

1 **Habitat disturbance alters color contrast and the detectability of cryptic and aposematic frogs**

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3

4 **ABSTRACT**

5 Animals use color both to conceal and signal their presence, with patterns that match the background,
6 disrupt shape recognition, or highlight features important for communication. The forms that these color
7 patterns take are responses to the visual systems that observe them and the environments within which
8 they are viewed. Increasingly, however, these environments are being affected by human activity. We
9 studied how pattern characteristics and habitat change may affect the detectability of three frog color
10 patterns from the Bocas del Toro archipelago in Panama: Beige-Striped Brown *Allobates talamancae* and
11 two spotted morphs of *Oophaga pumilio*, Black-Spotted Green and Black-Spotted Red. To assess
12 detectability, we used visual modeling of conspecifics and potential predators, along with a computer-
13 based detection experiment with human participants. Although we found no evidence for disruptive
14 camouflage, we did find clear evidence that *A. talamancae* stripes are inherently more cryptic than *O.*
15 *pumilio* spots regardless of color. We found no evidence that color pattern polytypism in *O. pumilio* is
16 related to differences in the forest floor between natural sites. We did, however, find strong evidence that
17 human disturbance affects the visual environment and modifies absolute and rank order frog detectability.
18 Human-induced environmental change reduces the effectiveness of camouflage in *A. talamancae*, reduces
19 detectability of Black-Spotted Green *O. pumilio*, and increases chromatic contrast, but not detectability, in
20 Black-Spotted Red *O. pumilio*. Insofar as predators may learn about prey defenses and make foraging
21 decisions based on relative prey availability and suitability, such changes may have wider implications for
22 predator-prey dynamics.

23 **KEYWORDS**

24 aposematism, camouflage, habitat change, human disturbance, *Oophaga pumilio*, *Allobates talamancae*.

25 **LAY SUMMARY**

26 Color patterns are used by animals to conceal, or signal, their presence, but the distinction between
27 camouflage and conspicuousness is often dependent on the background. We found that the absolute, and
28 rank-order, detectability of leaf litter frogs at a site of increased human activity differed from that at an
29 adjacent undisturbed site. These changes to detectability may affect the efficacy of individual defensive
30 strategies but may also influence how predators forage on multiple prey types.

31 INTRODUCTION

32 Color forms an important aspect of the lives of many different species (Cuthill et al., 2017): camouflage
33 allows animals to evade detection (Cott, 1940; Endler, 1978; Cuthill, 2019), aposematism warns predators
34 to stay away (Poulton, 1890; Cott 1940; Mappes et al., 2005; Stevens and Ruxton, 2012), and sexual
35 displays attract mates and intimidate rivals (Darwin 1871; Andersson, 1994; Weaver et al., 2017). These
36 colors, both cryptic and conspicuous, evolve as a product of the visual systems that observe them and the
37 backgrounds against which they are viewed (Stevens, 2007; Merilaita et al., 2017). The efficacy of
38 camouflage in particular often depends on specific background features (Troscianko et al., 2016; Michalis
39 et al., 2017), but conspicuous signals can also be affected by their surroundings (Gamberale-Stille, 2001;
40 Aronsson and Gamberale-Stille, 2009; Honma et al., 2015).

41 The perception of animal coloration can be described in relation to the processing of chromatic (hue) and
42 achromatic (luminance/brightness) information, as well as the structural arrangement of different pattern
43 components that may vary in spatial frequency (size), symmetry, and orientation (Troscianko et al., 2009;
44 Cuthill et al., 2017). In background matching camouflage, the signal-to-noise ratio between animal and
45 background characteristics is minimized with color and patterning that matches common features of the
46 background (Endler, 1978; Michalis et al., 2017; Cuthill, 2019). Disruptive camouflage, on the other
47 hand, prevents detection with high contrast patterns that differentially blend into the background and
48 break up the outline of otherwise recognizable features (Stevens and Cuthill, 2006; Stevens and Merilaita,
49 2009; Cuthill, 2019). In both instances, camouflage is most effective when hue and brightness are drawn
50 from the background distribution of colors (Stevens and Merilaita, 2009; Michalis et al., 2017). However,
51 whereas background matching is most effective when matching common background features, disruptive
52 coloring often favors patterns that maximize contrast between pattern elements (Schaefer and Stobbe,
53 2006; Stevens et al., 2006; Cuthill et al., 2006; Barnett et al., 2016; Michalis et al., 2017; Phillips et al.,
54 2017).

55 In aposematic signals, higher contrast against the background and between pattern components, is often
56 associated with higher detectability and more effective avoidance learning by potential predators
57 (Forsman and Merilaita, 1999; Forsman and Herrström, 2004; Aronsson and Gamberale-Stille, 2008).
58 The arrangement of pattern, however, may blur the distinction between cryptic and aposematic signals.
59 For instance, recognizable patterns can be aversive even without conspicuous colors (Wüster et al., 2004;
60 Valkonen et al., 2011), high contrast aposematic patterns can act as disruptive camouflage in certain
61 microhabitats (Honma et al., 2015), and when viewed from a distance high contrast patterning may blend
62 together to match the background (Marshall, 2000; Tullberg et al., 2005; Bohlin et al., 2012; Caro et al.,
63 2013; Barnett and Cuthill, 2014; Barnett et al., 2018).

64 Visual ecology, therefore, depends on a complex interaction between animal coloration and the
65 environmental features that form the visual background. Increasingly, however, human activity is
66 interfering with these processes and altering the background against which animals are observed
67 (Kettlewell, 1955; Mills et al., 2013; Zimova et al., 2016; Delhey and Peters, 2017; Walton and Stevens,
68 2018; Guiden et al., 2019; Spaniol et al., 2020). For example, the influence of humans on the visual
69 environment has been well illustrated by the classic evolutionary study of industrial melanism in the
70 peppered moth (*Biston betularia*; Kettlewell, 1955; Walton and Stevens, 2018), but such changes are also
71 seen as rising temperatures alter the extent and duration of snow cover (Imperio et al., 2013; Mills et al.,
72 2013; Zimova et al., 2016; Atmeh et al., 2018) and increase the frequency of coral bleaching events
73 (Coker et al., 2009).

74 The Neotropical poison frogs (Dendrobatidae) have become a model system for understanding visual
75 ecology due to their highly variable, and often very conspicuous, color patterns and their possession of
76 alkaloid toxins (Summers and Clough, 2001; Siddiqi et al., 2004; Roberts et al., 2007; Wang and Shaffer,
77 2008; Hoogmoed and Avila-Pires, 2012; Yeager et al., 2012; Twomey et al., 2016; Rojas, 2017). One
78 species, *Oophaga pumilio*, exhibits an extreme degree of color variation in the Bocas del Toro
79 archipelago in Panama. Throughout these islands, *O. pumilio* has diversified into both conspicuous and

80 cryptic color forms through interactions between genetic drift, sexual selection, and predation risk
81 (Summers et al., 1999; Siddiqi et al., 2004; Reynolds and Fitzpatrick, 2007; Saporito et al., 2007; Maan
82 and Cummings, 2008, 2009, 2012; Richards-Zawacki et al., 2012; Crothers and Cummings, 2015; Yang
83 et al., 2019). Conversely, co-occurring frogs in the closely related family Aromobatidae are
84 predominantly non-toxic and cryptic in color, despite sharing many features of their morphology,
85 behavior, and habitat requirements with dendrobatids (Grant et al., 2006; Grant et al., 2017; Mebs et al.,
86 2018).

87 Here, we examine how the interaction between frog coloration and background characteristics affects the
88 visual ecology of terrestrial frogs in the Bocas del Toro archipelago, using the non-toxic, Beige-Striped
89 Brown *Allobates talamancae* (Aromobatidae), and two allopatric color morphs of the toxic *O. pumilio*
90 (Dendrobatidae): Black-Spotted Green from Isla Colón and Black-Spotted Red from Isla Bastimentos.
91 Previous studies comparing the color and behavior of *O. pumilio* generally support the notion that,
92 although both morphs are chemically defended, red morphs utilize aposematism whereas green morphs
93 are cryptic (Pröhl and Ostrowski, 2011; Rudh et al., 2012; Rudh, 2013; Segami Marzal et al., 2017). The
94 frogs' natural habitats are, however, exposed to human activity, including tree removal and the
95 introduction of banana crops, that may alter the natural perception of frog coloration (Spalding, 2013;
96 Guiden et al., 2019).

97 By photographing frogs and their natural leaf litter backgrounds on Isla Colón and Isla Bastimentos, as
98 well as the leaf litter at a site of increased human activity on Isla Colón in which frogs were also present,
99 we sought to examine the role of pattern and habitat in producing frog camouflage or conspicuousness.
100 We measured the perceived contrast between the frogs and the three habitats with models of predator and
101 conspecific vision, in conjunction with a computer-based detection experiment with human participants
102 designed to assess whether these findings corresponded to differences in detectability. In particular, we
103 were interested in whether patterning reduced detection through disruptive camouflage or through
104 distance-dependent pattern blending, whether the polytypic color patterns of *O. pumilio* were specialized

105 towards particular local background characteristics, and whether human disturbance of habitats alters frog
106 detectability. We predicted i) that high contrast patterning combined with cryptic colors would act as
107 disruptive camouflage, ii) that the mean colors of the frogs would match the background and be
108 camouflaged when viewed from a distance, iii) that as camouflage and conspicuous signaling are both
109 affected by background features cryptic *O. pumilio* would be more cryptic, and conspicuous *O. pumilio*
110 more detectable, at their local sites than at alternate sites, and iv) that as camouflage is particularly
111 dependent on background characteristics habitat disturbance would make cryptic frogs more detectable.

112 **MATERIALS AND METHODS**

113 **Image analysis**

114 Photography

115 In May-June 2017, we photographed similarly sized, terrestrial leaf litter frogs and their natural habitats
116 in the Bocas del Toro archipelago, Republic of Panama (Figure 1). On Isla Colón, we photographed 10
117 non-toxic Beige-Striped Brown *A. talamancae* (SVL [\pm SD] = 20.93 \pm 2.86 mm) and 10 of the Black-
118 Spotted Green color form of the toxic *O. pumilio* (SVL = 18.28 \pm 1.89 mm). On Isla Bastimentos, we
119 photographed 10 of the Black-Spotted Red color morph of *O. pumilio* (SVL = 18.28 \pm 1.89 mm). We also
120 photographed both the natural rainforest leaf litter of Isla Colón (n = 40) and Isla Bastimentos (n = 35), as
121 a well as the leaf litter at a site of disturbed habitat, that included banana crops, adjacent to the Isla Colón
122 forest (n = 40). These background photographs were taken at ~1-2 m intervals along non-linear transects
123 through the habitat, and each was orientated to capture an unobscured section of the forest floor.

124 Each photograph was taken from a height of 50 cm with a Canon EOS Rebel T5i DSLR and Canon EF-S
125 18-55 mm IS STM lens (Canon Inc., Tokyo, Japan) and all images contained a ColorChecker Passport
126 (X-Rite Inc., Grand Rapids, MI, USA). We set the aperture to f8, the focal length to 30 mm, manually
127 adjusted the shutter speed (to avoid under or over exposed regions) and saved all files in RAW format. As
128 UV irradiance is minimal below the canopy (Théry, 2001) and there is no significant UV reflectance from

129 either the frogs or the leaf litter (Summers et al., 1999; Siddiqi et al., 2004; Maan & Cummings, 2009;
130 Flores et al., 2013; Chaves-Acuña et al., 2020; Yeager & Barnett, 2020), we did not include ultraviolet
131 light. For analysis we selected the dorsal pattern of each frog from its image and a randomly located
132 square region of interest from each of the background images covering ~200 mm² of the leaf litter.

133 Visual modeling

134 To quantify how easily the frogs' colors and patterns could be distinguished from the different
135 backgrounds, we used visual modeling. We modelled bird vision to assess how coloration may act as a
136 defense, *O. pumilio* vision to measure how differences in habitat may affect sexual signals, and human
137 vision to enable more intuitive interpretation of the image analysis and detection data.

138 We created a custom camera linearization profile using the 9% and 59% reflectance tiles from the
139 ColorChecker Passport and then converted each linearized photograph into relative cone capture rates
140 using the MICA toolbox (Troscianko and Stevens, 2015) in ImageJ v1.52k (Schneider et al., 2012). The
141 modeling protocol was repeated for the three visual systems: tetrachromatic Indian peafowl (*Pavo*
142 *cristatus*: λ_{\max} LWS = 605, MWS = 537, SWS = 477, VS = 432, and double cones = 567 nm (Hart,
143 2002)), trichromatic *O. pumilio* (λ_{\max} LWS = 561, MWS = 489, and SWS = 466 nm (Siddiqi et al.,
144 2004)), and trichromatic human (λ_{\max} LWS = 564, MWS = 534, and SWS = 420 nm (Smith and Pokorny,
145 1975)).

146 We calculated chromatic (hue) and achromatic (luminance) contrast using the receptor noise limited
147 visual discrimination model implemented through the MICA toolbox (Vorobyev and Osorio, 1998;
148 Troscianko and Stevens, 2015). All Weber fractions, estimates of intrinsic photoreceptor noise, were set
149 at 0.05 (Siddiqi et al., 2004; Maan and Cummings, 2012). The model generated 'just noticeable
150 differences' (JNDs), a measure of visual contrast in which higher values indicate that colors are more
151 likely to be discerned from each other. JNDs of <1 suggest that two colors are unlikely to be differentiated
152 even under ideal lighting conditions, values between 1 and 3 are a close match and difficult to distinguish

153 under natural lighting conditions, and values >3 are increasingly likely to be differentiated (Vorobyev and
154 Osorio, 1998; Nokelainen et al., 2019).

155 We calculated JNDs of chromatic contrast in a pairwise manner between each background and the frogs'
156 base colors (BC), stripe or spot colors (SC), and the mean color (MC) of each frog. The base colors
157 occupied the greatest area on the frog's body, with *A. talamancae* = brown, Black-Spotted Green *O.*
158 *pumilio* = green, and Black-Spotted Red *O. pumilio* = red. Whereas, the stripe/spots colors were *A.*
159 *talamancae* = beige, Black-Spotted Green *O. pumilio* = black, and Black-Spotted Red *O. pumilio* = black.
160 To assess the effect of habitat change, we compared each frog to the background at their native site (i.e.
161 *A. talamancae* and Black-Spotted Green *O. pumilio* to Isla Colón forest and Black-Spotted Red *O.*
162 *pumilio* to Isla Bastimentos forest) and to the disturbed habitat on Isla Colón. To investigate local
163 adaptation in polytypic *O. pumilio*, we also compared each *O. pumilio* morph to the natural background of
164 the other, i.e. "Allopatric", morph. The avian and human visual models used all three frog color patterns,
165 but for the *O. pumilio* visual model, we only used the two *O. pumilio* morphs to investigate intraspecific
166 communication.

167 We analyzed achromatic contrast and pattern matching (Fast Fourier bandpass filtering - granularity
168 analysis) using the luminance channels of each visual model (avian = double cone, *O. pumilio* = LWS,
169 and human = (LWS+MWS)/2). We generated JNDs of achromatic contrast using the mean luminance
170 response from each region of interest (BL = base luminance; SL = stripe/spot luminance; ML = mean
171 luminance) with the same pairwise comparisons as described for chromatic contrast. We measured pattern
172 energy, the standard deviation of the pixel values at each filter size, by doubling the wavelength at each
173 step along eight filter bands from 2 px (~ 0.07 mm) to 256 px (~ 9 mm), which was the approximate
174 width of the frogs, in the MICA toolbox. To compare how well each frogs' patterning matched the
175 background pattern, we calculated the area between the spatial frequency curves for each frog-
176 background pair using a piecewise linear function ('*approxfun*' function) in R 3.6.1 (R Core Team, 2019).

177 Smaller values indicated a closer match between frog and background patterning across the spatial
178 frequency range.

179 To assess how background affected visual contrast, we analyzed chromatic contrast, log-transformed
180 achromatic contrast, and the area between pattern energy curves, as the response variables in a series of
181 general linear mixed effects models in R 3.6.1 using R package *lme4* (Bates et al., 2014; R Core Team,
182 2019). Each of these models included background type as a fixed effect and both frog ID and background
183 ID as random factors. We performed pairwise Tukey tests to compare the natural background to the
184 alternative habitats (Disturbed and Allopatric) and adjusted *p*-values using the single-step method using R
185 package *multcomp* (Hothorn et al., 2008).

186 **Detection**

187 Detection stimuli

188 To assess how differences in visual contrast corresponded to detectability we ran a computer-based
189 detection experiment using human participants. Using humans as surrogate predators enabled us to
190 measure detectability under controlled conditions, without the potentially confounding factor of target
191 avoidance. Humans are unlikely to be a natural selective force on frog coloration and do differ in visual
192 processing from the frogs' natural predators (Kelber 2019; Hauzman 2020), however, there are important
193 similarities in visual perception and in direct comparisons of target detectability humans and birds have
194 repeatedly been shown to respond in similar ways when UV reflectance is minimal (Troscianko et al.,
195 2009; Olsson et al., 2015; Barnett et al., 2016; Xiao and Cuthill, 2016; Barnett et al., 2018; Barnett,
196 Michalis et al., 2020; Kjærnsmo et al. 2020). In this experiment, we manipulated frog color patterns to test
197 how the arrangement of pattern components may act as either camouflage or salient signaling. We also
198 manipulated the background both to test for local adaption in *O. pumilio* and to assess to how
199 anthropogenic changes may affect detection.

200 To create the stimuli, we first cropped the dorsal pattern (without legs) of each frog and the square
201 regions of each background used in the visual modeling from the standardized photographs (Figure 1). To
202 allow for pattern manipulations, we standardized the colors of each individual frog into two classes using
203 k-means clustering in MATLAB 2017a. The centroids of each cluster were then used to recolor specific
204 pattern regions of the frogs. We created a total of seven different pattern manipulations (A, B, C, D, E, F,
205 and G) that were applied to the three different frogs (1 = *A. talamancae*; 2 = Black-Spotted Green *O.*
206 *pumilio*, and 3 = Black-Spotted Red *O. pumilio*).

207 For our baseline control, we recreated the natural patterns of each frog with its standardized colors
208 (Treatment A1: brown with beige stripes, Treatment A2: green with black spots, and Treatment A3: red
209 with black spots). Next, to assess how the ratio of color components affected detectability, we reversed
210 these pattern regions (Treatment B1: beige with brown stripes, Treatment B2: black with green spots, and
211 Treatment B3: black with red spots). Then, to investigate how the presence of pattern affected detection,
212 we removed the frog's pattern to leave the base colors (Treatment C1: plain brown, Treatment C2: plain
213 green, and Treatment C3: plain red). Next, as adjacent patches of color will be summed perceptually into
214 an average color when viewed from a distance, we used the mean colors of the frogs and the backgrounds
215 to test for distance-dependent camouflage. In a fourth treatment, we recolored each frog with its mean
216 color (Treatments D1-D3), and in a fifth treatment, we recolored each frog with the mean color from a
217 randomly selected photograph of the its natural background: Isla Colón forest for *A. talamancae*
218 (Treatment E1) and Black-Spotted Green *O. pumilio* (Treatment E2), and Isla Bastimentos forest for
219 Black-Spotted Red *O. pumilio* (Treatment E3). Sixth, to represent random sample background matching
220 and evaluate camouflage efficacy, we used the shape of each frog to crop a random section from a
221 randomly selected patch of the frog's natural forest (Treatments F1-F3). The *A. talamancae* and Black-
222 Spotted Green *O. pumilio* replicates of Treatments E and F were both sampled from the same pool of
223 background images but were included to control for any differences in size or shape between frog types.
224 Finally, to investigate how pattern and color interact, in the seventh treatment, we swapped the colors

225 between the sympatric Beige-Striped Brown *A. talamancae* and the Black-Spotted Green *O. pumilio*
226 (Treatment G1: green-and-black stripes and Treatment G2: brown-and-beige spots).

227 These various frog treatments were then combined with the photographs of the background to create a
228 series of experimental stimuli. All frog treatments (A-G) were combined with their natural backgrounds
229 (Natural): *A. talamancae* and Black-Spotted Green *O. pumilio* with Isla Colón forest, and Black-Spotted
230 Red *O. pumilio* with Isla Bastimentos forest. To investigate how habitat disturbance may affect
231 detectability, the natural patterns of each frog type (Treatments A1-A3) were also combined with the
232 disturbed habitat (Disturbed), and to examine local adaptation in *O. pumilio*, the natural patterns of the
233 green and red morphs (Treatments A2-A3) were each combined with the other's natural background
234 (Allopatric).

235 For each of the human participants, we randomly selected five of each type of frog and all the stimuli
236 made using these individuals ($n = 125 / \text{participant}$). As the number of Isla Colón stimuli (75) was larger
237 than the number of background photographs (40), we randomly reselected 35 background photographs
238 and rotated each by 90° in a randomly selected direction. Each frog was then added to the background at a
239 random location (excluding a margin equal to the length of the frog) and with a randomly selected
240 orientation (integer values between 1 and 360). To remove edge artifacts, a Gaussian filter of one standard
241 deviation was applied to each image. Frog and background selection, background rotation, and frog
242 placement were randomized separately for each participant, such that all stimuli were unique.

243 Detection protocol

244 Twenty human participants, with normal or corrected to normal vision, were tasked with searching for the
245 frogs on a 13" MacBook Air (Apple Inc., Cupertino, CA, USA, 2018). Each image was presented at 150
246 x 150 mm, frogs were ~15 mm long, and participants sat ~0.5 m away from the screen. Consequently,
247 scenes and frogs occupied $\sim 17^\circ 00'$ and $\sim 1^\circ 40'$ of visual angle respectively. All images contained a frog
248 and each participant was shown a single block of all 125 stimuli in an individually randomized sequence.

249 All clicks within a circle centered on the frog with a diameter of the frog's length plus 10% were
250 classified as correct. Likelihood of detection (i.e. Detection Probability, DP) and time taken to click on
251 the frog (i.e. Reaction Time, RT) were recorded in Psychtoolbox (Brainard, 1997) in MATLAB 2017a.

252 Detection analysis

253 Using R package *lme4* (Bates et al., 2014), we analyzed Detection Probability with a binomial generalized
254 linear mixed effects model (with *nlsminb* optimizer from package *optimx* (Nash & Varadhan 2011)) and
255 analyzed log transformed Reaction Time with a general linear mixed effects model. Both models included
256 stimulus type as a fixed effect and participant number as a random effect. Pairwise Tukey tests,
257 prespecified to test particular hypotheses, were conducted in R package *emmeans* (Lenth, 2019), and as
258 the number of comparisons was equal to the degrees of freedom, *p*-values did not need to be adjusted.

259 To investigate whether *O. pumilio* color patterns were best matched with particular local background
260 characteristics, we first compared the detectability of the natural pattern of each color morph between its
261 Natural and Allopatric forests (Natural vs. Allopatric for Treatments A2 and A3). Second, to assess how
262 environmental change may affect the camouflage/signal efficacy of each frog, we compared the frogs'
263 natural patterns between the Natural and Disturbed habitats (Natural vs. Disturbed for Treatments A1, A2,
264 and A3). Third, to assess how habitat change may affect relative detectability, we then compared the
265 natural patterns of the sympatric *A. talamancae* and Black-Spotted Green *O. pumilio* both in their native
266 forest (Treatments A1 vs. A2 in Natural) and in the disturbed habitat (Treatments A1 vs. A2 in
267 Disturbed).

268 To investigate how different pattern components affected detection, we compared the natural patterns to
269 the reversed patterns (Treatments A vs. B in Natural) and to the patternless treatment (Treatments A vs. C
270 in Natural). To evaluate the potential for distance-dependent pattern blending camouflage, we compared
271 the natural pattern of each frog to random sample background matching (Treatments A vs. F in Natural)
272 and the mean frog colors to the mean background colors (Treatments D vs. E in Natural). Finally, to

273 determine how color affected pattern saliency, we compared brown-and-beige stripes to green-and-black
274 stripes (Treatment A1 vs. G1 in Natural), brown-and-beige spots to green-and-black spots (Treatment G2
275 vs. A2 in Natural), and brown-and-beige spots to red-and-black spots (Treatment G2 vs. A3 in Natural).

276 **RESULTS**

277 **Image analysis**

278 Hue and brightness

279 When using the avian visual model, we found a significant interaction between species and habitat type
280 for the chromatic and achromatic contrast of each frogs' base, pattern, and mean colors. We thus analyzed
281 the effect of habitat on chromatic and achromatic contrast separately for each species and conducted
282 pairwise tests to investigate habitat specificity in relation to anthropogenic change and local adaptation
283 (Figure 2; Tables 1 & 2). The general trends outlined below were also observed when using the *O.*
284 *pumilio* and human visual models although perceived chromatic contrast was consistently lower
285 (Supplementary Material: Tables S1-S4 and Figures S1-S2).

286 Habitat disturbance

287 The pattern of *A. talamancae* is made up of a dark brown base with two beige dorsolateral stripes. We
288 found that both of the natural colors (BC and SC) of *A. talamancae*, as well as the mean color (MC), were
289 significantly closer matches to the Natural forest than to the Disturbed habitat in chromatic contrast.
290 However, in achromatic contrast, the brown base (BL) was a closer match to the Natural background, the
291 beige stripes (SL) were closer to the Disturbed site, and there was no difference between backgrounds for
292 the mean luminance (ML) (Figure 2; Tables 1 & 2).

293 The Black-Spotted Green *O. pumilio* has a pattern consisting of a green base with irregular black spots.
294 We found that the green base color was significantly more distinct from the Natural forest than from the
295 Disturbed habitat in both chromatic (BC) and achromatic (BL) contrast. Whereas the black spots were a

296 closer match to the Natural forest in chromatic (SC) and achromatic (SL) contrast. With the mean color,
297 however, we did not find any difference between the Natural and Disturbed areas in chromatic contrast
298 (MC) but we did find that achromatic contrast (ML) was significantly higher in the Natural forest (Figure
299 2; Tables 1 & 2).

300 Black-Spotted Red *O. pumilio* have a red base color covered with irregular black spots. All pattern
301 components were a closer match to the Natural forest than to the Disturbed habitat in chromatic contrast
302 (BC, SC, and MC), but achromatic contrast (BL, SL, and ML) was not significantly different between
303 habitats (Figure 2; Tables 1 & 2).

304 Local adaptation in *Oophaga pumilio*

305 We found that, for the Black-Spotted Green *O. pumilio*, there was no difference in the chromatic contrast
306 of the green base color (BC) between Natural and Allopatric sites, but achromatic contrast (BL) was
307 significantly higher in the Natural forest. Conversely, the black spots were a closer match to the Natural
308 forest in both chromatic (SC) and achromatic contrast (SL). Whereas, for the mean color, there was no
309 significant difference in chromatic contrast (MC), but achromatic contrast (ML) was significantly higher
310 in the Natural habitat (Figure 2; Tables 1 & 2).

311 For the Black-Spotted Red *O. pumilio* the chromatic and achromatic contrast of the red base and mean
312 color (BC, BL, MC, and ML) were both significantly lower in the Natural forest than in the Allopatric
313 forest. The black spots, however, were not significantly different in chromatic contrast (SC) between
314 backgrounds, but we did find achromatic contrast (SL) to be significantly higher in the Natural habitat
315 (Figure 2; Tables 1 & 2).

316 Pattern analysis

317 Using the avian visual model, we found a significant interaction between species and habitat type ($\chi^2 =$
318 265.41, df = 3, $p < 0.001$; Figure 3) when comparing pattern contrast between the frogs and the three

319 habitats. When we examined the main effects of habitat and species separately, we found a significant
320 effect of species ($\chi^2 = 26.33$, $df = 2$, $p < 0.001$) but no significant effect of habitat type ($\chi^2 = 0.89$, $df = 2$,
321 $p = 0.642$), enabling us to remove habitat type from further analysis. The striped pattern of *A. talamancae*
322 was significantly more similar to the background than the spotted patterns of the Black-Spotted Green *O.*
323 *pumilio* ($z = -5.23$, $p < 0.001$) and the Black-Spotted Red *O. pumilio* ($z = -5.60$, $p < 0.001$). There was no
324 significant difference between the patterns of Black-Spotted Green *O. pumilio* and Black-Spotted Red *O.*
325 *pumilio* ($z = -0.37$, $p = 0.926$). The same trends were found with the human and *O. pumilio* visual models
326 (see Supplementary Material).

327 **Detection**

328 We found a significant effect of treatment on Reaction Time ($\chi^2 = 749.63$, $df = 24$, $p < 0.001$) and on
329 Detection Probability ($\chi^2 = 384.31$, $df = 24$, $p < 0.001$). We therefore conducted pairwise comparisons to
330 test specific hypotheses regarding two wider themes: i) habitat specificity (local adaptation and the effect
331 of anthropogenic change; Figure 4), and ii) the role of pattern in detectability (pattern distribution, pattern
332 blending, and the interaction between color and pattern; Figures 5-6).

333 Habitat specificity

334 We found no evidence of local adaptation in *O. pumilio*, as there was no significant difference in
335 detectability between the Natural and Allopatric backgrounds for either Black-Spotted Green *O. pumilio*
336 (A2 in Natural vs A2 in Allopatric – RT: $t = 0.10$, $p > 0.999$, DP: $z = 0.34$, $p > 0.999$) or Black-Spotted
337 Red *O. pumilio* (A3 in Natural vs A3 in Allopatric – RT: $t = 0.57$, $p > 0.999$, DP: $z = 1.13$, $p = 0.999$).

338 We found that *A. talamancae* were significantly more detectable in Disturbed habitat compared to Natural
339 habitat (A1 in Natural vs A1 Disturbed – RT: $t = 3.60$, $p = 0.008$, DP: $z = -3.96$, $p = 0.002$) but that co-
340 occurring Black-Spotted Green *O. pumilio* were significantly harder to find in the Disturbed habitat
341 compared to Natural habitat (A2 in Natural vs A2 Disturbed – RT: $t = -3.19$, $p = 0.035$, DP: $z = 2.02$, $p =$
342 0.652). Compared to Black-Spotted Green *O. pumilio*, *A. talamancae* were detected significantly more

343 slowly and less accurately in the Natural forest habitat (A1 in Natural vs A2 Natural – RT: $t = -6.61$, $p <$
344 0.001 , DP: $z = -3.92$, $p = 0.002$), but there was no difference in detectability in the Disturbed habitat (A1
345 in Disturbed vs A2 Disturbed – RT: $t = 0.18$, $p > 0.999$, DP: $z = -2.27$, $p = 0.429$). In contrast to the
346 Black-Spotted Green morph, however, there was no significant difference in the time taken to find Black-
347 Spotted Red *O. pumilio* between its Natural forest and the Disturbed habitat (A3 in Natural vs A3 in
348 Disturbed – RT: $t = -0.53$, $p > 0.999$, DP: $z = 0.46$, $p > 0.999$).

349 Pattern manipulations

350 We found that there was no significant difference in detectability between the natural and reversed
351 patterns for any of the three frogs: *A. talamancae* (A1 vs B1 - RT: $t = -1.41$, $p = 0.984$, DP: $z = 0.81$, $p >$
352 0.999), Black-Spotted Green *O. pumilio* (A2 vs B2 - RT: $t = -2.63$, $p = 0.186$, DP: $z = 1.42$, $p = 0.983$),
353 and Black-Spotted Red *O. pumilio* (A3 vs B3 - RT: $t = -0.54$, $p > 0.999$, DP: $z = 1.62$, $p = 0.931$). The
354 presence/absence of beige stripes on brown *A. talamancae* also had no effect on detectability (A1 vs C1 -
355 RT: $t = -1.59$, $p = 0.942$, DP: $z = 0.81$, $p > 0.999$). However, the presence of black spots significantly
356 decreased the time taken to find Black-Spotted Green *O. pumilio* (A1 vs C2 - RT: $t = -4.82$, $p < 0.001$,
357 DP: $z = 3.70$, $p = 0.005$) even though this had no discernable effect on the Black-Spotted Red *O. pumilio* (A3
358 vs C3 - RT: $t = 0.43$, $p > 0.999$, DP: $z = 1.39$, $p = 0.987$).

359 The natural pattern of each frog was detected significantly more quickly and more accurately than random
360 sample background matching: *A. talamancae* (A1 vs F1 - RT: $t = -5.71$, $p < 0.001$, DP: $z = 2.60$, $p =$
361 0.202), Black-Spotted Green *O. pumilio* (A2 vs F2 - RT: $t = -13.96$, $p < 0.001$, DP: $z = 6.62$, $p < 0.001$),
362 and Black-Spotted Red *O. pumilio* (A3 vs F3 - RT: $t = -13.16$, $p < 0.001$, DP: $z = 5.93$, $p < 0.001$). We
363 found no difference in Reaction Time and Detection Probability between the mean color of the
364 background and the mean colors of either *A. talamancae* (D1 vs E1 - RT: $t = -1.85$, $p = 0.795$, DP: $z =$
365 0.33 , $p > 0.999$) or Black-Spotted Red *O. pumilio* (D3 vs E3 - RT: $t = -2.97$, $p = 0.070$, DP: $z = 2.43$, $p =$
366 0.307), although the level of significance for this color pattern was marginal. By contrast, the mean color

367 of the Black-Spotted Green *O. pumilio* was found significantly more quickly than the mean of the
368 background (D2 vs E2 - RT: $t = -4.26$, $p < 0.001$, DP: $z = 2.31$, $p = 0.395$).

369 Spots were more conspicuous than stripes regardless of their color, with participants taking longer to
370 detect brown-and-beige stripes than brown-and-beige spots (A1 vs G2 - RT: $t = 3.93$, $p = 0.002$, DP: $z = -$
371 2.74 , $p = 0.139$). Similarly, green-and-black stripes were detected significantly more slowly than the
372 green-and-black spots (A2 vs G1 - RT: $t = -3.18$, $p = 0.036$, DP: $z = -2.20$, $p = 0.492$). Green was found to
373 be a more conspicuous color than brown. However, whereas stripe color affected detectability, with
374 brown-and-beige stripes being more cryptic than green-and-black stripes (A1 vs G1 - RT: $t = 3.43$, $p =$
375 0.015 , DP: $z = -2.35$, $p = 0.368$), there was no significant difference between brown-and-beige spots and
376 either the green-and-black spots (G2 vs A2 - RT: $t = -2.68$, $p = 0.164$, DP: $z = 1.83$, $p = 0.809$) or the red-
377 and-black spots (G2 vs A3 - RT: $t = 2.72$, $p = 0.147$, DP: $z = -2.34$, $p = 0.377$).

378 **DISCUSSION**

379 Our analyses reveal that the three different frogs that we studied exhibit three distinct defensive coloration
380 strategies formed from unique interactions between chromatic, achromatic, and pattern contrast.
381 Moreover, these different strategies were affected by habitat disturbance in different ways such that
382 absolute and rank order detectability differed between natural and disturbed habitat.

383 Under natural conditions, the non-toxic *A. talamancae* is camouflaged, with its color and patterning both
384 closely matched to the natural background. The toxic Black-Spotted Red *O. pumilio*, meanwhile,
385 advertises its presence with color and pattern that are both, independently, highly salient. In contrast,
386 Black-Spotted Green *O. pumilio*, which are also toxic, were detected quickly despite displaying colors
387 that closely matched the natural background, a result driven by the high saliency of the spotted pattern.
388 Frog detectability was, therefore, associated with pattern type, with the spotted patterns of both color
389 morphs of *O. pumilio* being more distinct from the background than the stripes of *A. talamancae*
390 regardless of color. Similar black spots found on several other color morphs of *O. pumilio* are also highly

391 salient (Qvarnström et al., 2014) and serve to reduce predation risk (Preißler and Pröhl, 2017), an effect
392 that appears to increase with larger spot size (Hegna et al., 2011; Qvarnström et al., 2014; Preißler and
393 Pröhl, 2017). Qvarnström et al. (2014) showed that Black-Spotted Green *O. pumilio* were as detectable as
394 Black-Spotted Red *O. pumilio* to domestic chickens, whereas although red patternless frogs were as
395 detectable as spotted frogs, green patternless frogs were significantly harder for the chickens to find. We
396 found the same, but our data also extend this finding to include the more cryptic colors of *A. talamancae*,
397 with no difference in detection being found between red-and-black, green-and-black, or brown-and-beige
398 spots.

399 Pattern is an important component of aposematic signaling. For example, predators find larger and more
400 symmetrical patterns more aversive (Forsman and Merilaita, 1999; Forsman and Herrström, 2004) and are
401 more likely to learn and remember patterns with high internal contrast (Aronsson and Gamberale-Stille,
402 2012; Green et al., 2018; Halpin et al., 2020). These studies, however, largely focus on artificial targets
403 presented against simple, unnatural backgrounds at close range, where the prey is always highly
404 detectable. The impact of pattern on detectability can, however, also depend on context and viewing
405 distance (Tullberg et al., 2005; Bohlin et al., 2012; Rojas et al., 2014; Honma et al., 2015; Barnett et al.,
406 2018). Despite the apparent high internal contrast of the three color patterns we examined here, there was
407 no evidence of disruptive camouflage in any of our frogs. Moreover, although the base colors appear to
408 cover the largest area of each frog, reversing the pattern had no effect on detection, and the presence of
409 pattern only affected the detectability of the Black-Spotted Green *O. pumilio*, where frog color and
410 patterning had opposing effects on detectability. Yet the mean color of *A. talamancae* was no more
411 detectable than the mean color of the background, suggesting that its camouflaged coloring matches the
412 background when viewed from a distance. However, although the same, was not observed in Black-
413 Spotted Green *O. pumilio*, we did find some evidence for distance-dependent camouflage in the Black-
414 Spotted Red *O. pumilio*. This effect, however, may only apply to observers with less effective longwave
415 sensitivity than birds (i.e., for humans and *O. pumilio*) and more work is needed to understand whether

416 distance-dependent signaling is effective under natural conditions with regard to this frog. The presence
417 of patterning, therefore, seems best explained by background matching camouflage in *A. talamancae* and
418 salient signaling in *O. pumilio*.

419 We also examined whether the detectability of these color patterns depended on the visual characteristics
420 of the background. We found no strong evidence to suggest that the detectability of either Black-Spotted
421 Green or Black-Spotted Red *O. pumilio* was significantly affected by local variation in the natural
422 background between islands. These data, therefore, suggest that island specific differences in the visual
423 background may have had a minimal role in the evolution of polytypism in *O. pumilio*.

424 We did, however, find evidence to suggest that a visual environment that is altered by human activity can
425 affect the detectability of frog coloration. Moreover, this anthropogenic change affected the three
426 different phenotypes in different ways. In the natural forests, where the ground was covered by a layer of
427 leaf litter, the brown, striped, *A. talamancae* was well camouflaged, whereas the sympatric, Black-Spotted
428 Green *O. pumilio*, was comparatively conspicuous. At the forest's edge, however, where human activity
429 has thinned the canopy, more light is able to penetrate through to the ground allowing for increased
430 growth of green mosses and herbaceous plants. We found that this greening of the background
431 undermined background color matching in *A. talamancae* but increased background color matching in
432 Black-Spotted Green *O. pumilio*. Consequently, although under natural conditions *A. talamancae* was the
433 more cryptic species, both frogs were equally detectable in the disturbed habitat. Furthermore, habitat
434 change may have also affected the conspicuous aposematic signal of Black-Spotted Red *O. pumilio*, but
435 this effect did not affect detection time, seemingly due to the frogs' high achromatic and pattern contrast.

436 Decreasing the efficacy of camouflage has clear implications for otherwise undefended prey. The risk of
437 predation rises dramatically with increasing detectability (Zimova et al., 2016; Delhey and Peters, 2017;
438 Atmeh et al., 2018). Conversely, for toxic prey, greater chromatic and achromatic contrast to the
439 background can increase the speed and accuracy of predator learning of warning signals (Gamberale-

440 Stille, 2001; Prudic et al., 2006; Aronsson and Gamberale-Stille, 2009; Stevens and Ruxton, 2012; Halpin
441 et al., 2020). Thus, our data suggest that habitat disturbance may undermine the camouflage of *A.*
442 *talamancae*, increase aversion learning in Black-Spotted Red *O. pumilio*, and have diverging effects on
443 Black-Spotted Green *O. pumilio*, where camouflage efficacy may increase but aposematic signaling may
444 be reduced. Indeed, such changes to visual contrast are also seen in the *O. pumilio* visual model and
445 similar effects may apply to important intraspecific signals where high visual contrast is used to mediate
446 mate choice, intra-sexual conflict, and territorial disputes (Summers et al., 1999; Reynolds and
447 Fitzpatrick, 2007; Maan and Cummings, 2008, 2009; Crothers and Cummings, 2015; Galeano and Harms,
448 2016). Poison frogs may be able to behaviorally mitigate some of these effects by selecting particular
449 microhabitats (Pröhl and Ostrowski, 2011; Willink et al., 2014), but the availability of such sites will
450 likely change as human activity alters the habitat.

451 Furthermore, beyond the direct effects of changing detectability, community wide shifts may have
452 broader effects on predator-prey dynamics (Guiden et al., 2019). Predators are frequently faced with a
453 community of prey that differ in nutritional content, ease of discovery and handling, toxicity, and in
454 abundance. The structure of the prey community will then affect predator decision-making as predators
455 trade off the costs and benefits of differently defended prey or alter foraging behavior (Skelhorn et al.,
456 2016; Skelhorn and Rowe, 2016; Smith et al., 2016; Spaniol et al., 2020). As such, predation risk may
457 also depend on changes occurring to the detectability and relative frequencies of heterospecifics. Thus, by
458 altering the rank-order detectability of these frogs, human disturbance could alter the capacity for the
459 frogs' predators to quickly learn important color-toxin associations.

460 It is important to also note that the perception of color contrast is not the only factor that may change in
461 human modified environments. Poison frogs rely on dietary derived carotenoid pigments and chemical
462 precursors to synthesize the colors and toxins underlying their aposematic defenses (Saporito et al., 2012;
463 Crothers et al., 2016). In disturbed habitat, frog diets, color, and alkaloid composition may change along
464 with the availability of their prey (McGugan et al., 2016; Moskowitz et al., 2020; Yeager et al., In

465 Review). As predators learn both about the frog's toxins and coloration (Skelhorn et al., 2016; Skelhorn
466 and Rowe, 2016; Smith et al., 2016), the delicate balance between detection and avoidance is potentially
467 disrupted further. Although it is unknown how changes to the interaction between detectability and
468 alkaloid profiles affects frog survival in the wild, our results highlight that these impacts may not be
469 safely ignored.

470 Overall, our analyses suggest that pattern is a major factor underlying differences in the detectability of
471 three frogs that differ greatly in appearance. However, color emerges as being particularly important in
472 explaining differences in the detectability of these frogs between different habitats. These findings
473 correspond to three phenotypes in the context of one instance of habitat disturbance but do highlight how
474 anthropogenic changes to the forest floor may alter visual contrast and detectability in ways that may
475 affect the performance of defensive and sexually selected color patterns. In turn, these changes to
476 detectability may have wide-reaching effects on animal behavior, not only with regard to individual
477 species but across entire communities as species of all kinds are confronted with changes to their relative
478 detectability.

479 **REFERENCES**

- 480 Aronsson M, Gamberale-Stille G. 2008. Domestic chicks primarily attend to colour, not pattern, when
481 learning an aposematic coloration. *Anim Behav.* 75:417-423.
- 482 Aronsson M, Gamberale-Stille G. 2009. Importance of internal pattern contrast and contrast against the
483 background in aposematic signals. *Behav Ecol.* 20:1356-1362.
- 484 Aronsson M, Gamberale-Stille G. 2012. Evidence of signaling benefits to contrasting internal color
485 boundaries in warning coloration. *Behav Ecol.* 24:349-354.
- 486 Andersson M. 1994. *Sexual selection*. Princeton, NJ, USA: Princeton University Press.
- 487 Atmeh K, Andruszkiewicz A, Zub K. 2018. Climate change is affecting mortality of weasels due to
488 camouflage mismatch. *Sci Rep.* 8:7648.
- 489 Barnett JB, Cuthill IC. 2014. Distance-dependent defensive coloration. *Curr Biol.* 24:R1157-R1158.
- 490 Barnett JB, Michalis C, Anderson HM, McEwen BL, Yeager J, Pruitt JN, Scott-Samuel NE, Cuthill IC.
491 2020. Imperfect transparency and camouflage in glass frogs. *Proc Natl Acad Sci USA.* 117:12885-12890.
- 492 Barnett JB, Michalis C, Scott-Samuel NE, Cuthill IC. 2018. Distance-dependent defensive coloration in
493 the poison frog *Dendrobates tinctorius*, Dendrobatidae. *Proc Natl Acad Sci USA.* 115:6416-6421.
- 494 Barnett JB, Redfern AS, Bhattacharyya-Dickson R, Clifton O, Courty T, Ho T, Hopes A, McPhee T,
495 Merrison K, Owen R, Scott-Samuel NE, Cuthill IC. 2016. Stripes for warning and stripes for hiding:
496 spatial frequency and detection distance. *Behav Ecol.* 28:373-381.
- 497 Barnett JB, Varela BJ, Jennings BJ, Lesbarrères D, Pruitt JN, Green DM. 2020. Data from: Habitat
498 disturbance alters color contrast and the detectability of cryptic and aposematic frogs. *Behav Ecol.*
499 <https://doi.org/10.5061/dryad.5tb2rbp2p>

500 Bates D, Mächler M, Bolker BM, Walker S. 2014. Fitting linear mixed-effects models using lme4. J Stat
501 Softw. 67:1-48.

502 Bohlin T, Gamberale-Stille G, Merilaita S, Exnerová A, Štys P, Tullberg BS. 2012. The detectability of
503 the colour pattern in the aposematic firebug, *Pyrrhocoris apterus*: an image-based experiment with human
504 'predators'. Biol J Linn Soc. 105:806-816.

505 Brainard DH. 1997. The Psychophysics Toolbox. Spat Vis. 10:433-436.

506 Caro T, Stankowich T, Kiffner C, Hunter J. 2013. Are spotted skunks conspicuous or cryptic? Ethol Ecol
507 Evol. 25:144-160.

508 Chaves-Acuña W, Sadoval L, Bitton PP, Barrantes G, García-Rodríguez A. 2020. Conspecific and
509 predator perception of the red *Oophaga pumilio* morph from the central Caribbean of Costa Rica. J
510 Herpetol. 54:361-370.

511 Coker DJ, Pratchett MS, Munday PL, 2009. Coral Bleaching and habitat degradation increase
512 susceptibility to predator for coral-dwelling fishes. Behav Ecol. 20:1204-1210.

513 Cott HB. 1940. Adaptive coloration in animals. London, UK: Methuen & Co., Ltd.

514 Crothers L, Saporito RA, Yeager J, Lynch K, Friesen C, Richards-Zawacki CL, McGraw K, Cummings
515 M. 2016. Warning signal properties covary with toxicity but not testosterone or aggregate carotenoids in a
516 poison frog. Evol Ecol. 30:601-621.

517 Crothers LR, Cummings ME. 2015. A multifunctional warning signal behaves as an agonistic status
518 signal in a poison frog. Behav Ecol. 26:560-568.

519 Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, Hill GE, Jablonski NG, Jiggins
520 CD, Kelber A, Mappes J, Marshall J, Merrill R, Osorio D, Prum R, Roberts NW, Roulin A, Rowland

521 HM, Sherratt TN, Skelhorn J, Speed MP, Stevens M, Stoddard MC, Stuart-Fox D, Talas L, Tibbetts E,
522 Caro T. 2017. The biology of color. *Science*. 357:eaan0221.

523 Cuthill IC, Stevens M, Windsor AMM, Walker HJ. 2006. The effects of pattern symmetry on detection of
524 disruptive and background-matching coloration. *Behav Ecol*. 17:828-832.

525 Cuthill IC. 2019. Camouflage. *J Zool*. 308:75-92.

526 Darwin C. 1871. *The decent of man, and selection in relation to sex*. London, UK: John Murray.

527 Delhey K, Peters A. 2017. Conservation implications of anthropogenic impacts on visual communication
528 and camouflage. *Conserv Biol*. 31:30-39.

529 Endler JA. 1978. A predator's view of animal color patterns. *Evol Biol*. 11:320-364.

530 Flores EE, Stevens M, Moore AJ, Blount JD. 2013. Diet, development and the optimization of warning
531 signals in post-metamorphic green and black poison frogs. *Funct Ecol*. 27:816-829.

532 Forsman A, Herrström J. 2004. Asymmetry in size, shape, and color impairs the protective value of
533 conspicuous color patterns. *Behav Ecol*. 15:141-147.

534 Forsman A, Merilaita S. 1999. Fearful symmetry: pattern size and asymmetry affects aposematic signal
535 efficacy. *Evol Ecol*. 13:131-140.

536 Galeano SP, Harms KE. 2016. Coloration in the polymorphic frog *Oophaga pumilio* associates with level
537 of aggressiveness in intraspecific and interspecific behavioral interactions. *Behav Ecol Sociobiol*. 70:83-
538 97.

539 Gamberale-Stille G. 2001. Benefit by contrast: an experiment with live aposematic prey. *Behav Ecol*.
540 12:768-772.

541 Grant T, Frost DR, Caldwell JP, Gagliardo R, Haddad CFB, Kok PJR, Means DB, Noonan BP, Schargel
542 WE, Wheeler WC. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia:
543 Athesphatanura: Dendrobatidae). *Bull Am Mus Nat Hist.* 2006:1-262.

544 Grant T, Rada M, Anganoy-Criollo M, Batista A, Dias PH, Jeckel AM, Machado DJ, Rueda-Almonacid
545 JV. 2017. Phylogenetic Systematics of Dart-Poison Frogs and Their Relatives Revisited (Anura:
546 Dendrobatoidea). *S Am J Herpetol.* 12:S1-S90.

547 Green NF, Urquhart HH, van den Berg CP, Marshall NJ, Cheney KL. 2018. Pattern edges improve
548 predator learning of aposematic signals. *Behav Ecol.* 29:1481-1486.

549 Guiden PW, Bartel SL, Byer NW, Shipley AA, Orrock JL. 2019. Predator–prey interactions in the
550 Anthropocene: reconciling multiple aspects of novelty. *Trends Ecol Evol.* 34:616-627.

551 Halpin CG, Penacchio O, Lovell PG, Cuthill IC, Harris JM, Skelhorn J, Rowe C. 2020. Pattern contrast
552 influences wariness in naïve predators towards aposematic patterns. *Sci Rep.* 10:9246.

553 Hart NS. 2002. Vision in the peafowl (*Aves: Pavo cristatus*). *J Exp Biol.* 205:3925-3935.

554 Hauzman E. 2020. Adaptations and evolutionary trajectories of the snake rod and cone photoreceptors.
555 *Semin Cell Dev Biol.* 106:86-93.

556 Hegna RH, Saporito RA, Gerow KG, Donnelly MA. 2011. Contrasting colors of an aposematic poison
557 frog do not affect predation. *Ann Zool Fenn.* 48:29-38.

558 Honma A, Mappes J, Valkonen JK. 2015. Warning coloration can be disruptive: aposematic marginal
559 wing patterning in the wood tiger moth. *Ecol Evol.* 5:4863-4874.

560 Hoogmoed MS, Avila-Pires TCS. 2012. Inventory of color polymorphism in populations of *Dendrobates*
561 *galactonotus* (Anura: Dendrobatidae), a poison frog endemic to Brazil. *Phyllomedusa.* 11:95-115.

562 Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. *Biom J.*
563 50:346-363.

564 Imperio S, Bionda R, Viterbi R, Provenzale A. 2013. Climate change and human disturbance can lead to
565 local extinction of alpine rock ptarmigan: new insight from the western Italian Alps. *PLOS ONE*
566 8:e81598.

567 Kelber A. 2019. Bird colour vision – from cones to perception. *Curr Opin Behav Sci.* 30:34-40.

568 Kettlewell HBD. 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity.* 9:323-
569 342.

570 Kjærsmo K, Whitney HM, Scott-Samuel NE, Hall JR, Knowles H, Talas L, Cuthill IC. 2020. Iridescence
571 as camouflage. *Curr Biol.* 30:551-555.

572 Lenth R, 2019. emmeans: estimated marginal means, aka least-squares means. R package version
573 1.4.3.01. <https://CRAN.R-project.org/package=emmeans>.

574 Maan ME, Cummings ME. 2008. Female preferences for aposematic signal components in a polymorphic
575 poison frog. *Evolution.* 62:2334-2345.

576 Maan ME, Cummings ME. 2009. Sexual dimorphism and directional sexual selection on aposematic
577 signals in a poison frog. *Proc Natl Acad Sci USA.* 106:19072-19077.

578 Maan ME, Cummings ME. 2012. Poison frog colors are honest signals of toxicity, particularly for bird
579 predators. *Am Nat.* 179:E1-E14.

580 Mappes J, Marples N, Endler JA. 2005. The complex business of survival by aposematism. *Trends Ecol*
581 *Evol.* 20:598-603.

582 Marshall NJ. 2000. Communication and camouflage with the same ‘bright’ colours in reef fishes. *Philos*
583 *Trans R Soc B.* 355:1243-1248.

584 McGugan JR, Byrd GD, Roland AB, Caty SN, Kabir N, Tapia EE, Trauger SA, Coloma LA, O'Connell
585 LA. 2016. Ant and mite diversity drives toxin variation in the little devil poison frog. *J Chem Ecol.*
586 42:537-551.

587 Mebs D, Yotsu-Yamashita M, Pogoda W, Vargas Alvarez J, Ernst R, Köhler G, Toennes SW. 2018. Lack
588 of alkaloids and tetrodotoxin in the neotropical frogs *Allobates* spp. (Aromobatidae) and *Silverstoneia*
589 *flotator* (Dendrobatidae). *Toxicon.* 152:103-105.

590 Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. *Philos Trans R Soc B.*
591 372:20160341.

592 Michalis C, Scott-Samuel NE, Gibson DP, Cuthill IC. 2017. Optimal background matching camouflage.
593 *Proc R Soc B.* 284:20170709.

594 Mills LS, Zimova M, Oyler J, Running S, Abatzoglou JT, Lukacs PM. 2013. Camouflage mismatch in
595 seasonal coat color due to decreased snow duration. *Proc Natl Acad Sci USA.* 110:7360-7365.

596 Moskowitz NA, Dorritie B, Fay T, Nieves OC, Vidoudez C, Fischer EK, Trauger SA, Coloma LA,
597 Donoso DA, O'Connell LA. 2020. Land use impacts poison frog chemical defenses through changes in
598 leaf litter ant communities. *Neotrop Biodivers.* 6:75-87.

599 Nash JC, Varadhan R. 2011. Unifying optimization algorithms to aid software system users: optimx for
600 R. *J Stat Softw.* 43:1-14.

601 Nokelainen O, Maynes R, Mynott S, Price N, Stevens M. 2019. Improved camouflage through
602 ontogenetic colour change confers reduced detection risk in shore crabs. *Funct Ecol.* 33:654-669.

603 Olsson P, Lind O, Kelber A. 2015. Bird colour vision: behavioural thresholds reveal receptor noise. *J Exp*
604 *Biol.* 218:184-193.

605 Phillips GAC, How MJ, Lange JE, Marshall NJ, Cheney KL. 2017. Disruptive colouration in reef fish:
606 does matching the background reduce predation risk? *J Exp Biol.* 220:1962-1974.

607 Poulton EB. 1890. *The colours of animals: their meaning and use, especially considered in the case of*
608 *insects.* London, UK: Kegan Paul, Trench & Trübner.

609 Preißler K, Pröhl H. 2017. The effects of background coloration and dark spots on the risk of predation in
610 poison frog models. *Evol Ecol.* 31:683-694.

611 Pröhl H, Ostrowski T. 2011. Behavioural elements reflect phenotypic colour divergence in a poison frog.
612 *Evol Ecol.* 25:993-1015.

613 Prudic KL, Skemp AK, Papaj DR. 2006. Aposematic coloration, luminance contrast, and the benefits of
614 conspicuousness. *Behav Ecol.* 18:41-46.

615 Qvarnström A, Rudh A, Edström T, Ödeen A, Løvlie H, Tullberg BS. 2014. Coarse dark patterning
616 functionally constrains adaptive shifts from aposematism to crypsis in strawberry poison frogs. *Evolution.*
617 68:2793-2803.

618 R Core Team. 2019. *R: A language and environment for statistical computing.* Version 3.6.1. Vienna,
619 Austria: R Foundation for Statistical Computing.

620 Reynolds RG, Fitzpatrick BM. 2007. Assortative mating in poison-dart frogs based on an ecologically
621 important trait. *Evolution.* 61:2253-2259.

622 Richards-Zawacki CL, Wang IJ, Summers K. 2012. Mate choice and the genetic basis for colour variation
623 in a polymorphic dart frog: inferences from a wild pedigree. *Mol Ecol.* 21:3879-3892.

624 Roberts JL, Brown JL, Schulte R, Arizabal W, Summers K. 2007. Rapid diversification of colouration
625 among populations of a poison frog isolated on sky peninsulas in the central cordilleras of Peru. *J*
626 *Biogeogr.* 34:417-426.

627 Rojas B, Rautiala P, Mappes J. 2014. Differential detectability of polymorphic warning signals under
628 varying light environments. *Behav Processes*. 109:164-172.

629 Rojas B. 2017. Behavioural, ecological, and evolutionary aspects of diversity in frog colour patterns. *Biol*
630 *Rev*. 92:1059-1080.

631 Rudh A, Breed MF, Qvarnström A. 2012. Does aggression and explorative behaviour decrease with lost
632 warning coloration? *Biol J Linn Soc*. 108:116-126.

633 Rudh A. 2013. Loss of conspicuous coloration has co-evolved with decreased body size in populations of
634 poison dart frogs. *Evol Ecol*. 27:755-767.

635 Saporito RA, Donnelly MA, Spande TF, Garraffo HM. 2012. A review of chemical ecology in poison
636 frogs. *Chemoecology*. 22:159-168.

637 Saporito RA, Zuercher R, Roberts M, Gerow KG, Donnelly MA. 2007. Experimental evidence for
638 aposematism in the dendrobatid poison frog *Oophaga pumilio*. *Copeia*. 2007:1006-1011.

639 Schaefer HM, Stobbe N. 2006. Disruptive coloration provides camouflage independent of background
640 matching. *Proc R Soc B*. 273:2427-2432.

641 Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat*
642 *Methods*. 9:671-675.

643 Segami Marzal JC, Rudh A, Rogell B, Ödeen A, Løvlie H, Rosher C, Qvarnström A. 2017. Cryptic
644 female strawberry poison frogs experience elevated predation risk when associating with an aposematic
645 partner. *Ecol Evol*. 7:744-750.

646 Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004. Interspecific and intraspecific views
647 of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol*. 207:2471-2485.

648 Skelhorn J, Halpin CG, Rowe C. 2016. Learning about aposematic prey. *Behav Ecol*. 27:955-964.

649 Skelhorn J, Rowe C. 2016. Cognition and the evolution of camouflage. *Proc R Soc B*. 283:20152890.

650 Smith KE, Halpin CG, Rowe C. 2016. The benefits of being toxic to deter predators depends on prey
651 body size. *Behav Ecol*. 27:1650-1655.

652 Smith VC, Pokorny J. 1975. Spectral sensitivity of the foveal cone photopigments between 400 and 500
653 nm. *Vis Res*. 15:161-171.

654 Spalding AK. 2013. Environmental outcomes of lifestyle migration: land cover change and land use
655 transitions in the Bocas del Toro Archipelago in Panama. *J Lat Am Geogr*. 12:179-202.

656 Spaniol RL, Mendonça MdS, Hartz SM, Iserhard CA, Stevens M. 2020. Discolouring the Amazon
657 rainforest: how deforestation is affecting butterfly coloration. *Biodivers Conserv*. 29:2821-2838.

658 Stevens M, Cuthill IC, Windsor AMM, Walker HJ. 2006. Disruptive contrast in animal camouflage. *Proc*
659 *R Soc B*. 273:2433-2438.

660 Stevens M, Cuthill IC. 2006. Disruptive coloration, crypsis and edge detection in early visual processing.
661 *Proc R Soc B*. 273:2141-2147.

662 Stevens M, Merilaita S. 2009. Defining disruptive coloration and distinguishing its functions. *Philos*
663 *Trans R Soc B*. 364:481-488.

664 Stevens M, Ruxton GD. 2012. Linking the evolution and form of warning coloration in nature. *Proc R*
665 *Soc B*. 279:417-426.

666 Stevens M. 2007. Predator perception and the interrelation between different forms of protective
667 coloration. *Proc R Soc B*. 274:1457-1464.

668 Summers K, Clough ME. 2001. The evolution of coloration and toxicity in the poison frog family
669 (*Dendrobatidae*). *Proc Natl Acad Sci USA*. 98:6227-6232.

670 Summers K, Symula R, Clough M, Cronin T. 1999. Visual mate choice in poison frogs. Proc R Soc B.
671 266:2141-2145.

672 Théry M. 2001. Forest light and its influence on habitat selection. Plant Ecol. 153:251-261.

673 Troscianko J, Stevens M. 2015. Image calibration and analysis toolbox – a free software suite for
674 objectively measuring reflectance, colour and pattern. Methods Ecol Evol. 6:1320-1331.

675 Troscianko J, Wilson-Aggarwal J, Stevens M, Spottiswoode CN. 2016. Camouflage predicts survival in
676 ground-nesting birds. Sci Rep. 6:19966.

677 Troscianko T, Benton CP, Lovell PG, Tolhurst DJ, Pizlo Z. 2009. Camouflage and visual perception.
678 Philos Trans R Soc B. 364:449-461.

679 Tullberg BS, Merilaita S, Wiklund C, 2005. Aposematism and crypsis combined as a result of distance
680 dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. Proc R Soc B.
681 272:1315-1321.

682 Twomey E, Vestergaard JS, Venegas PJ, Summers K, 2016. Mimetic divergence and the speciation
683 continuum in the mimic poison frog *Ranitomeya imitator*. Am Nat. 187:205-224.

684 Valkonen J, Niskanen M, Björklund M, Mappes J. 2011. Disruption or aposematism? Significance of
685 dorsal zigzag pattern of European vipers. Evol Ecol. 25:1047-1063.

686 Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. Proc R Soc B.
687 265:351-358.

688 Walton OC, Stevens M. 2018. Avian vision models and field experiments determine the survival value of
689 peppered moth camouflage. Commun Biol. 1:118.

690 Wang IJ, Shaffer HB. 2008. Rapid color evolution in an aposematic species: a phylogenetic analysis of
691 color variation in the strikingly polymorphic strawberry poison-dart frog. Evolution. 62:2742-2759.

692 Weaver RJ, Koch RE, Hill GE. 2017. What maintains signal honesty in animal colour displays used in
693 mate choice? *Philos Trans R Soc B*. 372:20160343.

694 Wüster W, Allum CSE, Bjargardóttir IB, Bailey KL, Dawson KJ, Guenioui J, Lewis J, McGurk J, Moore
695 AG, Niskanen M, Pollard CP. 2004. Do aposematism and Batesian mimicry require bright colours? A
696 test, using European viper markings. *Proc R Soc B*. 271:2495-2499.

697 Xiao F, Cuthill IC. 2016. Background complexity and the detectability of camouflaged targets by birds
698 and humans. *Proc R Soc B*. 283:20161527.

699 Yang Y, Blomenkamp S, Dugas MB, Richards-Zawacki CL, Pröhl H. 2019. Mate Choice versus mate
700 preference: inferences about color-assortative mating differ between field and lab assays of poison frog
701 behavior. *Am Nat*. 193:598-607.

702 Yeager J & Barnett JB. 2020. Ultraviolet components offer minimal contrast enhancement to an
703 aposematic signal. *Ecol Evol*. 10:13576-13582.

704 Yeager J, Brown JL, Morales V, Cummings M, Summers K. 2012. Testing for selection on color and
705 pattern in a mimetic radiation. *Curr Zool*. 58:668-676.

706 Yeager J, McGraw K, Saporito RA, Owens B, Giltz SM, Richards-Zawacki CL. Effects of habitat quality
707 on traits under multifarious selection for local adaptation. In Review.

708 Zimova M, Mills LS, Nowak JJ. 2016. High fitness costs of climate change-induced camouflage
709 mismatch. *Ecol Lett*. 19:299-307.

710 **Table 1. Visual contrast (JND means \pm SE) in luminance and hue between frog types and**
 711 **backgrounds according to an avian visual model.**

	Luminance (Achromatic)			Hue (Chromatic)		
	Base	Stripe/Spot	Mean	Base	Stripe/Spot	Mean
<i>Allobates talamancae</i>						
Natural	5.34 \pm 0.22	15.24 \pm 0.33	4.97 \pm 0.17	4.22 \pm 0.11	3.21 \pm 0.08	3.05 \pm 0.09
Disturbed	8.70 \pm 0.22	10.60 \pm 0.27	3.74 \pm 0.13	5.59 \pm 0.07	4.48 \pm 0.08	4.77 \pm 0.67
Black-Spotted Green <i>Oophaga pumilio</i>						
Natural	10.40 \pm 0.31	5.97 \pm 0.23	6.55 \pm 0.23	4.02 \pm 0.07	3.79 \pm 0.11	2.62 \pm 0.07
Disturbed	6.37 \pm 0.24	9.37 \pm 0.24	3.79 \pm 0.15	2.54 \pm 0.06	4.94 \pm 0.07	2.29 \pm 0.06
Allopatric	7.10 \pm 0.28	8.56 \pm 0.27	4.22 \pm 0.18	4.38 \pm 0.06	4.71 \pm 0.09	3.20 \pm 0.06
Black-Spotted Red <i>Oophaga pumilio</i>						
Natural	6.00 \pm 0.22	5.93 \pm 0.22	5.16 \pm 0.20	8.05 \pm 0.20	4.12 \pm 0.10	5.19 \pm 0.17
Disturbed	5.13 \pm 0.19	6.44 \pm 0.20	4.62 \pm 0.17	10.21 \pm 0.19	5.38 \pm 0.07	7.50 \pm 0.17
Allopatric	9.60 \pm 0.25	4.85 \pm 0.19	7.70 \pm 0.24	9.46 \pm 0.19	3.77 \pm 0.11	6.51 \pm 0.17

712 **Table 2. Statistical analysis of achromatic and chromatic contrast from the avian visual model.**

	Luminance (Achromatic)			Hue (Chromatic)		
	Base	Stripe/Spot	Mean	Base	Stripe/Spot	Mean
Full Model	$\chi^2 = 368.43,$ df = 3, p < 0.001	$\chi^2 = 199.10,$ df = 3, p < 0.001	$\chi^2 = 15.90,$ df = 3, p = 0.001	$\chi^2 = 868.07,$ df = 3, p < 0.001	$\chi^2 = 129.74,$ df = 3, p < 0.001	$\chi^2 = 8.25.86,$ df = 3, p < 0.001
<i>Allobates talamancae</i>						
Model	$\chi^2 = 25.62,$ df = 1, p < 0.001	$\chi^2 = 25.52,$ df = 1, p < 0.001	$\chi^2 = 3.04,$ df = 1, p = 0.081	$\chi^2 = 10.72,$ df = 1, p = 0.001	$\chi^2 = 18.29,$ df = 1, p < 0.001	$\chi^2 = 17.94,$ df = 1, p < 0.001
Natural vs Disturbed	z = -5.46, p < 0.001	z = 5.45, p < 0.001	z = 1.74, p = 0.082	z = -3.35, p = 0.001	z = -4.49, p < 0.001	z = -4.44, p < 0.001
<i>Black-Spotted Green Oophaga pumilio</i>						
Model	$\chi^2 = 25.18,$ df = 2, p < 0.001	$\chi^2 = 25.55,$ df = 2, p < 0.001	$\chi^2 = 22.55,$ df = 2, p < 0.001	$\chi^2 = 58.26,$ df = 2, p < 0.001	$\chi^2 = 9.84,$ df = 2, p = 0.007	$\chi^2 = 11.73,$ df = 2, p = 0.003
Natural vs Disturbed	z = 4.83, p < 0.001	z = -5.08, p < 0.001	z = 4.73, p < 0.001	z = 6.68, p < 0.001	z = -3.00, p = 0.005	z = 1.35, p = 0.301
Natural vs Allopatric	z = 4.15, p < 0.001	z = -3.77, p < 0.001	z = 3.54, p = 0.001	z = -1.56, p = 0.206	z = -2.34, p = 0.036	z = -2.15, p = 0.058
<i>Black-Spotted Red Oophaga pumilio</i>						
Model	$\chi^2 = 29.75,$ df = 2, p < 0.001	$\chi^2 = 14.20,$ df = 2, p < 0.001	$\chi^2 = 32.90,$ df = 2, p < 0.001	$\chi^2 = 39.27,$ df = 2, p < 0.001	$\chi^2 = 19.76,$ df = 2, p < 0.001	$\chi^2 = 52.98,$ df = 2, p < 0.001
Natural vs Disturbed	z = 1.11, p = 0.429	z = -1.03, p = 0.480	z = 0.41, p < 0.882	z = -6.72, p < 0.001	z = -3.31, p = 0.002	z = -8.13, p < 0.001
Natural vs Allopatric	z = -4.20, p < 0.001	z = 2.59, p = 0.018	z = -4.94, p < 0.001	z = -4.41, p < 0.001	z = 0.94, p = 0.538	z = -4.65, p < 0.001

713 **Figure 1**

714 Study system: frogs and detection experiment stimuli. Left, frog color forms (top to bottom): Isla Colón
715 *Allobates talamancae*, Isla Colón Black-Spotted Green *Oophaga pumilio*, and Isla Bastimentos Black-
716 Spotted Red *O. pumilio*. Middle, detection experiment treatment designs: A = natural pattern, B =
717 reversed pattern, C = patternless, D = mean frog, E = mean background, F = background matching, G =
718 switched colors; 1 = *A. talamancae*, 2 = Black-Spotted Green *O. pumilio*, and 3 = Black-Spotted Red *O.*
719 *pumilio*. Right, example stimuli (top to bottom): treatment A1 on an Isla Colón forest background,
720 treatment A2 on an Isla Colón disturbed background, and treatment A3 on an Isla Bastimentos forest
721 background.

722 **Figure 2**

723 Image analysis: chromatic contrast (ΔS) from the avian visual model (JND means \pm 95% CI from the
724 model) for each frog (left = Beige-Striped Brown *A. talamancae*; middle = Black-Spotted Green *O.*
725 *pumilio*; right = Black-Spotted Red *O. pumilio*) versus each background. Grey dashed lined represent
726 absolute (1.0) and conservative (3.0) visual discrimination thresholds.

727 **Figure 3**

728 Image analysis: pattern (granularity) analysis from the avian visual model (area between energy curves,
729 means \pm 95% CI from the model). Comparing each frog (*A. tal* = Beige-Striped Brown *A. talamancae*; *O.*
730 *pum* (G) = Black-Spotted Green *O. pumilio*; *O. pum* (R) = Black-Spotted Red *O. pumilio*) to the
731 backgrounds. There was no significant effect of background type on pattern contrast, so it was removed
732 from the model. The striped pattern of *A. talamancae* was a closer match to the background than the
733 spotted patterns of *O. pumilio*.

734 **Figure 4**

735 Detection experiment: habitat change and local adaption (reaction time (s) means \pm 95% CI from the
736 model: left = *A. talamancae*, middle = Black-Spotted Green *O. pumilio*, right = Black-Spotted Red *O.*
737 *pumilio*). Human disturbance affected reaction time: in the Disturbed habitat Beige-Striped Brown *A.*
738 *talamancae* were more easily found and Black-Spotted Green *O. pumilio* were more difficult to find than
739 they were on their Natural background. Conversely, the Black-Spotted Red *O. pumilio* were equally
740 detectable in both Natural and Disturbed habitats. There was no difference between Natural and
741 Allopatric background for either morph of *O. pumilio*.

742 **Figure 5**

743 Detection experiment: pattern distribution (reaction time (s) means \pm 95% CI from the model: left = *A.*
744 *talamancae*, middle = Black-Spotted Green *O. pumilio*, right = Black-Spotted Red *O. pumilio*). There
745 were no differences between Natural and Reversed patterns for any of the frogs. Removing pattern did not
746 affect detectability for *A. talamancae* nor Black-Spotted Red *O. pumilio*, but the presence of spots
747 decreased reaction time in Black-Spotted Green *O. pumilio*. All frogs were more detectable than random-
748 sample background matching, but there was no difference between the mean colors of *A. talamancae* or
749 Black-Spotted Red *O. pumilio* and the mean color of their backgrounds, suggesting these frogs may be
750 cryptic when viewed from a distance. The mean color of Black-Spotted Green *O. pumilio* was more
751 detectable than the mean color of the background.

752 **Figure 6**

753 Detection experiment: interaction between pattern and color (reaction time (s) means \pm 95% CI from the
754 model). Brown stripes (A1 - natural pattern of Beige-Striped Brown *A. talamancae*), green stripes (G1 –
755 switched colors), green spots (A2 - natural pattern Black-Spotted Green *O. pumilio*), brown spots (G2 –
756 switched colors), and red spots (A3 = natural pattern of Black-Spotted Red *O. pumilio*). Spots were a

757 more conspicuous pattern than stripes regardless of color. Brown stripes were more cryptic than green
758 stripes but there was no difference between differently colored spotted patterns.

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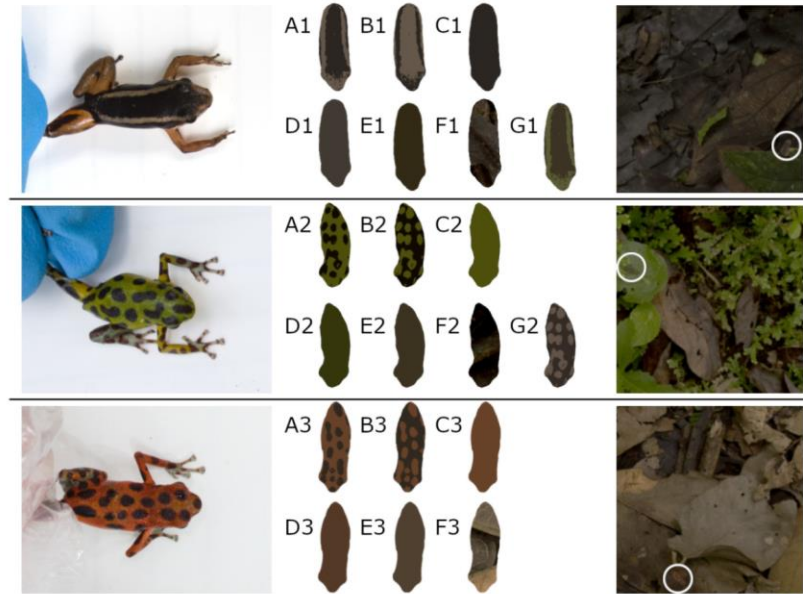


Figure 1

Study system: frogs and detection experiment stimuli. Left, frog color forms (top to bottom): Isla Colón *Allobates talamancae*, Isla Colón Black-Spotted Green *Oophaga pumilio*, and Isla Bastimentos Black-Spotted Red *O. pumilio*. Middle, detection experiment treatment designs: A = natural pattern, B = reversed pattern, C = patternless, D = mean frog, E = mean background, F = background matching, G = switched colors; 1 = *A. talamancae*, 2 = Black-Spotted Green *O. pumilio*, and 3 = Black-Spotted Red *O. pumilio*. Right, example stimuli (top to bottom): treatment A1 on an Isla Colón forest background, treatment A2 on an Isla Colón disturbed background, and treatment A3 on an Isla Bastimentos forest background.

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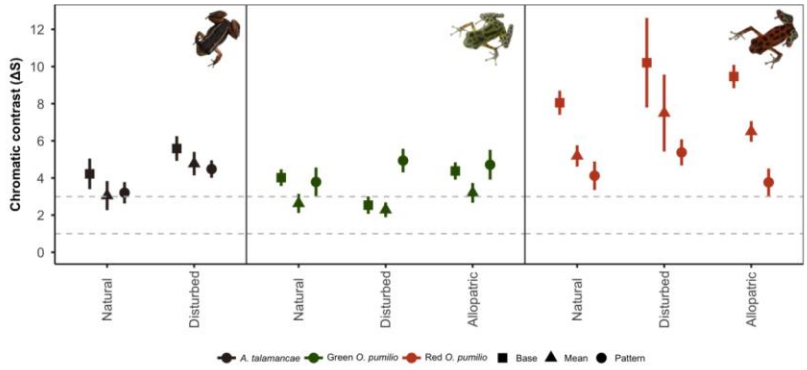


Figure 2

Image analysis: chromatic contrast (ΔS) from the avian visual model (JND means \pm 95% CI from the model) for each frog (left = Beige-Striped Brown *A. talamancae*; middle = Black-Spotted Green *O. pumilio*; right = Black-Spotted Red *O. pumilio*) versus each background. Grey dashed lined represent absolute (1.0) and conservative (3.0) visual discrimination thresholds.

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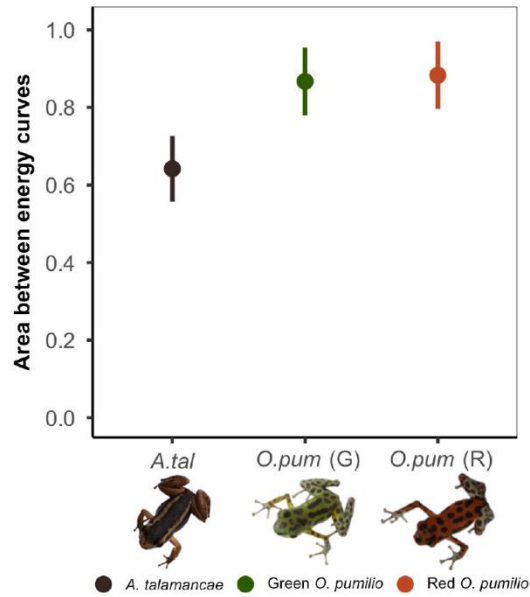


Figure 3

Image analysis: pattern (granularity) analysis from the avian visual model (area between energy curves, means \pm 95% CI from the model). Comparing each frog (*A. tal* = Beige-Striped Brown *A. talamancae*; *O. pum (G)* = Black-Spotted Green *O. pumilio*; *O. pum (R)* = Black-Spotted Red *O. pumilio*) to the backgrounds. There was no significant effect of background type on pattern contrast, so it was removed from the model. The striped pattern of *A. talamancae* was a closer match to the background than the spotted patterns of *O. pumilio*.

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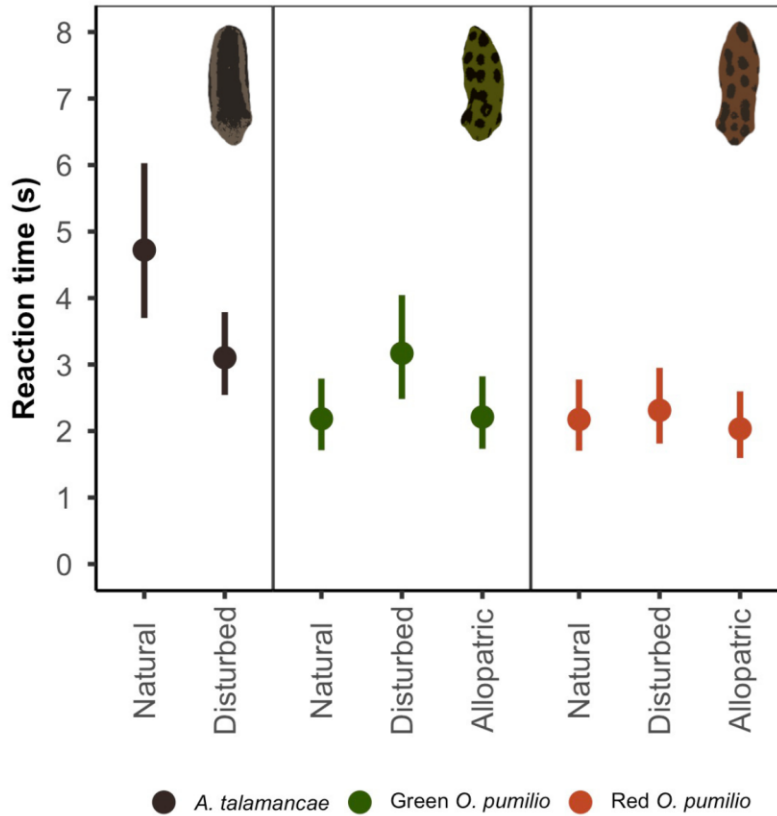


Figure 4

Detection experiment: habitat change and local adaption (reaction time (s) means \pm 95% CI from the model: left = *A. talamancae*, middle = Black-Spotted Green *O. pumilio*, right = Black-Spotted Red *O. pumilio*). Human disturbance affected reaction time: in the Disturbed habitat Beige-Striped Brown *A. talamancae* were more easily found and Black-Spotted Green *O. pumilio* were more difficult to find than they were on their Natural background. Conversely, the Black-Spotted Red *O. pumilio* were equally detectable in both Natural and Disturbed habitats. There was no difference between Natural and Allopatric background for either morph of *O. pumilio*.

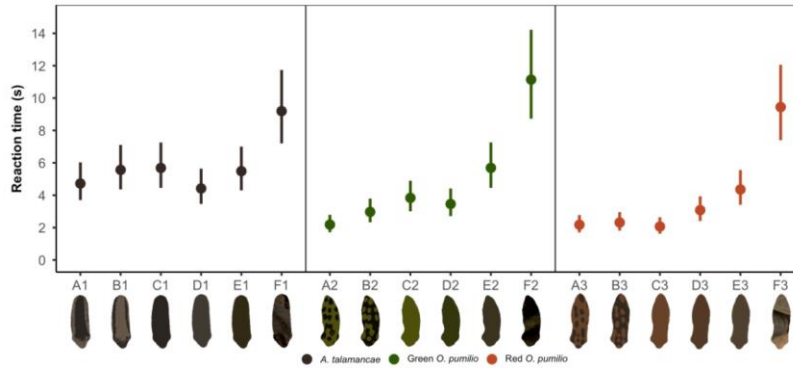


Figure 5
 Detection experiment: pattern distribution (reaction time (s) means \pm 95% CI from the model: left = *A. talamancae*, middle = Black-Spotted Green *O. pumilio*, right = Black-Spotted Red *O. pumilio*). There were no differences between Natural and Reversed patterns for any of the frogs. Removing pattern did not affect detectability for *A. talamancae* nor Black-Spotted Red *O. pumilio*, but the presence of spots decreased reaction time in Black-Spotted Green *O. pumilio*. All frogs were more detectable than random-sample background matching, but there was no difference between the mean colors of *A. talamancae* or Black-Spotted Red *O. pumilio* and the mean color of their backgrounds, suggesting these frogs may be cryptic when viewed from a distance. The mean color of Black-Spotted Green *O. pumilio* was more detectable than the mean color of the background.

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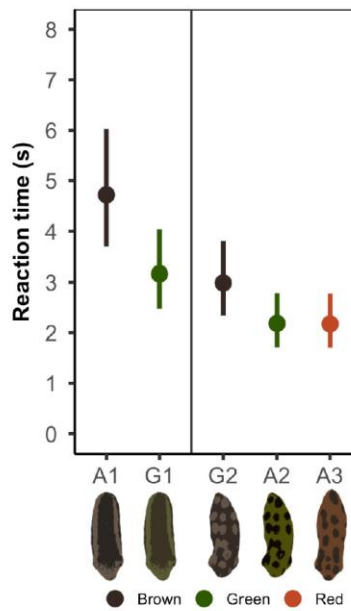


Figure 6
 Detection experiment: interaction between pattern and color (reaction time (s) means \pm 95% CI from the model). Brown stripes (A1 - natural pattern of Beige-Striped Brown *A. talamancae*), green stripes (G1 - switched colors), green spots (A2 - natural pattern Black-Spotted Green *O. pumilio*), brown spots (G2 - switched colors), and red spots (A3 = natural pattern of Black-Spotted Red *O. pumilio*). Spots were a more conspicuous pattern than stripes regardless of color. Brown stripes were more cryptic than green stripes but there was no difference between differently colored spotted patterns.

766