

Mimicry in coral reef fish: how accurate is this deception in terms of color and luminance?

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Batesian and aggressive mimics are considered to be under selective pressure to resemble their models, whereas signal receivers are under selection to discriminate between mimics and models. However, the perceptual ability of signal receivers to discriminate between mimics and models is rarely studied. Here we examined 15 model–mimic coral reef fish pairs using nonsubjective methods to judge the accuracy of mimics in terms of color and luminance. We then investigated the potential ability of fish with various visual systems to discriminate between model and mimic colors using theoretical vision models. We found the majority of mimics closely resembled models in terms of color and luminance from a nonsubjective perspective. However, fish that have potentially trichromatic (3 distinct cone photoreceptors) visual systems with ultraviolet sensitivity had a much better capacity to discriminate between models and mimics compared with fish with midrange sensitivity or dichromatic (2 cone photoreceptors) fish. The spectral reflectance of color patches reflected by models and mimics became more similar with an increase in depth, indicating that signal receivers may be more likely to distinguish mimics from models in habitats located closer to the surface. There was no such change in luminance contrast with depth. The selection pressure on mimics to accurately resemble their model is therefore predicted to vary depending on the visual system of the signal receiver and the light environment. **Key words:** aggressive mimicry, animal signaling, Batesian, color vision, signal accuracy. [*Behav Ecol* 20:459–468 (2009)]

Aggressive and Batesian mimics are often considered to be involved in an evolutionary arms race: mimics are under selection to appear more similar to their models to avoid recognition, whereas signal receivers are under selection to improve discrimination between models and mimics (Dawkins and Krebs 1979). However, inaccurate mimics exist in nature (Dittrich et al. 1993; Edmunds 2000); for example, many common hoverfly mimics resemble their models closely, whereas others only bear a crude resemblance (Azmeh et al. 1998; Edmunds 2000; Howarth and Edmunds 2000). Whether a mimic accurately resembles its model is often based on human perception and not what is perceived by the signal receiver (Lindström et al. 1997; Mappes and Alatalo 1997; but see Cuthill and Bennett 1993). Using our own perceptual abilities is often unsatisfactory, especially when investigating color signals (Lythgoe 1979; Endler 1990).

Body colors and patterns are the primary signaling mechanism for many mimicry systems (Wickler 1965; Zabka and Tembrock 1986). For example, the conspicuous red, yellow, and black markings of a venomous coral snake (e.g., *Micrurus fulvius*) are mimicked by nonvenomous king snakes (*Lampropeltis triangulum lapsoides*) in order to avoid predation (Pfenning et al. 2001). However, the perception of color signals depends on the visual system of signal receivers, which often vary considerably between species (e.g., Lythgoe 1979; Jacobs 1993; Hart 2001; Losey et al. 2003). The photic environment may also have dramatic influence on how color signals are viewed due to the attenuation of light with depth (Bowmaker 1990; Partridge 1990; Endler 1991; Marshall et al. 2003b). Therefore, to understand color signals in mimicry systems we should use a nonsubjective approach and view signals in their natural context from the signal receiver's perspective.

In the marine environment, around 60 species of coral reef fish are thought to mimic another species of fish (Moland et al. 2005), although evidence for this is often putative or circumstantial. Types of mimicry exhibited by coral reef fish include Batesian, aggressive, and social mimicry (Moland et al. 2005). In this study, we first used spectral reflectance measurements to quantify color signals on coral reef fish mimics and their models to examine whether mimics accurately resembled their models in terms of color from a nonsubjective perspective. Second, we used a color opponent discrimination model (Vorobyev and Osorio 1998) to examine whether particular fish visual systems were better at distinguishing mimics from models based on color and luminance. We predict that fish with trichromatic vision (3 distinct cone photoreceptors) should be better at distinguishing colors compared to fish with dichromatic vision (2 distinct cone photoreceptors). We then compared fish visual systems with the human visual system to enable us to compare our own sensory abilities with the ability of fish to discriminate colors. Third, we determined whether the accuracy of mimic color signals to model colors varied with depth due to variation in illumination. We predicted that model and mimic colors may become more similar with depth due to the attenuation of light.

METHODS

Study site and species

Fifteen pairs of putative mimic species and their models (Moland et al. 2005) were collected by SCUBA divers between 2005 and 2007 from reefs ranging from 2 to 18 m in depth around Palau Hoga 5°28'S, 123°45'E, southeast Sulawesi, Indonesia; Lizard Island 23°27'S and 151°55'E and Heron Island 23°45'S, 151°91'E, Great Barrier Reef, Australia (Table 1). Fish were caught using hand and barrier nets, placed in hermetically sealed (ziplock) bags or catch buckets, and transported back to the field station. Fish were housed in aquaria with running seawater or air pumps for 1–3 days

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Table 1
Coral reef fish putative model–mimic pairs

| | Model | Mimic | Type of mimicry | References | Sample size (pairs) | Location |
|-------|-------------------------------------|--|----------------------|---|---------------------|----------|
| i) | <i>Labroides dimidiatus</i> (adult) | <i>Aspidontus taeniatus</i> (adult) | Aggressive | Randall JE and Randall HA 1960; Kuwamura 1981 | 4 | 1,2,3 |
| ii) | <i>L. dimidiatus</i> (juvenile) | <i>A. taeniatus</i> (juvenile) | Aggressive | Randall JE and Randall HA 1960; Kuwamura 1981 | 1 | 1 |
| iii) | <i>L. dimidiatus</i> (juvenile) | <i>Plagiotremus rhinorhynchus</i> | Aggressive | Wickler 1965 | 5 | 1,2 |
| iv) | <i>Chromis viridis</i> | <i>P. rhinorhynchus</i> | Aggressive | Cheney et al. 2008 | 4 | 1 |
| v) | <i>Pseudanthias squamipinnis</i> | <i>P. rhinorhynchus</i> | Aggressive | Randall et al. 1997; Côté and Cheney 2005 | 5 | 1 |
| vi) | <i>Canthigaster valentini</i> | <i>Paraluteres prionurus</i> | Batesian | Caley and Schluter 2003 | 2 | 1,2 |
| vii) | <i>Meiacanthus atrodorsalis</i> | <i>Plagiotremus laudandus</i> | Aggressive, Batesian | Losey 1972; Springer and Smith-Vaniz, 1972; Smith-Vaniz et al. 2001 | 3 | 2,3 |
| viii) | <i>Ecsenius bicolor</i> | <i>P. laudandus</i> | Aggressive | Springer and Smith-Vaniz, 1972; Smith-Vaniz et al. 2001 | 4 | 2 |
| ix) | <i>Pomacentrus moluccensis</i> | <i>Pseudochromis fuscus</i> (yellow) | Aggressive | Munday et al. 2003 | 4 | 2 |
| x) | <i>Pomacentrus amboinensis</i> | <i>P. fuscus</i> (yellow) | Aggressive | Munday et al. 2003 | 4 | 2 |
| xi) | <i>Pomacentrus chrysurus</i> | <i>P. fuscus</i> (brown) | Aggressive | Munday et al. 2003 | 4 | 2 |
| xii) | <i>Chromis ternatensis</i> | <i>Lutjanus bohar</i> | Aggressive | Russell et al. 1976 | 2 | |
| xiii) | <i>Meiacanthus lineatus</i> | <i>Petroscirtes fallax</i> | Batesian | Springer and Smith-Vaniz 1972; Russell et al. 1976; Smith-Vaniz et al. 2001 | 2 | 3 |
| xiv) | <i>M. lineatus</i> | <i>Scolopsis bilineatus</i> (juvenile) | Batesian | Springer and Smith-Vaniz 1972 | 4 | 2,3 |
| xiii) | <i>Centropyge vrolikii</i> | <i>Acanthurus pyroferus</i> (juvenile) | Batesian | Randall JE and Randall HA 1960 | 3 | 1 |

Locations: 1 = Hoga, Indonesia; 2 = Lizard Island, Great Barrier Reef; 3 = Heron Island, Great Barrier Reef.

until their spectral reflectance could be measured. After measurements were taken, fish were released at the point of capture. Pairs of putative models and mimics were collected from the same locality. We attempted to collect 4–5 pairs of each model–mimic combination; however, due to the rarity of some species, collecting more than one pair was not always possible. Sample sizes of each pair of species are shown in Table 1. All experimental procedures were approved by the University of Queensland Animal Ethics Committee and collecting permits obtained from the Great Barrier Reef Marine Park Authority and the Wakatobi Marine Park (Indonesia).

Spectral analysis of color signals and illumination

Spectral reflectance measurements were obtained using an Ocean Optics (Dunedin, FL) USB2000 spectrometer and stored using a laptop computer running OOIBASE32 software. Fish were taken out of the water for a short amount of time (median 20 s, maximum 40 s) and placed on a damp cloth. Skin was kept moist during measurements. This technique provides similar results to measuring fish in the water and allows more accurate color quantification (Marshall 1996, 2000a). The light reflected from each color area of the fish were then measured through a 200- μ m bifurcated fiber optic ultraviolet (UV)/visible cable connected to a PX-2–pulsed xenon light source (Ocean Optics). Spectral reflectance measurements were taken within each colored body patch $> 4 \text{ mm}^2$. We considered the effects of signal transmission through water to be negligible as most coral reef fish would view models and mimics from a relatively close distance (ca. 1–2 m).

All fish that were measured have been previously screened with a UV camera (Marshall 2000b). This ensured that UV-colored areas were not ignored (e.g., *Pomacentrus amboinensis*, Figure 2x). Depending on the species, we sampled 1–5 color patches per species. The percentage of light reflected at each wavelength from 300 to 800 nm was calibrated against a Spectralon 99% white reflectance standard (LabSphere, North Sutton, NH). The bare end of the fiber was placed close to the fish so that it sampled from a small color region alone and was handheld at an approximate 45° angle to prevent specular reflection. The probe was cleaned with a soft tissue after each measurement. Each measurement was averaged from at least 10 samples of each colored area of the fish, taken in rapid succession. Spectra from individuals of each species ($n = 2$ –5) were then averaged, with the exception of juvenile *Aspidontus taeniatus* ($n = 1$) of which we only managed to find one individual (Table 1).

Illumination was measured underwater where fish were located using an Ocean Optics USB2000 spectrometer (Ocean Optics) enclosed in an underwater housing (Wills Camera Housings, Victoria, Australia). The spectrometer was powered by a battery pack and connected to handheld computer with modified Palm-Spec software (Ocean Optics). Irradiance measurements were taken with modified (shortened, length 60 cm) fiber optic cables (diameter 200 and 1000 μ m) over a 180° hemisphere, using a cosine corrector, taken 1–2 m away from reef and pointing horizontally at the reef. This is a more accurate estimate of light striking the side of a fish than the often-used vertical hemispheric irradiance.

Color discrimination capability

We calculated discriminability of color patches between each putative model–mimic pair using the well-established Vorobyev–Osorio color discrimination model (Vorobyev and Osorio 1998; Vorobyev et al. 2001). This model calculates the “distance” (ΔS) between the colors in a dichromatic, trichromatic, or tetrachromatic visual space, depending on the number of receptor types of the signal receiver. Here, we modeled dichromatic vision for fish with 2 distinct spectral sensitivities and trichromatic vision for fish with 3 cones possessing distinct spectral sensitivities. Colors that appear similar within each visual system result in low ΔS values, whereas those that are chromatically contrasting are high in value. This model assumes that the luminosity signal is disregarded, that colors are encoded by an opponent mechanism judged using the known cone sensitivity of the signal receiver, and that color discrimination in the perceptual space is limited by noise originating in the receptors and determined by the relative proportion of each photoreceptor (Vorobyev and Osorio 1998; Vorobyev et al. 2001).

The receptor quantum catch, q_i , in photoreceptor of type i (i.e., cone cell) is calculated as (Equation 1 of Vorobyev and Osorio 1998):

$$q_i = \int_{\lambda} R_i(\lambda) S(\lambda) I(\lambda) d\lambda, \quad (1)$$

where λ denotes wavelength, $R_i(\lambda)$ denotes the spectral sensitivity of a receptor i , $S(\lambda)$ is the reflectance spectrum of the color patch, $I(\lambda)$ is the irradiance spectrum entering the eye, and integration is over the range 300–700 nm. Color distances

were calculated with an illumination measured at 5-m depth. The signal of each receptor type f_i is proportional to the natural logarithm of the respective receptor quantum catch, which is normalized against an adaptive background. As a typical background color, an average spectrum from 250 corals of different species were used (Marshall et al. 2003b).

Color patches on our models and mimics were subjectively classified into the following color categories: dark blue, light blue, yellow/orange, white/gray, brown/black. Color distances were calculated for each model–mimic pair that had been captured at the same location. Each color distance was then averaged for each model–mimic combination and then averaged for each color category.

We modeled the visual responses of 3 potential trichromatic fish species: a UV-sensitive planktivorous damselfish, *Abudefduf abdominalis*; a violet/blue-sensitive piscivore, *Lutjanus bohar*; and a blue/green-sensitive herbivorous surgeonfish, *Ctenochaetus strigosus*. We make the assumption that fish with 3 distinct spectral sensitivities have trichromatic vision—however, signals from 2 members of a double cone may be optically coupled resulting in dichromatic vision. Therefore, we also modeled 2 dichromatic species, a piscivorous barracuda *Sphyræna helleri* and an omnivorous butterflyfish *Chaetodon kleinii* (Figure 1). These species will be subsequently referred to by their genus name only. These species were selected because their visual systems differed significantly and provided the best cross-section of reef fish spectral sensitivities that we currently have (Marshall et al. 2006). Also, they have differing ecological significance on coral reefs (i.e., can be predators or may be attacked by aggressive mimics; Cheney KL, unpublished data) and have similar geographical distributions as our model–mimic pairs. Spectral sensitivities were based on

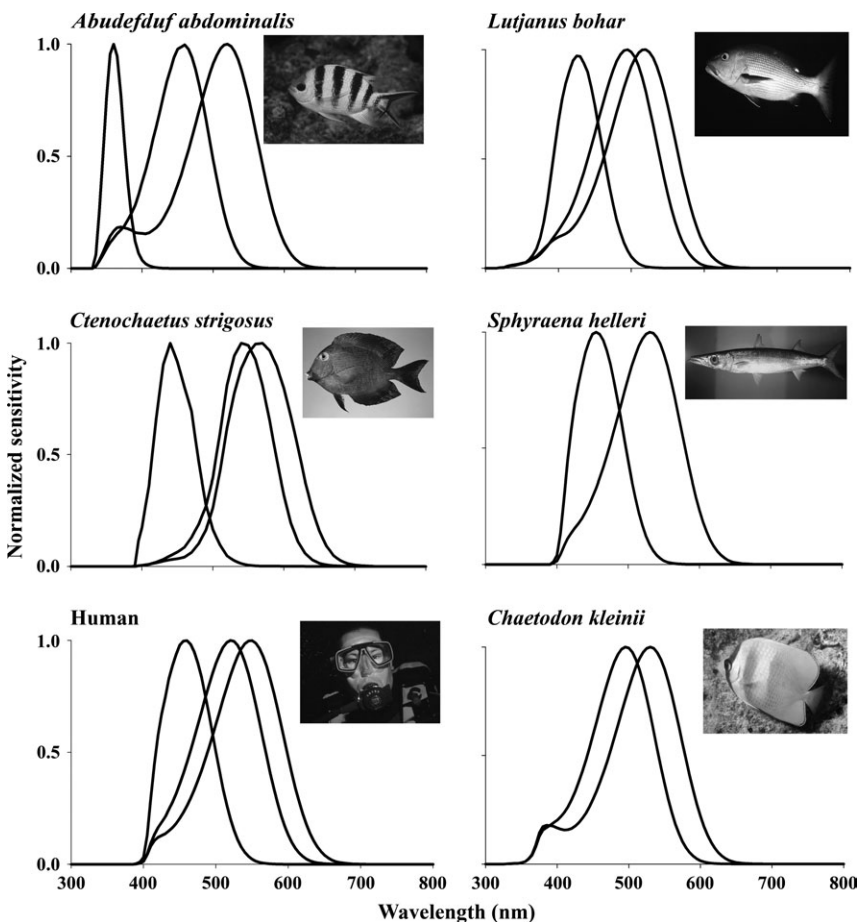


Figure 1
Relative spectral sensitivities of photoreceptors for the representative model species showing short wavelength receptor (dashed gray line), middle wavelength receptor (black line), and long wavelength receptor (solid gray line).

previous studies of reef fish and include the transmission properties of the cornea and lens (Losey et al. 2003; Marshall et al. 2006). These model species were then compared with human visual sensitivities as estimated psychophysically (Smith and Pokorny 1975; Dartnall et al. 1983; Figure 1).

In the absence of behavioral data on the visual thresholds of these species, the Weber fraction of the long-wavelength-sensitive (LWS) cone was set at 0.05; this value was chosen as a conservative measure of visual performance, being more than twice the measured value (half the sensitivity) of the human LWS cone system (Wyszecki and Stiles 1982). For humans, we set the Weber fraction to 0.02. Relative values of ω_i are defined by the proportion of receptor types in the eye, based on anatomical data. The relative proportions of the different spectral cone types in fangblennies and the other fish were based on morphological studies of reef fish retina (Marshall NJ, unpublished data). For trichromatic models, we used a ratio of 1:2:2 (short-wavelength-sensitive [SWS] cones to medium-wavelength-sensitive [MWS] cones to LWS cones; S:M:L). For dichromatic models, we used a ratio of 1:2 (S/M:L). We also modeled data with a ratio of 1:1:1 for trichromats and 1:1 for dichromats but found no significant differences in our overall conclusions. Calculations for human visual systems were done using cone proportions for a typical human observer 1:7:12 for S:M:L, respectively (Wyszecki and Stiles 1982). However, there was no difference in our qualitative results if we modeled human visual system with a ratio of 1:2:2.

General fish colors

In addition to assessing the discrimination ability of our signal receivers to distinguish between mimic and model spectral reflectance (mimic-model), we used another discrimination category to compare the differences in spectral reflectance of mimics and other non-model coral reef fish (mimic-general fish). To do this, we used spectral reflectance data from fish species that had been previously measured with a spectrophotometer using the same methodology (Marshall 2000b). Twelve fish species that had color patches that were categorized as dark blue, light blue, yellow, white, black (as per Marshall 2000b) and were found in the same habitat as our model-mimic pairs were randomly selected. ΔS was then calculated for randomly selected pairs of colors ($n = 12$ for each color category). We also compared a selection of general fish colors from the same category with each other (general-general fish; $n = 12$); however, these were not significantly different from the mimic-general fish color comparison (estimated marginal mean \pm standard error: mimic-general 4.38 ± 0.26 ; general-general 4.16 ± 0.20 ; pairwise comparison, $P = 0.49$); therefore, only mimic-model and mimic-general fish color distances are presented.

Luminance contrast

In addition to spectral differences, signal receivers may also use differences in luminance contrast to distinguish model signals from mimics. Long wavelength receptors are thought to be responsible for luminance contrast, as opposed to color (for discussion see Marshall et al. 2003b). Therefore, to determine differences in longwave cone luminance contrast between model and mimic spectral reflectance signals, we measured the difference in log quantum catch (Q) of the long wavelength receptor (L) for each spectral reflectance signal:

$$L = \ln(Q_{L\text{model}}) - \ln(Q_{L\text{mimic}}). \quad (2)$$

Changes in color and luminance contrast with depth

In the aquatic environment, spectra vary with depth. Color signals should be constant with increasing depth or in different

underwater environments in order to be effective in a range of circumstances. To test how depth affected signals, we compared spectral reflectance measurements at different illuminations at depths: surface and 5, 10, and 15 m. With increasing depth, the amount of light is attenuated both at the short and long wavelengths, but particularly beyond 600 nm (Barry and Hawryshyn 1999), which is common for shallow (<10 m) reef environments (McFarland 1991).

Statistical analyses

We used a gamma generalized linear model with a log-link function to test for differences in the discrimination ability between signal receivers color categories and discrimination category (mimic-model or mimic-general). Color distance was used as the dependent variable; whereas color category, signal receivers, and discrimination category were factors. Nonsignificant higher order interactions were deleted sequentially. Normal quantile-quantile plots of the residuals and plots of the residuals versus the fitted values were examined to check for the assumptions of normality and homoskedasticity, respectively. To test for differences between levels in each factor, we used estimated marginal means for pairwise multiple comparisons.

To test for changes in signal and luminance contrast with depth, we used a univariate Gaussian general linear model with an identity link function with difference in signal (compared with surface) as dependent variable, receiver and color category as fixed factor, and depth as covariate. Again, nonsignificant higher order interactions were deleted sequentially. All statistical analyses were conducted with R 2.4.1 using the "stats" package (R Foundation for Statistical Computing, Vienna; <http://www.R-project.org>).

RESULTS

Spectral analysis of color signals

In total, spectral reflectance measurements were taken from 102 individual fish from 30 species. Average spectra for model-mimic pairs are illustrated (Figure 2). All measurements could be described by color categories as identified by Marshall (2000b). Colors were qualitatively similar for the majority of model-mimic pairs (Figure 2). However, olive and orange color forms of *Plagiotremus rhinorhynchus* displayed an olive body and blue stripe, respectively, which was not found on their models (Figure 2iv,v). *Plagiotremus laudandus* colors differed to those of *Ecsenius bicolor*, particularly in orange markings present on the face of *E. bicolor* and in general body colors (Figure 2viii). Markings were also present on the face of *P. amboinensis* in the UV (<400 nm) range, and the presence of a black spot on the dorsal fin distinguished *P. amboinensis* from its model (Figure 2x). Finally, there were differences in the brightness of colors between *Meiacanthus lineatus* and *Scolopsis bilineatus* (Figure 2xiv).

For all species of signal receiver, color distances were significantly lower in the model-mimic discrimination category compared with the mimic-general category (estimated marginal mean \pm standard error: mimic-model 2.61 ± 0.18 , mimic-general 4.46 ± 0.27 ; wald $\chi^2 = 34.6$, degrees of freedom [df] = 1, $P < 0.001$; Figure 3). Luminance contrast for mimic-model color categories was also significantly lower than for mimic-general fish color categories (mimic-model 0.43 ± 0.03 ; mimic-general 0.70 ± 0.04 ; wald $\chi^2 = 35.3$, df = 1, $P < 0.001$).

Differences in signal receiver color discrimination capability

There were significant differences between trichromat signal receivers in their ability to discriminate between mimic and

model colors (*Abudefduf* 8.70 ± 0.87 ; *Lutjanus* 3.33 ± 0.34 ; *Ctenochaetus* 3.38 ± 0.35 ; human 5.87 ± 0.60 ; wald $\chi^2 = 65.0$, $df = 3$, $P < 0.001$; Figure 3). Color distances were significantly greater for *Abudefduf* (UV-sensitive fish), followed by *Lutjanus*, *Ctenochaetus*, and *Sphyaena*, which were all statistically similar (Figure 3). The receiver with the poorest discrimination ability was the dichromat *Chaetodon* (Figure 3). Human visual systems were significantly better at distinguishing between spectral reflectances compared with visual systems of all other fish species, with the exception of *Abudefduf* (Figure 3).

At 5 m, there were no significant differences between signal receivers for luminance contrast for either mimic–model color categories or mimic–general color categories (wald $\chi^2 = 0.16$, $df = 5$, $P = 0.98$; Figure 3). Luminance contrast varied significantly between color categories for both mimic–model and mimic–general (color category: wald $\chi^2 = 114.60$, $df = 4$, $P < 0.001$; Figure 3).

For signal receivers in the mimic–model category, there was a significant difference between color categories (wald $\chi^2 = 107.2$, $df = 4$, $P < 0.001$): yellow was significantly more distinguishable than any other color (yellow 5.31

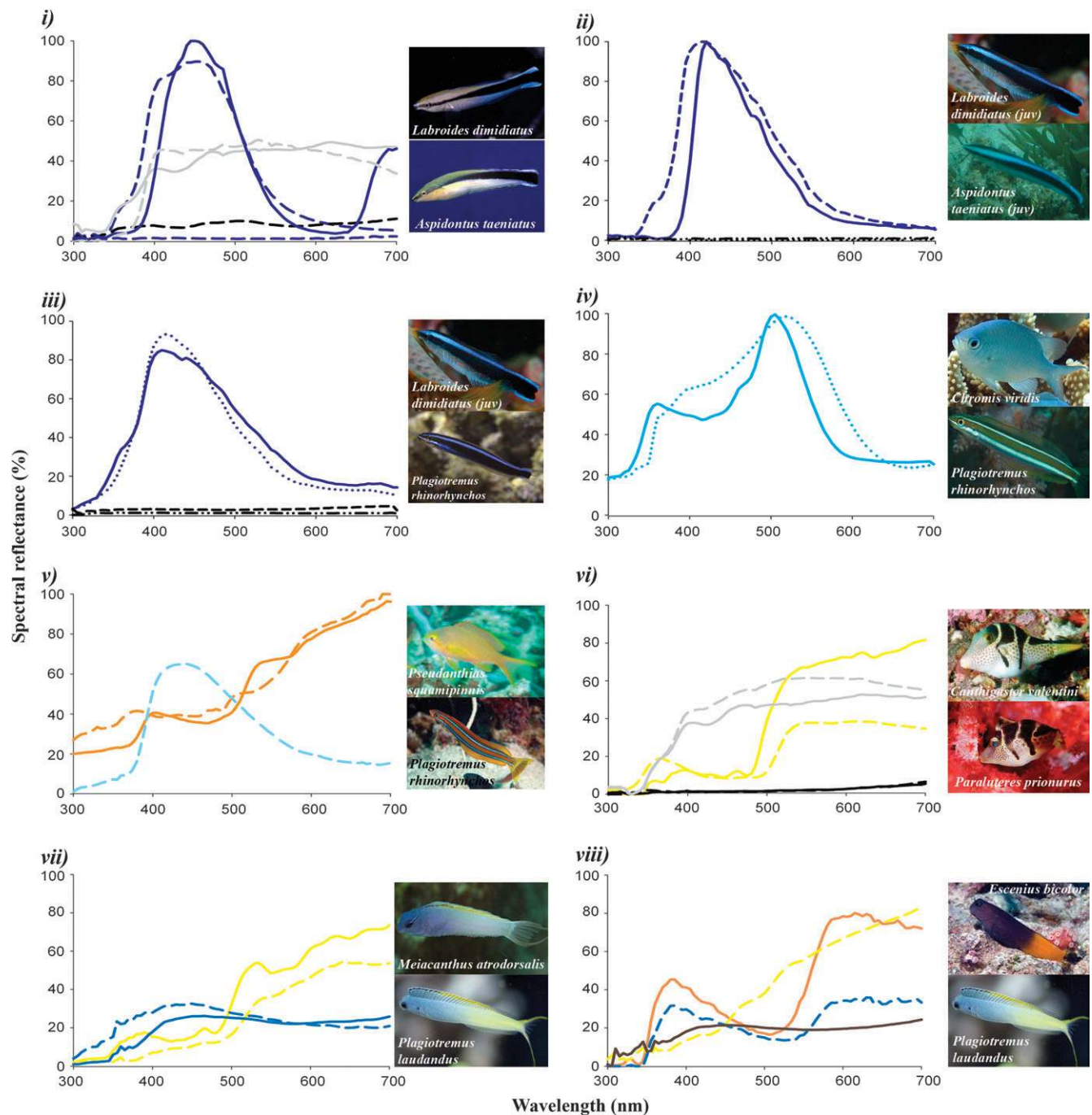


Figure 2
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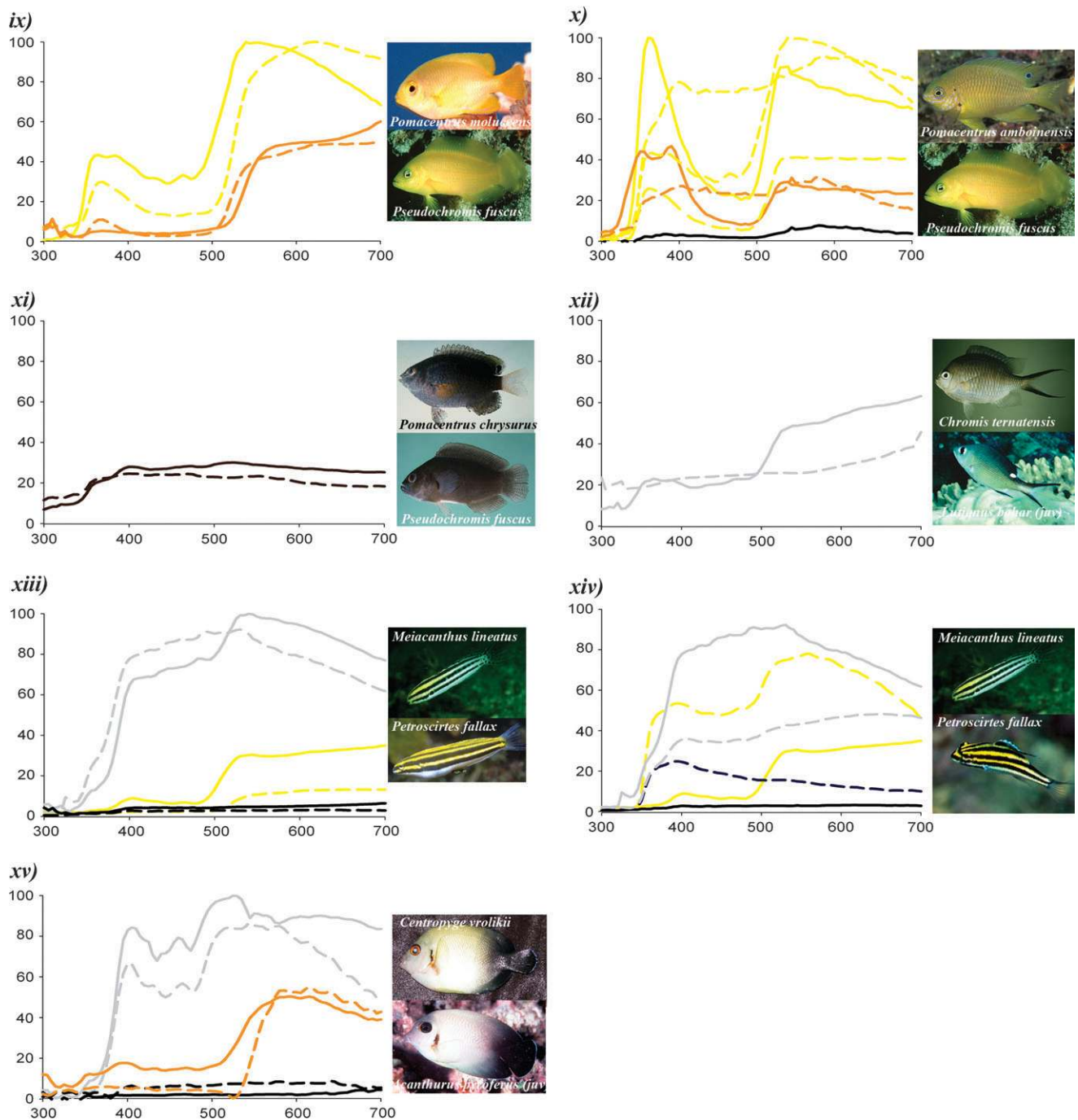


Figure 2

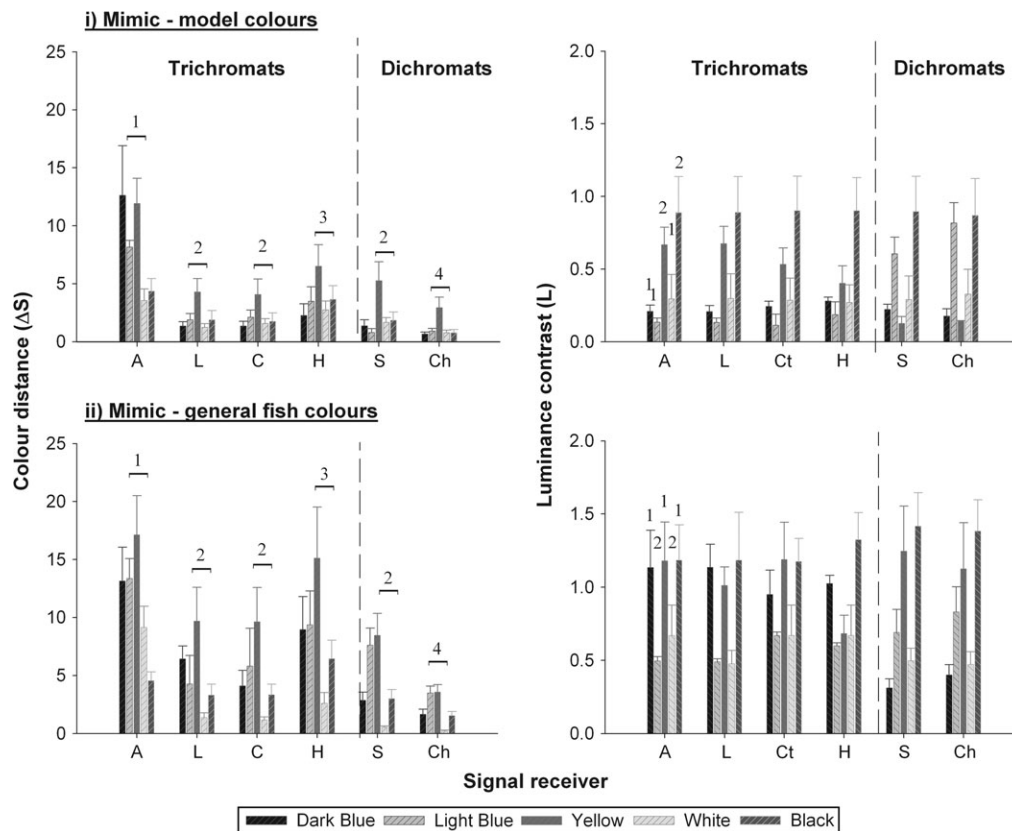
Spectral reflectance curves that are color coded to match photograph. Solid lines indicate model species (top photograph); dashed lines indicate mimic species (bottom photograph). Gray lines usually indicate white area. Photographs are © Karen Cheney and John Randall. In (iv) and (v), *Plagiotremus rhinorhynchus* is considered to be a social mimic, which hides in schools of similarly colored fish to avoid detection (Moland et al. 2005); therefore, in this scenario, they do not resemble the shape or body patterns of the fish they are mimicking.

± 0.56 ; light blue 2.21 ± 0.41 ; dark blue 2.08 ± 0.39 ; black 2.07 ± 0.24 ; white 1.72 ± 0.27 ; pairwise comparisons, $P < 0.04$). There were no other significant differences between color categories. For mimic-general fish spectral reflectances, again there was a significant difference between the color categories (wald $\chi^2 = 244.5$, $df = 4$, $P < 0.001$). All color categories were significantly different from one another (yellow 9.85 ± 1.00 ; light blue 8.26 ± 1.29 ; dark blue 4.72 ± 0.75 ; black 3.53 ± 0.45 ; white 1.31 ± 0.20 ; pairwise comparison, $P < 0.03$), with the

exception of yellow and light blue (pairwise comparison, $P = 0.19$).

Changes in color and luminance contrast with depth

There was a general and significant trend for color distances between model and mimic to decrease with depth ($F_{1,431} = 40.20$, $P < 0.001$; Figure 4i) for all signal receivers and colors. However, the amount that color distances became more similar with depth was similar between signal receivers

**Figure 3**

Color distances (ΔS) and luminance contrast (L) between (i) mimic–model pairs and (ii) mimic–general fish colors. Trichromat species are A = *Abudefduf abdominalis*, L = *Lutjanus bohar*, Ct = *Ctenochaetus strigosus*, H = humans. Dichromat species are S = *Sphyrna helleri* and Ch = *Chaetodon kleinii*. Error bars represent mean \pm 1 standard error. Numbers indicate receivers that are statistically similar to one another using pairwise multiple comparisons ($P > 0.05$).

($F_{5,88} = 2.42$, $P = 0.07$) and between colors ($F_{12,88} = 0.65$, $P = 0.80$; Figure 4i). For luminance contrast, there was no significant difference with depth ($F_{3,264} = 0.49$, $P = 0.97$; Figure 4ii) or between signal receivers ($F_{3,88} = 0.013$, $P = 0.99$). However, yellow was significantly different from the other colors ($F_{4,431} = 6.64$, $P < 0.001$; pairwise comparison, $P < 0.03$; Figure 4ii).

DISCUSSION

The spectral reflectance of color patches on coral reef fish mimics were qualitatively similar to their models for the majority of model–mimic pairs. Mimics resembled the colors of their models more accurately than general reef fish from the same habitat. However, the potential ability of reef fish to discriminate between models and mimics based on their coloration varied depending on their visual system. Fish with sensitivity in the UV region (*A. abdominalis*) had a greater capacity to discriminate between mimics and models based on color signals, compared with other trichromat and dichromat fish species that could come in to contact with model–mimic pairs. Dichromatic fish species (in particular, *C. kleinii*) had the poorest discrimination ability in distinguishing between mimics and models and reef fish colors in general. However, there was no difference between species in their ability to detect differences in luminosity. As depth increased, model and mimic colors became more similar; hence, mimics may resemble their models more closely in deeper habitats.

The selection pressures on mimics to resemble their models may therefore vary depending on the visual system of the signal

receiver and the light environment. In protective and aggressive mimicry systems, the predators of mimics and victims of attack, respectively, act as selective agents forcing mimics to accurately resemble their models (Sheppard 1958; Huheey 1988). Therefore, it is these visual systems we should consider when investigating how signal receivers shape the evolution of mimicry systems. In coral reef fish mimicry systems, many predators do not appear to have UV vision due to the absorbing properties of the ocular media (Siebeck and Marshall 2001; Losey et al. 2003), which may explain why many mimics do not resemble their models to UV-sensitive fish. In addition, many predators tested so far appear to be dichromats (Losey et al. 2003; Marshall et al. 2006) and therefore would be less likely to distinguish models from mimics based on color. Victims of aggressive mimicry vary widely and comprise of species with different visual capabilities (Cheney KL, unpublished data, 2004–2008), including those with UV sensitivity. Therefore, these systems would be ideal to further examine the extent to which interspecific variability in discrimination ability affects the success of mimics but requires a greater understanding of interactions of fish on the reef.

The absolute discrimination threshold at which signal receivers can detect mimics from models, and at which the mimic incurs a fitness cost, remains to be determined with behavioral experimentation. In previous studies, the threshold for discrimination between 2 colors has been set at $\Delta S = 0.5$ –2 and is expressed in just noticeable differences (JNDs) (Vorobyev et al. 2001; Siddiqi et al. 2004; Eaton 2005). For fish, it is predicted that this value will be much higher as reef fish have poor visual acuity relative to other animals (Marshall

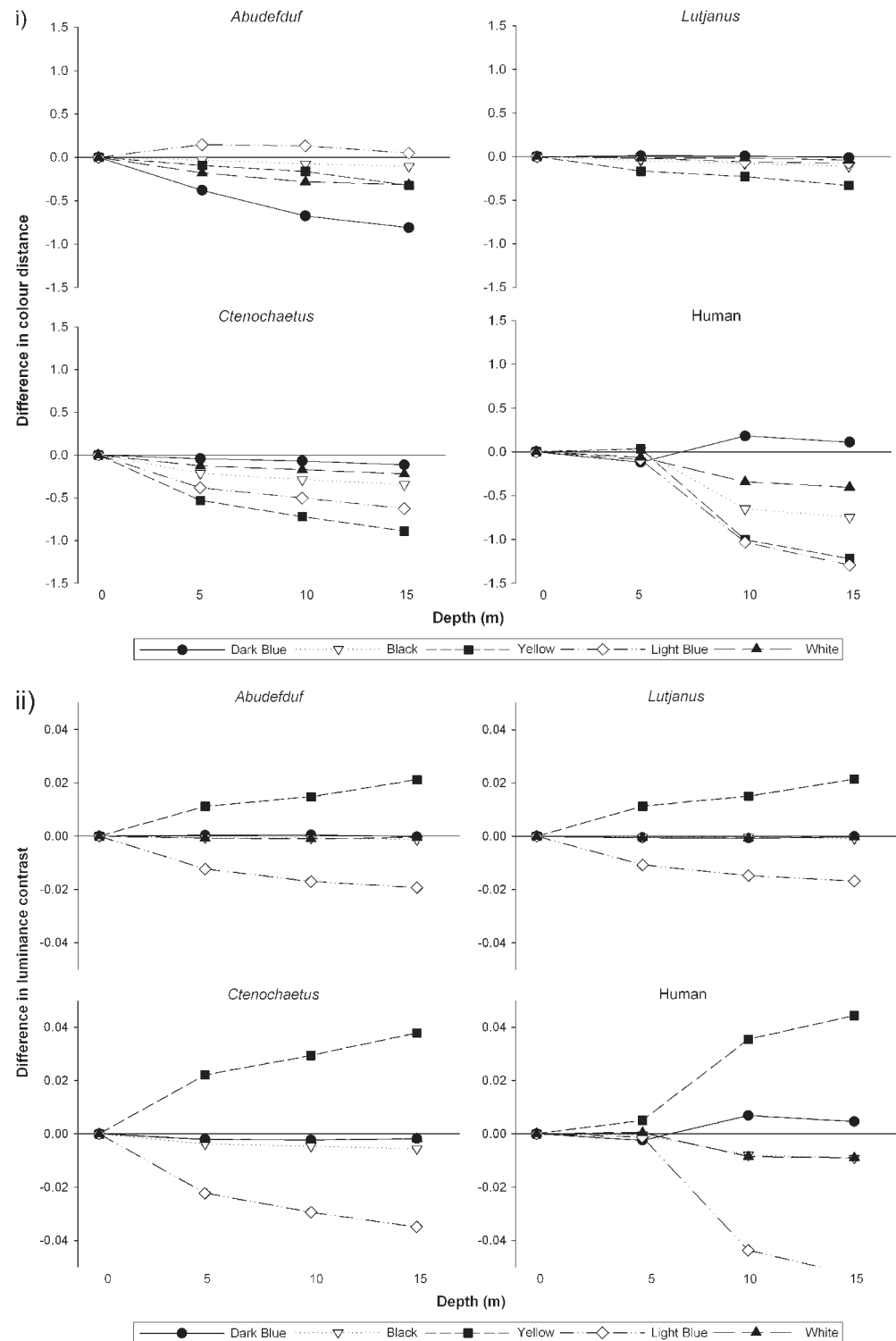


Figure 4
(i) Color and (ii) luminance contrast between mimic and model color signals with depth. Values were normalized by calculating color distance at depth minus color distance at surface; therefore, positive values indicate colors or luminance that become more distinguishable from each other, whereas negative values indicate colors or luminance that become less distinguishable.

2000a). If there is intraspecific variation in model color patterns, or if the model is very toxic, then only an approximation to the color signal by the mimic may be sufficient to gain a fitness benefit (Edmunds 2000; Sherratt 2002). In Batesian mimicry, predators would profit from detecting palatable mimics and unpalatable models, especially when alternative food sources are low; therefore, this may selectively drive mimics to be more accurate in terms of color. Further empirical

studies should be conducted using the signal detection theory (e.g., Swets 1964, Egan 1975), which provides a framework for identifying optimal predatory (or victim) behavior when the signal receiver is faced with discriminating between 2 species, for example, an unpalatable model and a palatable mimic. This theory predicts a critical threshold appearance beyond which prey items should be rejected or avoided by the signal receiver. The extent to which other signals could be used to detect

mimics from models should also be investigated; for example, body shape, color patterns, behavior, context-dependent discrimination, or a combination of signals (Cott 1940; Holen and Johnstone 2006).

Surprisingly, human visual systems were better at distinguishing between model and mimic colors in the aquatic environment compared with many trichromatic and dichromatic fish species (with the exception of *A. abdominalis*). This is perhaps unexpected as it is predicted that color vision would evolve in response to the environment (Lythgoe 1979). Generally, human observers are better at distinguishing colors in the green to red area of the spectrum compared with shorter wavelengths (Osorio and Vorobyev 1996). Longer wavelength colors, or parts of color spectra reflecting in this region, may appear more conspicuous as colors to humans than to reef fish (Marshall 2000a) and therefore may bias the data to indicate that humans are “better” at discriminating reef fish colors than the fish themselves. Comparing reef fish vision with a terrestrial species (humans) not only helps us to demonstrate the capabilities and limitations of reef fish vision but also provides insights into how the marine environment may influence the evolution of visual systems.

The majority of fish species examined in this study are generally found at depths between 2 and 30 m (Lieske and Myers 2001). Therefore, differences in habitat and light environment could affect the success of mimics. However, the maximum difference in color distance from the surface to 15 m was approximately $\Delta S = 1$ (Figure 4). Although statistically different, if ΔS is below the JND threshold, then model and mimic colors may remain close enough to be visually indistinguishable over depth. However, the threshold at which 2 colors become distinguishable for fish remains to be tested. There was no significant trend for the difference in luminance between model and mimic signals to increase or decrease with depth. Therefore, in terms of luminance, mimics appear to accurately resemble their models at all depths. The relative importance of different cues (e.g., hue, luminance, patterns, behavior) used by fish to recognize predators, food items, or a mate requires further investigation.

Some model–mimic pairs appeared to only vaguely resemble one another in color (e.g., *E. bicolor* and *P. laudandus*, Figure 2viii) or had obvious color patches that may enable signal receivers to distinguish models from mimics (e.g., *P. rhinorhynchus* and *Chromis viridis*, Figure 2iv). Furthermore, geographical variation in colors may occur so that in some areas putative model pairs may accurately resemble one another, whereas in others they are vastly different. Color analytical techniques may also help us to identify other model–mimic pairs that we, as humans, do not perceive. In conclusion, color spectrometry and visual modeling allow us to investigate color signaling from a signal receiver's perspective to provide a greater understanding of the evolution and ecology of mimicry systems.

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