

Cleaner gobies evolve advertising stripes of higher contrast

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SUMMARY

Elacatinus gobies of the Caribbean have undergone rapid speciation along ecological axes, and particular species from this genus act as ‘cleaners’ that remove ectoparasites from larger coral reef fish, termed ‘clients’. Evolutionary shifts in habitat use, behavior and lateral body stripe colors differentiate cleaners from ancestral sponge-dwelling lineages. High-contrast stripe colors associated with cleaning behavior on coral reefs may have evolved as a signal of cleaning status. We asked whether cleaner gobies with blue stripes are more conspicuous than ancestral yellow- and green-stripe phenotypes to a diverse set of potential client visual systems in the tropical reef environment where cleaning stations are commonly observed. Using spectrophotometric measurements of cleaners with blue and yellow stripes and their F₁ hybrid, we tested the contrast of each color stripe to both potential dichromatic and trichromatic reef fish visual systems, against typical coral and sponge microhabitat background colors. Blue stripes provide the highest average chromatic contrast across a range of possible microhabitat colors to the majority of fish visual systems tested. The contrast provided by yellow and hybrid green stripes are comparable across habitats to dichromatic visual systems. The green stripe is less contrasting than both blue and yellow to many potential trichromatic visual systems. We suggest that the evolution of blue stripes in *Elacatinus* gobies could be a result of natural selection for signals of high color contrast, driven by the sensory biases and visual systems of diverse reef fish clients.

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INTRODUCTION

In Caribbean *Elacatinus* (Jordan, 1904) (previously *Gobiosoma*) gobies, evolutionary shifts from non-mutualists to obligate generalist mutualists coincide with shifts in color patterns associated with advertising this derived status. This lineage of species provides a model framework in which to test signal evolution in a mutualism. *Elacatinus* (*E.*) gobies (*sensu lato-s.l.*) are small (approximately 2–4 cm in length) and habitat restricted, with limited mobility (Rüber et al., 2003; Colin, 1975). The striped pattern of the subgenus (*sensu stricto-s.s.*) *E.* is notably different from the most closely related sister species’ body patterns, which are more disruptive or banded (Rüber et al., 2003). These distinctive stripes are potentially conspicuous to visual detection, which makes it of particular interest that a lineage within the subgenus has evolved highly specialized parasite-cleaning behavior.

Molecular phylogenetic analysis shows that *E.* (*s.s.*) gobies diverged into two behaviorally distinct – obligate sponge-dwelling and cleaning – clades (Taylor and Hellberg, 2005; Rüber et al., 2003). Cleaners derive much or all of their nourishment by cleaning parasites from the bodies of visiting ‘clients’. Limited larval dispersal may contribute to the rapid speciation within the clade (Taylor and Hellberg, 2003) and may be an important mechanism by which selection on fitness-related traits varies and evolves in the marine environment. Sponge dwellers often associate with chemically defended sponge species such as *Xestospongia* spp. (Pawlik et al., 1995) and *Agelas* spp. (Assmann et al., 2000) and tend to retreat into sponge cavities if disturbed, while cleaners tend to be found on corals or on the outside of sponges, where they are

both more exposed and more visible to passers by and potential predators (L.L., personal observation). All species within the clade have distinctive stripe patterns, which set them apart from other *E.* (*s.l.*) species.

Basal species within the cleaner lineage have a lateral yellow stripe along both sides of the body, while more recently evolved species have derived green (broad spectrum reflectance that appears iridescent white) or blue lateral stripes (Taylor and Hellberg, 2005). In addition, two species of cleaners exhibit color stripe polymorphism, and the order of evolution within these stripes appears to follow this same trend (Taylor and Hellberg, 2005). Whereas bold black dorsal and sublateral stripes with a yellow or green lateral stripe can be found in both cleaning and non-cleaning gobies, the blue lateral stripe is only observed in cleaners and is significantly associated with a morphological change in mouth position that may be adaptive to cleaning (Taylor and Hellberg, 2005). It has been suggested that the black striped pattern is a conspicuous signal evolved to advertise cleaning behavior (Côté, 2000; Arnal et al., 2006; Stummer et al., 2004) and is a clear example of profile enhancing high contrast edge (Stevens, 2007). Paired with a blue, green or yellow stripe, the pattern may increase signal contrast against typical backgrounds (Marshall, 2000).

Interactions where fitness may be tied to visual signaling have the potential to exert selective pressure on color and pattern phenotypes (Stevens, 2007). Traits thought to have fitness consequences tied to contrast or chromatic distinctiveness may appear differently to many potential onlookers in the same microenvironment. Recent studies have used visual models to

estimate color conspicuousness of fruits or prey to potential observers (Håstad et al., 2005; Schaefer et al., 2007; Siddiqi et al., 2004; Stuart-Fox et al., 2003; Darst et al., 2006). Modeling of goby color stripes across a range of microhabitats, covering the potential diversity of client visual systems, may provide insight into the nature of signal evolution in an asymmetric mutualism (where many potential client species interact with one focal mutualist).

Mutualisms can be defined as interspecific interactions where both participants gain fitness benefits (Boucher et al., 1982; Cushman and Beattie, 1991). Evolution of specialist mutualisms often leads to traits that are coevolved communication signals from one partner class to the senses of a receiver class. In a diffuse mutualism, partner groups may exert differential selective pressure on traits of the shared mutualist; this could in turn lead to diffuse selection and evolution (Strauss et al., 2005). The ways in which signaling traits mediate interactions between mutualists and their potential partners are not well understood and may hold keys to understanding how asymmetric mutualisms promote diversity (Strauss et al., 2005; Bascompte et al., 2006). For obligate mutualists, especially those spatially restricted to habitat or by mobility, traits that signal to potential partner organisms may become strong arbiters of fitness. Evolutionary adaptations that increase the efficiency or reduce the cost of signaling to partners are likely to be favored and may exploit pre-existing biases of the intended receivers (Ryan and Rand, 1993). They may also increase visibility to potential eavesdroppers, thus affecting the potential risk of engaging in mutualism in an interaction network.

Our main hypothesis is that blue stripes of *E. gobies* are more conspicuous than other stripe colors to a larger pool of signal receivers. Although many species visit cleaning stations, more-abundant Caribbean species such as *Chromis* spp., *Clepticus* spp. and *Abudefduf* spp. have been suggested to contribute heavily to selection for traits that are integral to signaling cleaning behavior (Floeter et al., 2007); a general positive correlation between increased client abundance and increased cleaning interactions suggests that the signals indicating cleaner status are effective across broad taxonomic, trophic and social behavior groups (Floeter et al., 2007). First, we measured the colors of *Elacatinus oceanops* (blue), *Elacatinus randalli* (yellow) and their F_1 progeny (green) using spectrophotometry, as these three color classes represent the three phenotypes found across the species in the clade. The hybrid progeny are comparable in spectral reflectance to wild phenotypes often described as 'white' striped (e.g. *Elacatinus evelynae*, *Elacatinus illecebrosus* and *Elacatinus prochilos*) (L.L., unpublished data), although we will call them green as this most accurately describes the reflectance of the stripes. Next, we used color opponent models of reef fish visual sensitivity (Vorobyev and Osorio, 1998; Vorobyev et al., 2001; Kelber et al., 2003) to assess the likely contrast of these stripe colors against sponge and coral microhabitats. Because cleaners interact with a broad array of species, and different species make up the most abundant clients across geographic regions, we modeled chromatic contrast through the eyes of many client visual systems (Losey et al., 2003). This strategy allowed us to evaluate the conspicuousness of color stripes to a variety of model partner organisms. Color stripe may be under selective pressure to be more generally conspicuous to potential mutualist partners, given that evolution has resulted in species utilizing more-exposed habitat, engaging in more-specialized feeding behavior, and increasing interactions with potential predators (Rüber et al., 2003; Taylor and Hellberg, 2005; White et al., 2007).

MATERIALS AND METHODS

The model approach

To compare the visibility of goby advertising stripes, we used color vision models (Vorobyev and Osorio, 1998) that incorporate three main components: (1) spectral reflectance of the focal object or objects, (2) ambient environmental light and (3) color vision capabilities of the onlooker.

Component 1a: spectral reflectance of fish color stripes

Color stripe measurements were taken from eight individuals of each representative phenotype: blue-striped *Elacatinus oceanops* (Jordan, 1904), yellow-striped *Elacatinus randalli* (Böhlke and Robins, 1968) and an F_1 intercross of *E. oceanops* \times *E. randalli*. We measured spectral reflectance using an Ocean Optics S2000 spectrophotometer and OOIBASE32 software (Ocean Optics, Inc., Dunedin, FL, USA). The bare end of a 200 mm fiber optic UV/VIS cable was placed close to the fish so that it was sampled from the midlateral stripe color region alone and at a 45 deg. angle to prevent specular reflection. Illumination for both the sample and the reference (98% diffuse reflectance standard; Ocean Optics) was provided by a combination of light from a PX-2 xenon illuminator (Ocean Optics) and a Sunray 1000 video light (Light & Motion, Monterey, CA, USA). Fish were immediately returned to the water after measurement. Reflectances were smoothed using a 5-point boxcar average and 10 readings made at 15 ms intervals were averaged for each measurement. Two replicate measurements were averaged per individual for further calculations. Quantitative differences between the three stripe phenotypes were determined, first, objectively, statistically and predictively with discriminant function analysis (DFA) and, second, subjectively and in an ecologically relevant context for a range of potential fish visual systems. Stripe color reflectances were compared through the eyes of potential fish onlookers in two complementary ways described below.

Component 1b: coral and sponge microhabitat reflectance

In addition to stripe reflectances, we evaluated microhabitat colors either commonly occupied by or commonly available to the focal goby species (Fig. S2 in supplementary material). Coral and sponge reflectance readings were made in the Florida Keys, USA, using a diver-operated DiveSpec spectrophotometer (a self-contained reflectance and fluorescence measurement device using red, blue and white LEDs to obtain full-spectrum reflectance calculations without ambient light; NightSea, Andover, MA, USA). A Spectralon 99% reflectance standard (Labsphere, North Sutton, NH, USA) was first used to collect a reference reading, and reflectance was computed as the ratio of the sample to the reference measurement. Reflectances were then smoothed using a one-pass Savitzky-Golay 21-point algorithm and trimmed to show wavelength readings at 5 nm intervals from 400 nm to 750 nm. All coral species were identified to genus or species while sponges were not identified by species. However, Henkel and Pawlik found that *Callispongia vaginalis* was the most abundant species among Florida Keys vase sponges (43%) (Henkel and Pawlik, 2005), and this is likely the species used for vase sponge color reflectance in further calculations. Following extrapolation techniques used previously for terrestrial habitats (Endler, 1993), we extended the slope of reflectance in the 400–450 nm region down to 350 nm. Reflectance in this region is somewhat variable among coral species and even among colonies of the same species (Hochberg et al., 2004) but, on average, is fairly achromatic, exhibiting a relatively flat reflectance profile (Holden and LeDrew, 1998; Hochberg and Atkinson, 2000; Mazel and Fuchs, 2003). Little spectral reflectance data are available for sponges, but

our data show achromatic reflectance, if any, toward the UV end of the spectrum. Excluding UV-sensitive visual systems from our analyses, to avoid extrapolated data, did not change the interpretation of our results.

Component 2: environmental irradiance and sidewelling water background

In order to compare goby stripe and microhabitat colors under ecologically relevant light conditions, we incorporated ambient irradiance collected at depth into the visual models. Irradiance for daylight at open water near the reef habitat was collected at several locations using a 1 mm-diameter fiber optic probe fitted with a cosine collector attached to an Ocean Optics USB2000 spectrophotometer and recorded with a handheld computer with modified Palm-Spec software (Ocean Optics), encased in an underwater housing (Wills Camera Housings, Kaniva, VIC, Australia). We used a representative 6 m-depth irradiance (average of 15 technical replicate measurements) collected in October 2006 at West Palm Beach, FL, USA, mid-day, full sun, in our model as an ecologically relevant depth (all three stripe phenotypes have been documented at 1–40 m) (Colin, 1975). Sidewelling data toward and away from the sun were also collected at this time. Sidewelling quantum catch collected from the direction toward the sun was averaged with irradiance to represent the adaptive light field, and sidewelling data collected facing away from the sun were used as one of the potential background colors.

Component 3: fish visual capabilities

Cone sensitivities of reef fishes, measured using microspectrophotometry, were tested from 25 species (Table 1) representing 14 different families (Losey et al., 2003). Double cones were assumed to be neurally linked (Marshall and Vorobyev, 2003) and therefore to operate as a single (averaged) chromatic receptor channel. Representative cone sensitivities corrected for ocular media transmission (Siebeck and Marshall, 2001) were chosen to cover a range of ecological and sensitivity classes typical of tropical fish cone sensitivities (Marshall et al., 2006).

Color vision models

Receptor-noise-limited color opponent models of animal color vision (Vorobyev and Osorio, 1998; Vorobyev et al., 2001; Kelber et al., 2003) were used to map *E.* color stripes and coral and sponge microhabitat colors in a scaled coordinate space (Hempel de Ibarra et al., 2001; Marshall and Vorobyev, 2003; Siddiqi et al., 2004), or ‘chromaticity diagrams’. The exact proportion and number of individual cone types for the fish client visual systems is not known; however, if one assumes a 1:1 (dichromat) or a 1:1:1 (trichromat) ratio, the potential for chromatic contrast and color discriminability are maximized overall (relative to e.g. 1:2 or 1:2:2). We present results assuming cone ratios of 1:2 and 1:2:2 for reef fishes (N.J.M., unpublished data) and found similar results for ratios of 0.52:0.82:1, experimentally shown with ‘unsaturated blue’ light in goldfish (Dörr and Neumeyer, 2000). For the purposes of this experiment, we assume that spectral attenuation is negligible, to maximize comparisons among client visual systems, which likely makes our results more conservative as blue should transmit furthest in water (Barry and Hawryshyn, 1999). Quantum catches used in the analyses were von Kries transformed by each cone’s von Kries coefficient (Marshall and Vorobyev, 2003). The transformation adjusts sensitivities proportional to the illuminant, contributing to overall color constancy, which is a physiological adaptation likely to be used by many reef fish visual systems. We calculated the quantum catch of

Table 1. Blue-to-yellow contrast ratio for average coral, average sponge and sidewelling water for representative visual systems used in chromatic contrast analyses

	Average coral	Average sponge	Sidewelling
Dichromats			
<i>Acanthurus triostegus</i>	1.3	1.8	0.2
<i>Apogon kallopterus</i>	1.3	1.8	0.2
<i>Arothron melaegris*</i>	1.4	1.9	0.2
<i>Aulostomus chinensis*</i>	1.8	2.4	0.4
<i>Chaetodon kleini</i>	2.0	2.6	0.2
<i>Chromis ovalis</i>	2.1	2.9	0.4
<u><i>Chromis verater</i></u>	2.0	2.7	0.4
<i>Ctenochaetus strigosus</i>	1.5	2.0	0.2
<i>Forcipiger flavissimus</i>	1.4	1.9	0.2
<i>Lutjanus bohar*</i>	1.5	2.1	0.3
<i>Mulloidichthys flavolineatus</i>	2.0	1.9	2.0
<i>Naso lituratus</i>	1.6	2.2	0.3
<i>Pervagor spilosoma</i>	2.5	3.3	0.6
<i>Saurida variegatus*</i>	1.6	1.5	1.5
<i>Sphyrena helleri*</i>	1.4	1.9	0.2
<i>Stegastes fasciolatus</i>	1.6	1.6	1.5
<i>Zanclus cornutus</i>	1.3	1.8	0.2
<i>Zebrasoma flavescens</i>	1.3	1.8	0.2
Trichromats			
<i>Abudefduf abdominalis</i>	0.8	0.6	0.7
<i>Canthidermis maculata</i>	2.4	1.2	0.3
<u><i>Chromis hanui</i></u>	0.9	0.7	0.9
<i>Dascyllus albisella</i>	1.5	1.0	0.7
<i>Kuhlia sandvicensis</i>	0.9	0.7	0.9
<i>Myripristis berndti</i>	1.8	1.0	0.2
<i>Zebrasoma veliferum</i>	1.8	1.0	0.2

Species with asterisks are representative predator visual systems.
Underlined species represent those from particularly abundant families.

each cone as the product, integrated from 350 to 750 nm wavelength, of measured spectral reflectance, sensitivity spectrum, and illuminant.

We plotted stripe colors and microhabitat backgrounds into an onlooker color map [as illustrated in fig. 4D of Kelber et al. (Kelber et al., 2003)]. This chromaticity-diagram technique allowed us to compare stripe colors of gobies and to determine how different these and microhabitat colors would appear to representative onlooking client fishes. Distances between color points in the diagram represent chromatic stimulus with respect to individual cone classes, nominally assigned absolute values in the positive [longer wavelength sensitive (LWS) cones] or the negative direction [shorter wavelength sensitive (SWS) cones]. Each unit in the scale-free axis denotes a unit of increasing discriminability by the observer at decreased effort. In trichromats, axes are in two dimensions, each corresponding to a color opponent system between two cones with overlapping sensitivities. Colors were plotted following formulas described elsewhere (Vorobyev and Osorio, 1998; Hempel de Ibarra et al., 2001; Kelber et al., 2003). For double cones, we assumed that cone sensitivities were averaged; the opponent system contrasts the single cone and the averaged double cones to discriminate between colors. For all other cases, the axes of the diagrams are opponent contrasts between individual cone class sensitivities. Chromaticity values that plot at absolute distances, ΔS (Vorobyev and Osorio, 1998), of less than one scaled unit from one another are assumed to fall below a threshold of discrimination along that axis [i.e. for the cone LWS and medium wavelength sensitive (MWS) opponent discrimination along axis x_1]. This assumption is a best estimate for fish and could be incorrect for fish color vision, but, given that human and fish

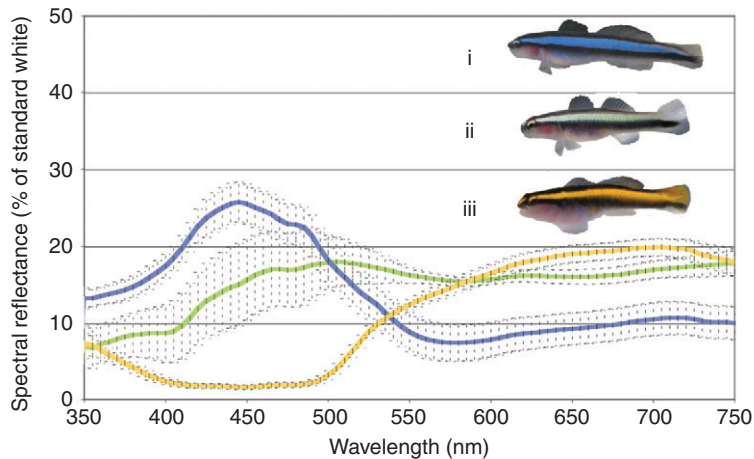


Fig. 1. Spectral reflectance curves of (i) *Elacatinus oceanops* (ii) *E. hybrid* and (iii) *E. randalli* are color coded to match their stripe color. Mean \pm s.d. for eight individuals per phenotype shown.

color constancy responses are highly similar (Neumeyer et al., 2002) and that these estimates have been used as a discrimination cutoff in other visual systems, e.g. primates (Osorio and Vorobyev, 1996) and bird (Schaefer et al., 2007), we argue that they are reliable in this comparative context. In the chromaticity diagram, the origin of the map corresponds to all achromatic reflectances, including white, shades of achromatic gray, and black. As chromatic distances between points increase, colors are distinct and differentiable under a wider range of conditions and at decreased effort to the observer.

Models of client fish visual systems (potential dichromat and trichromat) were also used to calculate the magnitude of color differences (ΔS) between each *E.* stripe color and representative background microhabitat colors. To calculate the dichromatic and trichromatic ΔS between color stripe and microhabitat background (based on noise-limited color-opponent cone sensitivities), we employed formulas 3 and 4 from Vorobyev and Osorio (Vorobyev and Osorio, 1998). This calculated ΔS gives a sense of how differentiable the stripe is from a specific background color rather than from an arbitrary achromatic value.

RESULTS

Color stripes are distinctly and categorically different

Fig. 1 shows the averaged color spectrum of stripes. Blue stripes reflect in a peak waveform around 445 nm. Yellow stripes have a characteristic step-shaped reflectance function, with 50% of maximum reflectance reached at around 525 nm and leveling to a flat line at around 625 nm. The hybrid stripe color was uniformly green (Marshall, 2000) with a wide but apparent peak at 500–510 nm (Fig. 1). We refer to hybrid color as green, and it is comparable in phenotype to wild ‘white stripe’ *E.* species.

The color reflectance functions for blue, yellow and green are distinctly and categorically different. With *a priori* assignments of *E. randalli*, *E. oceanops* or hybrid color class, stripes reflectances could be clustered with 100% cumulative accuracy (Fig.S1 in supplementary material) into respective categories, using discriminant function analysis (DFA), with a reduced number of wavelengths (10) in linear combination (Table S1 in supplementary material). Although standardized reflectance with respect to full spectrum illumination shows the potential for differential chromatic signal, it does not necessarily represent the actual signal variation in an ecologically relevant context. To filter the stripe phenotypes through the spectral window of downwelling and sidewelling irradiance, we next incorporated environmental light (Fig. 2) to assess ecologically relevant differences among the three stripes, between stripe colors and possible backgrounds and to compare the

effectiveness of each color as a signal against typical microhabitats and water color.

Stripe colors are differentially discernable to fish clients

Trophically and ecologically divergent onlooker visual systems may see stripe and microhabitat colors differently. We wanted to, first, get a sense of how alike or different the stripe colors may be and, second, evaluate to what extent they differentiate from microhabitat colors. Two dichromats and two trichromats are represented in color vision chromaticity maps (Fig. 3). Unit-less opponency-based coordinate distance represents the ease with which colors can be discriminated to the modeled observer. Hybrid stripes are more chromatically similar to blue than yellow *E.* stripes to modeled fish visual systems in all cases. Yellow stripes plot furthest away from blue and closest to sponge and coral microhabitat colors. Coral and sponge microhabitats are likely chromatically similar in many cases to fish onlookers, as suggested by the overlapping standard deviation around the group centroids. Green stripes seem to be most achromatic to fish visual systems (as they are to humans) among the three colors and also seem to be a close match to sidewelling water color among the representative fish onlookers tested. Blue stripes also closely match both the sidewelling water color in three

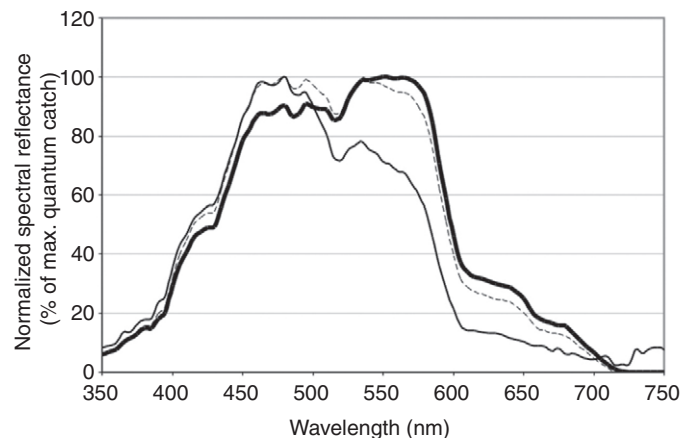


Fig. 2. Downwelling and sidewelling light spectral envelope at 6 m depth, normalized to show differences in color transmittance or reflectance. Representative curves, collected at West Palm Beach, FL, USA, midday, full sun are downwelling onto cleaning station (thick line), sidewelling toward the sun and away from coral head (broken line), and sidewelling away from the sun and away from coral head (thin line).

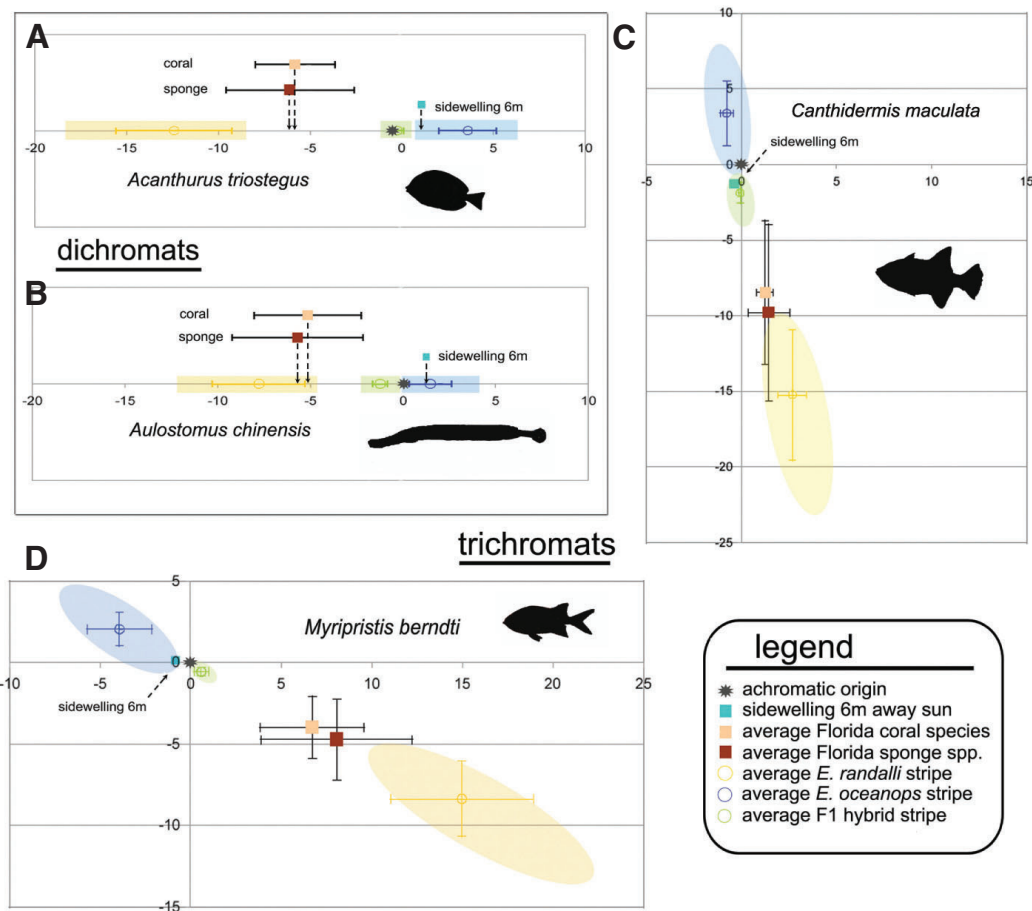


Fig. 3. Chromaticity diagrams to represent two dichromat (A,B) and trichromat (C,D) visual systems plotted at 6 m depth downwelling light spectral envelope adjusted for sidewelling light coming from the direction of the sun. Averaged stripes ($N=8$ individuals per phenotype) and microhabitats ($N=10$ sponges and $N=11$ corals) are shown with 1 s.d. whiskers. x and y -axis coordinates represent unit-less color opponency values for dichromat or trichromat models (Kelber et al., 2003) calculated from the two or three (respectively) cone visual systems. Colored clouds encompass the entire span of the stripe color values.

out of four and the achromatic origin in two out of four modeled cases (although see further discussion below for extended absolute chromatic contrast values across all modeled visual systems).

Representative dichromat plots (Fig. 3A,B) show blue stripe points furthest offset from coral or sponge microhabitats, while yellow and green may be essentially the same color as some habitats to onlooking fish, if they fall below a threshold of discrimination ability. Dichromats may not chromatically distinguish between yellow stripes and many microhabitat colors, especially sponges. The representative predatory onlooker *Aulostomus chinensis*, the trumpetfish, may not be able to reliably use chromatic cues to distinguish yellow-striped *E. gobies* from many typical backgrounds. Blue-striped gobies, for this same predator, are potentially almost a perfect match to the sidewelling water color. Green stripes fall below discrimination thresholds with a few habitat colors to the modeled trumpetfish and are most achromatic. For the surgeonfish, *Acanthurus triostegus*, green may be more easily distinguishable from microhabitats. In both dichromat cases shown, blue and green stripes are likely more achromatic, plotting closer to the achromatic origin, than yellow stripes. A potentially ecologically relevant achromatic color for the gobies is their black dorsal and lateral stripes (reflectance is achromatic black). These stripes can vary in saturation and can fade to dusky achromatic gray if the fish is stressed or during social interactions (L.L., personal observation) The pairing of a color stripe against an achromatic black stripe is likely to enhance signal

visibility overall (see Appendix, caveat 1 for discussion of brightness and signals). If we compare yellow to green stripe discrimination potential against background habitats and stripes, models suggest that each maximizes offset from one but not both, while blue accomplishes both chromatic contrast from habitat and the bordering stripes.

In the plots of possible trichromats – the cardinalfish, *Myripristis berndti*, and the triggerfish, *Canthidermis maculata* – yellow is furthest from green and blue stripe points, which again map more closely to each other and to the achromatic origin than either does to yellow. Colors falling on a straight line through the origin are likely complementary in the visual system represented (Fig. 3C,D; but this is not *always* the case in trichromats). Both green and yellow are nearly equidistant (on average) from average coral and sponge habitats but are not chromatically similar; they are different in color but potentially equally contrasting from habitat colors. The standard deviation of yellow stripes from the group centroid is larger, suggesting that variation in hues of yellow are greater than those of blue and green. In general, trichromats are likely to be better able to distinguish all stripes from possible microhabitat colors than are dichromats.

Overall, there was only slight variation in results between 1 m, 6 m and 17 m depth (only 6 m results shown), which is not surprising as the model assumes von Kries color constancy. All chromaticity points plotted at 17 m shifted slightly towards the center (more

achromatic) of the plot. To the representative client fishes, sidewelling 'blue' water plots within the standard deviation (on at least one opponent axis) of blue stripes and closest to the mean value for green stripes. The color of shallow tropical water is likely to be categorically different from all goby stripe colors to potential clients at shallow depth but is likely to be more similar to blue or green stripes at increased depth. Yellow stripes are likely discernable from most microhabitats at shallow depth but trend toward chromatic similarity with more microhabitats at deeper depths, at least for the representative species mapped. All three phenotypes are potentially effective communication colors against most microhabitats [see discussions of blue and yellow as signals by Lythgoe (Lythgoe, 1968) and Marshall (Marshall, 2000)], but blue stripes should operate as a more chromatically distinct color against corals and sponges of many colors.

Blue is higher contrast against microhabitat colors

In order to focus on the potential contrast of each stripe color to relevant microhabitats, we next used a complementary approach. We compared absolute chromatic distances of individual color stripes from selected coral and sponge microhabitats (Fig. 4). For pairwise comparisons between stripes and microhabitat colors to any particular onlooker, chromatic distance (ΔS) can differ from background color in absolute value or in direction (represented by \pm direction along an opponent system axis, e.g. differential contrast between cones). Contrast results consider only *absolute* color distances and therefore do not reflect the likeness or difference of stripe colors, but the relative ease of discrimination by the observer with respect to the microhabitat reference color (rather than an achromatic origin). This approach allowed us to ask how well each stripe performs in terms of color contrast as a signal against a particular microhabitat across many visual systems. We found that, overall, blue stripes provide the highest chromatic contrast across a range of possible microhabitat colors to the majority of client visual systems, especially to dichromatic visual systems (Table 1).

Against the coral and sponge microhabitats examined (Fig. 4A), possible dichromats see blue in higher contrast to microhabitat background than both yellow and green stripes in all cases. The yellow stripe of *E. randalli* is likely to be of equal contrast compared with hybrid green for dichromats against all focal backgrounds except *Montastrea cavernosa* and sidewelling blue water (higher for both). The blue stripe color is not significantly different in contrast magnitude from yellow against sidewelling blue in the combined possible dichromat cases tested at the 6 m depth. Although contrast potentials of blue compared with yellow differ among dichromats (Table 1), for the average sponge and coral microhabitats, blue is higher contrast in all cases. Depending on the visual sensitivity, blue stripes ranged in added contrast potential from 0.3 to 2.5-fold on corals and from 0.8 to over 3-fold on sponges.

For the same potential microhabitat or background colors tested, possible trichromats show a slightly different pattern (Fig. 4C). Yellow is just as contrasting as blue on average against all microhabitat colors and sidewelling color to the combined trichromats. No significant difference in the absolute magnitude of contrast value among stripes was found for average trichromats against the coral *D. strigosa* color, average sponge and vase sponge; all three are equally effective. In the cases tested, possible trichromats are better able to distinguish both blue and yellow stripe colors than green stripe from the background colors (see Appendix, caveat 2 for further discussion of green stripes and coral fluorescence) with higher overall contrast values compared with dichromats. When UV-sensitive trichromats were excluded from

the analysis (in order to avoid using any extrapolated data), contrast values mimicked the patterns seen in dichromats, where blue was consistently higher contrast than yellow. In all tested microhabitats, except vase sponge, both the minimum contrast value and the median contrast value for blue were higher than for yellow. For the vase sponge case, the median yellow contrast was slightly higher, although no significant differences were found among absolute contrast values across stripes (Friedman non-parametric ANOVA test statistic, $P=0.486$). Average sponges were also equally contrasting as a microhabitat background to all three phenotypes ($P=0.118$). Blue and yellow appear to be equally effective contrast colors against average coral colors to trichromats. Minimum values for yellow were often below a chromatic distance of 4 (the average standard deviation of yellow stripe contrast values against the least contrasting background microhabitat), while blue was always above $\Delta S=5$. Yellow stripes produced the overall highest chromaticity values of all, with some ΔS values reaching >25 , suggesting that variation in contrast potential is higher with ancestral yellow stripes. Among possible trichromats analyzed (Table 1), contrast potential for yellow compared with blue varies. For some species, blue is potentially more effective, and for others, yellow. A few trichromats see blue and yellow with equal contrast potential against average sponge colors.

In all, 25 fish visual systems were modeled in order to ask how the three stripe phenotypes compared against typically used backgrounds. Among predators (Table 1; asterisks denote species representing piscivores), blue was on average 0.6 and 2-fold more contrasting against average corals and sponges, respectively. Among representative species from particularly abundant families (underlined in Table 1), yellow and blue are both potentially effective contrast colors. Cone sensitivities from representative abundant dichromat species seem to have a blue contrast bias, while abundant trichromat species may see yellow more easily compared with blue. Against average sponge color, a total of 19 species have higher blue contrast than yellow. An additional three have equivalent contrast values for blue and yellow. Overall, 22 out of 25 species likely perceive blue with higher contrast on coral microhabitats.

DISCUSSION

We compared the signal chromatic contrast of *E. goby* color stripes to 25 different modeled fish onlookers. Using a modeling approach, we evaluated three representative phenotypes against many microhabitats on which the cleaners would advertise to passing clients. While spectral reflectance of stripe colors among the three *E. goby* phenotypes measured shows statistically distinct and categorical differences (Fig. S1 in supplementary material), we considered the colors in the context of the natural surroundings and in the sense-perceived context of trait-mediated signals that they communicate. In order to better evaluate the potential in signal variation on which selection could act, we needed to compare the potential signaling ability of the advertising stripes through the eyes of client beholders. We found that variation in signal ability among stripes does exist among different onlooker visual systems and against different microhabitat backgrounds and that derived blue stripes are on average a more robust signal.

We know from previous research that both yellow and blue are potentially good signal colors in the tropical marine environment and are known to be commonly occurring signaling colors in fishes (Lythgoe, 1968; Lythgoe 1979; Marshall, 2000; Marshall and Vorobyev, 2003) as the wavelengths reflected are complementary colors to many fishes and effectively exploit the many blue-shifted (and UV-shifted) visual systems found in tropical marine fishes

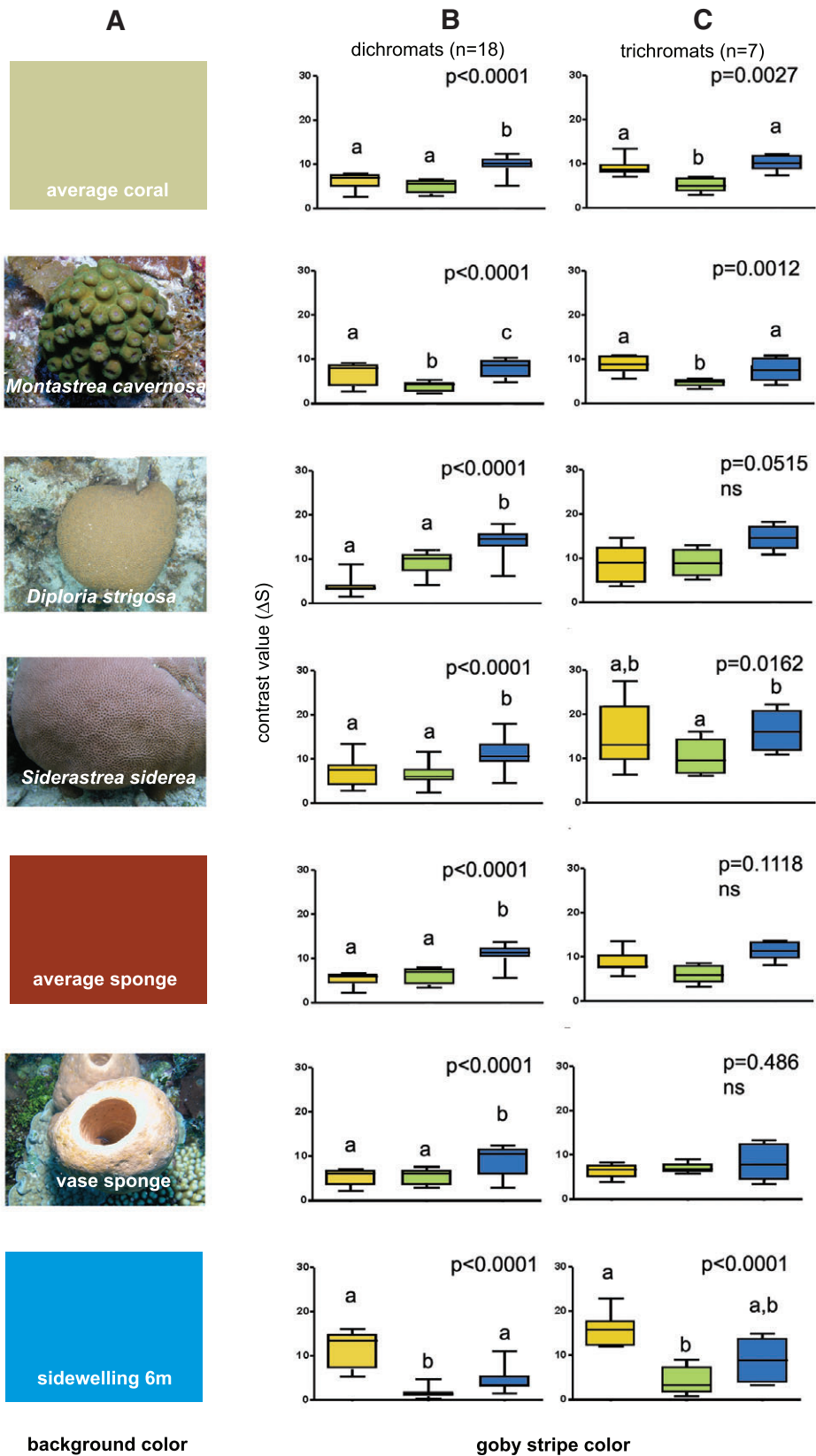


Fig. 4. Contrast value (ΔS) box-and-whisker plots of stripe colors against each of seven microhabitat background colors (A; coral and vase sponge photographs courtesy of R. Ritson-Williams) tested within dichromat (B) and trichromat (C) visual systems (showing median, upper and lower quartile, and least and greatest values). Eight color stripe replicates were used to calculate chromatic contrast values for each stripe color in 18 dichromat visual systems and seven trichromats using cone sensitivity data from Losey et al. (Losey et al., 2003). Friedman non-parametric ANOVA *P*-values shown. Significant Bonferroni–Dunn post-test differences between stripe contrasts against each microhabitat indicated by different letters above values for each stripe.

(Bowmaker, 1990; Losey et al., 1999; Lythgoe, 1984; Loew and Lythgoe, 1978; Marshall, 2000). We showed that *E. blue* stripes may be more distinguishable to a larger pool of species or to a particular type of visual system (dichromat) against typical

microhabitat backgrounds. Blue is consistently different chromatically from microhabitat hues, although certain yellow-striped individuals produced the highest single contrast potentials in both potential di- and trichromats. In the representative client

visual system examples we show (Fig. 3), blue stripes fall below discrimination thresholds with sidewelling water blue (6m) color in a few cases, but overall contrast values across both dichromat and trichromat visual systems (Fig. 4) suggest that, on average, reef fish are able to chromatically distinguish yellow and blue equally well (no significant difference between ΔS value) against sidewelling water color. The cleaners and sponge dwellers in this family, however, do not typically advertise against a water backdrop. Cleaner gobies typically rest on sponge and coral surfaces before approaching visiting clients (L.L., personal observation) and do not engage in the elaborate dances that characterize their Indo-Pacific cleaner wrasse counterparts, *Labroides dimidiatus*. The use of color signals is likely to be a reliable communication method (in this case to advertise cleaning status) among fishes (Chiao et al., 2000; Cummings, 2004). It is possible, alternatively, that evolutionary pressure selecting for increased brightness (achromatic signal) of the pattern has led to the observed changes in stripe colors (see Appendix, caveat 1 for further discussion) but we did not explicitly test this hypothesis. Perception of stripe colors against the microhabitat to potential observers will vary depending on the ambient downwelling and sidewelling light, background against which the signal is observed, visual system and sensitivity of the observer, as well as the size, shape and overall pattern of the color signal perceived (Lythgoe, 1968; Loew and Lythgoe, 1985; Lythgoe and Partridge, 1989; Barry and Hawryshyn, 1999; Partridge and Cummings, 1999; Marshall and Vorobyev, 2003). The wide range of visual systems analyzed encompasses a variety of tropical reef species and feeding strategies and are likely to be a good representation of potential client visual systems. The vast majority of these species has a blue stripe advertising bias compared with the ancestral yellow phenotype.

Blue signal increases opportunity

Visual cues to attract cooperative partners must be both visible and recognizable to their intended targets, and color stripe traits may respond to selection mediated by the sensory biases of various receivers, both intentional partners and unintentional eavesdroppers (Endler et al., 2005; Cummings, 2007). In the genus *E. gobies*, basal sponge-dwelling as well as facultative and obligate cleaners share black-stripe patterns that enhance the visibility of a lateral colored stripe, but only the cleaners use their pattern to recruit a mobile food source. Our results suggest that stripe evolution tends toward more conspicuous signaling to dichromats in particular, a potentially larger pool of onlookers. The black stripes paired with a colored stripe distinguish this entire subgenus *E.* lineage from other cryptic or disruptively marked congeners. Independent contrasts among both cleaner and non-cleaner species indicate that these long lateral stripes are linked to obligate cleaning (Côté, 2000) and longer stripes (relative to body length) have been experimentally verified to attract more clients (Stummer et al., 2004). Among potential client visual systems, abundant dichromats (Table 1) are much more likely to see blue stripes with greater ease than yellow stripes. Blue may be a more visible signal to the many tropical marine species and trophic groups that are likely to have dichromatic color vision. Many of the potential trichromats we analyzed (including representative abundant family species) showed similar discrimination distance values for yellow and blue, suggesting that signal potential is roughly equivalent between basal and derived stripes to the most abundant reef dwellers. Evolution of stripe colors in these mutualisms seems to be linked to cleaning,

suggesting that within this lineage, the benefits of evolving novel blue advertising stripes may lie in the broader pool of species whose visual senses are likely to see blue with greater ease on typical habitat backgrounds.

Blue signal may increase risk

Cleaning interactions are dependent on the action of the intended client fish, which must approach and accept cleaning from the cleaner. The potential for cheating by clients includes attack and predation on these small, relatively immobile fishes, but they are rarely found in the guts of predatory species (K.L.C., personal observation). The types of clients visiting stations can vary considerably by depth, geography and habitat (Colin, 1975; Cheney and Côté, 2003; Arnal et al., 2001; Côté, 2000; Floeter et al., 2007), and stripes may communicate different information to different species and may initiate different responses. The average blue-to-yellow contrast ratio among all piscivores that we included was 1.6 on average coral color and 2.0 on average sponge color. Our models predict that blue stripes should be more conspicuous than yellow and green stripes to a wide range of potential client visual systems across multiple possible background colors, and they may also be much more conspicuous to potentially dangerous clients. By advertising to a more diverse client pool (more potential 'partner' mutualists) while simultaneously making cleaning more risky (more exposed microhabitats and predator interactions) as a strategy, selective pressure may be increased on traits associated with altering partner behavior. Tradeoffs between attracting partners and deterring predation are likely to be ubiquitous challenges for immobile mutualists (e.g. Kessler et al., 2008) and may lead to the adaptive evolution of traits designed to manipulate the behavior of partners through various sensory channels. Mechanisms for the increased diversity exhibited in asymmetric mutualisms (Bascompte et al., 2006) may lie in the interaction of these traits as they evolve to broadcast to cooperators in the audience and simultaneously deter cheating behavior in potentially risky partners.

Distinction from co-occurring fishes (Merilaita and Ruxton, 2007) could have evolved to indicate aposematism, as preliminary feeding tests (Colin, 1975) with predatory reef fish showed avoidance and rejection of several *E. gobies*, although conclusive evidence that any one species is chemically defended remains to be tested. Since pattern and defensive chemistry need not coincide (Darst et al., 2006; Endler and Mappes, 2004), the ultimate cause of evolution of the stripe pattern could be different from the proximate selective forces maintaining the pattern and driving color change across the *E.* clade. If mediating risk is indeed a tradeoff for increasing visibility, then it may explain why all cleaners are not blue.

Potential for diffuse evolution in choice-based mutualisms

Strong local selection pressures have been suggested to influence geographic variation in the color of cleaners among *E. evelynae* (and *E. illecebrosus*) populations (Palumbi and Warner, 2003). Interactions with different combinations of client species in choice-based mutualisms may alter the evolutionary trajectory of stripe colors, even though, on average, blue is of higher contrast. If diffuse evolution occurs, where traits in the cleaners are differentially selected in the presence or absence of key consortia (e.g. clients) (Strauss et al., 2005), we might expect that yellow and green could be favored in certain cases. We suggest that inherent sensory biases of clients and local microhabitat availability may also contribute to the maintenance and evolution of color variation and ultimately reinforce mechanisms of speciation among mutualist species.

APPENDIX

Caveat 1: brightness and saturation

All three *E. (s.s.)* stripe colors are paired with the black stripes dorsal and ventral, and there is potential for effective achromatic brightness variation that does not correspond to the patterns we see with chromatic color signal. The visual channels used in detecting achromatic and chromatic signals are likely to be different in fishes (Cummings, 2004) and both systems may contribute to transmitting reliable signals to an intended receiver, whether interspecific mutualists or predators or intraspecific mates or competitors. We did not specifically test these potential differences in luminance to the fish visual systems. Brightness and saturation are likely also under physiological control by movement of melanophores in the color stripe, in order to highlight or obscure iridophores, similar to color changes described in *Paracanthus* surgeonfish by Goda and Fujii (Goda and Fujii, 1998), and may regulate visibility of the overall stripe pattern. Under variable illumination, as is characteristic of coral reef habitats, chromatic signals are often more reliable and may be more important for identifying objects than achromatic (brightness) signals for fishes (Chiao et al., 2000; Cummings, 2004). Comparisons of color hue and saturation (chroma) regardless of brightness differences when comparing between color stripes and backgrounds is evolutionarily relevant given the novelty of blue stripes within the *E. cleaners* but may not fully explain the selective paradigm in which signal evolution is occurring.

Caveat 2: microhabitat color variation and fluorescence

Reflected and emitted light from corals can include light fluorescing from coral pigments in the coral host tissue (Mazel and Fuchs, 2003), with the most common pigments having fluorescence emission peaks at 486 nm, 515 nm and 575 nm. The effect of fluorescence on overall exitance (total flux per unit area leaving the surface of the coral from emission, reflectance and transmittance) can vary from coral to coral, across depth and at changing zenith angle of the sun; however, in our measurements, no significant contribution to color was noted in the reflectance data. The results of contrast calculations could be affected by increased contribution of the most chromatically saturated pigments, namely p515 and p575, named after the emission wavelength peak, which would likely reduce chromatic contrast values for the hybrid green stripe color.

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REFERENCES

- Arnal, C., Côté, I. M. and Morand, S. (2001). Why clean and be cleaned? The importance of client ectoparasites and mucus in a marine cleaning symbiosis. *Behav. Ecol. Sociobiol.* **51**, 1-7.
- Arnal, C., Verneau, O. and Desdèvises, Y. (2006). Phylogenetic relationships and evolution of cleaning behaviour in the family Labridae: importance of body colour pattern. *J. Evol. Biol.* **19**, 755-763.
- Assmann, M., Lichte, E., Pawlik, J. R. and Köck, M. (2000). Chemical defenses of the Caribbean sponges *Agelas wiedenmayeri* and *Agelas conifera*. *Mar. Ecol. Prog. Ser.* **207**, 255-262.
- Barry, K. L. and Hawryshyn, C. W. (1999). Effects of incident light and background conditions on potential conspicuousness of Hawaiian coral reef fish. *J. Mar. Biol. Assoc. UK* **79**, 495-508.
- Bascompte, J., Jordano, P. and Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431-433.
- Böhle, J. E. and Robins, C. R. (1968). Western Atlantic seven-spined gobies, with descriptions of ten new species and a new genus, and comments on Pacific relatives. *Proc. Acad. Nat. Sci. Phila.* **120**, 45-174.
- Boucher, D. H., James, S. and Keeler, K. H. (1982). The ecology of mutualism. *Ann. Rev. Ecol. Syst.* **13**, 315-347.
- Bowmaker, J. K. (1990). Visual pigments of fishes. In *The visual systems of fish* (ed. M. B. A. Djamgoz), pp. 81-107. London: Chapman and Hall.
- Cheney, K. L. and Côté, I. M. (2003). Do ectoparasites determine cleaner fish abundance? Evidence on two spatial scales. *Mar. Ecol. Prog. Ser.* **263**, 189-196.
- Chiao, C.-C., Vorobyev, M., Cronin, T. W. and Osorio, D. (2000). Spectral tuning of dichromats to natural scenes. *Vis. Res.* **40**, 3257-3271.
- Colin, P. (1975). *The Neon Gobies*. Neptune City, NJ: TFF Publications, Inc.
- Côté, I. M. (2000). Evolution and ecology of cleaning symbioses in the sea. *Ocean Mar. Biol. Annu. Rev.* **38**, 311-355.
- Cummings, M. E. (2004). Modelling divergence in luminance and chromatic detection performance across measured divergence in surfperch (*Embiotocidae*) habitats. *Vis. Res.* **44**, 1127-1145.
- Cummings, M. E. (2007). Sensory trade-offs predict signal divergence in surfperch. *Evolution* **61**, 530-545.
- Cushman, J. H. and Beattie, A. J. (1991). Mutualisms – assessing the benefits to hosts and visitors. *Trends Ecol. Evol.* **6**, 193-195.
- Darst, C. R., Cummings, M. E. and Cannatella, D. C. (2006). A mechanism for diversity in warning signals: conspicuousness versus toxicity in poison frogs. *Proc. Nat. Acad. Sci.* **103**, 5852-5857.
- Dörr, S. and Neumeyer, C. (2000). Color constancy in goldfish: the limits. *J. Comp. Physiol. A* **186**, 885-896.
- Endler, J. A. (1993). The color of light in forests and its implications. *Ecol. Monogr.* **63**, 2-27.
- Endler, J. A. and Mappes, J. (2004). Predator mixes and the conspicuousness of aposematic signals. *Am. Nat.* **163**, 532-547.
- Endler, J. A., Westcott, D. A., Madden, J. R. and Robson, T. (2005). Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* **59**, 1795-1818.
- Floeter, S. R., Vázquez, D. P. and Grutter, A. S. (2007). The macroecology of marine cleaning mutualisms. *J. Anim. Ecol.* **76**, 105-111.
- Goda, M. and Fujii, R. (1998). The blue coloration of the common surgeonfish, *Paracanthurus hepatus*-II. Color revelation and color changes. *Zool. Sci.* **15**, 323-333.
- Håstad, O., Victorsson, J. and Ödeen, A. (2005). Differences in color vision, make passerines less conspicuous in the eyes of their predators. *Proc. Nat. Acad. Sci. USA* **102**, 6391-6394.
- Hempel de Ibarra, N., Giurfa, M. and Vorobyev, M. (2001). Detection of coloured patterns by honeybees through chromatic and achromatic cues. *J. Comp. Physiol. A* **187**, 215-224.
- Henkel, T. P. and Pawlik, J. R. (2005). Habitat use by sponge-dwelling brittlestars. *Mar. Biol.* **146**, 301-313.
- Hochberg, E. J. and Atkinson, M. J. (2000). Spectral discrimination of coral reef benthic communities. *Coral Reefs* **19**, 164-171.
- Hochberg, E. J., Atkinson, M. J., Apprill, A. and Andréfouët, S. (2004). Spectral reflectance of coral. *Coral Reefs* **23**, 84-95.
- Holden, H. and LeDrew, E. (1998). Spectral discrimination of healthy and non-healthy corals based on cluster analysis, principal components analysis, and derivative spectroscopy. *Remote Sens. Environ.* **65**, 217-224.
- Jordan, D. S. (1904). Notes on fishes collected in the Tortugas Archipelago. *Bull. US Fish Comm.* **22**, 539-544.
- Kelber, A., Vorobyev, M. and Osorio, D. (2003). Animal colour vision – behavioural tests and physiological concepts. *Biol. Rev.* **78**, 81-118.
- Kessler, D., Gase, K. and Baldwin, I. T. (2008). Field experiments with transformed plants reveal the sense of floral scents. *Science* **321**, 1200-1202.
- Loew, E. R. and Lythgoe, J. N. (1978). The ecology of cone pigments in teleost fishes. *Vision Res.* **18**, 715-722.
- Loew, E. R. and Lythgoe, J. N. (1985). The ecology of colour vision. *Endeavour* **14**, 170-174.
- Losey, G. S., Cronin, T., Goldsmith, T. H., Hyde, D., Marshall, N. J. and McFarland, W. N. (1999). The UV visual world of fishes: a review. *J. Fish Biol.* **54**, 921-943.
- Losey, G. S., McFarland, W. N., Loew, E. R., Zamzow, J. P., Nelson, P. A. and Marshall, N. J. (2003). Visual biology of Hawaiian coral reef fishes. I. Ocular transmission and visual pigments. *Copeia* **3**, 433-454.
- Lythgoe, J. N. (1968). Visual pigments and visual range underwater. *Vision Res.* **8**, 997-1012.
- Lythgoe, J. N. (1979). *The Ecology of Vision*. Oxford, UK: Oxford University Press.
- Lythgoe, J. N. (1984). Visual pigments and environmental light. *Vision Res.* **24**, 1539-1550.
- Lythgoe, J. N. and Partridge, J. C. (1989). Visual pigments and the acquisition of visual information. *J. Exp. Biol.* **146**, 1-20.
- Marshall, N. J. (2000). Communication and camouflage with the same 'bright' colours in reef fishes. *Phil. Trans. R. Soc. Lond. B* **355**, 1243-1248.
- Marshall, N. J. and Vorobyev, M. (2003). The design of color signals and color vision in fishes. In *Sensory Processing in Aquatic Environments* (ed. S. P. Colin and N. J. Marshall), pp. 194-235. New York: Springer.
- Marshall, N. J., Vorobyev, M. and Siebeck, U. E. (2006). What does a reef fish see when it sees a reef fish? Eating 'Nemo'. In *Communication in Fishes* (ed. F. Ladich, S. P. Colin, P. Moller and B. G. Kapoor), pp. 394-422. Enfield, NH: Science Publishers.
- Mazel, C. H. and Fuchs, E. (2003). Contribution of fluorescence to the spectral signature and perceived color of corals. *Limnol. Oceanogr.* **48**, 390-401.
- Merilaita, S. and Ruxton, G. D. (2007). Aposematic signals and the relationship between conspicuousness and distinctiveness. *J. Theor. Biol.* **245**, 268-277.
- Neumeyer, C., Dörr, S., Fritsch, J. and Kardelky, C. (2002). Color constancy in goldfish and man: influence of surround size and lightness. *Perception* **31**, 171-187.
- Osorio, D. and Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proc. R. Soc. Lond. B* **263**, 593-599.

- Palumbi, S. R. and Warner, R. R. (2003). Why gobies are like hobbits. *Science* **299**, 51-52.
- Partridge, J. C. and Cummings, M. E. (1999). Adaptations of visual pigments to the aquatic environment. In *Adaptive Mechanisms in the Ecology of Vision* (ed. S. N. Archer, E. R. Djamgoz, E. R. Loew, J. C. Partridge and S. Vallerga), pp. 251-284. Dordrecht, Boston, London: Kluwer.
- Pawlik, J. R., Chanas, B., Toonen, R. J. and Fenical, W. (1995). Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrence. *Mar. Ecol. Prog. Ser.* **127**, 183-194.
- Rüber, L., Van Tassel, J. L. and Zardoya, R. (2003). Rapid speciation and ecological divergence in the American seven-spined gobies (Gobiidae, Gobiosomatini) inferred from a molecular phylogeny. *Evolution* **57**, 1584-1598.
- Ryan, M. J. and Rand, A. S. (1993). Sexual selection and signal evolution: the ghosts of biases past. *Phil. Trans. R. Soc. Lond. B* **340**, 187-195.
- Schaefer, H. M., Schaefer, V. and Vorobyev, M. (2007). Are fruit colors adapted to consumer vision and birds equally efficient in detecting colorful signals? *Am. Nat.* **169**, S159-S169.
- Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M. and Summers, K. (2004). Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* **207**, 2471-2485.
- Siebeck, U. E. and Marshall, N. J. (2001). Ocular media transmission of coral reef fish – can coral reef fish see ultraviolet light? *Vision res.* **41**, 133-149.
- Stevens, M. (2007). Predator perception and the interrelation between different forms of protective coloration. *Proc. R. Soc. Lond. B* **274**, 1457-1464.
- Strauss, S. Y., Sahli, H. and Conner, J. K. (2005). Toward a more trait-centered approach to diffuse (co)evolution. *New Phytol.* **165**, 81-90.
- Stuart-Fox, D. M., Moussalli, A., Marshall, N. J. and Owens, I. P. F. (2003). Conspicuous males suffer higher predation risk: visual modeling and experimental evidence from lizards. *Anim. Behav.* **66**, 541-550.
- Stummer, L. E., Weller, J. A., Johnson, M. L. and Côté, I. M. (2004). Size and stripes: how fish clients recognize cleaners. *Anim. Behav.* **68**, 145-150.
- Taylor, M. S. and Hellberg, M. E. (2003). Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* **299**, 107-109.
- Taylor, M. S. and Hellberg, M. E. (2005). Marine radiations at small geographic scales: speciation in Neotropical reef gobies (*Elacatinus*). *Evolution* **59**, 374-385.
- Vorobyev, M. and Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. Lond. B* **265**, 351-358.
- Vorobyev, M., Brandt, R., Peitsch, D., Laughlin, S. B. and Menzel, R. (2001). Colour thresholds and receptor noise: behaviour and physiology compared. *Vis. Res.* **41**, 639-653.
- White, J. W., Grigsby, C. J. and Warner, R. R. (2007). Cleaning behavior is riskier and less profitable than an alternative strategy for a facultative cleaner fish. *Coral Reefs* **26**, 87-94.