

Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*

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Accepted 21 April 2004

Summary

Poison frogs in the anuran family Dendrobatidae use bright colors on their bodies to advertise toxicity. The species *Dendrobates pumilio* Schmidt 1858, the strawberry poison frog, shows extreme polymorphism in color and pattern in Panama. It is known that females of *D. pumilio* preferentially choose mates of their own color morph. Nevertheless, potential predators must clearly see and recognize all color morphs if the aposematic signaling system is to function effectively. We examined the ability of conspecifics and a model predator to discriminate a diverse selection of *D. pumilio* colors from each other and from background colors. Microspectrophotometry of isolated rod and cone photoreceptors of *D. pumilio* revealed the presence of a trichromatic photopic visual system. A typical tetrachromatic bird system was used for the model predator. Reflectance spectra of frog and

background colors were obtained, and discrimination among spectra in natural illuminants was mathematically modeled. The results revealed that both *D. pumilio* and the model predator discriminate most colors quite well, both from each other and from typical backgrounds, with the predator generally performing somewhat better than the conspecifics. Each color morph displayed at least one color signal that is highly visible against backgrounds to both visual systems. Our results indicate that the colors displayed by the various color morphs of *D. pumilio* are effective signals both to conspecifics and to a model predator.

Key words: visual ecology, aposematism, poison frog, *Dendrobates pumilio*, color vision, color signal.

Introduction

Many anurans (frogs and toads) use toxins as an effective defense against predators and are conspicuous in color, a combination of features known as aposematism (Cott, 1940). Use of prominent coloration is a widespread visual aposematic technique. A classic example of aposematic color signals is found in poison frogs of the family Dendrobatidae, which are found in Central and South America where they occupy a wide range of habitats.

The species *Dendrobates pumilio* Schmidt 1858, commonly called the 'strawberry poison frog', offers an excellent case study of how color and, therefore, aposematic signaling may vary within a single species. *D. pumilio* is a toxic species, generally about 1 to 2 cm in size, that inhabits the forest floor throughout Central America. A group of islands in Panama's Bocas del Toro Archipelago is populated with these poison frogs (see Summers et al., 2003). Here, *D. pumilio* has evolved to become chromatically distinct between islands, and single populations of *D. pumilio* on the adjacent mainland of Panama may also have striking color variations (Myers and Daly, 1983). Fig. 1 depicts typical *D. pumilio* color morphs, all of

which have been classified into one species based on call parameters, toxicity and mitochondrial DNA sequence comparisons (Summers et al., 1997).

Warning coloration in poison frogs seems to be very effective, as predation is rarely observed. Unlike most frogs, poison frogs are active during the daytime when predators can easily see them. The toxins that are released from their skin are some of the most potent animal poisons known, and the bright daylight environment favors advertisement based on color (Myers and Daly, 1983). The polymorphic appearance of *D. pumilio* is not obviously deleterious to the species in terms of predation. The divergence is a recent phenomenon. Today's color morphs have apparently arisen within the last 6000 years, as the geography of the archipelago has altered with the rise of sea level (Summers et al., 1997). Notably, other monomorphic species of dendrobatid frogs are sympatric with *D. pumilio* (Summers et al., 1997). *D. pumilio*'s variability is not explained by Mullerian mimicry, where natural selection should favor convergence of color and pattern in unpalatable species (Summers et al., 1997; Mallet and Joron, 1999).

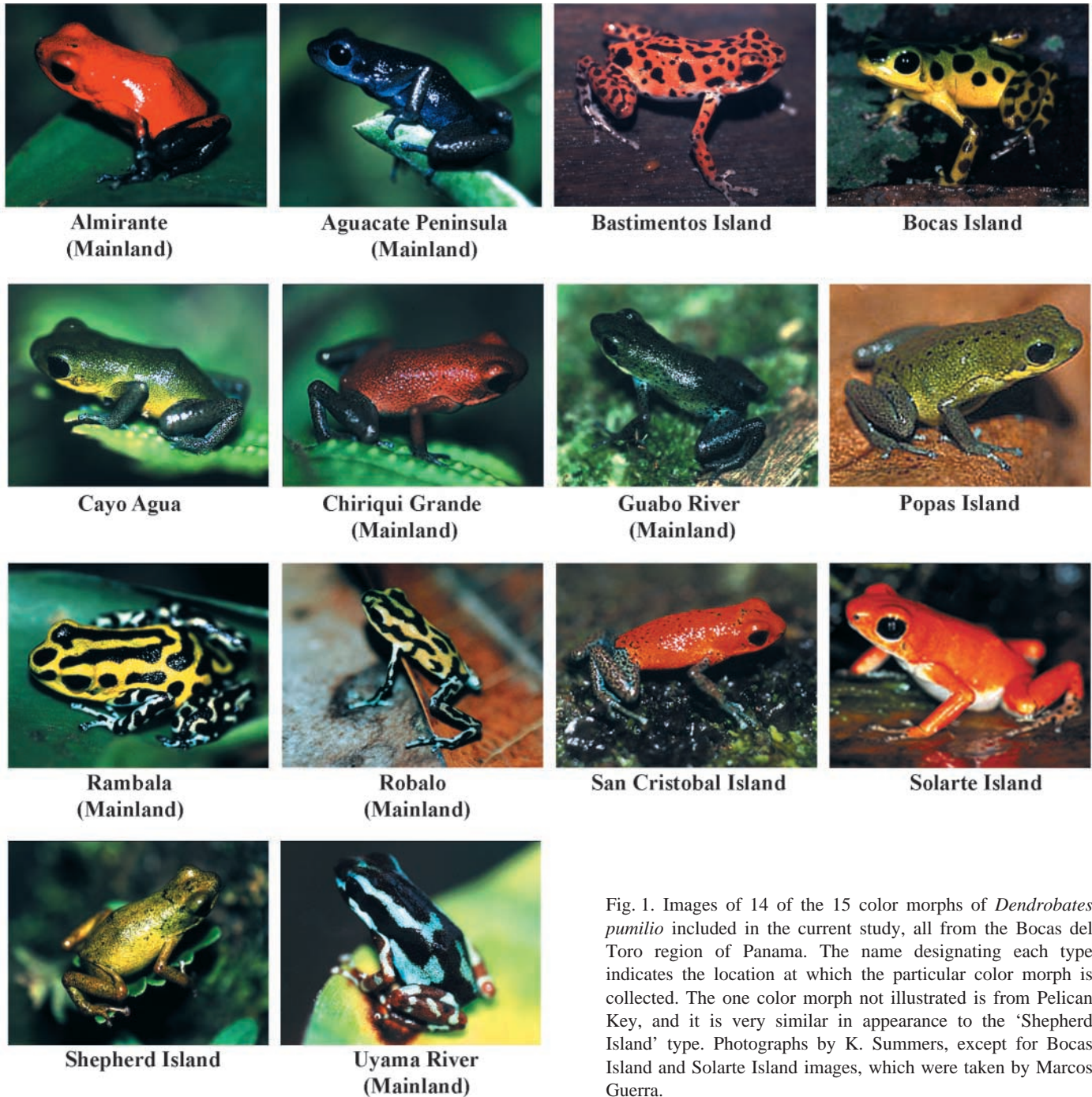


Fig. 1. Images of 14 of the 15 color morphs of *Dendrobates pumilio* included in the current study, all from the Bocas del Toro region of Panama. The name designating each type indicates the location at which the particular color morph is collected. The one color morph not illustrated is from Pelican Key, and it is very similar in appearance to the 'Shepherd Island' type. Photographs by K. Summers, except for Bocas Island and Solarte Island images, which were taken by Marcos Guerra.

Instead, it is apparently driven by mate selection by females. Unlike other dendrobatid species, where males and females have equal parental roles, parental investment in *D. pumilio* is higher in females, and gives them a strong role in sexual selection (Summers et al., 1997). Female choice can be an important factor in the divergence of populations. Fisher theorized that a preference and the preferred trait may coevolve, resulting in an exaggeration of the trait in a positive-feedback cycle known as the runaway process (reviewed by Pomiankowski, 1988).

If mate choice explains *D. pumilio* color diversity, then signals are not only important for signaling to potential predators – they also effect communication between conspecifics. Summers et al. (1999) explored the role of vision in mate choice in *D. pumilio*. When individual *D. pumilio* females were given a choice between frogs having different color morphs, they preferentially chose their own type. Under light conditions where frogs were unable to tell the difference in color between the color morphs, they expressed no preference. Thus, female *D. pumilio* use visual cues to assess

possible mates. The relatively lengthy courtship behavior of *D. pumilio* potentially gives a female ample opportunity to observe and examine the coloration and patterning of a possible mate (Limerick, 1980).

D. pumilio shares its range with other dendrobatid species; consequently, species recognition is vital for successful reproduction. Acoustic signals are species-specific and aid in the recognition of possible mates and conspecifics, but (as just noted) visual cues are also important in this task (Summers et al., 1999). The color signals expressed by *D. pumilio* should be discriminable between color morphs by conspecifics. Frogs should also be detected easily against backgrounds such as foliage or tree bark. This is important for finding mates and for facilitating social interactions between conspecifics.

Since *D. pumilio* colors also serve as aposematic color signals, potential predators should recognize them as indicators of unpalatability and move on without an attempted attack. Therefore, the signals should be well tuned to the vision of predators. The polymorphic character of *D. pumilio* motivates the question of how potential predators perceive these differences in coloration. For instance, are color morphs that are seemingly cryptic (see examples of green frogs in Fig. 1) easily discriminated from backgrounds by visual systems of predators? Here we investigate the question of how the signals of many *D. pumilio* color morphs are perceived and discriminated by conspecifics and by a potential predator. Since birds are predators on many anurans (Myers and Daly, 1983; Poulin et al., 2001), and avian visual systems are well studied (Hart, 2001), we use a typical passerine bird as a model predator on *D. pumilio*.

This study thus addresses the effectiveness of color signals used by *D. pumilio* as perceived both by conspecifics and by a potential predator. The effectiveness is assessed by determining how discriminable colors are to each viewer, quantifying the viewer's ability to discriminate frog colors from each other and from background colors. Our study of the frogs' color signals will help to comprehend the effectiveness of the polymorphic nature of *D. pumilio* in Panama.

Materials and methods

Microspectrophotometry

One adult *Dendrobates pumilio* Schmidt 1858 was provided by the National Aquarium in Baltimore (NAIB) and taken to Loew's laboratory at Cornell University the same day. The animal was kept in a warm, lit environment before examination. After 4 h of dark adaptation, the frog was euthanized with MS-222 (3-aminobenzoic acid ethyl ester) and the eyes enucleated under dim red light (safelight No. 2, 15 W bulb; Kodak, Rochester, NY, USA). Further preparations and measurements were done under infrared illumination (>800 nm, Kodak safelight No. 11), using image converters. The eyes were hemisected and the retinas carefully removed under buffer solution (cold Ca/Mg-free Ringer's solution, pH 7.4, supplemented with 5% sucrose). Pieces of retina were macerated on a coverslip and then sandwiched using a second

coverslip edged with silicone grease. The computer-controlled, single-beam microspectrophotometer (MSP) used in this study has been previously described (Loew, 1994). The 2 μm × 3 μm measuring beam was produced by demagnification using a Leitz (Oberkochen, Germany) 180X quartz mirror objective. A Zeiss 100X Ultrafluor (0.85 NA) collected the transmitted light and focused it onto the photomultiplier photocathode. Baseline and sample spectra were obtained at 100 nm s^{-1} from 750 to 350 nm, and back from 350 to 750 nm, with a wavelength accuracy of approximately 1 nm (Loew, 1994). Individual cells were selected for measurement under infrared illumination, using an image converter. In cases where it was not certain that an actual photoreceptor was being measured, the putative photoreceptor was exposed to 60 s of white light and scanned once more to look for evidence of photobleaching.

The selection criteria used for data inclusion into the λ_{max} analysis pool were the same as those used by Loew (1994). Each acceptable spectrum was smoothed prior to normalization using a digital filter routine ('smooft'; Press et al., 1987). The smoothed spectrum was overlaid on the unsmoothed one and checked by eye to make sure that over-filtering or spurious data points had not shifted the apparent maximum. The peak absorbance used for normalization prior to template fitting was the calculated maximum of the best-fit Gaussian to the data points 20 nm either side of the estimated-by-eye absorbance maximum of the alpha band and is referred to as X_{max} . For those curves meeting the selection criteria, the λ_{max} (the wavelength at maximum absorbance for a template-derived visual pigment best fitting the experimental data) of the smoothed, normalized (using X_{max}) visual pigment absorbance spectrum was obtained using the method of Mansfield as presented by MacNichol (1986). The templates used were those of Lipetz and Cronin (1988). In some cases the data were not of sufficient quality for template matching, but were usable for qualitative estimation of λ_{max} .

Reflectance measurements

Summers et al. (2003) measured reflectances in the field in Panama from various *D. pumilio* color morphs. Some colors, generally those of small or insignificant body parts, were not measured in the field or did not produce good quality data. To include the colors not represented in the data from Panama (invariably black or dark brown patches), reflectance measurements were taken from similar patches on dendrobatid frogs at NAIB. Altogether, 47 reflectance spectra were used, representing 15 color morphs.

To measure background spectra, tropical plants were acquired from the University of Maryland, Baltimore County's greenhouse. These included aglonema (*Aglaonema commutatum*), bromeliads (including *Neoreglia carolinae*), rubber plant (*Ficus elastica*), maranta (*Maranta leuconeure*), monstera (*Monstera deliciosa*), and *Zebrina pendula* (see examples in Fig. 2). Dry leaves, rocks, dirt, sand, sticks, and moss were also collected on campus for measurements of background reflectance.

Reflectance spectra were taken using an Ocean Optics

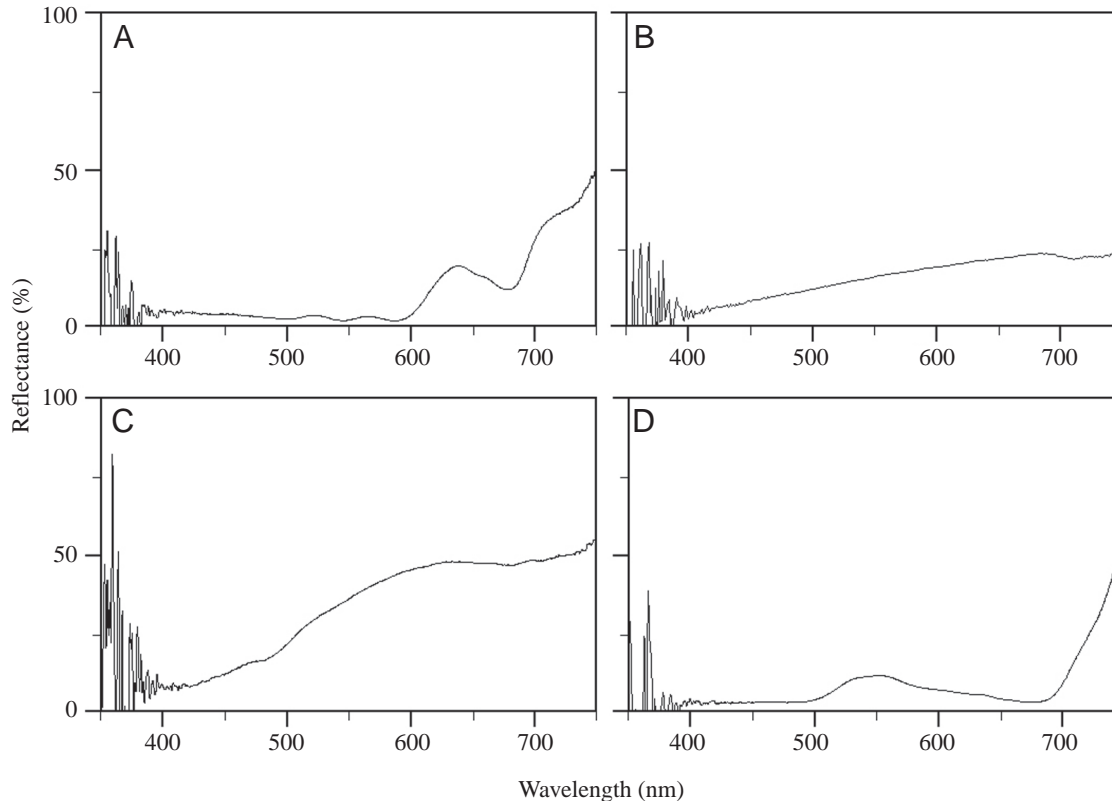


Fig. 2. Representative reflectance spectra from leaves used as backgrounds for spectral comparisons. (A) Purple leaf from *Zebrina pendula*. (B) Red leaf from *Neoreglia caroliniae*. (C) Yellow dry leaf. (D) Green leaf of *Aglaonema commutatum*.

(Dunedin, FL, USA) S2000 spectrometer, connected to a portable computer. A Labsphere (North Sutton, NH, USA) certified WS-1 Diffuse Reflectance Standard was used as a reference. A WILD Heerbrugg (Leica Microsystems, Wetzlar, Germany) photomicroscope connected to the spectrometer was used to isolate specific locations on the surface of the sample to be measured. A fiber optic light source illuminated samples, providing a measurable spectral range of about 350–750 nm. Various areas of plants were measured to ensure that dark, bright, and colored spots were included.

Irradiance spectra

To define lighting conditions where *D. pumilio* are found, four irradiance spectra were used (Fig. 3A): standard D55, D65 and D75 irradiance spectra (Wyszecki and Stiles, 1982), and a forest shade green light measured in *D. pumilio* habitat by Summers et al. (2003). The spectrum labeled D65 is the 'standard daylight', D55 is illumination dominated by sunlight, D75 is 'north' light dominated by sky, and Green is taken in shade, under the forest canopy.

Quantitative model

To analyze the perception of signals, we used the model developed by Vorobyev et al. (2001), which assumes that receptor noise limits discrimination (see Vorobyev and Osorio, 1998). Noise in frog photoreceptors was estimated using

behavioral data from birds and humans, as no appropriate measurements exist for amphibians. Signal-to-noise estimates are used to estimate the visual Weber fractions, the ratio of intensity between two lights that is just perceived by a visual system (i.e. at threshold). The Weber fraction estimated in bird long-wavelength sensitive class (LWS) cone is 0.1 (Vorobyev et al., 1998), calculated from behavioral experiments. In frogs, we assume that the Weber fraction of 0.05 (at threshold) for the LWS mechanism, which is an intermediate value between the Weber fraction of human LWS cones (0.02; Wyszecki and Stiles, 1982) and birds (0.1; Vorobyev et al., 1998). Since absolute values of Weber fractions are not known, we perform calculations for several values of the signal-to-noise ratio (or the jnd, see below). Noise decreases with the number of receptors in a given type, because more individual receptors provide a signal to the system. Thus, the signal-to-noise ratio (Equation 5) takes into account both the visual Weber fraction (v_i) and the number of cone per type (n_i). The ratios of cones between classes were estimated from MSP preparations, assuming that the relative encounter rates in these preparations are similar to the actual proportions of cone types found in the eye. The bird ratios were refined by accurately matching behavioral spectral sensitivities (see Maier and Bowmaker, 1993; Vorobyev et al., 1998), providing ratios of cone types as follows: LWS 4 : MWS 2 : SWS 2 : UVS 1 (MWS, middle-wavelength-sensitive class; SWS, short-wavelength-sensitive

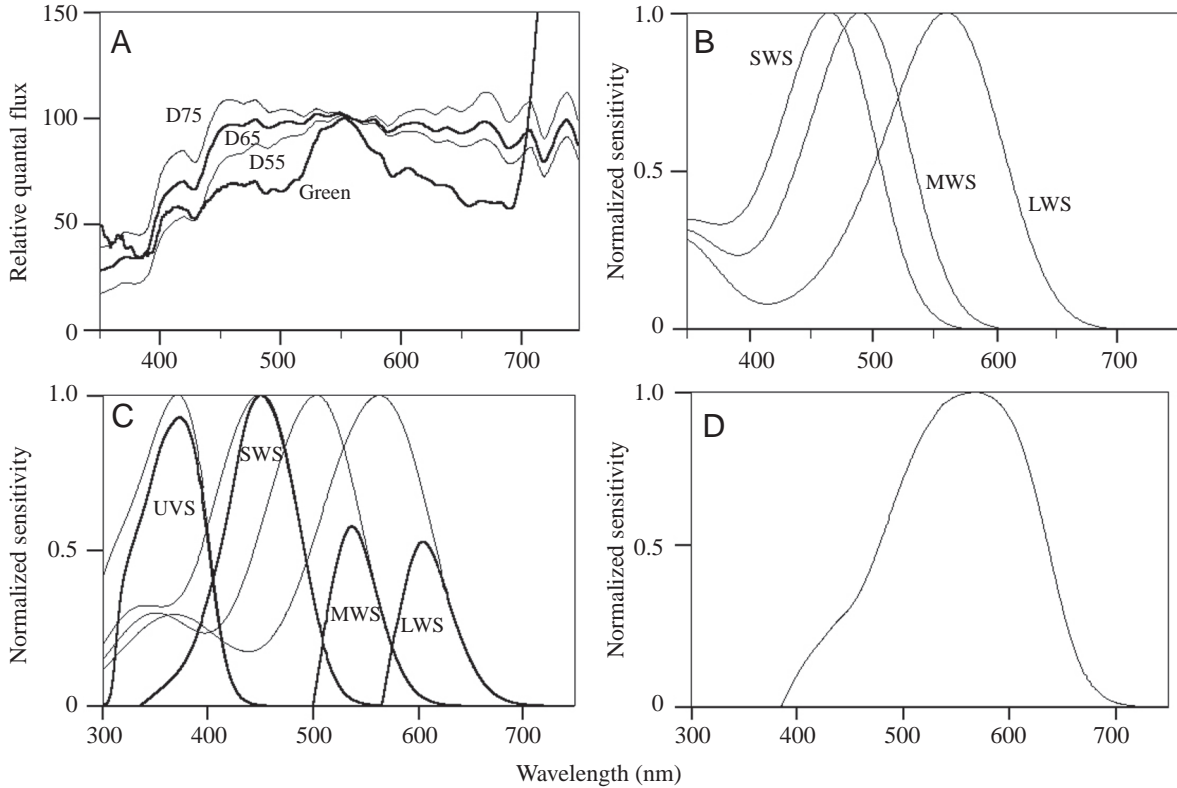


Fig. 3. Spectra used in data analyses of spectral discriminability. See text for a description of the model used for this analysis. (A) Irradiance spectra. D65 (standard daylight), D55 (direct sunlight) and D75 ('north' skylight), from Wyszecki and Stiles (1982). Green (light under the natural forest canopy in *D. pumilio* habitat, Pelican Key), from Summers et al. (2003). (B) Templates representing cone visual pigments of *D. pumilio*. (C) Spectral sensitivities of avian cones, taken from *Parus caeruleus* (generously provided by N. Hart). Thin lines indicate visual pigments, while thick lines represent spectral sensitivities computed taking cone oil droplet absorption into account, used for actual analyses. (D) Normalized absorbance of an avian double cone, including the contribution of the associated oil droplet, used in achromatic analyses (provided by N. Hart). UVS, ultraviolet sensitive; SWS, short-wavelength sensitive; MWS, medium-wavelength sensitive; LWS, long-wavelength sensitive.

class; UVS, ultraviolet-sensitive class). Using data from our MSP results, receptor ratios in *D. pumilio* were taken as: LWS 4 : MWS 3 : SWS 1.

The model was run using a program written in Mathematica (Version 4.0, Wolfram Research). The program requires the photopic sensitivity functions of the frog (Fig. 3B) and bird (Fig. 3C,D) visual systems, using templates fitted to MSP data in *D. pumilio* and taken directly from avian templates generously provided by Nathan Hart. It also requires the selection of one of the irradiance spectra (Fig. 3A) and of a pair of reflection spectra measured from frog skin or background. First, we calculate the quantum catch Q_i of each receptor class, denoted by the subscript i , over the wavelength range 350–750 nm, as the integrated product of the receptor sensitivity spectrum (R_i), reflectance spectrum (S), and illumination spectrum (I):

$$Q_i = R_i(\lambda)S(\lambda)I(\lambda)d\lambda . \quad (1)$$

Equation 2 accounts for the adaptation of a receptor to its light environment, using the von Kries transformation. This assumes that receptors adapt their sensitivities in proportion to

the light they absorb from the illuminant, a property that contributes to color constancy (Foster and Nascimento, 1994), thus:

$$k_i = 1 / \int R_i(\lambda)I(\lambda)d\lambda , \quad (2)$$

where k is the von Kries adaptation coefficient. The product of Equations 1 and 2 gives the quantum catch q_i of each receptor class, adapted to its background.

$$q_i = k_i Q_i . \quad (3)$$

Equation 4 is then applied to find the contrast between two spectra, as the logarithm of the quotient of quantum catches from spectrum 1 and spectrum 2. The result of this calculation is the contrast Δf for each receptor type i :

$$\Delta f_i = \ln[q_i(\text{spec1})] - \ln[q_i(\text{spec2})] = \ln[q_i(\text{spec1})/q_i(\text{spec2})] . \quad (4)$$

For quantum catches that differ only slightly, the contrast is equal to the relative difference between these catches, $\Delta q_i/q_i$, where $\Delta q_i = q_i(\text{spec1}) - q_i(\text{spec2})$, because $\Delta f_i = \ln[q_i(\text{spec1})/q_i(\text{spec2})] = \ln(1 + \Delta q_i/q_i(\text{spec2})) = \Delta q_i/q_i(\text{spec2})$

(Vorobyev et al., 2001). Note that this relation holds only if the natural logarithms are used.

The contrast, so defined, does not depend on the adaptation of receptors to their light environment, k_i , because Δf_i depends on the ratio of quantum catches. Nevertheless, it is convenient to use adapted receptor responses to compare the quantum catches from different spectral types of cones.

To quantify discrimination using all receptor types in a given visual system, each receptor class is first assigned a noise value ω based on its individual Weber fraction (v) and on the receptor proportion (n); see also Vorobyev et al. (2001):

$$\omega_i = v_i / n_i. \quad (5)$$

Then, we calculate discrimination values for trichromatic and tetrachromatic visual systems. The subscript number of each variable in Equations 6i, ii is again the value given for a particular receptor class (1 to 3 for frogs, 6i; 1 to 4 for birds, 6ii):

Trichromat:

$$(\Delta S)^2 = [\omega_1^2(\Delta f_3 - \Delta f_2)^2 + \omega_2^2(\Delta f_3 - \Delta f_1)^2 + \omega_3^2(\Delta f_1 - \Delta f_2)^2] / [(\omega_1\omega_2)^2 + (\omega_1\omega_3)^2 + (\omega_2\omega_3)^2], \quad (6i)$$

Tetrachromat:

$$(\Delta S)^2 = [(\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2] / [(\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2]. \quad (6ii)$$

Results of calculations using Equations 6i, ii provide the chromatic distance (ΔS) separating the perceptual values of two spectra in receptor space. The units for ΔS are jnds (just noticeable differences), where 1 jnd is at the threshold of discrimination, values <1 jnd indicate that the two colors are indistinguishable, and values above 1 jnd indicate how much above threshold a pair of spectra is discriminated. The higher the value, the more 'distance' in color space there is between the two spectra and the more distinguishable the two colors are, providing increasingly rapid discrimination under difficult conditions.

We also performed an achromatic (brightness contrast) analysis similar to the chromatic analysis, where comparisons are based on brightness differences alone.

$$\Delta S = |\Delta f_i / \omega|. \quad (7)$$

In birds, it is assumed that the double cone class (which contains LWS pigment; Fig. 3D) is responsible for achromatic tasks (Maier and Bowmaker, 1993; Campenhausen and Kirschfeld, 1998; Hart et al., 1998; Vorobyev et al., 1998; Osorio et al., 1999b). The double cone's principal member contains an oil droplet that absorbs at short wavelengths, but does not displace the λ_{\max} of the visual pigment (Hart, 2001). In frogs, the LWS class is again assumed to be responsible for the achromatic task, based on evidence from birds, bees and turtles that the LWS receptor is the most numerous type and is commonly used in achromatic tasks (Srinivasan, 1985; Campenhausen and Kirschfeld, 1998). As before, the quantum

catches and contrasts are calculated using Equations 1 to 4, and the separation in receptor space of the two spectra is determined using Equation 7. We estimated the Weber fraction as 0.05 (at threshold) for the double cone in birds and for the LWS cone in frogs.

Results

Microspectrophotometry

All averaged data from *Dendrobates pumilio* (Fig. 4) were best fit using A1 visual pigment templates, suggesting that in this diurnal species, 3,4-didehydroretinal (from vitamin A2), is not used as a visual pigment chromophore. The results obtained suggested the presence of one rod and three cone types, with no evidence for the existence of a cone class specialized for ultraviolet vision, as follows.

Rod

The average λ_{\max} of all individual rod cells measured in *D. pumilio* was 491 ± 2 nm (mean \pm S.D., $N=16$). The average spectrum can be seen in Fig. 4A, together with the template fit to the curve ($\lambda_{\max}=491 \pm 1$ nm (mean \pm S.D.)). Amphibians typically have two distinct rod types, 'red' rods (with λ_{\max} near or above 500 nm) and 'green' rods (λ_{\max} in the mid 400 nm range). Our measurements provided no evidence for the presence of 'green' rods in this species.

SWS cone

The shortest-wavelength-absorbing cone class was found to absorb maximally at a mean of 466 ± 5 nm (mean \pm S.D., $N=5$). Measurements were noisier for cones of this class, and template fits had larger standard deviations than for other receptor types. In individual fits, λ_{\max} ranged from 457 nm to 471 nm. Fig. 4B shows the average absorbance curve of the measured receptors and the best-fit template spectrum ($\lambda_{\max}=467 \pm 3$ nm, mean \pm S.D.).

MWS cones

The second type of cone had an average λ_{\max} of 489 ± 8 nm (mean \pm S.D., $N=14$). The average spectrum and its best template fit, seen in Fig. 4C, had a λ_{\max} of 488 ± 1 nm (mean \pm S.D.).

LWS cones

This was the most frequently encountered cone type, and it had an average λ_{\max} of 561 ± 3 nm (mean \pm S.D., $N=14$). The average absorbance curve, shown in Fig. 4D, had its best template fit with a λ_{\max} of 563 ± 1 nm (mean \pm S.D.).

Oil droplets

Oil droplets were associated with some cones. The absorbance spectrum of one such droplet, from an LWS cone, is displayed in Fig. 4E and shows very low absorbance from 350 nm to 750 nm. All oil droplets that were observed looked similar to the one that was measured, and we assume that these droplets have no significant influence on light absorption by the underlying visual pigment.

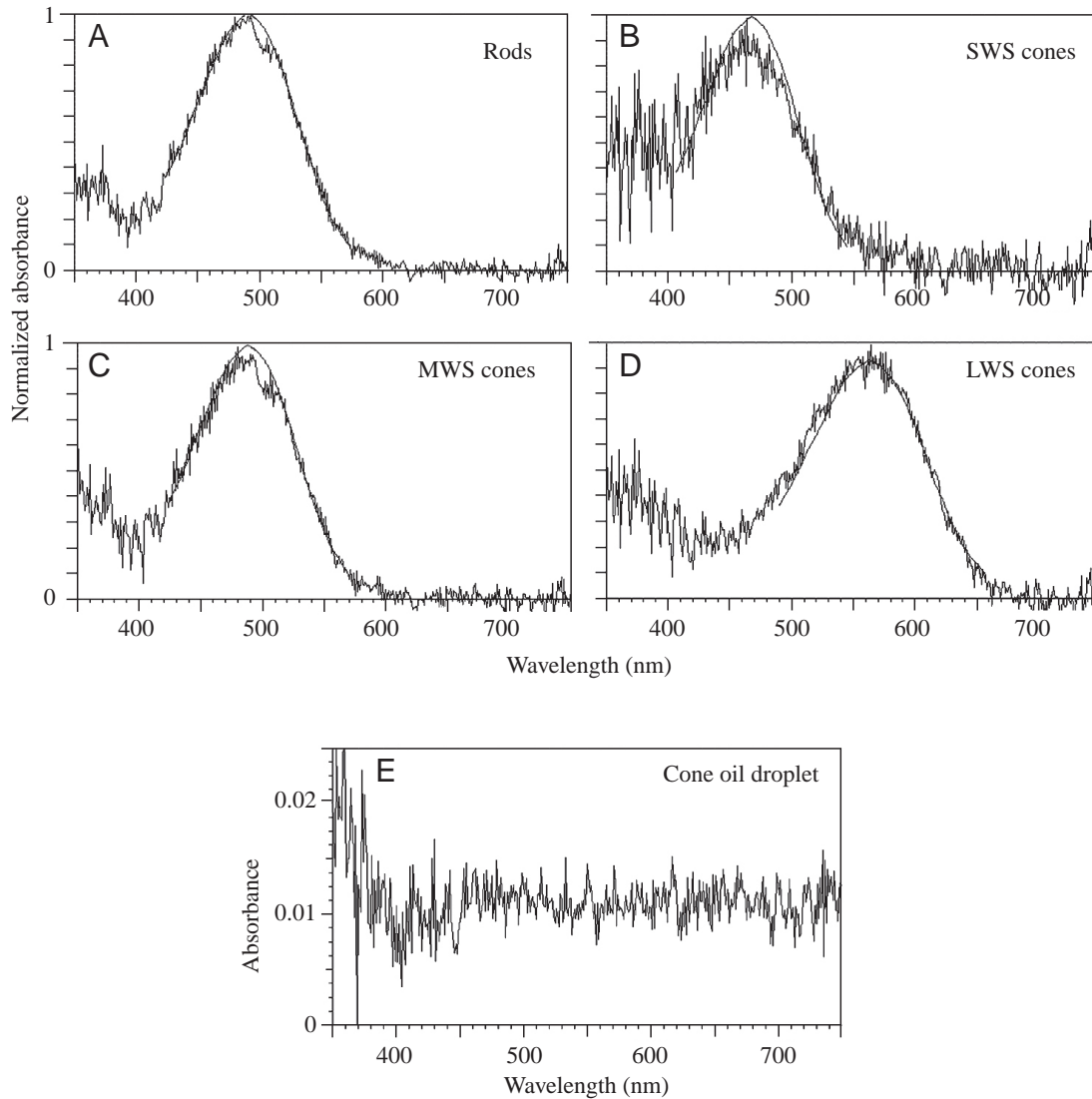


Fig. 4. Results from microspectrophotometric analyses of photoreceptors of *D. pumilio*, together with best-fit rhodopsin templates (smooth lines; from Lipetz and Cronin, 1988). (A) Rod photoreceptors ($\lambda_{\max}=491$ nm; $N=16$). (B) SWS cone photoreceptors ($\lambda_{\max}=466$ nm; $N=5$). (C) MWS cone photoreceptors ($\lambda_{\max}=488$ nm; $N=14$). (D) LWS cone photoreceptors ($\lambda_{\max}=560$ nm; $N=20$). (E) Single oil droplet from a single LWS cone inner segment, showing no significant absorption throughout the visual spectrum.

Reflectance spectra

Most reflectance spectra from frogs that were used (a total of 47 spectra) came from work published by Summers et al. (2003) and can be seen in the figures of that paper. Fig. 2 shows some representative spectra (of a total of 15 background spectra) from several leaf backgrounds against which individuals of *D. pumilio* might be viewed by predators or conspecifics.

Frog colors discriminated

Using our model, color signals were quantified pairwise for their contrast as viewed by conspecifics or by a typical passerine bird. Forty-seven spectra were compared to each other resulting in 1081 [(47×46)/2] comparisons. The results are displayed as histograms showing the number of cases

occurring at each jnd (just-noticeable-difference) level (Figs 5–9). In general, when jnd=1, the spectral pair is barely discriminable under ideal conditions, and as jnd becomes greater, discrimination can be made more rapidly and under increasingly unfavorable viewing conditions.

Four different lighting conditions were considered: standard daylight, sunlight, sky light and under the canopy (Fig. 3A). Results varied only slightly among the different illuminations tested, most likely because the model used incorporates von Kries color constancy (see Materials and methods). Here, we typically display analyses using the 'forest shade' illuminant, as poison frogs are found under the forest canopy, where they are most commonly viewed by conspecifics and by predatory birds, but results from all illuminants are given in the Tables.

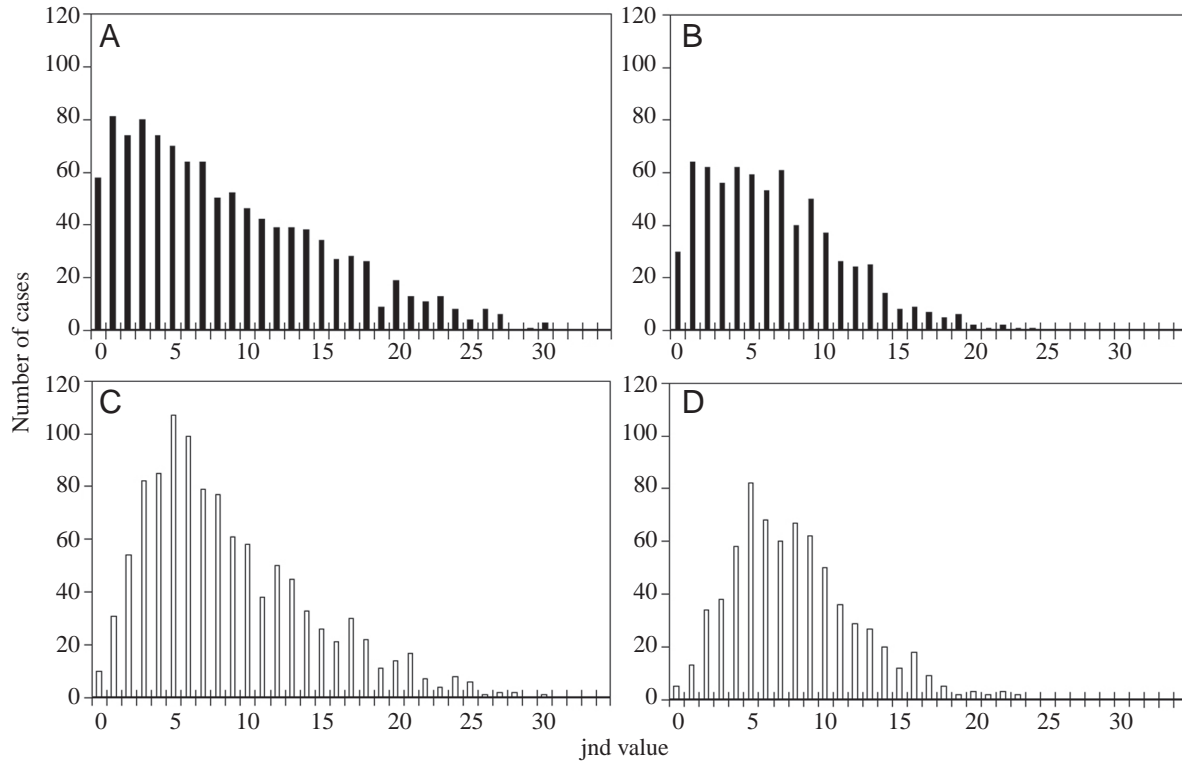


Fig. 5. Results of analyses comparing frog spectral reflectances as discriminated by frog or bird visual systems. Each panel is a histogram plot of the number of comparisons (each a pair of spectra) vs. jnds ('just-noticeable-differences'); see text for details. Data plotted here represent results for the 'Green' illuminant, but overall results were similar for all illuminants; see also Table 1. (A) Frog spectral pairs, as seen by frog vision. (B) Frog spectra compared to background spectra, as seen by frog vision. (C) Frog spectral pairs, as seen by bird vision. (D) Frog spectra compared to background spectra, as seen by bird vision.

Frogs are able to discriminate many frog colors well, but about 27% of color pairs are relatively poorly discriminable, producing values that are <4 jnds (Fig. 5A, Table 1). About 5% of pairs have a value of 0 jnds, and are thus never discriminable by frogs. Birds discriminate frog colors even better: only about 18% of frog color pairs are separated by <4 jnds, and less than 1% have a value of 0 jnds (Fig. 5C, Table 1). Overall, then, it appears that birds discriminate similar frog colors better than frogs, but both appear to discriminate many dissimilar colors equally well.

In an attempt to discover whether the colors within each color morph contrast well, perhaps for pattern displays (see Fig. 1), we compared them pairwise. Results are presented in Table 2 and in Fig. 6A (frog vision) and Fig. 6C (bird vision). Again, results were generally similar among the different light regimes tested. Table 2 contains the extreme values from this analysis and lists the color morphs expressing them (see also Fig. 1). Frogs of most morphotypes have color pairs with very low visual contrast, often just above 0 jnd. The Uyama type generally has the very least internal color contrast between two

Table 1. Percentage of spectra with low chromatic discriminability in frog and bird visual systems

Irradiance	Visual system							
	Frog (f×f)		Bird (f×f)		Frog (f×b)		Bird (f×b)	
	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds
D65	5.00	26.55	0.83	18.41	5.11	29.93	0.43	15.03
D55	5.09	25.81	0.65	18.78	4.96	19.79	0.43	15.04
D75	5.18	27.29	0.83	17.95	5.39	30.64	0.43	14.47
Green	5.37	27.10	0.93	16.37	4.26	30.07	0.71	14.61

jnds, just-noticeable differences.

Values are percent of total spectra compared. (f×f), frog colors compared; (f×b), frog colors compared to backgrounds. Lower percentages show higher discrimination ability of the viewer.

Table 2. Frog morphotype with low and high contrasting colors within a frog and against a background for bird and frog visual systems

Irradiance	Visual system							
	Frog (f×f)		Bird (f×f)		Frog (f×b)		Bird (f×b)	
	LC	HC	LC	HC	LC	HC	LC	HC
D65	Uyama	Almirante	Uyama	Almirante	Shepard	Solarte	Uyama	Almirante
D55					vs.	vs.	vs.	vs.
D75					Yellow	Zebrina	Moss	Sticks
Green			San Cristobal		Bromiliad leaf	plant	Solarte vs. Moss	

LC, low contrast colors; HC, high contrast colors.

(f×f), frog colors compared; (f×b), frog colors compared to backgrounds.

Morphotype in each column represents the lowest or highest contrasted colors to the visual system viewing the frog.

of its colors, but for bird vision in the green illuminant, the San Cristobal type has the color pair with the lowest value. Both frog and bird vision see the greatest color contrast in the Almirante type. In general, both frogs and birds have similar discrimination abilities within a frog coloration scheme, and all color morphs of frogs contain at least one color pair that is easily discriminated.

Frogs compared to backgrounds

Contrasts of frog colors against backgrounds involved

analysis of all 47 frog reflectance spectra against 15 background spectra, yielding 705 (47×15) comparisons. Each test was conducted for both model visual systems under the four illuminants; results were similar under all lighting conditions (Table 1). Analytical results using the green illuminant for frog and bird vision are displayed in Fig. 5B and Fig. 5D, respectively. In the case of the frog visual system, most discrimination values are found at relatively low jnd values (Fig. 5B). For frogs, about 28% of frog/background comparisons are discriminable at <4 jnd, and 5% of the pairs

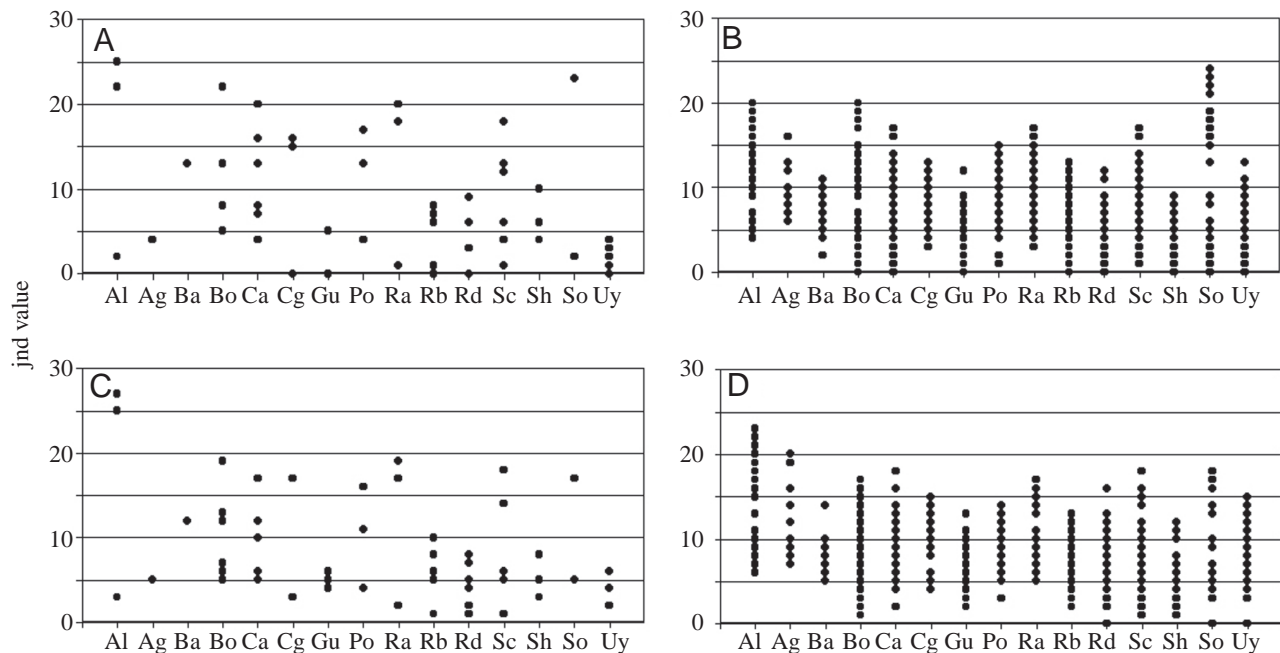


Fig. 6. Results of analyses comparing frog spectral reflectances within single color morphs, as viewed by frog or bird visual systems. Each panel plots the discriminability (in jnds; just-noticeable-differences) of spectral pairs, each indicated by a dot, for color morphs indicated along the abscissa. Al, Almirante; Ag, Aguacate; Ba, Bastimentos; Bo, Bocas; Ca, Cayo Agua; Cg, Chiriqui Grande; Gu, Guabo; Po, Pope; Ra, Rambala; Rb, Robalo; Rd, Roldan (Pelican Key); Sc, San Cristobal; Sh, Shepherd; So, Solarte; Uy, Uyama. Results plotted here are for the ‘Green’ illuminant, but similar results were found for all illuminants. See also Table 2. (A) Frog spectral pairs, as seen by frog vision. (B) Frog spectra compared to background spectra, as seen by frog vision. (C) Frog spectral pairs, as seen by bird vision. (D) Frog spectra compared to background spectra, as seen by bird vision. Note that there are many more points in the panels for frogs vs. backgrounds, because each frog color was compared to all background colors, not only to the few colors present in any given frog color morph as in A and C.

are never discriminable (Table 1). Birds are better than frogs at this discrimination task, as there are very few comparisons that give a value less than 1 jnd (<1%) and only about 15% of spectral pairs are barely discriminable (less than 4 jnd) (Tables 1 and 2). While birds generally outperform frogs in this discrimination task, the highest discrimination value (24 jnd) occurred with the frog visual system.

For a frog to contrast well with its background, only one of the colors it displays need be very different from the background spectrum. Thus, we analyzed the visual contrast of colors within each of the 13 color morphs of Fig. 1 in turn to background colors. Such an approach suggests which color morphs are always highly detectable and which may always be

difficult to see. The results are seen in Fig. 6B (frog vision) and Fig. 6D (bird vision). Each color morph has at least one color that is discriminable from any background color with a value of at least 8 jnd for frogs and at least 10 jnd for birds. The Shepherd Island type was generally the most difficult to detect against background, while the most detectable was the Solarte type (for frogs) or the Almirante type (for birds, Table 2). Both frogs and birds can discriminate each color morph from any background quite well, but birds are able to discriminate better overall. Interestingly, the most discriminable of the color morphs that were tested differs for the two visual systems.

Many of the non-discriminable frog colors (as viewed by

Table 3. Percentage of spectra with low chromatic discriminability of 'bright' frog colors in frog and bird visual systems

Irradiance	Visual system							
	Frog (f×f)		Bird (f×f)		Frog (f×b)		Bird (f×b)	
	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds
D65	3.99	17.39	0.36	13.04	3.60	18.06	0	8.06
D55	3.99	16.67	0.36	13.41	3.33	17.50	0	8.06
D75	3.99	18.48	0.36	13.04	4.17	19.17	0	7.22
Green	3.62	16.67	0.72	13.04	3.06	19.72	0.56	7.78

Values are percentage of total spectra compared. (f×f), frog colors compared; (f×b), frog colors compared to backgrounds. Lower percentages show higher discrimination ability of the viewer.

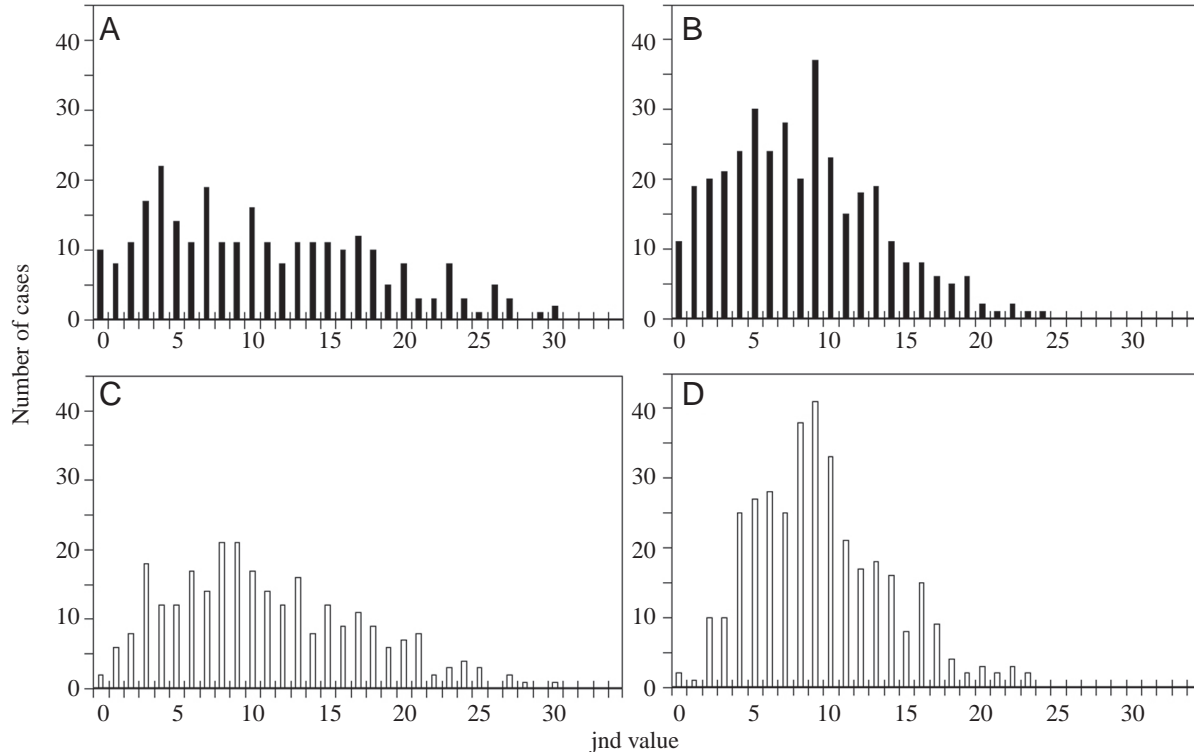


Fig. 7. Results of analyses comparing frog spectral reflectances as discriminated by frog or bird visual systems, using only 'bright' frog colors in the analysis. Each panel is a histogram plot of the number of comparisons (each a pair of spectra) vs. jnds ('just-noticeable-differences'); see text for details. Data plotted here represent results for the 'Green' illuminant, but overall results were similar for all illuminants; see also Table 3. (A) Frog spectral pairs, as seen by frog vision. (B) Frog spectra compared to background spectra, as seen by frog vision. (C) Frog spectral pairs, as seen by bird vision. (D) Frog spectra compared to background spectra, as seen by bird vision.

frogs) may be dark colors, present on the body to produce patterns. We therefore compared only the 'bright' colors found in the frogs, disregarding 'patterning' colors. 'Patterning' colors were identified by eye, and included black, brown or other generally dark colors that form stripes or spots and visually break the uniform coloration of the animal. All other colors were classified as 'bright' colors and compared both to each other and to backgrounds, pairwise. This analysis reduced the number of spectra compared to 24, resulting in 276 $((24 \times 23)/2)$ comparisons of frog colors. Results for frog and bird visual systems are tabulated in Table 3 and displayed in Fig. 7A and Fig. 7C, respectively. Comparing Fig. 7A to Fig. 5A, a small shift to the right is observed, but still 4% of colors remain indiscriminable (0 jnd). The number of poorly discriminable spectra (<4 jnd) is reduced to 17%. Therefore, disregarding 'patterning' colors and only considering those that are 'bright' only slightly increases discriminability, at least to frogs. The bird visual system analysis, Fig. 7C compared to Fig. 5C, also shows a shift to the right when only 'bright' colors are analyzed, but still some spectra can hardly be discriminated. About 13% of all spectral pairs are discriminable at <4 jnd, while less than 1% are completely indiscriminable (Table 3). Thus, birds better discriminate 'bright' colors compared to 'patterning' colors, and birds remain better at discriminating frog colors than are frogs (compare Table 3 to Table 1).

The analysis of 'bright' frog colors compared to backgrounds is given in Fig. 7B and Fig. 7D, where the pairing of 24 frog colors with 15 background colors results in 360 comparisons. In frogs, comparing Fig. 7B to Fig. 5B shows that 'bright' colors are discriminated better, but many spectral pairs remain indistinguishable; about 19% fall in the 0–3 jnds range and about 3.5% are not discriminable at all (Table 3). The analysis for bird vision (Fig. 7D compared to Fig. 5D) also shows a slight improvement in discriminability. Birds can discriminate all 'bright' spectra from backgrounds, and only about 8% of spectral pairs fall in the 1–3 jnd range (Table 3).

Dorsal vs. ventral colors

The color signals received by conspecifics and predators

may come from different body regions. Birds normally view frogs from above, so they would see aposematic signals on the dorsal parts of the frog. However, interactions among frogs occur mainly at eye level, while facing each other. Therefore, signals to conspecifics are commonly produced by ventral body parts. For example, during courtship, males will distend the throat pouch while calling to females (Wells, 1978; Limerick, 1980). *D. pumilio* has often been observed on elevated perches (Graves, 1999), where the ventral parts would be particularly prominent. Similarly, territorial behaviors of males include vocalization, postural changes and fighting (Donnelly, 1989), making ventral body parts potentially influential in male–male interactions as well. To assess how such signals may differ, dorsal and ventral colors were separated for analysis, comparing them to background spectra. The results are plotted in Fig. 8, where dorsal colors are represented by white bars and ventral colors by dark bars. To both frog (Fig. 8A) and bird (Fig. 8B) systems, ventral colors are more discriminable from backgrounds overall. This may aid frogs in finding conspecifics in their environment. Birds may not view these ventral colors very often; nevertheless, for birds the dorsal colors are still quite discriminable from the background colors (Fig. 8B).

Achromatic analysis

Discriminations among frogs, or between frogs and backgrounds, may also be based on brightness (achromatic) cues alone. Fig. 9A (frog vision) and Fig. 9C (bird vision) represent frog colors compared to each other using only achromatic cues. In both frog and bird vision, many spectral pairs have low discrimination values; about 14% of the frog–frog pairs are barely discriminable (0–3 jnd) to frogs and birds (Table 4). Frog colors compared to background colors are represented in Fig. 9B (frog vision) and Fig. 9D (bird vision). Here, approximately 12% of the spectra compared are barely discriminable to frogs and about 15% are barely discriminable to birds (Table 4). Surprisingly, in both frog and bird vision fewer spectral pairs generally have jnd values <4 in the achromatic quantification than in the chromatic, with the exception of birds viewing frogs against backgrounds (both $\sim 15\%$). Some pairs of frog and background spectra are

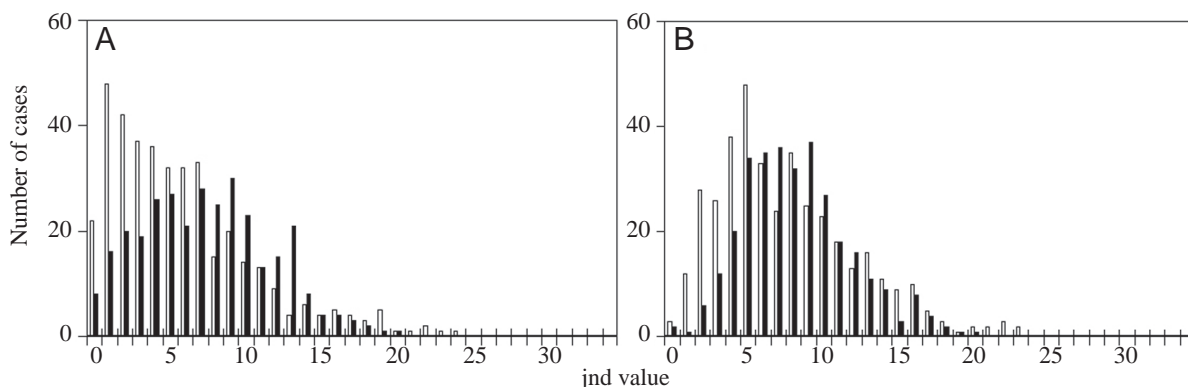


Fig. 8. Results of analyses comparing spectral reflectances from dorsal or ventral frog body regions, as discriminated from backgrounds by frog or bird visual systems. All discriminations plotted here are for the 'Green' illuminant, but results were similar for all illuminants. Open bars, dorsal frog colors; solid bars, ventral frog colors. (A) Frog visual systems, (B) bird visual systems.

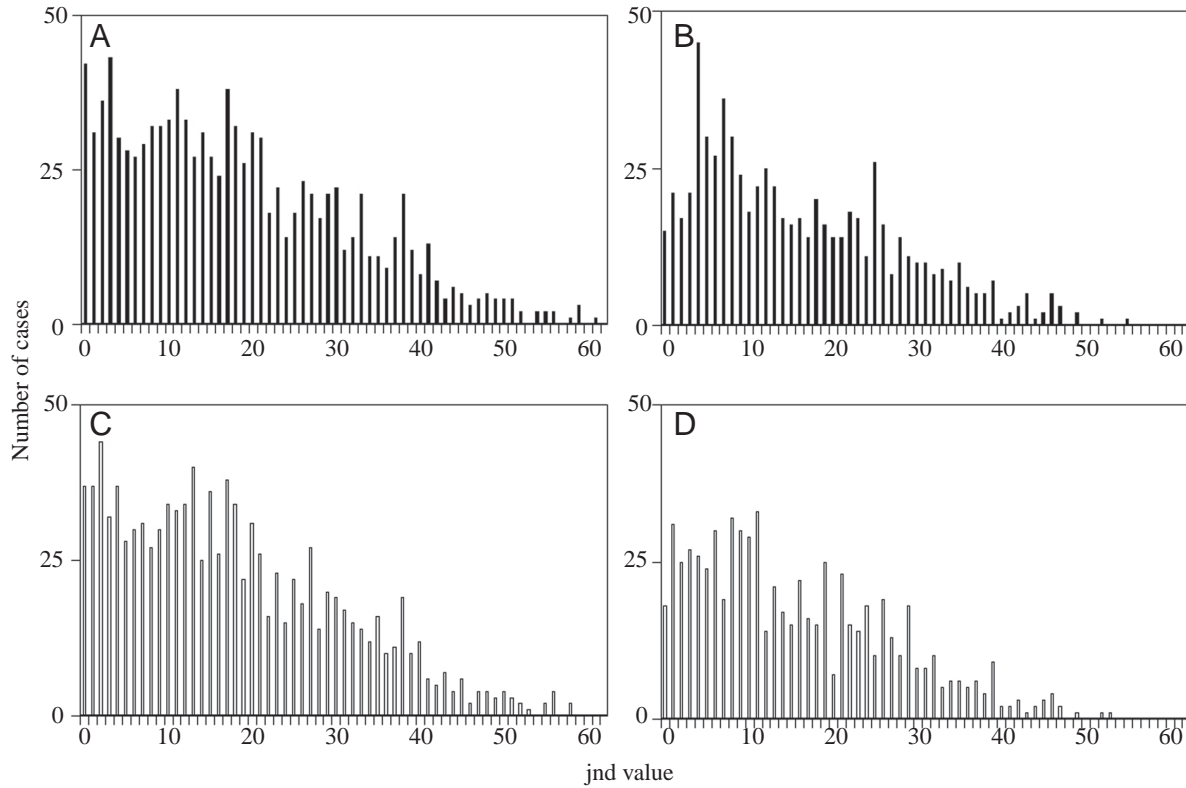


Fig. 9. Results of analyses comparing frog spectral reflectances as discriminated by only the achromatic channel of frog or bird visual systems. Data plotted here represent results for the ‘Green’ illuminant, but overall results were similar for all illuminants; see also Table 4. (A) Frog spectral pairs, as seen by frog vision. (B) Frog spectra compared to background spectra, as seen by frog vision. (C) Frog spectral pairs, as seen by bird vision. (D) Frog spectra compared to background spectra, as seen by bird vision.

perceptually very different, with high values reaching 56 jnds for frog vision and 53 jnds for bird vision. Such high contrasts may be useful for both frogs and birds, particularly for spotting *D. pumilio* frogs against their backgrounds.

Discussion

Color signals throughout the animal kingdom can be directed at a variety of viewers. Here, we have examined the effectiveness of a given signal system by analyzing how well potential recipients can discriminate color signals in natural environments. Our results indicate the degree to

which each color might be discriminated from other analogous color signals or from other colors found in the environment. Our investigation addresses two main questions concerning the effectiveness of color signals of the strawberry poison frog species *Dendrobates pumilio* as viewed by conspecifics or by a potential predator. First, are the color signals discriminable from each other? Second, how well is each color signal discriminated from its background?

Like most amphibians (Liebman and Entine, 1968), poison frogs have three cone classes, but unusually, they have only one type of rod receptor. Many frogs are active during twilight

Table 4. Percentage of spectra with low achromatic discriminability in frog and bird visual systems

Irradiance	Visual system							
	Frog (f×f)		Bird (f×f)		Frog (f×b)		Bird (f×b)	
	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds	0 jnds	0–3 jnds
D65	3.24	13.51	3.52	13.88	2.13	11.91	3.26	15.32
D55	3.61	14.15	2.96	13.23	2.84	13.19	3.4	14.61
D75	3.89	13.23	3.33	13.6	2.7	11.21	2.98	14.89
Green	3.89	14.06	3.42	13.88	2.13	10.50	2.55	14.33

Values are percentage of total spectra compared. (f×f), frog colors compared; (f×b), frog colors compared to backgrounds. Lower percentages show higher discrimination ability of the viewer.

Table 5. Frog morphotypes with the greatest and least color contrasts to a given morphotype

Morphotype	Almirante	Aguacate	Basti-mentos	Bocas	Cayo Agua	Chiriqui Grande	Gila Rambala	Guabo	Pope Is	Robalo	Roldan	San Cristobal	Shepherd	Solarte	Uyama
Minimum contrast	Basti-mentos (1.21)	San Cristobal (0.60)	Uyama (0.09)	Pope Is. (0.49)	Aguacate (0.60)	Guabo (0.14)	Uyama (0.11)	Chiriqui Grande (0.14)	Bocas (0.49)	Uyama (0.11)	Gila Rambala (0.21)	Basti-mentos (0.32)	Roldan (0.57)	Uyama (0.57)	Basti-mentos (0.09)
Maximum contrast	Solarte (29.02)	Solarte (30.48)	Solarte (27.85)	San Cristobal (26.77)	Solarte (30.88)	Solarte (26.86)	Solarte (27.71)	Solarte (26.76)	San Cristobal (22.03)	Solarte (27.37)	Solarte (26.02)	Solarte (30.88)	Solarte (23.60)	San Cristobal (30.88)	Solarte (27.60)

In each column the type having a color with the least difference from one color in the morphotype given at the top, and the type with a color having the greatest difference from a color in the given type.

Also given is the perceptual distance between the color pairs in jnds.

and some are nocturnal (Duellman and Trueb, 1986), so having two types of rods may be useful to them. With the exception of one species in the genus *Colostethus*, dendrobatid frogs are diurnal animals (Graves, 1999). Therefore, the presence of two rod receptor classes, specialized for use in scotopic conditions, may have been lost over evolutionary time.

Most poison frogs are active in the early morning and again in the late afternoon (Poulin et al., 2001). *D. pumilio* become active at dawn and peak in activity early in the morning (07:45 h to 09:15 h); then activity gradually decreases to midday, after which a moderate level of activity is observed until dusk (Graves, 1999). Avian foraging also peaks in the early morning and late afternoon (Poulin et al., 2001). Thus, while poison frogs are rarely preyed upon by birds, the likelihood of birds viewing frogs is high.

This study focuses on photopic conditions, when frogs and birds are active and color vision is utilized. The results from color comparisons indicate that birds (potential predators) readily discriminate colors within the species *D. pumilio*, and are particularly adept at discriminating the frogs from their backgrounds. While it is important for a potential predator to recognize an aposematic signal, the ability to differentiate between toxic frogs has little relevance unless there are differences between frogs, such as toxin levels, that a predator profits from knowing. Such differences do occur in *D. pumilio* (Daly and Myers, 1967), but it is not known whether they affect predation rates. The use of color signals in *D. pumilio* seemingly flies in the face of the theory of Mullerian mimicry, where natural selection favors sharing of color and pattern in unpalatable species (Summers et al., 1997; Mallet and Joron, 1999).

Predators often have little time to make the decision of whether or not to attack a potential prey item once it is seen. Therefore, unpalatable prey should be as visible as possible to deter incorrect decisions by predators (Guilford, 1986). The advantage of increased conspicuousness has been demonstrated with chicks (*Gallus gallus domesticus*) feeding on aposematic insect larvae (*Tropidothorax leucopters*) (Gamberale and Tullberg, 1996). Naïve chicks attacked larger (presumably more conspicuous) prey less frequently than the smaller larvae.

The uniquely unusual feature of the various populations of *D. pumilio* is that the aposematic signals have diverged into a variety of conspicuous signals. In this species, conspicuousness expressed by bright coloration may in itself be enough to ward off predation. If so, the aposematic signal does not arise from a specific color or pattern. Instead, all conspicuous, colored signals would be interpreted by potential predators as warnings. Other poison frog species are diverse in coloration and pattern, although to a much lesser extent than what is observed in *D. pumilio*, and the poison frogs as an ensemble of species exhibit great diversity. All of these diverse signals are evidently effective, and the frogs are successful throughout the neotropics.

Nevertheless, the basis of the diversity demands explanation. Coloration can be an important signal in mate

selection in birds and fish, where specific colors enhance success for mating (Withgott, 2000; Ryan, 2001; Arnold et al., 2002). As noted above, *D. pumilio* females discriminate among potential mates using visual cues (Summers et al., 1999), and it is female choice that best accounts for the diversity seen in Panama today. Our analytical results suggest that in general, color morphs should be effectively distinguished by conspecifics, a factor that may be important in maintaining the identities of the various populations (Table 5).

Ventral colors were better discriminated against backgrounds than dorsal colors, both by conspecifics and predators. These ventral colors may be particularly important as signals in frog-to-frog interactions. For birds, normally viewing the frog from overhead, the ventral signals probably play little role in communication. However, it is interesting to note that the dorsal colors tend to be far more saturated than ventral shades (see photographs of Fig. 1). Reflectance spectra from the dorsal regions almost always have steep changes in spectral height in a particular spectral region, and tend to have strong spectral contrast, but those from the ventral regions are often spectrally flatter (Summers et al., 2003). Saturation of the color is likely to be an important component of its signal quality.

Achromatic aspects of colors and patterns are important in spatial vision, texture, shape and movement detection (Maier and Bowmaker, 1993; Hart et al., 1998; Osorio et al., 1999a,b). Our analysis indicates that achromatic aspects of *D. pumilio* signal colors permit the differentiation of *D. pumilio* from backgrounds both by birds and frogs, even in the absence of color vision. Birds do not outperform frogs in achromatic discrimination, as only one spectral channel contributes. On the other hand, the superb chromatic discrimination ability of birds is probably owed to the extra receptor type found in bird eyes compared to frog eyes (i.e. tetrachromatic vision vs. trichromatic vision) and to the narrow sensitivity curves produced by filtering by oil droplets in birds (Vorobyev et al., 1998). Thus, while elevated values of achromatic discrimination aid in the detection of *D. pumilio* in its environment, chromatic discrimination remains important for recognizing signals and color morphs.

This study indicates that the signal colors used throughout the complex of color morphs of *Dendrobates pumilio* are easily seen and potentially easily recognized, both by conspecifics and by a model predator. Bright, often unsaturated ventral colors seem to be particularly important in frog–frog interactions and may play important roles in female choice, driving the divergence of color morphs between isolated populations. A diversity of saturated dorsal colors effectively signal prey toxicity to avian predators and contrast well to typical forest backgrounds under the typical range of natural illuminants. Aposematic signaling in poison frogs is particularly interesting for its diversity, both within and between species. It appears that predators recognize their toxic prey not through the perception of particular colors, but instead simply because they are brightly colored objects in a world of green and brown.

List of Abbreviations

jnd	Just-noticeable difference
k	Adapted response of a receptor class
$I(\lambda)$	Irradiance spectrum
LWS	Long-wavelength-sensitive receptor class
MSP	Microspectrophotometry
MWS	Middle-wavelength-sensitive receptor class
n	Proportion of a given photoreceptor class
Q	Quantum catch of a receptor class
q	Quantum catch of an adapted receptor class
$R(\lambda)$	Reflectance spectrum
SWS	Short-wavelength-sensitive receptor class
$S(\lambda)$	Sensitivity spectrum of a receptor class
UWS	Ultraviolet-sensitive receptor class
Δf	Spectral contrast of two stimuli to one receptor class
ΔS	Overall chromatic difference between two stimuli
λ_{\max}	Wavelength of the maximum value
v	Weber fraction of a given receptor class
ω	Noise in one receptor class

The National Aquarium in Baltimore, and most particularly J. Cover and Z. Zamora, generously provided specimens and gave all possible assistance. C. Greitner was most helpful in providing tropical plants for measurements of background spectra. N. Hart shared his analyses of avian spectral systems with us for use in this project. This research was supported by the National Science Foundation under Grants nos. IBN-0118793 and IBN-0235820.

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