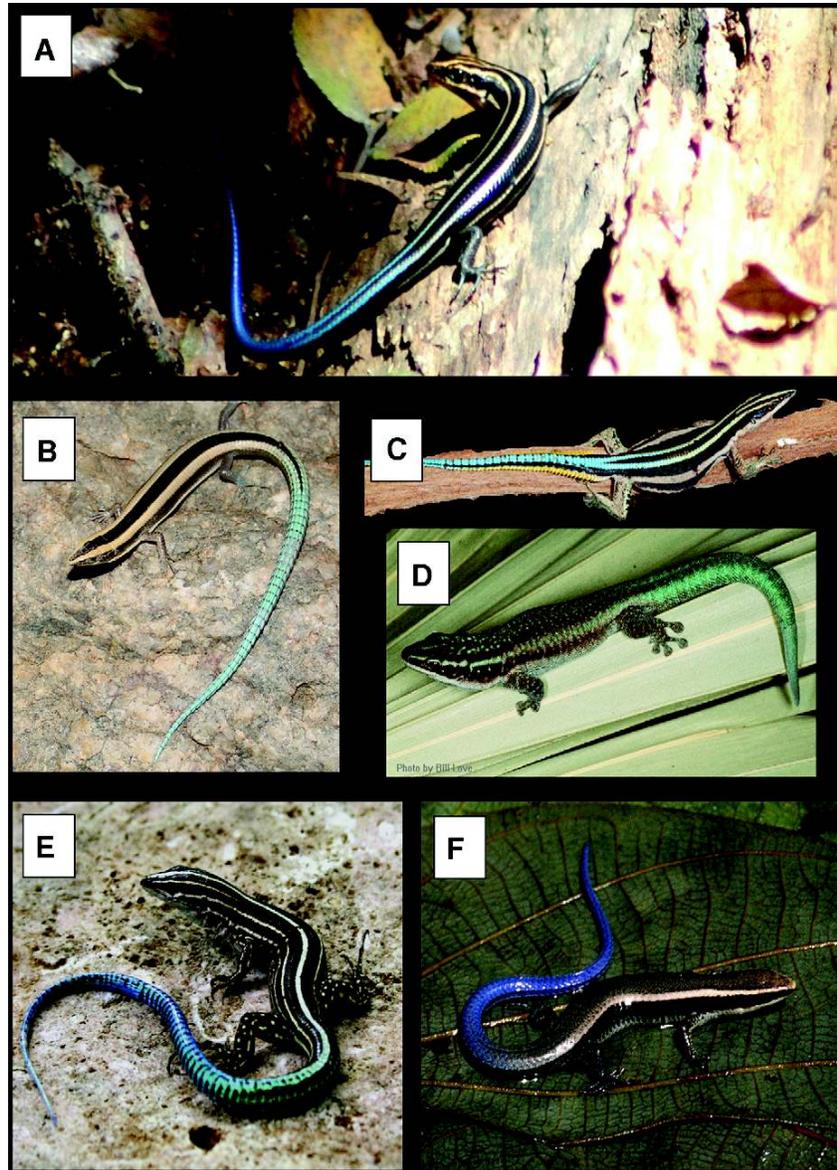 *E-mail address:* cwatson@mcneese.edu (C.M. Watson).

Fig. 1. Examples of species within different lizard families that possess the autotomous blue tail: (A) *Plestiodon fasciatus* (Scincidae) of North America, (B) *Cordylosaurus subtessellatus* (Gerrhosauridae) of Southern Africa, (C) *Holaspis guentheri* (Lacertidae) of Central Africa, (D) *Phlesuma barbouri* (Gekkonidae) of Madagascar, (E) *Ameiva wetmorei* (Teiidae) of Puerto Rico, and (F) *Micrablepharus maximiliani* (Gymnophthalmidae) of Brazil.

Hall, 1970; Arnold, 1984). As a result, several hypotheses have been posited to explain the origin of the autotomous blue tail in lizards. The decoy hypothesis states that the blue tail serves to divert predatory attacks away from vital areas, such as the head and body, to the autotomous tail (Barbour, 1926; Fitch, 1954). A decoy function for the tail has been noted for taxa other than lizards (e.g., tadpoles: Johnson et al., 2008). The intraspecific signaling hypothesis states that the blue coloration serves as a social signal, perhaps in decreasing aggression towards juveniles, and is relegated to a nonvital region, the autotomous tail (Clark and Hall, 1970). Lastly, the aposematism hypothesis proposes that the blue coloration is a signal to predators that the lizard is noxious (Arnold, 1984; Castilla et al., 1999). Despite this literature, it is not known if blue tail coloration increases conspicuousness and predation on lizards, and whether this coloration is used as a decoy or is an aposematic signal.

The efficacy of clay models in measuring avian predation has been demonstrated for lizards as well as salamanders and snakes

(Brodie and Janzen, 1995; Castilla et al., 1999; Kuchta, 2005). In the present study, we empirically examined the functional significance of the blue tail using in situ clay models. We used the resulting data to test whether (i) the blue tail increases conspicuousness and hence whether models with blue coloration are attacked with greater frequency than all-dark models, (ii) the blue tail serves as warning coloration and thus decreases avian attacks, and (iii) whether blue coloration is an effective decoy, directing avian attacks away from more vital parts of the body.

2. Materials and methods

2.1. Clay models

We constructed 180 models out of commercially available pre-tinted oil-based modeling compound (Plastalina; Van Aken International, Rancho Cucamonga, CA, USA). Plastalina was pressed
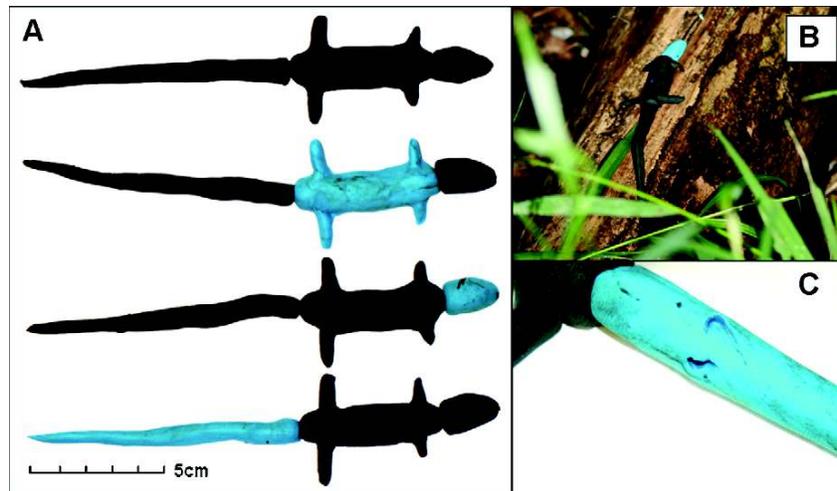
Fig. 2. (A) Examples of clay models used in this study. (B) An example of a clay model in situ. (C) An enlarged example of the traces of an avian attack on the blue tail.

into plaster molds of a head, body, and tail with body sections connected by 24-gauge metal wire. Body dimensions of the models (total length = 18.5 cm, mid-body diameter = 1.5 cm, head = 2.0 cm, body = 5.5 cm, tail = 11 cm) were based on lizard morphology reported by Davis (1968). We constructed 4 color categories of models (Fig. 2): all-dark models (n = 45), dark models with blue bodies (n = 45), dark models with blue heads (n = 45), and dark models with blue tails (n = 45). Our models did not possess longitudinal striping, which we considered a potential confounding factor. Each model type was photographed from above, and ImageJ (Rasband, 1997–2012) was used to calculate the area of each body section (head, body, and tail).

Identification of predators was based upon the markings left on the clay during an attack. Birds typically leave U- or V- shaped marks or puncture marks in the clay while mammals leave toothmarks (Brodie, 1993; Castilla et al., 1999).

2.2. Field placement

We deployed the lizard models in a riparian habitat in River Legacy Park in Tarrant County, Texas (32°47′39.72″N, 97°06′59.79″W). The models were placed 5–50 m apart on horizontal logs and low-lying tree limbs to mimic the natural basking behavior of these lizards (Fitch, 1954). Two species of five-lined skinks (*Plestiodon laticeps* and *Plestiodon fasciatus*) naturally occur at this site (Conant and Collins, 1998) as well as their primary avian predators, birds of the families Corvidae and Accipitridae (Cooper and Vitt, 1985; Rappole and Blacklock, 1994). Birds of these families see the blue color spectrum well (Håstad et al., 2005) and create a distinct pattern on the models when they attack, allowing accurate identification of each attack (Castilla et al., 1999; Brodie, 1993). We inspected the models after 48 h and avian attacks were recorded from the head, body, and tail sections of each model.

2.3. Statistical analysis

We used either a Chi-square test (expected frequencies >5) or a Fisher's exact test (FET, expected frequencies <5) to determine whether the frequencies of avian attacks on body sections of the models with blue body sections differed significantly from the frequency of avian attacks on body sections of the all-dark models. For all analyses, expected frequencies were calculated based upon (i) the proportion of hits on each body section of the all-dark model and (ii) the proportion of hits based on the area of each body section.

First, we compared the frequency of attacked and non-attacked models using the Chi-square test to determine whether the blue coloration made the models more conspicuous to predators. Second, we analyzed data from models that exhibited avian attacks on a single body section (n = 67), because multiple avian attacks on a single model are not independent. We then used the single-attack data to test key predictions of the decoy, intraspecific signal, and aposematism hypotheses. To ensure that our results were verified with our entire dataset we analyzed all models (including multiply attacked models). We also analyzed our data (including multiply attacked models) assuming different orders of attack sequence for body sections (head, tail, body; head, body, tail; etc.), using the frequency of attacks on each body segment of the all-dark model as our expected frequencies.

3. Results

3.1. Avian strikes on clay models

Avian attacks were observed on 70.6% of all models, which although comparable to a similar study in temperate climates (Castilla et al., 1999) is notably higher than attack rates for other studies in temperate and tropical climates (e.g., Brodie and Janzen, 1995; Pfennig et al., 2001; Kuchta, 2005; Shepard, 2007). This high attack rate is likely due to high predator (mostly bird) density in the field site due to anthropogenic effects.

We found no significant difference in avian attack frequency when comparing attacked all-dark models to all attacked models with a blue body section (X^2 = 0.13, P = 0.718). Furthermore, there was a similar number of unattacked models (X^2 = 0.66, P = 0.883) in each category. We found that in the all-dark model, the head and body attracted significantly more attacks than the tail (P's < 0.05). Among all single-attack models with any blue body section, there was a significant difference in the frequency of avian attacks on each body section among the three model types. Based upon expected frequencies from the all-dark model (P < 0.001, FET) or area of body section (X^2 = 6.86, P < 0.05), the blue section of each model was attacked much more frequently (82.3%) than the dark body sections (17.6%; Fig. 3.). The blue head (P < 0.001, FET) and the blue tail (P < 0.001, FET) were both effective in diverting avian attacks, based upon expected frequencies calculated assuming equal probability of attacks for each body section or calculated using the relative area of each body section. The blue body was not significantly different in effectiveness from the all-dark models (P > 0.1, FET). This is likely
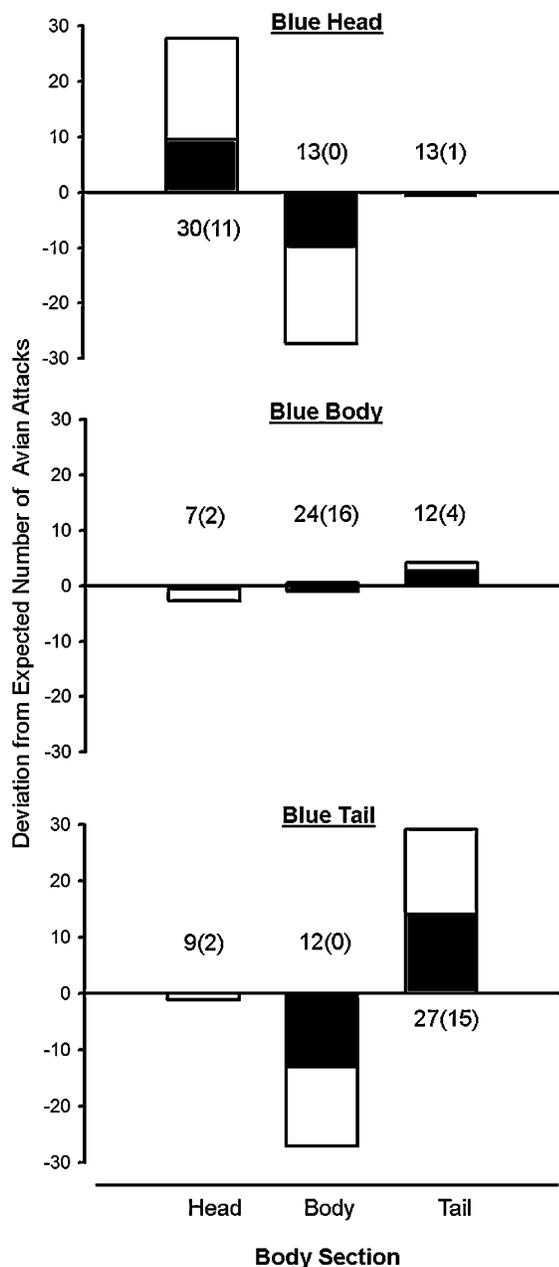
Table 1
Chi-square and P-values for the complete dataset assuming different attack sequences. The values refer to expected frequencies based upon the proportion of hits to the body sections of the all-dark model.

Model type	X^2	P
Head, body, tail		
Blue head	48.16	<0.0001
Blue body	9.18	0.0102
Blue tail	9.81	0.0074
Head, tail, body		
Blue head	48.8	<0.0001
Blue body	57.04	<0.0001
Blue tail	524.58	<0.0001
Body, head, tail		
Blue head	122.38	<0.0001
Blue body	11.86	0.0027
Blue tail	244.64	<0.0001
Body, tail, head		
Blue head	104.48	<0.0001
Blue body	18.49	<0.0001
Blue tail	278.06	<0.0001
Tail, head, body		
Blue head	42.5	<0.0001
Blue body	2.51	0.2851
Blue tail	27.65	<0.0001
Tail, *body, head*		
Blue head	4.43	0.1092
Blue body	4.32	0.1153
Blue tail	26.79	<0.0001

head or tail (P's < 0.001, FET; Fig. 3). The blue coloration of each model type effectively diverted avian attacks in all attack sequence scenarios for all data with the exception of the two scenarios where we assumed that the tail was preferentially attacked first (Table 1). When we assumed that the tail was hit first, then the head, and lastly the body, the frequency of attacks to the blue head and the blue tail were both significantly increased, but not that to the blue body (Table 1). When we assumed that the tail was hit first, then the body, and finally the head, only the blue tail significantly increased avian attacks (Table 1). In all scenarios, the blue coloration was consistently effective at directing avian attacks to the tail.

4. Discussion

We found no increase in the frequency of predatory attacks between models with blue coloration and all-dark models, which suggests that blue coloration does not increase the conspicuousness of the lizard models. Neither did we document a reduction in the frequency of avian attacks associated with blue coloration, which is inconsistent with the notion that the blue tail is a warning that the lizard is noxious or otherwise undesirable as prey (i.e., the aposematism hypothesis). Instead, we found that avian attacks can be directed to any section of the lizard model simply by coloring that region blue. These results support the theory that the blue tail is an effective decoy for attracting attacks towards a non-vital body segment.

Another study (Castilla et al., 1999) used clay models in much the same way as the present study to determine the frequency of attacks on lizard models with green and brown tails. However, this previous methodology (Castilla et al., 1999) could not disentangle predator attack propensity for a particular body region or the decoy color. By changing the position of the blue coloration on the model body, we determined that blue coloration effectively directed attacks to the smallest body section (the head) and that it decreased the proportion of attacks to the much larger body to zero in both models where the head or tail was blue. We found the same general pattern when analyzing single attack models,

Fig. 3. Deviation of observed avian attacks from expected avian attacks based upon the frequency of attacks on each body section of the all-dark models. Open bars represent all data, while the solid portion of each bar is from single-hit models. Body section attack frequencies significantly deviate from the expected frequency ($\alpha = 0.05$) for blue head and blue body models. Total number of avian attacks per body section is noted for all models with single-attack model data in parentheses.

due to the fact that the all-dark models were attacked primarily in the larger and less protected (at least for *Plestiodon*) body and a blue body would simply reinforce that result. Interestingly, 95% of the models exhibiting multiple attacks possessed predation marks in the blue body section.

3.2. Multiple attack data

Generally, multiple attack results were almost identical to single attack results, with the blue color attracting more attacks to the

all data (including multiply attacked models) and considering all possible sequences of attacks (see Section 3, Table 1). While many lizard species with blue tails have longitudinal striping, our models were unpatterned and so we cannot determine the role of longitudinal striping in the phenotype of blue-tailed lizards. Nonetheless, our results suggest that a predatory attack, once initiated, will be focused on the largest body segment (the body) or the head unless directed elsewhere by blue coloration.

Like Castilla et al. (1999), we found no measurable increase in the frequency of predatory attacks between models with blue coloration and all-dark models. This suggests that stationary, exposed lizards are already evident to sharp-eyed avian predators and the blue tail may serve as a diversion of the attack at close range (Arnold, 1984). Our study cannot parse whether the response of an avian predator to our clay models is a lizard-specific or a generalized predation response. In fact, it is not known whether the avian predation response to an actual lizard is generalized or specific. Nonetheless, we note that the fitness consequences of a successful predation attempt, either generalized or lizard-specific, are identical for a lizard killed by the predator.

Although the present study focused on avian predators, the blue tail may also effectively divert non-avian attacks due to visual cues other than color. Experimental research found that a nocturnal predator that does not employ color vision, the scarlet kingsnake (*Lampropeltis elapsoides*), struck the body of lizards with blue-painted tails less frequently than that of lizards with darkly painted tails (Walls, 1963; Cooper and Vitt, 1991). We found little evidence of mammalian attacks (only 2 of the 180 models), with one all-dark model and one model with a blue body severely disfigured by presumably mammalian predators. Predators that are not sensitive to the color blue may focus on the blue autotomous tail for reasons other than coloration such as contrast with the body or movement (Arnold, 1984; Cooper and Vitt, 1985). Decoy coloration other than the blue tail (red or green) occurs in some lizards and may also be effective in diverting predatory attacks. Specifically, the green tail coloration of another lizard (*Podarcis bocagei*) also increases the frequency of predatory strikes on the tail, but does not reduce predatory attacks to the vital parts of the lizard's body (Castilla et al., 1999). Although a brightly colored, autotomous tail is an effective decoy in lizards, the precise color of the tail may be driven by selection from the most important predators of each species.

Many lizard species with blue tail coloration experience an ontogenetic loss of this color in adults (Taylor, 1935; Fitch, 1954; Hawlena et al., 2006). This ontogenetic shift seems to be limited to lizards with relatively large adult body size, such as *Plestiodon laticeps*, and large male specimens of *Plestiodon fasciatus* and *Plestiodon inexpectatus* (Taylor, 1935; Conant and Collins, 1998). Conversely, many relatively small lizards such as smaller *Plestiodon* sp., *Holaspis guentheri* and *Micrablepharus maximiliani* maintain the blue tail coloration as mature adults (Taylor, 1935; Avila-Pires, 1995; Spawls et al., 2004). This ontogenetic shift in color could be related to intraspecific signaling, with immature lizards signaling their juvenile status to adult conspecifics (Clark and Hall, 1970; Arnold, 1984). Another potential explanation for this shift is that large mature lizards may experience different predation environments than smaller lizards (Booth, 1990) due to ontogenetic changes in behavior or predation susceptibility (Hawlena et al., 2006; Hawlena, 2009). A final explanation is that as these species shift energy allocation from growth to reproduction, the tail may serve as an energy reservoir (Vitt et al., 1977) and may become too costly to lose. Future research in this area should clarify the mechanisms underlying the ontogenetic loss of blue tail coloration for some lizards.

Our findings are in agreement with theoretical models that predict a brightly colored decoy phenotype to be favored over a cryptic phenotype in a population if the benefit of an increased ability to escape outweighs the cost of increased detection by predators (Cooper and Vitt, 1991; Wilkinson, 2003). Given the ubiquity of this trait (Fig. 1, see also Table S1 in Appendix A) and the global distribution of predatory birds (Beletsky, 2006), we find it plausible that the selective pressures identified in the current study could have led to the convergent evolution of the autotomous blue tail in lizards. While only a detailed phylogenetic analysis can clarify the evolutionary origins of the blue tail in lizards, our results suggest that selection mediated by avian predators is a possible mechanism underlying the origin of this trait.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.zool.2012.04.001.

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