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Mimicry, colour forms and spectral sensitivity of the bluestriped fangblenny, *Plagiotremus rhinorhynchos*

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Animals change their body coloration for a variety of purposes including communication, thermoregulation and crypsis. The cues that trigger adaptive colour change are often unclear, and the role of colour vision remains largely untested. Here, we investigated the bluestriped fangblenny (*Plagiotremus rhinorhynchos*), an aggressive mimic that changes its body coloration to impersonate a variety of coral reef fishes. In this field, we determined the fish species that the fangblenny associated with and measured the spectral reflectance of mimics and their models. We measured the spectral absorbance characteristics of the retinal photoreceptor visual pigments in the bluestriped fangblenny using microspectrophotometry and found it to have rod photoreceptors (λ_{max} 498 nm), single cones (449 nm) and double cones (561 nm principal member; 520 nm accessory member). Using theoretical vision models, fangblennies could discriminate between the colours they adopted and the colours of the fish they associated with. Potential signal receivers (*Abudefduf abdominalis* and *Ctenochaetus strigosus*) perceived colours of most mimics to closely resemble fishes they associated with. However, fishes with ultraviolet-sensitive visual pigments were better at discriminating between mimics and models. Therefore, colour vision could be used by fangblennies when initiating colour change enabling them to accurately resemble fishes they associate with and to avoid detection by signal receivers.

Keywords: facultative mimicry; microspectrophotometry; colour vision; colour change; spectral reflectance; coral reef fish

1. INTRODUCTION

Many animal species can quickly alter their body patterns and coloration to communicate with conspecifics (e.g. Hanlon & Messenger 1996; Kodric-Brown 1998), regulate body temperature (e.g. Stevenson 1985), warn predators of toxicity (e.g. Hanlon & Messenger 1996) or match the colour of their surrounding habitat to avoid detection from predators or prey (e.g. Ramachandran *et al.* 1996; Stuart-Fox *et al.* 2006). In most cases, the exact cues that initiate adaptive colour changes are uncertain. One system that has been studied in some detail is the ability of cephalopods to use visual information—including the brightness and spatial frequency structure of the underlying substrate—to alter body patterns and coloration for the purposes of camouflage (Hanlon & Messenger 1988, 1996; Marshall & Messenger 1996). However, most cephalopods are colour blind and cannot use chromatic signals when matching background patterns (Hanlon & Messenger 1988; Marshall & Messenger 1996; Mathger *et al.* 2006). By contrast, the physiological basis for colour vision is common in many other species that act as dynamic mimics or cryptic species, including coral reef fishes (e.g. Losey *et al.* 2003; Marshall *et al.* 2006). For these species, it is unclear whether colour vision is an important component in attaining an accurate

resemblance to their background. Colour vision in signal receivers viewing these species may also influence their success; signal receivers with good colour vision may be able to distinguish mimetic/cryptic species from their background based on colour alone. Therefore, to investigate the selective pressures on adaptive colour change, we should consider colour vision in the species that is changing colour, and in species that act as signal receivers (e.g. Chittka 2001; Théry & Casas 2002; Stuart-Fox *et al.* 2003; Théry *et al.* 2005).

Many coral reef fishes are capable of rapid colour change within a few seconds or minutes (Crook 1997*a,b*; Mathger *et al.* 2003), e.g. the coral trout *Plectropomus leopardus* can switch its coloration from black to striped to white in a matter of seconds, depending on its background (Marshall *et al.* 2006). However, few studies have attempted to quantitatively measure and analyse the colour change (but see Mathger *et al.* 2003). The bluestriped fangblenny *Plagiotremus rhinorhynchos*, an aggressive mimic, attacks larger reef fish to feed on pieces of fin, mucus and body tissue (Kuwamara 1981), and can alter its body colour depending on the availability of fish that it is mimicking (Cheney *et al.* 2008). The repertoire of disguises displayed by the fangblenny appears to prevent or reduce detection by potential victims, and possibly by predators (Côté & Cheney 2007). In its 'mimic' colour form, which is characterized by a black body with a lateral neon blue stripe (Randall *et al.* 1997;
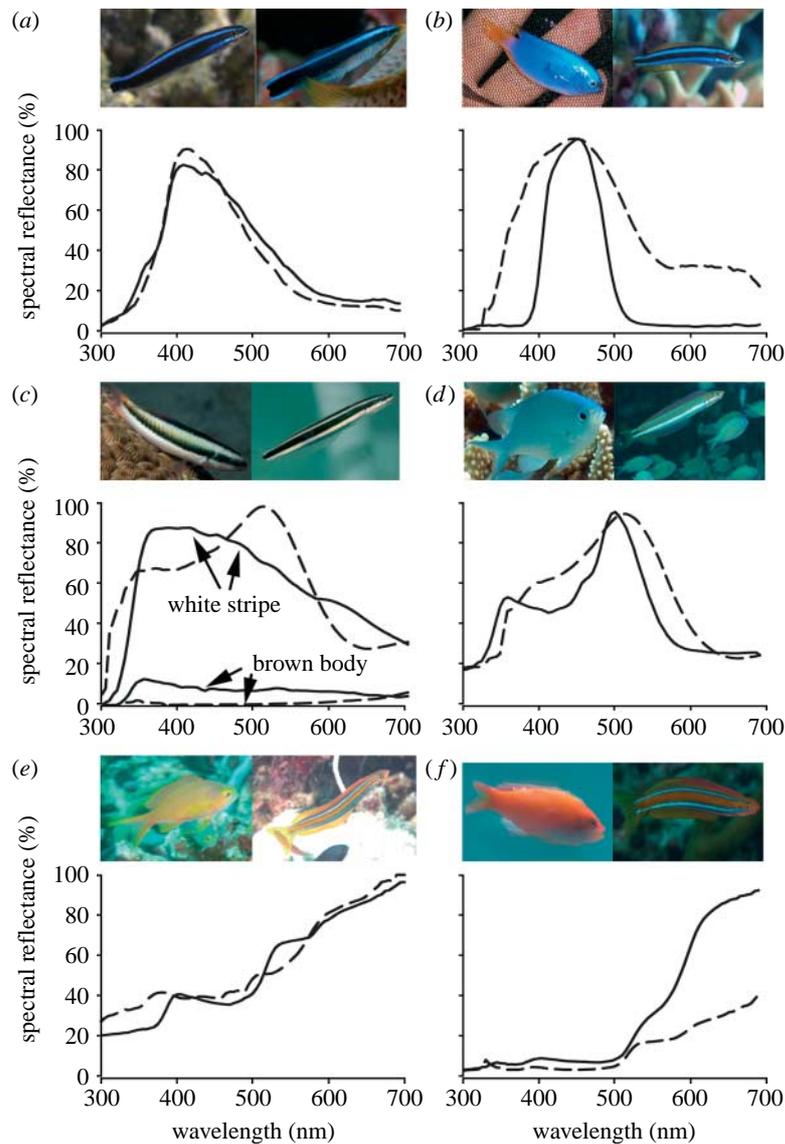
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Figure 1. Mean spectral distribution of colours measured on each fish species. Solid curves indicate the colours of associated fish and dashed curves indicate the colours of fangblennies. (*a*) Blue stripe of juvenile *Labroides dimidiatus* and blue stripe of black/blue fangblenny, (*b*) blue body of *Chrysiptera parasema* and blue stripe of brown fangblenny/two blue stripes, (*c*) *Thalassoma amblycephalum* and brown/white fangblenny, (*d*) body colour of *Chromis viridis* and stripe of olive/light blue fangblenny, (*e*) orange body colour of *Pseudanthias huchtii* and body colour of orange fangblenny and (*f*) orange body colour *Pseudanthias dispar* and body colour of orange fangblenny.

Côté & Cheney 2005; figure 1*a*), the bluestriped fangblenny closely resembles and associates with juvenile cleaner wrasse, *Labroides dimidiatus*. Other 'non-mimic' colour forms include orange, brown or olive body colour with two pale blue stripes that are often found hiding within similarly coloured shoals of fish (Russell *et al.* 1976; Côté & Cheney 2005; Cheney *et al.* 2008; figure 1*b*–*f*). In these non-mimic colour forms, only a portion of their body approximates the colour of the fish they associate with (either their body colour or lateral stripes). However, this appears to be sufficient to allow them to blend in with the shoals of fish making them difficult to detect—at least from a human's perspective. Bluestriped fangblennies can switch between the colour forms, particularly in the presence or the absence of juvenile cleaner wrasse (Moland & Jones 2004; Côté & Cheney 2005; Cheney *et al.* 2008). However, whether colour vision is important to fangblennies when changing colour or selecting shoal mates is unclear.

In this study, we first identified whether different colour forms of bluestriped fangblennies were associated with particular species of shoaling fish. Second, we used spectroradiometry to measure the colours of each fangblenny and those of the shoaling fish with which they associated. We have presented some preliminary colour data on this previously (Cheney *et al.* 2008); however, a new study site provided more colour forms of fangblenny and an increased variety of associated shoaling fish species. Third, we examined the visual system of the bluestriped fangblenny using microspectrophotometry and measured the spectral absorption characteristics of photoreceptor visual pigments found in the retina. Finally, we used a photoreceptor noise-limited colour discrimination model (Vorobyev & Osorio 1998) to assess whether fangblennies could discriminate between the various colorations they adopt and the different colours of the fish they associate with. If so, colour vision could be used to initiate colour change in the fangblenny mimic. It is

possible that fangblennies can view some of their own body coloration: they swim in an 'S' shape motion and often adopt a head-to-tail circular pose. We also examined whether potential signal receivers perceive fangblennies to be accurate mimics of the fish they are attempting to impersonate. If so, fangblenny coloration should be used to avoid detection by signal receivers.

2. MATERIAL AND METHODS

(a) *Study site and species*
The field component of this study was conducted on coral reefs around Pulau Hoga 05°28′ S, 123°45′ E, southeast Sulawesi, Indonesia in July–August 2006. We located 60 bluestriped fangblennies (*P. rhinorhynchos*) on eight different reefs at depths between 2 and 18 m. Fangblennies were classified subjectively by eye into five different colour categories: (i) black body with one neon blue lateral stripe (figure 1*a*), (ii) black/dark brown with two lateral blue body stripes (figure 1*b*), (iii) brown with two light blue/white body stripes (figure 1*c*), (iv) olive with two light blue/white body stripes (figure 1*d*), and (v) orange body with two light blue/white stripes (figure 1*e,f*). The size (total length, TL) of each fangblenny was estimated underwater from a distance of approximately 2 m, and estimated to the nearest 5 mm using a ruler placed on the substrate as a reference. In a preliminary study, fangblenny TL was estimated by the observer under similar conditions and compared with actual length measured with a ruler once the fishes had been captured ($n=25$). Differences between the estimated and actual length were calculated (mean±s.d.: 3.5 mm±4.4). We also recorded the number and species of fishes that were located within an estimated 2 m radius of the location where fangblenny was first seen, for a period of 5 min. Shoaling fish were considered to be groups of more than 20 individual fish from the same species located in the same area.

(b) *Underwater spectroradiometry*
We caught and measured the colours of fangblennies ($n=17$) that were associating with shoals of fish and also one to three of the shoaling fish ($n=35$). We also caught and measured the colours of five black and blue fangblennies and five juvenile *L. dimidiatus* (figure 1*a*) with which these fangblennies were associating and potentially mimicking. The fish were caught with the hand and barrier nets and placed into a clear plastic bag that was equally permeable to all wavelengths of light between 300 and 900 nm, and absorbed less than 1 per cent of the incident light across this wavelength range. The fish were held in one corner of the bag and colour measurements were taken immediately after capture in an attempt to avoid any colour change associated with capture. These colour changes are observed typically 10–30 min after capture (Cheney *et al.* 2008) and in particular on transfer to aquaria, hence the necessity of measuring fish *in situ*. The colours were measured underwater using an Ocean Optics USB2000 spectrometer (Ocean Optics, Dunedin, FL) enclosed in an underwater housing (Wills Camera Housings, Victoria, Australia). The spectrometer was powered by a battery pack and connected to a handheld computer with modified PALM-SPEC software (Ocean Optics). The light reflected from each coloured area of the fish (including background body colour and stripes of fangblenny, and the overall body colour of shoaling fish) was measured through a modified (shortened,

length 60 cm) fibre-optic cable (diameter 200 and 1000 μm) and stored by the spectrophotometer. The bare end of the fibre was placed close to the fish so that it sampled from that colour region alone and at a 45° angle to reduce specular reflectance. Each measurement was an average of at least 10 randomly selected spots of each coloured area (more than 5 mm²) of the fish. Colour measurements were calibrated against a Spectralon 99 per cent white reflectance standard (LabSphere, USA) placed in the bag along with the fish. After colour measurements were taken, fish were measured for TL, which were 2.5±2.3 mm (mean±s.d.) different from our estimates, and released back at the location where they were caught.

Illumination was measured underwater where the fish were located using the underwater spectrometer (as described above). Sidewelling irradiance measurements were taken with modified (shortened, length 60 cm) fibre-optic cables (diameter 200 and 1000 μm) fitted with a cosine corrector, 1–2 m away from reef and pointing horizontally at the reef.

(c) *Microspectrophotometry*
Bluestriped fangblennies used for microspectrophotometry ($n=8$) were collected using hand nets from coral reefs around Lizard Island (14°40′ S 145°28′ E) and Heron Island (23°26′ S 151°55′ E), Great Barrier Reef, Australia between January 2006 and February 2007, and were transported to the University of Queensland in oxygenated seawater. They were housed in aquaria under ultraviolet wavelength-enhanced fluorescent strip lighting on a 12 L : 12 D photo-period until use (1–10 weeks), and were maintained on a diet of finely chopped prawn. Prior to each experiment, the fish were dark adapted overnight, anaesthetized using clove oil (1 ml of 20% clove oil/ethanol solution sprayed into a 5 l container) and killed by decapitation under dim red light.

Eyes were removed and dissected under infrared (IR) illumination with the aid of a dissecting microscope fitted with an IR image converter (FJW Optical Systems, Inc., Palatine, IL, USA). Retinae were removed from the back of the eye and placed in cold (4°C) phosphate-buffered saline (PBS, Oxoid Australia Pty Ltd, Thebarton, Australia; osmolality 340 mOsmol kg^{-1}). Small pieces of retinal tissue (approx. 1 mm²) were mounted on a 22×64 mm no. 1 glass cover-slip in a drop of PBS containing 10 per cent dextran (MW 282 000; Sigma D-7265). The retina was then teased apart using fine needles to detach individual photoreceptors from other retinal tissue. The preparation was covered with an 18×18 mm no. 0 glass cover-slip and sealed using clear nail varnish to prevent dehydration and movement of the specimen.

Absorbance spectra (350–800 nm) of individual rod and cone outer segments were measured using a computer-controlled, single-beam, wavelength-scanning microspectro-meter as described in detail elsewhere (Hart 2004). Each pre-bleach absorbance spectrum consisted of a sample scan of the outer segment and a baseline scan of a cell-free area of the preparation adjacent to the outer segment. Following the pre-bleach scans, the outer segments were bleached with full spectrum 'white' light from the monochromator for 3 min and a further sample and baseline scan made 'post-bleach'. The post-bleach spectrum was then subtracted from the pre-bleach spectrum in order to produce a difference spectrum for each outer segment and to confirm photolability. Spectral data were processed and analysed as described in detail elsewhere (Hart *et al.* 2004; Mosk *et al.* 2007). Pre-bleach

and difference spectra from each photoreceptor type that satisfied established selection criteria (Levine & MacNichol 1985; Hart *et al.* 1998) were averaged and reanalysed to obtain mean absorbance spectra for display.

(d) *Modelling visual systems*

We used a photoreceptor noise-limited colour discrimination model (Vorobyev & Osorio 1998; Vorobyev *et al.* 2001) to assess how fangblennies perceive the various colours they can adopt and those of the fishes they are trying to mimic. We also assessed how the colours of fangblenny mimics and their associated fish appear to other reef fishes. The model application used here involves the calculation of colour distances (ΔS) within the visual 'space' of the fish. Essentially, different colours that appear similar to a signal receiver (either because of the nature of their visual system or an absolutely small difference in the reflectance spectra of the colours) result in small ΔS values, while those that have high chromatic contrast have large ΔS values. We calculated the colour distances (ΔS) between the body colours of fangblennies and their associated shoaling fish species when viewed by two representative reef fish species for which spectral sensitivity data are available. When fangblennies were in their non-mimic colour forms, we modelled the colour patch that they had altered to match the fish they were associated with (figure 1). The two fish species selected as signal receivers in the fangblenny mimicry system were the planktivorous damselfish *Abudefduf abdominalis* and the herbivorous surgeonfish *Ctenochaetus strigosus*. These species were selected because their visual systems differ markedly (especially in their sensitivity to ultraviolet wavelengths), they are attacked by fangblennies (K. L. Cheney 2006, personal observation), they inhabit different areas of the coral reef, and both species were found at our study site. The spectral absorbance properties of the visual pigments in these two species have been measured previously using microspectro-photometry (Losey *et al.* 2003).

Colour vision is assumed when animals possess more than one spectral sensitivity measured in the retina (Lythgoe 1979). In studies with animals where behavioural trials testing colour vision have been conducted, this has been shown to be the case (for review see Kelber *et al.* 2003), and fishes are no exception (Siebeck *et al.* 2008). The different functions of each type of receptor are still unclear, but here we assume that both double cones (paired cones with different visual pigments) and twin cones (paired cones with similar morphology and visual pigment type) are used in colour vision. However, in some animal groups, such as birds, double cones are thought to be used in luminance vision (Osorio & Vorobyev 2005).

We modelled two scenarios for each fish, that the two members of the double cone (i) can be used independently in the visual process and (ii) may be optically coupled owing to the lack of pigmented screening pigment between their outer segments. *Abudefduf abdominalis* is reported to have four pigments: 347 nm (single cone); 464 nm (single); and 519 nm and 457 nm (double) (Losey *et al.* 2003). Owing to the significant overlap in the long-wavelength-sensitive (LWS) single cone (464 nm) and the accessory member of the double cone (457 nm), we modelled *A. abdominalis* as a trichromat with three cone pigments: λ_{max} at 347 nm; 457 nm; and 519 nm (one UV single and one double cone) and as a trichromat with λ_{max} 347 nm, 464 nm and the double cone pigments combined. *Ctenochaetus strigosus* was modelled

as a tetrachromat with four pigments: λ_{max} at 453 nm; 501 nm; 521 nm; and 548 nm (one single, one twin and one double cone), and as a trichromat with pigments 521 and 548 nm combined. However, we found no difference in our conclusions when we modelled each scenario. Therefore, we present the data assuming that the members of the double cone work independently from one another. Calculated quantal spectral sensitivities for each of the cones were multiplied by the spectral transmittance of the ocular media measured in each of these species previously (Siebeck & Marshall 2001; Losey *et al.* 2003).

In the absence of the behavioural data on the visual thresholds of these species, the Weber's fraction of the 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 & Stiles 1982). Should the Weber's fraction be twice higher or twice lower than our estimated value of 0.05, the colour distances would increase or decrease by a factor of 2. Although this may affect the absolute values of colour distances, the relative difference between different visual systems would not be affected. The relative proportions of the different spectral cone types in fangblennies and the other fishes were based on the morphological studies of reef fish retina (N. J. Marshall 2000, unpublished data). We used a ratio of 1 : 2 : 2 (short-wavelength-sensitive (SWS) cones to medium-wavelength-sensitive (MWS) double cone members to LWS double cone members; S : M : L). We also modelled the data with a ratio of 1 : 1 : 1 for trichromats and 1 : 1 for dichromats, but found no significant differences in our overall conclusions.

Colour 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 are normalized against an adaptive background. As a typical background colour, an average spectra from 210 corals of different species was used (Marshall *et al.* 2003).

(e) *Statistical analysis*

We used a general linear model to test for differences between the calculated colour distances of fangblenny and associated fish species. Colour distances were log transformed to fit a normal distribution and were used as the dependent variable. Signal receiver and fangblenny-associated fish pairs were factors. Least significant difference *post hoc* tests were used to identify differences between signal receivers and fangblenny-associated fish species. All statistical analyses were conducted with R v. 2.4.1 (R Foundation for Statistical Computing, Vienna; http://www.R-project.org).

3. RESULTS

(a) *Fangblenny associations with shoaling fish*

Light brown fangblennies were significantly more likely to associate with *Thalassoma amblycephalum*, olive fangblennies with *Chromis viridis* and orange fangblennies with *Pseudanthias huchtii* or *Pseudanthias dispar*, compared to any other fangblenny colour form or with any other shoaling or non-shoaling fish species (table 1). Black and blue mimic fangblennies were significantly more likely to associate with juvenile cleaner wrasse (table 1). There was no significant association for fangblennies that were black with two blue stripes ($\chi^2_4 = 6.4$, $p = 0.17$; table 1).

Table 1. Number of fangblennies that were found associated with different species of shoaling or non-shoaling fishes. (Asterisks indicate that fangblenny colour form is more likely to be associated with that particular species compared to other colour forms ($\chi_4^2 > 12.3$, $p < 0.05$). In the categories 'other', a particular fish species was not present more than once.)

|	shoaling fishes					non-shoaling fishes	
	Chromis viridis	*Pseudanthias huchtii* or *P. dispar*	*Thalassoma amblycephalum*	*Chrysiptera parasema*	other	juvenile *Labroides dimidiatus*	other
fangblenny colour form							
black and blue ($n=15$)	0	0	1	0	0	12*	2
black and two blue stripes ($n=7$)	1	0	0	2	1	2	1
light brown with two stripes ($n=17$)	1	0	6*	0	2	1	7
olive with two stripes ($n=10$)	5*	1	0	0	1	0	3
orange with two stripes ($n=11$)	0	8*	0	0	1	0	2
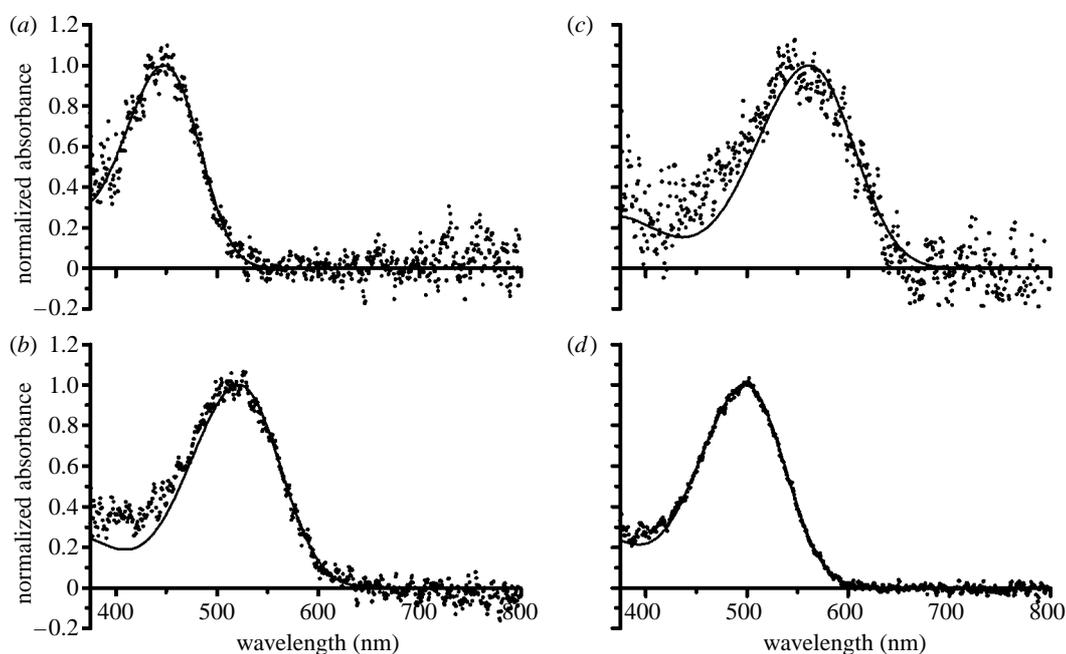
Figure 2. Normalized pre-bleach absorbance spectra for (*a*) the SWS single cones, (*b*) the MWS visual pigment found in one member of the double cone pair, (*c*) the LWS visual pigment found in the other member of the double cone pair and (*d*) the MWS visual pigment found in the rod photoreceptors of the bluestriped fangblenny, *P. rhinorhynchos*. Spectra are fitted with rhodopsin (vitamin A$_1$ based) templates of the appropriate λ_{max}, calculated using the equations of Govardovskii *et al.* (2000).

Other non-shoaling fishes found in the vicinity of fangblennies included damselfish (Pomacentridae), wrasse (Labridae), butterfly fish (Chaetodontidae), parrotfish (Scaridae), snapper (Lutjanidae) and surgeon-fish (Acanthuridae); however, we found no other patterns of association with these fishes and fangblennies ($\chi^2 < 0.15$, $p > 0.52$).

Smaller fangblennies were more likely to be found with shoals of fish compared to larger fangblennies (mean ± s.d. (TL mm); with shoal 46.8 ± 5.3; no shoal 54.9 ± 8.6; independent *t*-test: $t_{57.6} = -2.82$, $p = 0.007$).

(**b**) *Spectral reflectance of fish colours*
The colours were measured from 62 individual fishes, comprising 22 fangblennies and 40 associated fishes. Average spectra for fangblenny-associated fish pairs are

illustrated (figure 1). All colours could be described by colour categories as identified by Marshall (2000).

(**c**) *Microspectrophotometry*
Microspectrophotometric data for visual pigments of the bluestriped fangblenny are summarized in figure 2 and table 2. A total of 18 rods and 64 cones were scanned, and some records were rejected because they were of insufficient quality. Twenty-three spectra were retained for further analysis. The retina of the bluestriped fangblenny contained four different types of visual pigments. Rods contained a medium-wavelength ('green')-sensitive visual pigment with a mean ($n=8$) pre-bleach maximum absorbance (λ_{max}) at 498 nm. There was one spectrally distinct type of single cone with a short-wavelength ('blue')-sensitive type with a 449 nm λ_{max}

Table 2. Spectral characteristics of visual pigments found in the rod, single cone and double cone photoreceptors of the bluestriped fangblenny *P. rhinorhynchos*. (Each double cone had the MWS visual pigment in one member and the LWS visual pigment in the other.)

| | | double cone | | |
	single cone	MWS	LWS	rod
mean λ_{max} of pre-bleach absorbance spectra (nm)	448.7 ± 4.5	520.0 ± 3.6	560.6 ± 6.6	498.3 ± 2.0
λ_{max} of mean pre-bleach absorbance spectrum	447.6	521.0	561.0	498.0
mean λ_{max} of difference spectra (nm)	446.4 ± 5.3	519.8 ± 2.1	563.8 ± 7.2	500.9 ± 2.6
λ_{max} of mean difference spectrum (nm)	448.5	520.9	565.6	500.5
absorbance at λ_{max} of mean difference spectrum	0.011	0.015	0.016	0.024
no. of cells used in analysis	5	7	3	8
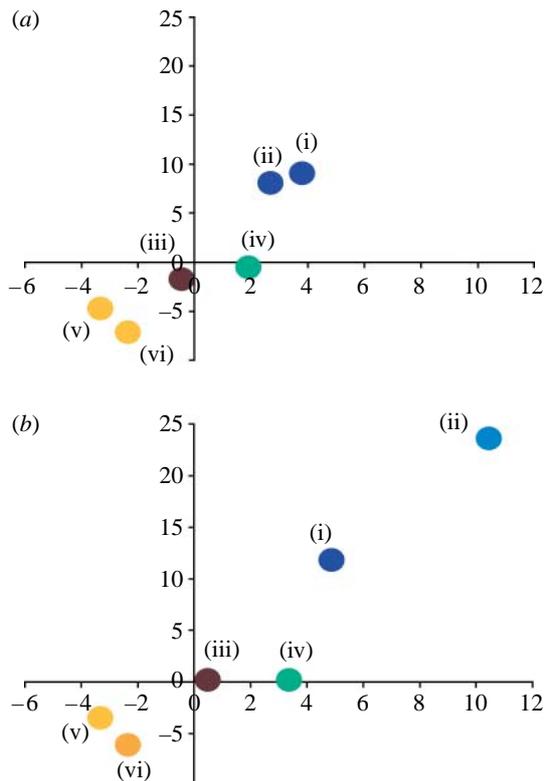
Figure 3. The trichomatic visual system of *P. rhinorhynchos* represented with a two-dimensional chromaticity diagram corresponding to the photoreceptor noise-limited colour opponent model. The colours from (a) fangblennies and (b) associated fish (as shown in figure 1) were plotted according to eqn (B5) in Kelber *et al.* (2003). Chromaticity values that plot at a distance of less than one unit are unlikely to be discriminable along that axis. As the plots increase in distance from one another, colours are more distinguishable from one another. The origin corresponds to all achromatic colours including white, black and grey.

visual pigment ($n = 5$). The double cone members had a medium-wavelength member (green) at 520 nm λ_{max} ($n = 7$) and a long-wavelength ('red')-sensitive cone of 561 nm λ_{max} ($n = 3$; figure 2).

To model the visual system of the bluestriped fangblenny (*P. rhinorhynchos*), the visual pigment absorbance spectrum template of Stavenga *et al.* (1993) was used in preference to data obtained by microspectrophotometry to remove noise from the calculations and eliminate measurement artefacts. The effective absorbance was then calculated for an outer segment with a path length of 7 μm and a specific absorbance of

0.08 μm^{-1}. The effective absorbance of the outer segment was then converted into absorptance and multiplied with the transmissions of the combined ocular media at each wavelength. In a comparable way to our other signal receivers, we modelled *P. rhinorhynchos* as a trichromat ($\lambda_{max} = 449$, 520 and 561 nm) and as a dichromat (with double cone optically coupled), but did not find a significant difference in our results. Again, we present results assuming that the double cone members work independently from one another.

(d) Colour discrimination by fangblennies and other signal receivers

Fangblennies appear capable of distinguishing between their various colour morphs (figure 3a) and between the colours of the fish they associate with (figure 3b). There was no overlap between colours in the chromaticity diagrams, and the colours were distributed across different areas of the plot.

There were significant differences in mean colour distances (ΔS) between pairs of fangblennies and their associated fish species ($F_{5,87} = 5.60$, $p < 0.001$; figure 4). For all signal receivers, brown fangblennies with two stripes that were associated with *Chrysiptera parasema*, and brown and white fangblennies associated with *T. amblycephalum* had relatively large colour distances. Other pairs (four out of six pairs) had relatively small colour distances, with the exception of *A. abdominalis* viewing black and blue fangblennies and *L. dimidiatus* (figure 4).

Overall, there were also significant differences between signal receivers in their ability to discriminate between the body colours of fangblennies and their associated fish models ($F_{3,87} = 3.27$, $p = 0.03$). *Abudefduf abdominalis* was also significantly different from *C. strigosus* (estimated marginal mean $\pm$ s.e.: *C. strigosus* 0.32 ± 0.09; $p < 0.05$). There were no other differences between the species ($p > 0.26$).

In their ability to discriminate between their own colours and associated fish colours, fangblennies were significantly different from *A. abdominalis* (estimated marginal mean $\pm$ s.e.: *P. rhinorhynchos* 0.43 ± 0.09, *A. abdominalis* 0.81 ± 0.09; $p < 0.05$) but not significantly different from *C. strigosus* ($p > 0.05$).

4. DISCUSSION

Using microspectrophotometry, fangblennies were shown to have three types of cone visual pigment within one single (λ_{max} 449 nm) and one double (λ_{max} 520 and
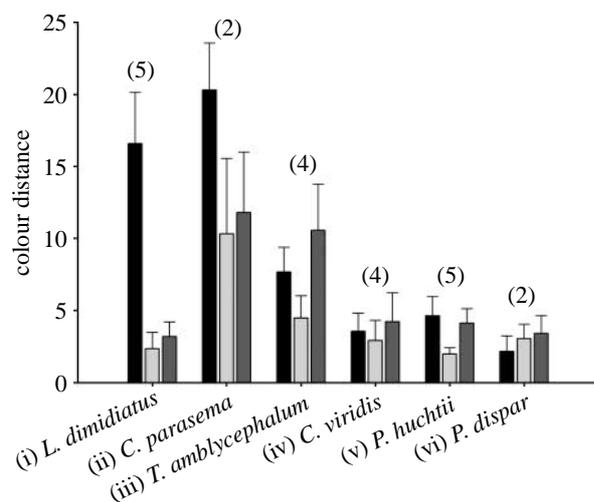
Figure 4. Mean colour distance (ΔS) between fangblenny colour and their associated fish species (pairs as per figure 1). Shaded bars indicate different signal receivers: *A. abdominalis* (black bars), *C. strigosus* (light grey bars) and *P. rhinorhynchos* (dark grey bars). Error bars represent $+1$ s.e. Sample sizes for each pair of species are shown in parentheses.

561 nm) cone. Based on this visual system, we have shown that fangblennies should be capable of discriminating between the various colour morphs they adopt and the colours of the fish they associate with. Therefore, colour vision could potentially be used to initiate colour change in this mimicry system. Different colour forms of the bluestriped fangblenny associated with a variety of similarly coloured species. Fangblennies were successful at camouflaging themselves chromatically against the fish they associated with from the perspective of potential signal receivers. Therefore, fangblenny coloration should help to avoid detection by victims of attack or potential predators. Signal receivers with high UV sensitivity were potentially better at discriminating between fangblennies and their associated fish species. Fangblennies did not appear to be better at discriminating between the colours of conspecifics and the fish they may impersonate compared to other potential signal receivers.

Orange fangblennies associated with orange anthias *P. huchtii* and *P. dispar*, while olive-coloured fangblennies sought protection in similarly coloured shoals of damselfish *C. viridis*. The body colours and/or stripes of both orange and olive colour forms closely matched their shoal mates. Mimic black and blue fangblennies were more likely to associate with juvenile *L. dimidiatus* compared to any other fish species (also shown in Côté & Cheney 2005), and also closely matched their coloration (see also Cheney et al. 2008).

Brown and white fangblennies were found to significantly associate with *T. amblycephalum*; however, our vision models suggest that most assumed trichromatic signal receivers may be able to distinguish them from their shoal mates based on colour. *Thalassoma amblycephalum* is of a similar shape and size to fangblennies, with a similar lateral stripe on their body; therefore, when the body shape and patterns are more similar, a close match in colour may be less important. Black fangblennies with two lateral blue stripes did not appear to associate with or resemble the colours of *C. parasema*, or any other fish

species. This colour form may be an intermediate phase from mimic black and blue neon stripe to non-mimic, as fangblennies tend to gain another stripe when changing coloration. However, our sample size was small and this requires further investigation.

Not all *P. rhinorhynchos* individuals were found associated with shoaling fish species or with juvenile *L. dimidiatus*. The ratio of fangblennies associating with other fish varies considerably between sites (Moland & Jones 2004; Cheney et al. 2008); the distribution of other reef fish species and availability of particular habitats may affect the numbers of different non-mimic colour morphs and should be included in future studies. Smaller fangblennies were more likely to be associated with shoals of fish compared with larger individuals. Fangblennies may be more susceptible to predation when they are small or they may lose their ability to change colour as they grow (Cheney et al. 2008). Additionally, if fangblennies become larger than their shoal mates, then they may be more detectable to signal receivers and thus lose the benefits gained from associating with shoals.

The bluestriped fangblenny has three types of cone visual pigments, similar to many other coral reef fishes (Losey et al. 2003; Marshall et al. 2006). Fangblennies were found to have one type of SWS single cone ($\lambda_{max}=$ 449 nm), and one type of double cone with a MWS visual pigment in one member ($\lambda_{max}=520$ nm) and LWS visual pigment in the other ($\lambda_{max}=561$ nm). Compared to other species of reef fishes, the sensitivity of the long-wavelength cone was longer than as is often found (Losey et al. 2003), with the exception of the sea horse *Hippocampus barbouri* (Mosk et al. 2007) and giant shovelnose ray (Hart et al. 2004). However, this did not significantly affect the fangblennies' ability to discriminate between their colours morphs or fishes they may impersonate.

We did not find evidence of a UV-sensitive receptor in fangblennies (Losey et al. 1999, 2003). Whether fangblennies are dichromatic or trichromatic also remains to be determined. If the signals from each member of the double cones—with their different spectral sensitivities—can be compared with each other and with the single cones, there is the possibility for trichromatic colour vision. If the signals from the two members of the double cone are pooled, then this combined signal with a broad spectral sensitivity function could be compared with the single cones to provide a dichromatic colour sense. Of course, if double cones are not involved in colour vision, then the fangblenny may lack colour vision altogether.

This is the first time that underwater spectroradiometry, microspectrometry and theoretical vision models have been used in combination to examine colour mimicry in fish, enabling us to determine how signal receivers view colour signals independently of our own visual bias.

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