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# Both novelty and conspicuousness influence selection by mammalian predators on the colour pattern of *Plethodon cinereus* (Urodela: Plethodontidae)

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3 1 Title: Both novelty and conspicuousness influence selection on *Plethodon cinereus*  
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5 2 (Urodela: Plethodontidae) color pattern by mammal predators  
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29 12 Running Title: Mammalian influence on salamander coloration  
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13 **Abstract**

14 Predators influence the evolution of color pattern in prey species, yet how these selective  
15 forces might differ among predators is rarely considered. In particular, prey color patterns  
16 that indicate unpalatability to some predator species may not carry the same signal for  
17 other predators. We test several hypotheses of selection on patterning between mammal  
18 predators and the polymorphic salamander *Plethodon cinereus*, which, under an avian  
19 visual system appears as a mimic of the toxic newt *Notophthalmus viridescens*. We fit  
20 each hypothesis against field observations of mammalian attacks on salamander clay  
21 replicas. We then develop a novel analytical procedure that enables the combination of  
22 multiple non-exclusive models in a likelihood framework. We find that mammals do not  
23 follow any single hypothesis proposed, including the hypothesis of mimicry. Instead,  
24 mammals in this system use visual cues while foraging to avoid unfamiliar, novel prey  
25 and attack conspicuous prey. We propose that mammals may help to maintain color  
26 pattern polymorphism within populations of *P. cinereus* by avoiding novel, unfamiliar  
27 color morphs. Additionally, selective pressures from multiple predators and variation in  
28 predator communities among sites may contribute to the maintenance of color  
29 polymorphism within and among localities in this salamander species.

30 Keywords: *Plethodon* – non-exclusive hypotheses – mimicry – color polymorphism –  
31 clay replicas

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3 32 Predation exerts strong selective pressures on prey phenotype, often acting as a creative  
4  
5 33 force driving the evolution of new phenotypic traits that deter predators (Endler, 1988).  
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8 34 For example, defensive structures present in prey populations that are sympatric with  
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10 35 predators are frequently lost in predator-poor environments (Bell, Orti, Walker &  
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12 36 Koenings, 1993; Pafilis *et al.*, 2009; Reimchen, 2000), and experimental evidence has  
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15 37 shown that the presence of predators exerts strong selective pressures on life history and  
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17 38 other phenotypic traits (Reznick, Bryga & Endler, 1990; Reznick *et al.*, 1997). High rates  
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19 39 of predation can drive prey species to mature at smaller sizes (Reznick and Endler, 1982)  
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21 40 or to evolve extremely high toxicity (Brodie Jr., Ridenhour & Brodie III, 2002).  
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24 41 However, while such studies inform on how predation can act as a constructive force of  
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26 42 selection that drives the evolution of new phenotypes, less attention has been given to  
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28 43 how predation can maintain standing phenotypic diversity within prey species (Bond,  
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30 44 2007).  
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36 46 A common phenotypic trait to evolve in response to predation is patterning, which can  
37  
38 47 directly influence predator detection and identification of potential prey (Endler, 1986).  
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40 48 In many species, selection from predators has resulted in color pattern polymorphism,  
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42 49 where multiple distinct morphs exist for a single prey species (reviewed in Bond, 2007).  
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45 50 The evolution of such polymorphism is strongly directed by the visual capabilities of  
46  
47 51 potential predators, which can vary greatly among species (Ruxton, Sherratt & Speed,  
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49 52 2004). Once detected, the behavioral response of a predator to potential prey can fit  
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51 53 several different hypotheses, which may or may not maintain color pattern  
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54 54 polymorphisms. First, predators may avoid prey color pattern morphs that resemble an  
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3 55 unpalatable species, thus driving the evolution of Batesian mimics that closely resemble  
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5 56 their unpalatable models (the Mimicry Hypothesis, Figure 1A; Bates, 1862).  
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8 57 Alternatively, foraging predators may detect and target prey whose patterning has greater  
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10 58 contrast with the background environment (i.e. more conspicuous), thereby driving the  
11  
12 59 evolution of cryptic morphs difficult for predators to initially detect (the Conspicuousness  
13  
14 60 Hypothesis, Figure 1B; Endler, 1978). Predators may also recognize, and then attack,  
15  
16 61 those prey that are most common in the environment, resulting in frequency-dependent  
17  
18 62 selection against common morphs (the Apostatic Selection Hypothesis, Figure 1C; Allen,  
19  
20 63 1988). On the other hand, predators may avoid unfamiliar prey (the Novel Avoidance  
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22 64 Hypothesis; also called ‘dietary conservatism’, Figure 1D; Marples *et al.*, 2007), or  
23  
24 65 predators may not use patterning in any way during foraging, perhaps instead utilizing  
25  
26 66 other senses, such as smell (the Non-Visual Hypothesis; Endler, 1986; Hughes *et al.*,  
27  
28 67 2010; Ruxton, 2009). Importantly, these hypotheses are not necessarily exclusive.  
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30 68 Predators may incorporate several of the above strategies into a single composite  
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32 69 behavior when responding to visual cues in potential prey (the Combined Hypothesis;  
33  
34 70 Endler, 1986). These hypotheses can be difficult to observe directly, and are best tested  
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36 71 through the observation of predation events themselves (e.g. Kikuchi & Pfennig, 2010).  
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40 73 In salamanders, predation is a major source of mortality, and a diversity of patterning has  
41  
42 74 consequently evolved in response to predators (Petranka, 1998). In some taxa, this  
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44 75 includes color pattern polymorphism, or multiple color morphs, within species. In the  
45  
46 76 salamander *Plethodon cinereus*, three distinct color morphs are typically encountered,  
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48 77 including the solid red-orange ‘erythristic’ morph, the solid black ‘unstriped’ morph, and  
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3 78 the 'striped' morph that possesses a single red dorsal stripe on a dark background (Lotter  
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5 79 & Scott, 1977; Figure 2A-C). Birds are hypothesized to associate erythristic *P. cinereus*,  
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7  
8 80 which are palatable (Tilley, Lundrigan & Brower, 1982), with similarly colored juveniles  
9  
10 81 of the highly toxic newt *Notophthalmus viridescens*, making erythristic *P.*  
11  
12 82 *cinereus* Batesian mimics of *N. viridescens* (Lotter & Scott, 1977; Brodie & Brodie,  
13  
14 83 1980; Tilley *et al.*, 1982). A recent study found that bird predators with tetrachromatic  
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16 84 vision are able to discriminate non-mimetic *P. cinereus* from *N. viridescens*, but not  
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18 85 mimetic *P. cinereus* from *N. viridescens* on the basis of coloration (Kraemer & Adams,  
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20 86 2014). Birds are thus capable of imposing selection on *P. cinereus* patterning consistent  
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22 87 with Batesian mimicry. In contrast, this study found that visual models for diurnal,  
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24 88 dichromatic mammals are unable to discriminate salamanders on the basis of coloration,  
25  
26 89 suggesting that visual constraints might prevent diurnal mammal predators from selecting  
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28 90 for mimicry in this system. However, these visual models indicated that mammals are  
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30 91 able to discriminate salamanders on the basis of brightness. Mammalian predators may  
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32 92 thus use visual cues distinct from coloration when hunting, thereby selecting for  
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34 93 patterning in a manner different from birds.  
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43 94  
44 95 In the present study, we test five hypotheses of selection on *P. cinereus* color pattern by  
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46 96 mammal predators, specifically the Mimicry, Conspicuousness, Apostatic Selection,  
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48 97 Novel Avoidance, and Non-Visual hypotheses as described above. We test the fit of each  
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50 98 hypothesis against field observations of mammalian predation on clay replicas of each *P.*  
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52 99 *cinereus* color morph. We then use a novel analytical procedure that, given a set of non-  
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55 100 exclusive explanatory models, enables us to identify a 'combined' model that  
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3 101 incorporates aspects of multiple predation hypotheses within a single likelihood  
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5 102 framework.  
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## 11 105 **Materials and Methods**

### 12 106 *Study System*

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15 107 The salamander species *Plethodon cinereus* is the most common vertebrate species in  
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17 108 New England forests (Burton & Likens, 1962), and many populations have two of the  
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19 109 three typical *P. cinereus* color morphs (Lotter & Scott, 1977). While avian predators are  
20  
21 110 thought to drive the evolution of color mimicry in this system (Brodie & Brodie, 1980;  
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23 111 Tilley *et al.*, 1982; Kraemer & Adams, 2014), the impacts of additional predators, such as  
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25 112 mammals and snakes, are less well understood. In North America, mammals are  
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27 113 important salamander predators (Petranka, 1998). However, mammalian attacks on  
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29 114 salamanders are harder to observe and are less well documented as compared to attacks  
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31 115 from snakes and birds (e.g. Lotter & Scott, 1977; Arnold, 1982; Fenster & Fenster, 1996;  
32  
33 116 Adams, 1999). Nonetheless, prior work has shown that common mammalian predators on  
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35 117 salamanders are opossums, raccoons, skunks, opportunistic rodents, and other small  
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37 118 carnivorous mammals (Stebbins, 1954; Huheey & Stupka, 1967; Brodie Jr., Nowak,  
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39 119 Harvey, 1979; Beachy, 1991; Dodd, 1991; Petranka, 1998). These typically dichromatic  
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41 120 mammalian species have visual capabilities far different from bird predators, particularly  
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43 121 through a narrower range of visual sensitivities (Chen & Goldsmith, 1986; Jacobs, 1993;  
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45 122 Kraemer & Adams, 2014; see supporting information Table S1). While mammals are  
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47 123 known to use non-visual senses while foraging (e.g., smell: Pyare & Longland, 2001;  
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3 124 Hughes, Price & Banks, 2010; but see Discussion), they also utilize visual cues during  
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5 125 the predation process. As such, it is of interest to determine whether mammalian  
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8 126 predators differentially attack *P. cinereus* color morphs in accordance with several  
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10 127 hypotheses in which predator behavior is mediated by visual cues (see *Expected Attacks*  
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12 128 *For Each Hypothesis* below). We tested predictions in the field using clay replicas of  
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15 129 salamander morphs that were exposed to mammalian predators for four to five days. At  
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17 130 the conclusion of this period, we collected the replicas, scored them for mammalian  
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20 131 attacks, and compared observed attack rates to attack rates expected under each  
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22 132 hypothesis (described below).  
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#### 26 27 134 *Replica Construction*

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29 135 We constructed clay replicas out of Sculpey III<sup>®</sup> polymer clay. This clay does not harden  
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31 136 under field conditions but retains impressions made by potential predators, thus serving  
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34 137 as a record of attack events over several days. Similar approaches have been used to  
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36 138 document predator-mediated selection on color patterns in diverse taxa, including snakes  
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38 139 (Madsen, 1987; Pfennig, Harcombe & Pfennig, 2001), lizards (Husak *et al.*, 2006), mice  
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40 140 (Vignieri, Larson & Hoekstra, 2010), frogs (Noonan & Comeault, 2009; Willink *et al.*,  
41  
42 141 2014; McElroy, 2015), and salamanders (e.g. Brodie, 1993; Kuchta, 2005). We formed  
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44 142 replicas to resemble *P. cinereus* morphs that were present at the four localities (striped,  
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46 143 unstriped, and erythristic; Figure 2A-C). To construct the replicas, we hand-shaped 1.5  
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48 144 grams of black or red clay to resemble a basic salamander form with a head and tapered  
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50 145 body (Figure 2D). We made 300 replicas of each salamander color morph, for a total of  
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53 146 900 clay replicas.  
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5 148 *Replica Distribution and Retrieval*

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8 149 We chose four locations in western Massachusetts based on the presence and frequency  
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10 150 of *P. cinereus* color morphs, which we estimated by visiting each locality on three  
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12 151 separate occasions in May and June of 2011. During each visit we searched under cover  
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14 152 objects (e.g. logs, rocks, leaf litter) for one hour and noted each salamander encounter. In  
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16 153 total, we observed 247 salamanders (72 at Fisk, 97 at Lily, 56 at Coys, and 22 at Palmer).  
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18 154 At two locations striped and erythristic *P. cinereus* are present (Fisk and Lily; located in  
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20 155 Fisk Meadows Wildlife Management Area and Lily Pond Wildlife Management Area,  
21  
22 156 respectively), while at the other two locations striped and unstriped *P. cinereus* are  
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24 157 frequently encountered (Coys and Palmer; located in Coys Hill Wildlife Management  
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26 158 Area and Palmer Wildlife Management Area, respectively; Figure 3A). At three of the  
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28 159 four localities *N. viridescens* are regularly encountered, while at the fourth locality (Coys)  
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30 160 *N. viridescens* have been observed on the road directly adjacent to the wildlife  
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32 161 management area. Historical records of morph frequencies in this region (Tilley *et al.*,  
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34 162 1982) are similar to modern morph frequencies (A. Kraemer, *unpublished*), suggesting  
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36 163 that morphs we identify as novel are likely to be the same as those local mammals would  
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38 164 identify as novel. We placed the replicas in the field from 28 May to 31 May 2012, and  
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40 165 we collected the replicas from 1 June to 5 June 2012 such that each replica was exposed  
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42 166 to predators for four to five days. At each locality there was complete overhead canopy,  
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44 167 while understory vegetation was sparse. Although there was some variation in understory  
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46 168 coverage within sites, the large number of replicas distributed at each site ( $N = 225$ ) led  
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48 169 to even replica placement across all possible understory densities.  
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We distributed an equal proportion of each color morph at all four localities, so any deviation from equal predation across morphs strongly suggests that predators are using coloration to identify potential prey. We placed 15 replicas (five of each morph) along 75 m transects, each separated by 5 m. All replicas were placed directly on leaf litter five meters perpendicular to the transect line. Each locality had 15 transects and all transects had at least 20 m between them. After four (for Fisk Meadows) or five days (for Lily Pond, Coys Hill, and Palmer) replicas were retrieved, though not all replicas could be recovered (Fisk: 28 lost; Lily: 3; Coys: 6; Palmer: 8). This may be due in part to predators removing replicas from the transects, but may also be in part a result of our inability to relocate replicas placed in heterogeneous terrain (e.g. among boulders or vegetation). In such cases where models could not be recovered, they were removed from the analysis. We then scored replicas as either attacked if mammalian incisors or other indications of teeth could be identified in the clay, or not attacked if mammalian marks were absent (for similar scoring procedures, see: Brodie, 1993; Pfennig *et al.*, 2001; Kutcha, 2005; Low *et al.*, 2014). Raw totals are given in supporting information Table S2.

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#### 187 *Expected Attacks for Each Hypothesis*

188 Figure 1 provides a general schematic of attack frequencies under each predation  
189 hypothesis. To quantitatively characterize these into the expected attack rates under each  
190 hypothesis for our dataset, the following procedure was utilized.

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3 192 *Mimicry Hypothesis* – The Mimicry Hypothesis states that predators will avoid attacking  
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6 193 prey that resemble unpalatable models (Bates, 1862). Thus, the most parsimonious  
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8 194 expectation for the Mimicry Hypothesis is predators will avoid mimics and attack the two  
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10 195 non-mimetic morphs at equal frequency. Because no prior data was available for this  
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12 196 taxon from which to generate prior expectations under this hypothesis, we consequently  
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14 197 set expected attack rates at: 50% of observed attacks on unstriped replicas, 50% on  
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16 198 striped replicas, and 0% on erythristic replicas (Figure 3B).  
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22 200 *Conspicuousness Hypothesis* – The Conspicuousness Hypothesis states that attacks will  
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24 201 be distributed among prey such that the most conspicuous prey morphology will be  
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26 202 attacked at the greatest frequency (Endler, 1978). We used previously published  
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28 203 estimates of spectral reflectance for salamander morphs (collected from the mid-dorsal  
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30 204 point of over 1000 salamanders; Kraemer & Adams, 2014), a local background (wet leaf  
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32 205 litter; Kraemer & Adams, 2014), a measure of nocturnal irradiance (Veilleux &  
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34 206 Cummings, 2012), and the achromatic spectral sensitivities of a mammal (Jacobs *et al.*,  
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36 207 1993) to estimate salamander conspicuousness for a nocturnal mammal (*sensu* Vorobyev  
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38 208 *et al.*, 1998). This approach estimates the discriminability of visual signals from the  
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40 209 signal to noise ratio of predator photoreceptors (Vorobyev *et al.*, 1998). The units are  
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42 210 calculated as just-noticeable-difference units (jnd), where 1 jnd is the difference  
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44 211 necessary for predators to detect a distinction between two spectra. Erythristic *P. cinereus*  
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46 212 are most conspicuous (conspicuousness score = 3.59 jnd), unstriped *P. cinereus* are  
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48 213 moderately conspicuous (conspicuousness score = 3.28 jnd), and striped *P. cinereus* are  
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50 214 least conspicuous (conspicuousness score = 3.07 jnd; see Kraemer & Adams, 2014).  
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3 215 Although all color morphs were conspicuous against wet leaf litter, there were clear  
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5 216 differences in conspicuousness among morphs. From these estimates of relative  
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8 217 conspicuousness we set expected attack rates at: 36.1% on erythristic replicas, 33% of  
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10 218 attacks on unstriped replicas, and 30.9% on striped replicas (Figure 3C).  
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15 220 *Apostatic Selection Hypothesis* – The Apostatic Selection Hypothesis states that most  
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17 221 attacks will occur on morphs that are most common in the environment, such that  
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19 222 common morphs will be attacked frequently, rare morphs will be attacked rarely, and  
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21 223 novel morphs will be avoided (Allen, 1988). We thus set separate expected attack rates  
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23 224 for each morph by locality (Figure 3D), with expected attack rates corresponding to the  
24  
25 225 relative frequency of each morph naturally found at that locality (Figure 3D).  
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31 227 *Novel Avoidance Hypothesis* – The Novel Avoidance Hypothesis states that predators  
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33 228 will avoid morphs not previously encountered (Marples *et al.*, 2007). We classified  
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35 229 morphs naturally present at a locality as ‘previously encountered’ by predators and thus  
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37 230 predicted that they would not be avoided. Conversely, we considered novel morphs at a  
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39 231 locality as ‘not previously encountered’ and predicted that they would be avoided by  
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41 232 predators. For example, at the Fisk locality unstriped *P. cinereus* are absent, while striped  
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43 233 and erythristic salamanders are present. We thus set attack rates at Fisk as 0% of  
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45 234 observed attacks on unstriped replicas, 50% attacks on striped replicas, and 50% attacks  
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47 235 on erythristic replicas (Figure 3E).  
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3 237 *Non-Visual Hypothesis* – The Non-Visual Hypothesis states that color pattern will not  
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5 238 influence attacks on potential prey (Endler, 1986). This hypothesis is derived from cases  
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7 239 where predators locate prey items primarily using other senses (such as smell) or if visual  
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9 240 cues not related to coloration are utilized. As such, the Non-Visual Hypothesis predicts  
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11 241 equal attacks across color morphs, or 33% of the attacks on unstriped replicas, 33% on  
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13 242 striped replicas, and 33% on erythristic replicas.  
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20 244 *Combined Hypothesis* – Finally, the Combined Hypothesis states that several of these  
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22 245 factors jointly influence predator attacks on different color morphs, and thus predicts  
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24 246 attack rates intermediate between the above predictions (Figure 3F; see *Combined*  
25  
26 247 *Hypothesis* below). For example, if predators avoid mimics and unfamiliar color morphs,  
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28 248 attacks will be distributed between non-mimetic and locally abundant color morphs.  
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### 35 36 251 **Statistical Analyses**

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38 252 We evaluated observed predation rates on salamander replicas relative to alternative  
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40 253 hypotheses using several analytical approaches. First, we calculated the binomial log-  
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42 254 likelihood of each hypothesis given the observed data by setting  $n$  as the number of  
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44 255 retrieved replicas for a given morph,  $x$  as the number of replicas that were attacked, and  $p$   
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46 256 as the expected attack rate on that morph for a particular hypothesis (Sokal & Rohlf,  
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48 257 2012). Second, we determined which hypotheses provided the best ‘fit’ to the observed  
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50 258 data using AIC scores. Next, we performed a series of pair-wise likelihood ratio tests  
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52 259 (LRTs). These tests compared the likelihood of the observed data given each model of  
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3 260 predator behavior through a non-nested LRT approach (see *Simulation LRT*). Finally,  
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5 261 because not all biological hypotheses were mutually exclusive, there existed the  
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8 262 possibility that some combination of these hypotheses provided the best explanation of  
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10 263 the observed data. We therefore developed a novel likelihood procedure to combine non-  
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12 264 exclusive biological hypotheses (see *Combined Hypothesis* below).  
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16  
17 266 *Simulation LRT*

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19 267 Simulation LRT is an approach where non-nested models may be compared using  
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21 268 likelihood ratio tests (Williams, 1970; Lewis, Butler & Gilbert, 2011). The procedure  
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23 269 consists of several steps, which are outlined briefly here. First, for two non-nested  
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25 270 models, ‘A’ and ‘B,’ calculate the likelihood of models ‘A’ and ‘B’ given the parameters  
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27 271 of the models and observed data. Next, simulate a large number of datasets under the null  
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29 272 model ‘A,’ fit each dataset to the null ‘A’ and alternative ‘B’ models, and calculate  
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31 273 Likelihood Ratio Test Statistics (LRTS) for each simulated dataset as well as the  
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33 274 observed dataset. The proportion of LRTS from the simulated datasets that are more  
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35 275 extreme than the observed data is then estimated, and if the observed LRTS is more  
36  
37 276 extreme than 95% of the simulated datasets, the LRT is judged as ‘significant.’ Finally,  
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39 277 the steps are repeated with the role of ‘null’ and ‘alternative’ model reversed.  
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48 279 The procedure above provides a means of evaluating the fit of data to multiple models  
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50 280 that are not statistically nested (as is the case here). As noted by Lewis *et al.* (2011), this  
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52 281 analysis has four potential outcomes. 1) The LRT with A as the null model is non-  
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54 282 significant, but the LRT with B as the null is significant. In this case, model A is a better  
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3 283 fit than model B. 2) The LRT with B as the null model is non-significant, but the LRT  
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5 284 with A as the null is significant. In this case, model B is a better fit than model A. 3) If  
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7 285 both LRTs are significant, neither model fits the data well. 4) If neither LRT is  
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9 286 significant, the two models cannot be distinguished given the available data. We used this  
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11 287 procedure on each pair of the hypotheses described above to determine which hypothesis  
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13 288 (if any) provided a better explanation for the observed attack rates.  
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20 290 *Combined Hypothesis*

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22 291 The LRT procedure described above is quite flexible, in that it allows one to compare the  
23  
24 292 fit of non-nested models to data using likelihood ratio tests. However, the method  
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26 293 assumes that all models are mutually exclusive, which is not always case. With respect to  
27  
28 294 predation, predators may use prey color patterning differently throughout the predation  
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30 295 process, which suggests the above hypotheses (Conspicuousness, Apostatic Selection,  
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32 296 Mimicry, Novel Avoidance) are not necessarily exclusive of one another (Endler, 1986).  
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34 297 Because of this, predators may, in essence, combine information from multiple sources,  
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36 298 effectively utilizing multiple strategies that fall within the previously defined hypotheses.  
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38 299 In such cases, the best explanation for the observed attack rates would be from a model  
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40 300 that does not exclusively describe one or another scenario, but rather combines multiple  
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42 301 models (akin to model averaging using AIC weights). To address this possibility, we  
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44 302 developed a likelihood procedure that, given a set of explanatory models, identified the  
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46 303 best fitting model (based on likelihood) where this model consisted of combinations of  
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48 304 the previously stated hypotheses. Procedurally, this was accomplished by incorporating  
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50 305 weights ( $w$ ) for each model, which were multiplied by the parameters of each hypothesis  
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3 306 (i.e. Conspicuousness:  $\beta_{\text{conspic}}$ , Apostatic Selection:  $\beta_{\text{apo}}$ , Mimicry:  $\beta_{\text{mim}}$ , Novel  
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5 307 Avoidance:  $\beta_{\text{novel}}$ ). These weights were then adjusted to maximize the likelihood of a  
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8 308 combined hypothesis, with the constraint that the weights sum to 1.0. Thus, the best  
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10 309 fitting combined model was found as:

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$$\beta_{\text{combined}} = w_{\text{conspic}}\beta_{\text{conspic}} + w_{\text{freq}}\beta_{\text{apo}} + w_{\text{mim}}\beta_{\text{mim}} + w_{\text{novel}}\beta_{\text{novel}},$$

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19 313 with  $\beta_{\text{combined}}$  signifying the parameters of a combined model that maximizes the  
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21 314 likelihood of a hypothesis incorporating aspects of each single hypothesis. Note that for a  
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23 315 ‘pure’ model, the weight for that component would be  $w = 1.0$ , and the weights for the  
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25 316 remaining model contributions would be  $w = 0.0$ . We implemented this procedure using  
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27 317 the ‘optim’ function in the ‘stats’ package found in ‘R.’ We then compared the fit of the  
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29 318 combined hypothesis to each ‘pure’ hypothesis using likelihood, Akaike Information  
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31 319 Criterion (AIC), and simulation LRT. All analyses were conducted in R 3.2.2 (R  
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33 320 Development Core Team, 2015). Associated R code for this procedure can be found in  
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35 321 supporting information S3.

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## 40 41 324 **Results**

### 42 43 325 *Likelihood and AIC*

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45 326 We found likelihood scores and AIC scores reflected similar patterns of fit among single  
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47 327 models (Table 1). In both cases, the Novel Avoidance Hypothesis was a much better fit to  
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49 328 the observed data than were the remaining models. The next best-fitting models (Non-



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3 329 Visual and Conspicuousness) were  $>6 \Delta AIC$  units from the Novel Avoidance  
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6 330 Hypothesis, implying that the Novel Avoidance Hypothesis represented a substantially  
7  
8 331 better fit to the observed attack rates (Table 1). Further, two models that described strict  
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10 332 avoidance of one morph (Mimicry and Apostatic Selection hypotheses) provided the  
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12 333 poorest fit to the data, implying that these models did not describe how predators attacked  
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14 334 potential prey in this system (Table 1).  
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20 336 *Simulation LRT*

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22 337 Pairwise comparisons of models through simulation LRT corroborated the findings  
23  
24 338 described above, indicating that the Mimicry and Apostatic Selection hypotheses were  
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26 339 particularly poor predictors of the observed data (Table 2). In no comparisons did either  
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28 340 of these models fit better than the alternative. Comparisons between the remaining single  
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30 341 models were more equivocal, and we were unable to determine whether the Novel  
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32 342 Avoidance, Conspicuousness, or Non-Visual models provided the best fit.  
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39 344 *Combined Hypothesis*

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41 345 Interestingly, the combined hypothesis that best predicted our observed data was most  
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43 346 strongly influenced by the Conspicuousness Hypothesis ( $w_{\text{conspic}} = 0.61$ ) and Novel  
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45 347 Avoidance Hypothesis ( $w_{\text{novel}} = 0.39$ ), with no contribution from the remaining  
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47 348 hypotheses. All other combinations of hypotheses, including those that included the Non-  
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49 349 Visual Hypothesis, provided a poorer fit to the data, regardless of their AIC scores as  
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51 350 calculated singly. Consequently, only the parameters from the Conspicuousness and  
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53 351 Novel Avoidance hypotheses were considered in calculating the AIC score for the  
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3 352 combined hypothesis. Note that the best-fitting combined hypothesis does not weight the  
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5 353 Conspicuousness and Novel Avoidance hypotheses according to AIC or likelihood  
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8 354 scores, but by the predictions made by each resulting model. Both likelihood and AIC  
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10 355 scores indicated that the Combined Hypothesis was a far better predictor of our observed  
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12 356 data than any single hypothesis (Table 1). Likewise, the Combined Hypothesis was a  
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14 357 better fit than any single hypothesis as indicated by simulation LRT (Table 2).  
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20 359 Overall, results from AIC, simulation LRT, and combined LRT consistently group the  
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22 360 Novel Avoidance Hypothesis among the best-fitting hypotheses. Results from the  
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24 361 combined LRT test found the highest support for the combination of the Novel  
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27 362 Avoidance and Conspicuousness hypotheses. It should be noted here that although our  
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29 363 clay replicas appeared similar to the salamander color morphs they represented, there was  
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31 364 a possibility that dichromatic mammals viewed them differently. To account for this we  
32  
33 365 recalculated all analyses using conspicuousness estimates of clay reflectance in the place  
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35 366 of salamander reflectance (in this case, striped morph conspicuousness was estimated as  
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37 367 the average reflectance of red and black clay: results not shown). Under this formulation  
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39 368 the Conspicuousness Hypothesis yielded a somewhat poorer fit to the observed data and  
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41 369 was excluded from the combined model.  
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## 50 372 **Discussion**

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52 373 Selection on color pattern can be strongly driven by predators (Endler, 1988), yet how  
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54 374 multiple predators influence selection on the same color patterns is understudied (Endler,  
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3 375 1986). Importantly, prey color patterns that signify toxicity to some predator species may  
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5 376 not carry the same indication of unpalatability to other predators (Pekár *et al.*, 2011;  
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7 377 Willink *et al.*, 2014). In this study, we tested several hypotheses of selection on color  
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9 378 pattern between mammal predators and the salamander *Plethodon cinereus*. We found  
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11 379 consistent support for the single hypothesis that mammals avoid novel and unfamiliar  
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13 380 prey, an observation that has been made in experimental settings (Chitty & Kempson,  
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15 381 1949; Mitchell, 1976), and we found the highest support for a combined hypothesis in  
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17 382 which mammalian predators preferentially attack the most conspicuous prey while  
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19 383 avoiding unfamiliar color morphs.  
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27 385 Avian predators avoid erythristic *P. cinereus* because they appear similar in coloration to  
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29 386 the toxic salamander *Notophthalmus viridescens* (Brodie & Brodie, 1980; Tilley *et al.*,  
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31 387 1982). Selection for Batesian mimicry in *P. cinereus* may or may not extend to additional  
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33 388 predator species, such as mammals. We tested this hypothesis by fitting our observed  
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35 389 data to a model in which mammals avoided erythristic replicas while not discriminating  
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37 390 between either striped or unstriped replicas. We found no support for this hypothesis  
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39 391 alone or as a component of the Combined Hypothesis. The lack of support for mimicry  
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41 392 between erythristic *P. cinereus* and *N. viridescens* from the perspective of mammalian  
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43 393 predators suggests that mammals do not associate erythristic *P. cinereus* with  
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45 394 unpalatability, which aligns well with recent research in the system. For example,  
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47 395 Kraemer and Adams (2014) found evidence that the dichromatic mammalian visual  
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49 396 system allows mammals to use visual stimuli to differentiate salamander species from  
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51 397 each other and common backgrounds on the basis of brightness, but not coloration. This  
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3 398 is significant with regards to mimicry because erythristic *P. cinereus* and *N. viridescens*  
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5 399 are similar with respect to color, while they differ substantially with respect to brightness  
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8 400 (Kraemer & Adams, 2014). Predators that select for mimicry between *P. cinereus* and *N.*  
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10 401 *viridescens* must be capable of identifying prey by color while foraging, which  
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12 402 monochromatic and dichromatic mammals appear unable to do. When paired with our  
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15 403 findings, this research strongly indicates that monochromatic and dichromatic mammals  
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17 404 do not select for mimicry in this system.  
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22 406 By contrast, in this study we found strong statistical support for a composite hypothesis  
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24 407 that incorporates aspects of two modes of prey selection that utilize visual information,  
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27 408 Novel Avoidance (Marples *et al.*, 2007) and Conspicuousness (Endler, 1978), with Novel  
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29 409 Avoidance previously observed in mammal taxa (Chitty & Kempson, 1949). Mammals  
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31 410 are well known to use olfactory cues while foraging (Pyare & Longland, 2001; Hughes *et*  
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33 411 *al.*, 2010). However, our data support two hypotheses that each indicate mammals also  
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35 412 utilize visual cues, specifically by attacking prey that most strongly contrast with local  
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37 413 backgrounds and that are most familiar in appearance. This result implies that mammals  
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39 414 use visual cues both during the detection and identification phase of foraging, which  
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41 415 allows for the possibility that these predators use visual cues of their prey at different  
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43 416 stages of a single predation event (Endler, 1986). For example, a color pattern that  
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45 417 influences a predator's ability to first detect potential prey (the Conspicuousness  
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47 418 Hypothesis; Endler, 1978), may also impact whether that predator then recognizes the  
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49 419 potential prey as a prey item (i.e. the Novel Avoidance, Batesian Mimicry, or Apostatic  
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51 420 Selection hypotheses; summarized in Endler, 1986). Furthermore, both our approaches to  
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3 421 estimate salamander conspicuousness suggest that, although conspicuousness may be  
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5 422 important, novel avoidance likely plays a far more important role in determining attack  
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8 423 likelihood on salamanders by mammal predators. Our findings indicate selection on *P.*  
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10 424 *cinereus* by mammalian predators is complex, with a combination of directional selection  
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12 425 favoring inconspicuous individuals and frequency-dependent selection favoring novel  
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15 426 color morphs. Interestingly, this selection could result from a complex predator  
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17 427 community consisting of several species with each species responding to salamander  
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19 428 visual cues differently, a predator community with behavioral plasticity among  
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21 429 individuals, or a single predator type that incorporates visual cues relating to prey  
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23 430 conspicuousness and novelty at every encounter with potential prey. The next, and  
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25 431 perhaps more technically challenging, research direction will be to identify all members  
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27 432 of these salamander predator communities and characterize how each interacts with  
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29 433 individual salamander prey.  
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36 435 Salamander conspicuousness and novelty to predators are strongly influenced by local  
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38 436 community structure and environmental factors, which may result in selection pressures  
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40 437 that differ among localities. For example, conspicuousness is determined by the contrast  
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42 438 between prey and background (Endler, 1978). Importantly, background may differ by  
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44 439 locality and therefore be influenced by factors such as the composition of tree species,  
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46 440 precipitation, vegetative cover, and time of year (Endler, 1993). Likewise, the  
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48 441 contribution of Novel Avoidance in the best-fitting combined hypothesis supports the  
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50 442 hypothesis that predators avoid prey they have not previously encountered (e.g. Mitchell,  
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52 443 1976; Lindström *et al.*, 2001). Furthermore, when classified as either local (if  
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3 444 corresponding *P. cinereus* morphs were present at the locality) or novel (if corresponding  
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5 445 *P. cinereus* morphs were absent), local salamander replicas were twice as likely to be  
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8 446 attacked than novel replicas (local proportion attacked = 0.23; novel proportion attacked  
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10 447 = 0.11). Thus, our Combined Hypothesis indicates that mammal predators are strongly  
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12 448 influenced by local factors. Variation in potential backgrounds and prior predator  
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14 449 experience may contribute to the variability observed between natural predator-prey  
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16 450 studies conducted under similar, but not identical conditions (e.g., as seen between  
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18 451 Saporito *et al.*, 2007 and Hegna, Saporito & Donnelly, 2013).  
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23 453 *Plethodon cinereus* are likely hunted by several predator taxa (Lotter & Scott, 1977),  
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25 454 with each species potentially directing the evolution of *P. cinereus* phenotype along a  
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27 455 different evolutionary trajectory. Previous research suggests that bird predators select *P.*  
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29 456 *cinereus* coloration such that erythristic individuals evolve coloration that is similar to *N.*  
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31 457 *viridescens* (Brodie & Brodie, 1980; Tilley *et al.*, 1982; Kraemer & Adams, 2014). Here,  
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33 458 we present evidence that mammal predators may select for inconspicuousness in *P.*  
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35 459 *cinereus* as well as for novel color morphs. This complex selective regime may contribute  
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37 460 to the maintenance of polymorphism in *P. cinereus* through variation in predator  
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39 461 communities within and among localities as well as consistent selection for novel,  
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41 462 unfamiliar color morphs. Research on other taxa has likewise found support for  
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43 463 frequency-dependent selection (Pfennig *et al.*, 2007; Karpestam, Merilaita & Forsman,  
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45 464 2014), though under different mechanisms (i.e. apostatic selection and limited attention,  
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47 465 respectively). Selection on prey that depends on the relative abundance of different  
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49 466 morphologies is relatively understudied, though findings like these suggest that  
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3 467 mechanisms such as these may play a large role in maintaining phenotypic diversity.  
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8 469 Color pattern polymorphism is widespread in many species in addition to *P. cinereus*  
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10 470 (e.g. frogs: Hoffman & Blouin, 2000; moths: Poulton, 1890; land snails: Cain &  
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12 471 Sheppard, 1954; reptiles: Norris & Lowe, 1964, Olsson, Stuart-Fox & C Ballen, 2013;  
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14 472 insects: Karpestam *et al.*, 2014), though the mechanisms maintaining polymorphisms are  
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16 473 hotly debated (Bond, 2007). Polymorphisms can be maintained by frequency-dependent  
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18 474 selection (such as novel avoidance or limited attention; Marples *et al.*, 2007; Karpestam  
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20 475 *et al.*, 2014), variation in prey community structure (Merilaita & Kaitala, 2002), multiple  
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22 476 predators with variable behavior (Nokelainen *et al.*, 2014), gene flow among populations  
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24 477 (Slatkin, 1987), or habitat heterogeneity (Sandoval & Nosil, 2005). In many species,  
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26 478 including *P. cinereus*, polymorphism is likely maintained by a complex bricolage of the  
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28 479 above mechanisms. The results of this study demonstrate that prey selection by predators  
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30 480 is complex and is best understood when considering the joint influence of multiple non-  
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32 481 exclusive hypotheses.  
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34 482  
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36 483 Analyses that combine hypotheses as we have done have important strengths over  
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38 484 traditional analyses that compare single hypotheses. First, many biological phenomena  
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40 485 are subject to multiple factors that interact in complex ways (e.g. Prum & Brush, 2002).  
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42 486 Hypotheses that can account for such interactions have the potential to make biological  
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44 487 predictions that more closely approximate biological reality. Second, analytical  
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46 488 frameworks like our combined analysis can be used to propose hypotheses regarding the  
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48 489 relative importance of different, non-exclusive phenomena. For example, our combined  
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3 490 analysis found that the familiarity and conspicuousness of prey was more important for  
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5 491 predicting mammal attack rates than the similarity of prey to other, toxic species. These  
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8 492 hypotheses can then be further tested in more explicit studies. Similar combined  
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10 493 approaches can be used to disentangle other, complex phenomena such as community  
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12 494 assembly, colonization processes, and adaptive landscapes.

13 495

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3 502 Potential Conflicts of Interest:  
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## REFERENCES

- 1  
2  
3 505  
4  
5  
6 506 **Adams DC. 1999.** *Plethodon hoffmani* (Valley and Ridge Salamander). Predation.  
7  
8 507 Herpetological Review **30**: 160.  
9  
10 508 **Allen JA. 1988.** Frequency-dependent selection by predators. Philosophical Transactions  
11  
12 509 of the Royal Society B **319**: 485-503.  
13  
14 510 **Arnold SJ. 1982.** A quantitative approach to antipredator performance: salamander  
15  
16 511 defense against snake attack. Copeia **1982**: 247-253.  
17  
18 512 **Bates HW. 1862.** Contributions to an insect fauna of the Amazon valley (Lepidoptera:  
19  
20 513 Heliconidae). Biological Journal of the Linnaean Society **23**: 495-556.  
21  
22 514 **Beachy CK. 1991.** *Ambystoma maculatum* (spotted salamander). Predation.  
23  
24 515 Herpetological Review **22**: 128.  
25  
26 516 **Bell MA, Orti G, Walker JA, Koenings JP. 1993.** Evolution of pelvic reduction in  
27  
28 517 threespine stickleback fish: a test of competing hypotheses. Evolution **47**: 906-914.  
29  
30 518 **Bond AB. 2007.** The evolution of color polymorphism: crypticity, searching images, and  
31  
32 519 apostatic selection. Annual Review of Ecology, Evolution and Systematics **38**: 489-  
33  
34 520 514.  
35  
36 521 **Brodie ED III. 1993.** Differential avoidance of coral snake banded patterns by free-  
37  
38 522 ranging avian predators in Costa Rica. Evolution **47**: 227-235.  
39  
40 523 **Brodie ED Jr., Brodie ED III. 1980.** Differential avoidance of mimetic salamanders by  
41  
42 524 free-ranging birds. Science **208**: 181-182.  
43  
44 525 **Brodie ED Jr., Nowak RT, Harvey WR. 1979.** Effectiveness of antipredator secretions  
45  
46 526 and behavior of selected salamanders against shrews. Copeia **1979**: 270-274.  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 527 **Brodie ED Jr., Ridenhour BJ, Brodie ED III. 2002.** The evolutionary response of  
4  
5 528 predators to dangerous prey: hotspots and coldspots in the geographic mosaic of  
6  
7 529 coevolution between garter snakes and newts. *Evolution* **56**: 2067-2082.
- 8  
9  
10 530 **Burton TM, Likens GE. 1975.** Salamander populations and biomass in the Hubbard  
11  
12 531 Brook Experimental Forest, New Hampshire. *Copeia* **1975**: 541-546.
- 13  
14  
15 532 **Cain AJ, Sheppard PM. 1954.** Natural Selection in *Cepaea*. *Genetics* **39**: 89-116.
- 16  
17 533 **Chen DM, Goldsmith TH. 1986.** Four spectral classes of cone in the retinas of birds.  
18  
19 534 *Journal of Comparative Physiology A* **159**: 473-479.
- 20  
21  
22 535 **Chitty D, Kempson DA. 1949.** Prebaiting small mammals and a new design of live trap.  
23  
24 536 *Ecology* **30**: 536-542.
- 25  
26  
27 537 **Dodd CK Jr. 1991.** The status of the Red Hills salamander *Phaeognathus hubrichti*,  
28  
29 538 Alabama, USA, 1976-1988. *Biological Conservation* **55**: 57-75.
- 30  
31  
32 539 **Endler JA. 1978.** A predator's view of animal color patterns. In: *Evolutionary Biology*  
33  
34 540 (MK Hecht & WC Steere, eds), pp. 319-364 Plenum Press, New York and London.
- 35  
36 541 **Endler JA. 1986.** Defense against predators. In: *Predator-Prey Relationships* (M Feder &  
37  
38 542 G Lauder), pp. 109-134 University of Chicago Press, Chicago, Illinois.
- 39  
40  
41 543 **Endler JA. 1988.** Frequency-dependent predation, crypsis and aposematic coloration.  
42  
43 544 *Philosophical Transactions of the Royal Society B* **319**: 505-523.
- 44  
45  
46 545 **Endler JA. 1993.** The color of light in forests and its implications. *Ecological*  
47  
48 546 *Monographs* **63**: 1-27.
- 49  
50  
51 547 **Fenster TLD, Fenster CB. 1996.** *Plethodon Cinereus* (redback salamander) predation.  
52  
53 548 *Herpetological Review* **27**: 194.
- 54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 549 **Hegna RH, Saporito RA, Donnelly MA. 2013.** Not all colors are equal: predation and  
4  
5 550 color polytypism in the aposematic poison frog *Oophaga pumilio*. Evolutionary  
6  
7 551 Ecology **27**: 831-845.
- 8  
9  
10 552 **Hughes NK, Price CJ, Banks PB. 2010.** Predators are attracted to the olfactory signals  
11  
12 553 of prey. PLOS ONE **5**: e13114.
- 13  
14  
15 554 **Hoffman EA, Blouin MS. 2000.** A review of colour and pattern polymorphisms in  
16  
17 555 anurans. Biological Journal of the Linnaean Society **70**: 633-665.
- 18  
19  
20 556 **Huheey JE, Stupka A. 1967.** Amphibians and Reptiles of the Great Smoky Mountains  
21  
22 557 National Park. University of Tennessee Press, Knoxville, Tennessee, 98 p.
- 23  
24 558 **Husak JF, Macedonia JM, Fox SF, Saucedo RC. 2006.** Predation cost of conspicuous  
25  
26 559 male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using  
27  
28 560 clay-covered model lizards. Ethology **112**: 572-580.
- 29  
30  
31 561 **Jacobs GH. 1993.** The distribution and nature of colour vision among the mammals.  
32  
33 562 Biological Reviews **68**: 413-471.
- 34  
35  
36 563 **Karpestam E, Merilaita S, Forsman A. 2014.** Natural levels of colour polymorphism  
37  
38 564 reduce performance of visual predators searching for camouflaged prey. Biological  
39  
40 565 Journal of the Linnean Society **112**: 546-555.
- 41  
42  
43 566 **Kikuchi DW, Pfennig DW. 2010.** Predator cognition permits imperfect coral snake  
44  
45 567 mimicry. The American Naturalist **176**: 830–834.
- 46  
47  
48 568 **Kraemer AC, Adams DC. 2014.** Predator perception of Batesian mimicry and  
49  
50 569 conspicuousness in a salamander. Evolution **68**: 1197-1206.
- 51  
52  
53 570 **Kuchta SR. 2005.** Experimental support for aposematic coloration in the salamander  
54  
55 571 *Ensatina eschscholtzii xanthoptica*: implications for mimicry of pacific newts. Copeia

- 1  
2  
3 572       **2005:** 265-271.  
4  
5  
6 573       **McElroy MT. 2015.** Teasing apart crypsis and aposematism – evidence that disruptive  
7  
8 574       coloration reduces predation on a noxious toad.  
9  
10 575       **Lewis F, Butler A, Gilbert L. 2011.** A unified approach to model selection using the  
11  
12 576       likelihood ratio test. *Methods in Ecology and Evolution* **2:** 155-162.  
13  
14 577       **Lindström L, Alatalo RV, Lyytinen A, Mappes J. 2001.** Predator experience on cryptic  
15  
16 578       prey affects the survival of conspicuous aposematic prey. *Proceedings of the Royal*  
17  
18 579       *Society B* **268:** 357-361.  
19  
20 580       **Lotter F, Scott NJ Jr. 1977.** Correlation between climate and distribution of the color  
21  
22 581       morphs of the salamander *Plethodon cinereus*. *Copeia* **1977:** 681-690.  
23  
24 582       **Low PA, Sam K, McArthur C, Posa MRC, Hochuli DF. 2014.** Determining predator  
25  
26 583       identity from attack marks left in model caterpillars: guidelines for best practice.  
27  
28 584       *Entomologia Experimentalis et Applicata* **152:** 120-126.  
29  
30 585       **Madsen, T. 1987.** Are juvenile grass snakes, *Natrix natrix* aposematically colored?  
31  
32 586       *Oikos* **48:** 265-267.  
33  
34 587       **Marples NM, Quinlan M, Thomas RJ, Kelly DJ. 2007.** Deactivation of dietary  
35  
36 588       wariness through experience of novel food. *Behavioural Ecology* **18:** 803-810.  
37  
38 589       **Merilaita S, Kaitala V. 2002.** Community structure and the evolution of aposematic  
39  
40 590       coloration. *Ecology Letters* **5:** 495-501.  
41  
42 591       **Mitchell D. 1976.** Experiments on neophobia in wild and laboratory rats: a reevaluation.  
43  
44 592       *Journal of Comparative and Physiological Psychology* **90:** 190-197.  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
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- 1  
2  
3 593 **Nokelainen O, Valkonen J, Lindstedt C, Mappes J. 2014.** Changes in predator  
4  
5 594 community structure shifts the efficacy of two warning signals in Arctiid moths.  
6  
7 595 *Journal of Animal Ecology* **83**: 598-605.  
8  
9  
10 596 **Noonan BP, Comeault AA. 2009.** The role of predator selection on polymorphic  
11  
12 597 aposematic poison frogs. *Biology Letters* **5**: 51-54.  
13  
14  
15 598 **Norris KS, Lowe CH. 1964.** An analysis of background color-matching in amphibians  
16  
17 599 and reptiles. *Ecology* **45**: 565-580.  
18  
19  
20 600 **Olsson M, Stuart-Fox D, Ballen C. 2013.** Genetics and evolution of colour patterns in  
21  
22 601 reptiles. *Seminars in Cell & Developmental Biology* **24**: 529-541.  
23  
24  
25 602 **Pafilis P, Foufopoulos J, Poulakakis N, Lymberakis P, Valakos ED. 2009.** Tail  
26  
27 603 shedding in island lizards: decline of antipredator defenses in relaxed predation  
28  
29 604 environments. *Evolution* **63**: 1262-1278.  
30  
31  
32 605 **Pekár S, Jarab M, Fromhage L, Herberstein ME. 2011.** Is the evolution of inaccurate  
33  
34 606 mimicry a result of selection by a suite of predators? A case study using  
35  
36 607 myrmecomorphic spiders. *The American Naturalist* **178**: 124-134.  
37  
38  
39 608 **Petranka J. 1998.** Salamanders of the United States and Canada. Smithsonian Books,  
40  
41 609 Washington, DC.  
42  
43  
44 610 **Pfennig DW, Harcombe WR, Pfennig KS. 2001.** Frequency-dependent Batesian  
45  
46 611 mimicry *Nature* **410**: 323.  
47  
48  
49 612 **Pfennig DW, Harper GR, Brumo AF, Harcombe WR, Pfennig KS. 2007.** Population  
50  
51 613 differences in predation on Batesian mimics in allopatry with their model: selection  
52  
53 614 against mimics is strongest when they are common. *Behavioral Ecology and*  
54  
55 615 *Sociobiology* **61**: 505-511.  
56  
57  
58  
59  
60

- 1  
2  
3 616 **Poulton EB. 1890.** The Colours of Animals: Their Meaning and Use, Especially  
4  
5  
6 617 Considered in the Case of Insects. Appleton, New York.  
7  
8 618 **Prum RO, Brush AH. 2002.** The evolutionary origin and diversification of feathers. The  
9  
10 619 Quarterly Review of Biology **77**: 261-295.  
11  
12 620 **Pyare S, Longland WS. 2001.** Mechanisms of truffle detection by northern flying  
13  
14 621 squirrels. The Canadian Journal of Zoology **79**: 1007-1015.  
15  
16  
17 622 **R Core Development Team. 2015.** R: a language and environment for statistical  
18  
19 623 computing. Foundation for Statistical Computing, Vienna.  
20  
21  
22 624 **Reimchen TE. 2000.** Predator handling failures of lateral plate morphs in *Gasterosteus*  
23  
24 625 *aculeatus*: functional implications for the ancestral plate condition. Behaviour **137**:  
25  
26 626 1081-1096.  
27  
28  
29 627 **Reznick DN, Bryga H, Endler JA. 1990.** Experimentally induced life-history evolution  
30  
31 628 in a natural population. Nature **346**: 357-359.  
32  
33  
34 629 **Reznick DN, Shaw FH, Rodd FH, Shaw RG. 1997.** Evaluation of the rate of evolution  
35  
36 630 in natural populations of guppies (*Poecilia reticulata*). Science **275**: 1934-1937.  
37  
38  
39 631 **Reznick D, Endler JA. 1982.** The impact of predation on life history evolution in  
40  
41 632 Trinidadian guppies (*Poecilia reticulata*). Evolution **36**: 160-177.  
42  
43  
44 633 **Ruxton GD. 2009.** Non-visual crypsis: a review of the empirical evidence for  
45  
46 634 camouflage to senses other than vision. Philosophical Transactions of the Royal  
47  
48 635 Society B **364**: 549-557.  
49  
50  
51 636 **Ruxton GD, Sherratt TN, Speed MP. 2004.** Avoiding attack: the evolutionary ecology  
52  
53 637 of crypsis, warning signals and mimicry. Oxford Univ Press, Oxford, UK.  
54  
55  
56  
57  
58  
59  
60

- 1  
2  
3 638 **Sandoval CP, Nosil P. 2005.** Counteracting selective regimes and host preference  
4  
5 639 evolution in ecotypes of two species of walking-sticks. *Evolution* **59**: 2405-2413.  
6  
7  
8 640 **Saporito RA, Zuercher R, Roberts M, Gerow KG, Donnelly MA. 2007.** Experimental  
9  
10 641 evidence for aposematism in the dendrobatid poison frog *Oophaga pumilio* Copeia  
11  
12 642 **2007**: 1006-1011.  
13  
14  
15 643 **Slatkin M. 1987.** Gene flow and the geographic structure of natural populations. *Science*  
16  
17 644 **236**: 787-792.  
18  
19  
20 645 **Sokal RR, Rohlf FJ. 2012.** *Biometry* 4th ed. New York: W.H. Freeman.  
21  
22 646 **Stebbins RC. 1954.** Natural history of the salamanders of the plethodontid genus  
23  
24 647 *Ensatina*. University of California Publications in Zoology **54**: 47-124.  
25  
26  
27 648 **Tilley SG, Lundrigan BL, Brower LP. 1982.** Erythrism and mimicry in the salamander  
28  
29 649 *Plethodon cinereus*. *Herpetologica* **38**: 409-417.  
30  
31  
32 650 **Vignieri SN, Larson JG, Hoekstra HE. 2010.** The selective advantage of crypsis in  
33  
34 651 mice. *Evolution* **64**: 2153-2158.  
35  
36  
37 652 **Veilleux CC, Cummings ME. 2012.** Nocturnal light environments and species ecology:  
38  
39 653 implications for nocturnal color vision in forests. *Journal of Experimental Biology*  
40  
41 654 **215**: 4085-4096.  
42  
43  
44 655 **Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998.** Tetrachromacy,  
45  
46 656 oil droplets and bird plumage colours. *Journal of Comparative Physiology A* **183**:  
47  
48 657 621–633.  
49  
50  
51 658 **Williams DA. 1970.** Discrimination between regression models to determine the pattern  
52  
53 659 of enzyme synthesis in synchronous cell cultures. *Biometrics* **26**: 23-32.  
54  
55  
56  
57  
58  
59  
60



- 1  
2  
3 6601. **Willink B, García-Rodríguez A, Bolaños F, Pröhl H. 2014.** The interplay between  
4  
5  
6 661 multiple predators and prey colour divergence. **113**: 580-589.  
7  
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3 662 **Table 1.** Likelihood and AIC scores for each hypothesis. Both approaches indicate that,  
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6 663 of the hypotheses tested, Novel Avoidance is the best fitting single hypothesis, while the  
7  
8 664 Combined Hypothesis best fits the observed data over all single hypotheses.  
9

10 665

Model	-lnL	AIC
Combined	-3.76	15.52
Novel Avoidance	-7.65	19.31
Non-Visual	-10.58	25.16
Conspicuousness	-10.93	25.86
Mimicry	-19.18	42.36
Apostatic	-35.14	74.28
Selection		

32 666

667 **Table 2.** Pairwise comparisons of each hypothesis using simulation-based LRT.  
 668 ‘Apostatic’ refers to the Apostatic Selection Hypothesis, ‘Conspic.’ refers to the  
 669 Conspicuousness Hypothesis, ‘Novel Avoid.’ refers to the Novel Avoidance Hypothesis,  
 670 and ‘Non-V’ refers to the Non-Visual Hypothesis. Row names that correspond to each  
 671 cell indicate the model treated as the ‘null’ hypothesis, while column names denote the  
 672 ‘alternative’ hypothesis. Note that the Combined Hypothesis is the best fit among all  
 673 comparisons, because all comparisons with the Combined Hypothesis as the null are non-  
 674 significant and all comparisons with the Combined Hypothesis as the alternative are  
 675 significant.

676

	Apostatic	Mimicry	Conspic.	Novel Avoid.	Non-V	Combined
Apostatic	-	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Mimicry	<b>&lt;0.001</b>	-	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Conspic.	0.120	0.540	-	<b>0.005</b>	0.420	<b>&lt;0.001</b>
Novel Avoid.	0.798	<b>&lt;0.001</b>	<b>&lt;0.001</b>	-	<b>&lt;0.001</b>	<b>&lt;0.001</b>
Non-V	0.343	0.877	0.991	<b>0.020</b>	-	<b>&lt;0.001</b>
Combined	0.775	0.552	0.922	0.616	0.766	-

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3 678 **Figure 1.** Schematic of predator attacks expected under each single hypothesis. A) The  
4  
5 679 Mimicry Hypothesis states that mimics will be avoided, resulting in 100% of attacks on  
6  
7 680 non-mimetic morphs. B) The Conspicuousness Hypothesis states that prey with the  
8  
9 681 highest contrast with background will be attacked most. In this example, the gray morph  
10  
11 682 is twice as conspicuous as the black morph, thus sustaining twice as many attacks. C) The  
12  
13 683 Apostatic Selection Hypothesis states that rare morphs will be attacked less frequently  
14  
15 684 and common morphs will be attacked more. In this example, the gray morph is rare  
16  
17 685 (making up 25% of the local population and thus 25% of total attacks), while the black  
18  
19 686 morph is more common (making up 75% of the local population and thus 75% of total  
20  
21 687 attacks). D) The Novel Avoidance Hypothesis states that morphs not locally encountered  
22  
23 688 are avoided. In this example, the gray morph is locally encountered by predators and thus  
24  
25 689 attacked, while the black morph is absent and is thus avoided by predators. Note that the  
26  
27 690 Non-Visual Hypothesis predicts no difference in attacks among morphs (not depicted),  
28  
29 691 and the Combined Hypothesis has different predictions depending on the weights given  
30  
31 692 for each single hypothesis (not depicted).  
32  
33  
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41 694 **Figure 2.** *Plethodon cinereus* color morphs, clay replicas, and typical mammalian  
42  
43 695 impressions. A) An erythristic *P. cinereus* salamander; B) a striped *P. cinereus*  
44  
45 696 salamander; C) an unstriped *P. cinereus* salamander. D) Representative clay replicas of  
46  
47 697 each salamander morph: Left, erythristic; center, striped; right, unstriped. Typical  
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49 698 mammalian impressions on an E) unstriped replica and an F) striped replica.  
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3 700 **Figure 3.** Predator attacks A) observed, B) predicted under the Mimicry Hypothesis, C)  
4  
5 701 the Conspicuousness Hypothesis, D) the Apostatic Selection Hypothesis, E) the Novel  
6  
7 702 Avoidance Hypothesis, and F) the Combined Hypothesis. Black bars represent the  
8  
9 703 unstriped color morph, striped bars represent the striped morph, and red bars represent  
10  
11 704 the erythristic morph. The pie charts in panel ‘A’ denote the proportion of each  
12  
13 705 *Plethodon cinereus* color morph locally present at each locality. Fisk: 28% erythristic and  
14  
15 706 72% striped; Lily: 21% erythristic and 79% striped; Coys: 38% unstriped and 62%  
16  
17 707 striped; Palmer: 18% unstriped and 82% striped.  
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708 **Appendix S1: Potential Mammalian Predator Visual Abilities**

709 **Table S1.** Potential mammalian predators of *Plethodon cinereus* listed by family,  
 710 including their activity patterns and known visual systems. List taken from  
 711 <http://www.mass.gov/eea/agencies/dfg/dfw/fish-wildlife-plants/state-mammal-list.html>  
 712 Sources are listed below table.

Family	Time Active	Visual System
Canidae (foxes and coyotes)	mostly nocturnal	dichromatic
Cricetidae (deermice and voles)	varies	unknown
Didelphidae (opposums)	nocturnal	monochromatic
Dipodidae (jumping mice)	nocturnal	unknown
Erethizontidae (porcupines)	nocturnal	unknown
Felidae (cats)	varies	dichromatic
Mephitidae (skunks)	nocturnal	unknown
Muridae (old world rats and mice)	varies	dichromatic
Mustelidae (weasels)	varies	dichromatic
Procyonidae (racoons)	nocturnal	monochromatic
Sciuridae (squirrels)	diurnal (squirrels)	dichromatic
	nocturnal (flying squirrels)	monochromatic
Soricidae (shrews)	nocturnal	dichromatic
Talpidae (moles)	varies	dichromatic
Ursidae (bears)	varies	dichromatic

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714 Carvalho LS, Cowing JA, Wilkie SE, et al (2006) Shortwave visual  $\square$  sensitivity in tree

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2  
3 715 and flying squirrels reflects changes in lifestyle. *Curr Biol* 16:R81–83  
4  
5  
6 716 Glösmann M, Fliesser M, Ahnelt PK (1999) Cone opsin topography in the retina of the  
7  
8 717 European mole. *Invest Ophthalmol Vis Sci* 40:S158  
9  
10 718 Jacobs GH (1993) The distribution and nature of colour vision among the mammals. *Biol*  
11  
12 719 *Rev* 68:413-471  
13  
14  
15 720 Jacobs GH (2009) Evolution of colour vision in mammals. *Phil Trans Roy Soc B*  
16  
17 721 364:2957-2967  
18  
19 722 Jacobs GH, Deegan JF II (1992) Cone photopigments in nocturnal and diurnal  
20  
21 723 procyonids. *J Comp Physiol A* 171:351-358  
22  
23 724 Jacobs GH, Williams GA (2010) Cone pigments in a North American marsupial, the  
24  
25 725 opossum (*Didelphis virginiana*). *J Comp Physiol A* 196:379-384  
26  
27  
28 726 Martin IG (1983) Daily activity of short-tailed shrews (*Blarina brevicauda*) in simulated  
29  
30 727 natural conditions. *Am Mid Nat* 109:136-144  
31  
32  
33 728 Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining  
34  
35 729 activity patterns of rodents. *Evol Ecol* 20:479-490  
36  
37  
38 730 Samson C, Raymond M (1995) Daily activity pattern and time budget of stoats (*Mustela*  
39  
40 731 *erminea*) during summer in southern Quebec. *Mammalia* 59:501-510  
41  
42  
43 732 Stebbins LL (1971) Seasonal variations in circadian rhythms of deer mice, in  
44  
45 733 Northwestern Canada. *Arctic* 24:124-131  
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734 **Appendix S2: Clay Replicas Recovered and Attacked**

735 **Table S2. Number of replicas attacked and recovered at each locality. Values above**  
 736 **the slash indicate the number attacked, while values below the slash indicate the**  
 737 **total number recovered (from a possible 75).**

Locality	Unstriped	Striped	Erythristic
Fisk	9/61	14/66	17/70
Lily	7/73	12/74	20/75
Coys	11/73	7/73	3/73
Palmer	10/72	18/72	9/73

738

739



```

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4 740 Appendix S3: R Code For Combined Analysis
5
6 741
7
8 742 Note: this code is organized for the data presented in this paper, but can be reformulated
9
10 743 for any other data/hypothesis structure for which like likelihood can be calculated.
11
12
13 744 # General order of operations:
14
15 745 # 1) Set up data
16
17 746 # 2) Combine models
18
19
20 747 # 3) Find optimum combination of models to maximize likelihood
21
22 748 # 4) Identify weights
23
24 749 # 5) Calculate new predictions
25
26
27 750
28
29 751 ##### Step 1 #####
30
31 752 obs.x<- #vector of 'successes' in n trials
32
33 753 obs.y<- #vector of 'failures in n trials
34
35 754 n<- #number of trials
36
37 755 A.x.exp<- #expected number of 'successes' under hypothesis 'A'
38
39 756 B.x.exp<- #expected number of 'successes' under hypothesis 'B'
40
41 757 x.exp<-cbind(A.x.exp, B.x.exp)
42
43 758 p.exp<- #similar matrix to x.exp, but with expected proportion of 'successes' under each
44
45 759 hypothesis
46
47 760 p.obs<- #observed proportion of 'successes'
48
49 761
50
51 762 ##### Step 2 #####
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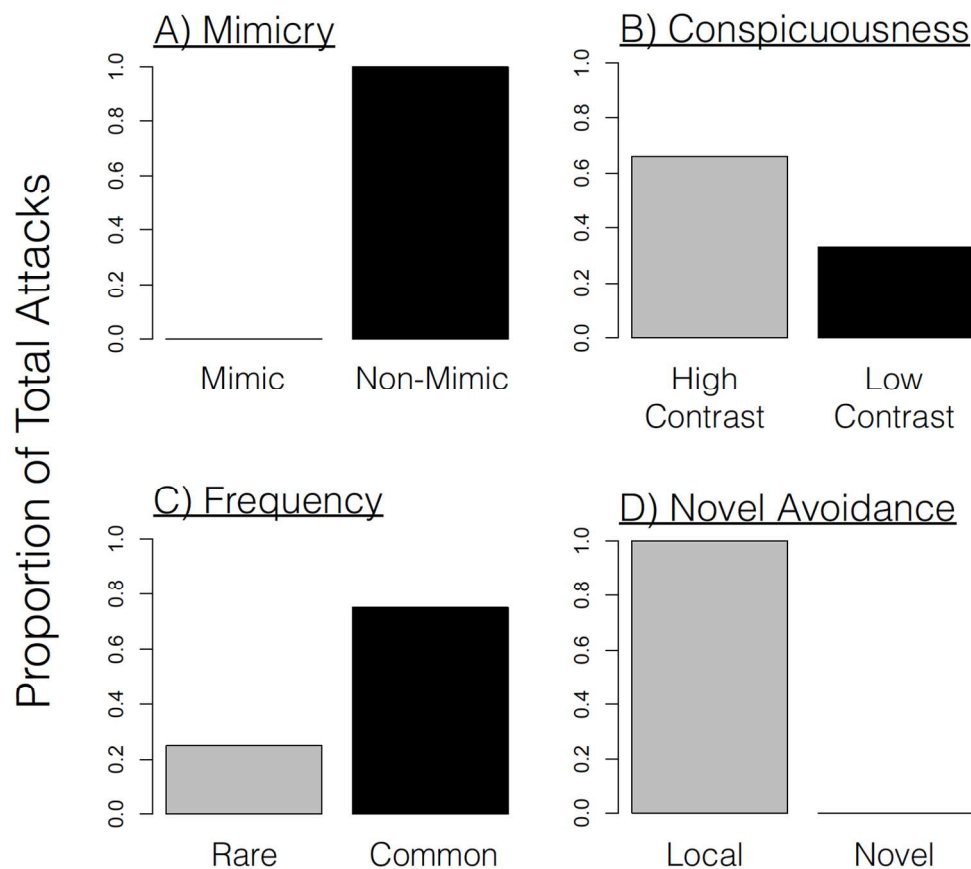
```

```

1
2
3   763   propAB<-function(a,b){
4
5   764       tot<-sum(a,b)
6
7   765       a<-a/tot; b<-b/tot
8
9
10  766       return(c(a,b))
11
12
13  767   }
14
15  768   comb.like.fit<-function(AB){
16
17  769       abVec<-propAB(AB[1],AB[2])
18
19
20  770       p.combine<-(abVec[1]*P.exp[,1] + abVec[2]* P.exp[,2])
21
22  771       comb.like<-log((p.combine/p.obs)^obs.x*((1-p.combine)/(1-p.obs))^(obs.y))
23
24  772       mask<-apply(as.matrix(comb.like),2,is.infinite) #finds all 'Inf'
25
26
27  773       comb.like2<-comb.like
28
29  774       comb.like2[mask]<-0 #replaces 'Inf' with 0 (because integer/0 can not be
30
31  775       calculated; this should     result in a more conservative likelihood for all model-
32
33  776       dataset combinations)
34
35
36  777       mask<-apply(as.matrix(comb.like2),2,is.nan) #finds all 'NaN'
37
38
39  778       comb.like3<-comb.like2
40
41  779       comb.like3[mask]<-0 #replaces 'NaN' with 0 (these were all instances in which 0/0
42
43  780       = NaN)
44
45
46  781       result<-sum(comb.like3)
47
48  782       return(result)
49
50
51  783   }
52
53  784
54
55  785   ##### Step 3 #####
56
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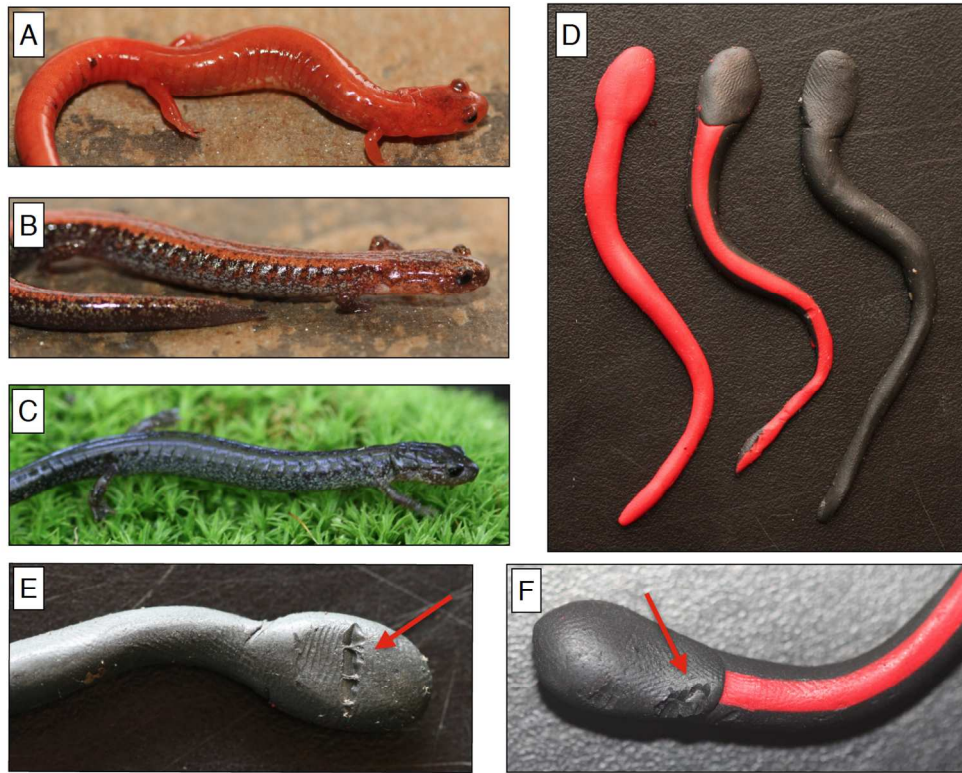
```

```
1
2
3 786 AB<-c(1,1)
4
5 787 comb.like.fit(AB)
6
7
8 788 optim(AB,comb.like.fit,method="L-BFGS-B",control=list(fnscale=-1),lower=0)
9
10 789 solution<-optim(AB,comb.like.fit,method="L-BFGS-B",control=list(fnscale=-
11
12           1),lower=0)$par
13
14 791 solution
15
16
17 792
18
19
20 793 ##### Step 4 #####
21
22 794 A.weight<-solution[1]/sum(solution)
23
24 795 B.weight<-solution[2]/sum(solution)
25
26
27 796
28
29 797 ##### Step 5 #####
30
31 798 combined.p.exp<-A.weight*p.exp[,1]+B.weight*p.exp[,2]
32
33
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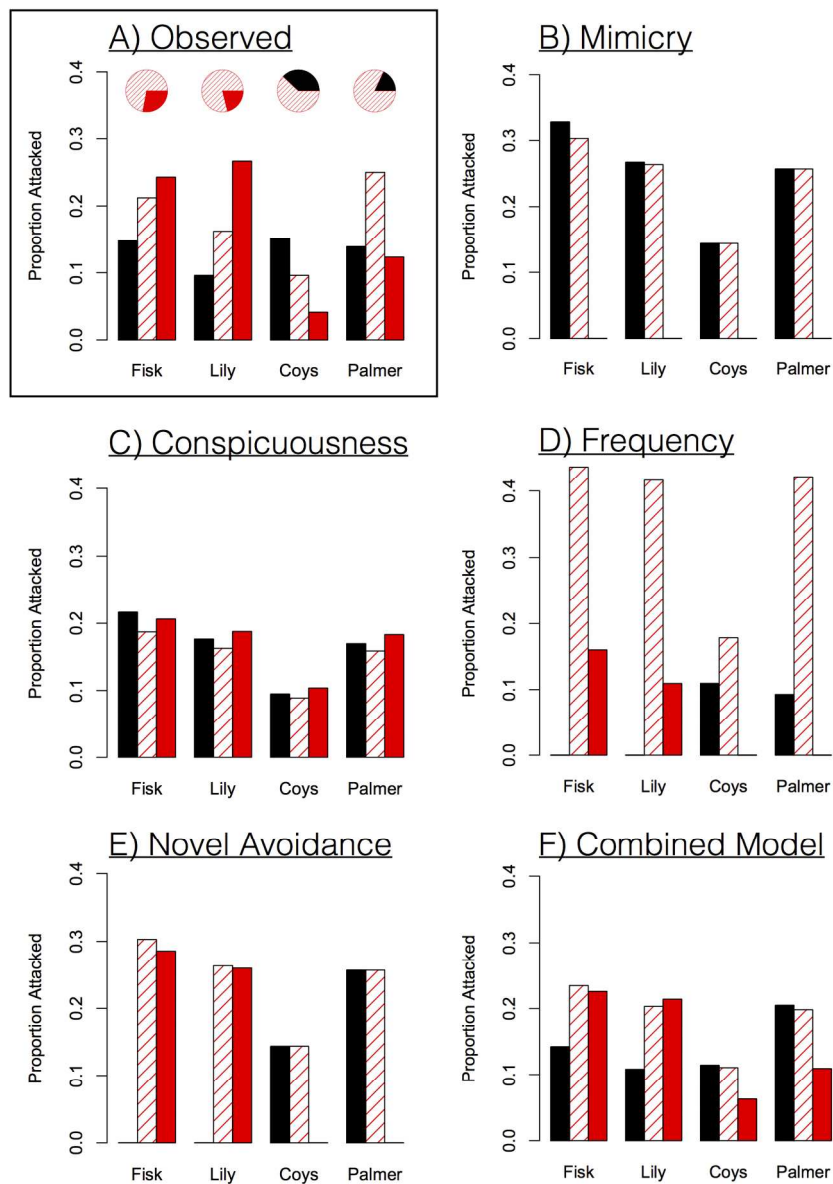


Schematic of predator attacks expected under each single hypothesis. A) The Mimicry Hypothesis states that mimics will be avoided, resulting in 100% of attacks on non-mimetic morphs. B) The Conspicuousness Hypothesis states that prey with the highest contrast with background will be attacked most. In this example, the gray morph is twice as conspicuous as the black morph, thus sustaining twice as many attacks. C) The Apostatic Selection Hypothesis states that rare morphs will be attacked less frequently and common morphs will be attacked more. In this example, the gray morph is rare (making up 25% of the local population and thus 25% of total attacks), while the black morph is more common (making up 75% of the local population and thus 75% of total attacks). D) The Novel Avoidance Hypothesis states that morphs not locally encountered are avoided. In this example, the gray morph is locally encountered by predators and thus attacked, while the black morph is absent and is thus avoided by predators. Note that the Non-Visual Hypothesis predicts no difference in attacks among morphs (not depicted), and the Combined Hypothesis has different predictions depending on the weights given for each single hypothesis (not depicted).

274x245mm (144 x 144 DPI)



*Plethodon cinereus* color morphs, clay replicas, and typical mammalian impressions. A) An erythristic *P. cinereus* salamander; B) a striped *P. cinereus* salamander; C) an unstriped *P. cinereus* salamander. D) Representative clay replicas of each salamander morph: Left, erythristic; center, striped; right, unstriped. Typical mammalian impressions on an E) unstriped replica and an F) striped replica.  
279x220mm (144 x 144 DPI)



Predator attacks A) observed, B) predicted under the Mimicry Hypothesis, C) the Conspicuousness Hypothesis, D) the Apostatic Selection Hypothesis, E) the Novel Avoidance Hypothesis, and F) the Combined Hypothesis. Black bars represent the unstriped color morph, striped bars represent the striped morph, and red bars represent the erythristic morph. The pie charts in panel 'A' denote the proportion of each *Plethodon cinereus* color morph locally present at each locality. Fisk: 28% erythristic and 72% striped; Lily: 21% erythristic and 79% striped; Coys: 38% unstriped and 62% striped; Palmer: 18% unstriped and 82% striped.

300x422mm (150 x 150 DPI)