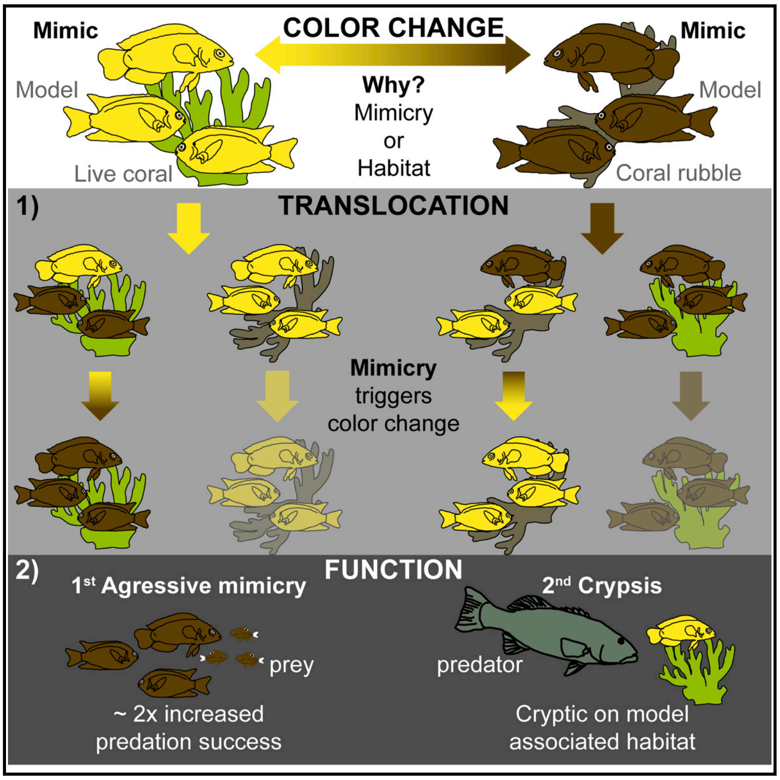
Report

Current Biology

Phenotypic Plasticity Confers Multiple Fitness Benefits to a Mimic

Graphical Abstract



Highlights

- Fish mimics can flexibly change color to imitate multiple model species
- Flexible mimicry increases predation success by preventing detection by prey
- Changing color also increases protection by deceiving larger predatory fish
- Phenotypic plasticity thus enables the continuous use of deceptive signals

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In Brief

Cortesi et al. show that a predatory fish changes color to mimic various surrounding fishes. This prevents detection by prey, increasing predation success, and reduces detection by larger predators. Phenotypic plasticity is a novel strategy to maintain the effectiveness of deceptive signals.

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Report

Phenotypic Plasticity Confers Multiple Fitness Benefits to a Mimic

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SUMMARY

Animal communication is often deceptive; however, such dishonesty can become ineffective if it is used too often, is used out of context, or is too easy to detect [1–3]. Mimicry is a common form of deception, and most mimics gain the greatest fitness benefits when they are rare compared to their models [3, 4]. If mimics are encountered too frequently or if their model is absent, avoidance learning of noxious models is disrupted (Batesian mimicry [3]), or receivers become more vigilant and learn to avoid perilous mimics (aggressive mimicry [4]). Mimics can moderate this selective constraint by imperfectly resembling multiple models [5], through polymorphisms [6], or by opportunistically deploying mimetic signals [1, 7]. Here we uncover a novel mechanism to escape the constraints of deceptive signaling: phenotypic plasticity allows mimics to deceive targets using multiple guises. Using a combination of behavioral, cell histological, and molecular methods, we show that a coral reef fish, the dusky dottyback (*Pseudochromis fuscus*), flexibly adapts its body coloration to mimic differently colored reef fishes and in doing so gains multiple fitness benefits. We find that by matching the color of other reef fish, dottybacks increase their success of predation upon juvenile fish prey and are therefore able to deceive their victims by resembling multiple models. Furthermore, we demonstrate that changing color also increases habitat-associated crypsis that decreases the risk of being detected by predators. Hence, when mimics and models share common selective pressures, flexible imitation of models might inherently confer secondary benefits to mimics. Our results show that phenotypic plasticity can act as a mechanism to ease constraints that are typically associated with deception.

RESULTS AND DISCUSSION

Animals commonly use deceptive signals to increase access to food [1], reproductive opportunities [8], or protection from predation [9]. These uses of deception, however, bear a common risk: if deceptive signals are used too frequently or out of context, receivers can learn to recognize them and eventually ignore or even punish the signaler [1–3, 10]. Animals are known to “negotiate” such deceptive constraints with genetic adaptations (i.e., polymorphisms) [6] or by opportunistically switching between deceptive and nondeceptive signals [1, 7, 8]. Nonetheless, how obligate deceivers, such as many mimics, limit the costs imposed by deceptive constraints remains unclear.

In this context, we explored the function of color changes in the dusky dottyback, *Pseudochromis fuscus*, a small predatory fish (total length [TL] ~ 8 cm) common to Indo-Pacific coral reefs [11]. Dottybacks vary in coloration, with brown, yellow, pink, orange, and gray morphs being reported throughout their range [11]. On the reefs surrounding Lizard Island, Great Barrier Reef, Australia, two of these color morphs (yellow and brown) co-occur, and while yellow morphs are mostly seen on live coral together with similar-looking yellow damselfishes (*Pomacentrus* spp., such as the Ambon damselfish, *P. amboinensis*, and lemon damselfish, *P. moluccensis*) (Figure 1A), brown morphs are mostly seen on coral rubble together with similar-looking brown damselfishes (such as the whitetail damselfish, *P. chrysurus*) [12] (Figure 1B). In general, dottybacks are solitary and territorial, and although both yellow and brown damselfishes, live coral, and coral rubble habitat can be found within their territories [12], yellow morphs occupy significantly smaller home ranges compared to brown morphs (home range size, n = 10 morphs each, mean ± SEM: yellow dottyback 5.5 ± 1.6 m^2, brown dottyback 11.2 ± 1.7 m^2; independent t test, $t_{18} = 2.86$, p = 0.01). Color dimorphism is not sex linked [12], though, and yellow and brown morphs are genetically indistinguishable using either mitochondrial [13] or microsatellite markers (this study; n = 31 yellow/39 brown morphs, $F_{ST} = 0$, p = 0.68; Figure S1), precluding color assortative mating as a driver for color dimorphism. Yellow dottybacks have previously

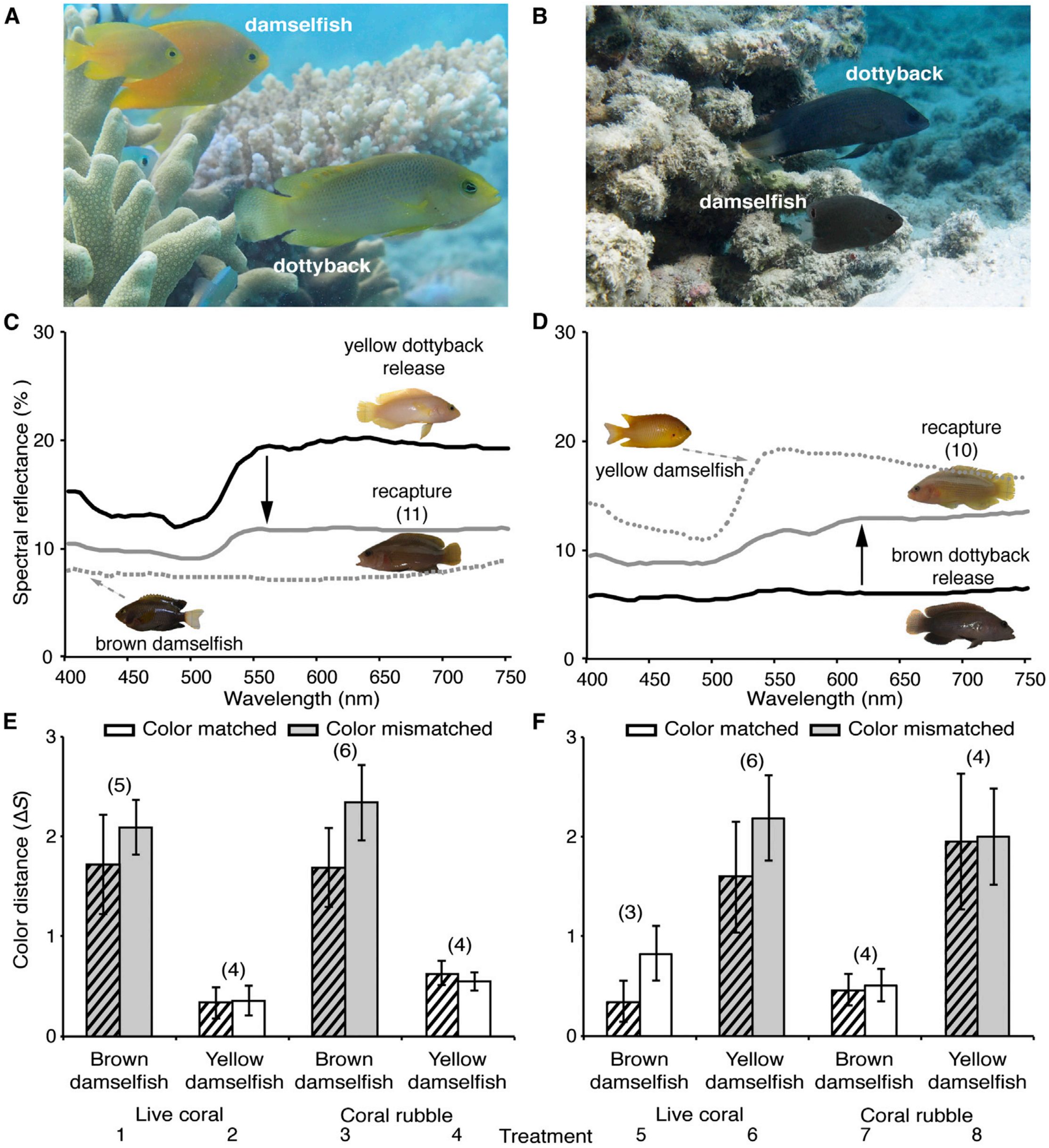

Figure 1. Environmental Cues for Color Change in Dottybacks

(A and B) In the field, yellow dottybacks associate with yellow damselfish on live coral (A), and brown dottybacks associate with brown damselfish on coral rubble (B). (See Figure S1 for population genetic assessment.)

(C and D) Mean spectral reflectance measurements from yellow dottybacks (C) and brown dottybacks (D) that changed color during the translocation experiment. (See Figure S3 for histological assessments of color change.)

(E and F) Color distances (Δ*S*, mean ± SEM) between body coloration before release and after recapture for yellow dottybacks (E) and brown dottybacks (F) as perceived by the potentially tetrachromatic visual systems of a dottyback predator, the coral trout (hatched bars), and a dottyback prey, the juvenile Ambon damselfish (plain bars). (See Figure S2 for Δ*S* of potentially trichromatic visual systems.) Numbers in parentheses denote sample size.

Images by K.L.C. and F.C.

been shown to change their body coloration to brown within two weeks when translocated to artificial patch reefs comprising primarily dark coral rubble [13], indicating that coloration is a plastic trait. Furthermore, it has been suggested that dottybacks aggressively mimic similarly colored adult damselfishes to gain increased access to juvenile damselfishes, upon which they prey [12]. However, the cues that drive color change and the associated fitness benefits remain unclear.

In this study, we first conducted a translocation experiment to investigate whether habitat composition or, alternatively, the color of resident adult damselfish would induce color change in dottybacks. To this end, we built experimental patch reefs

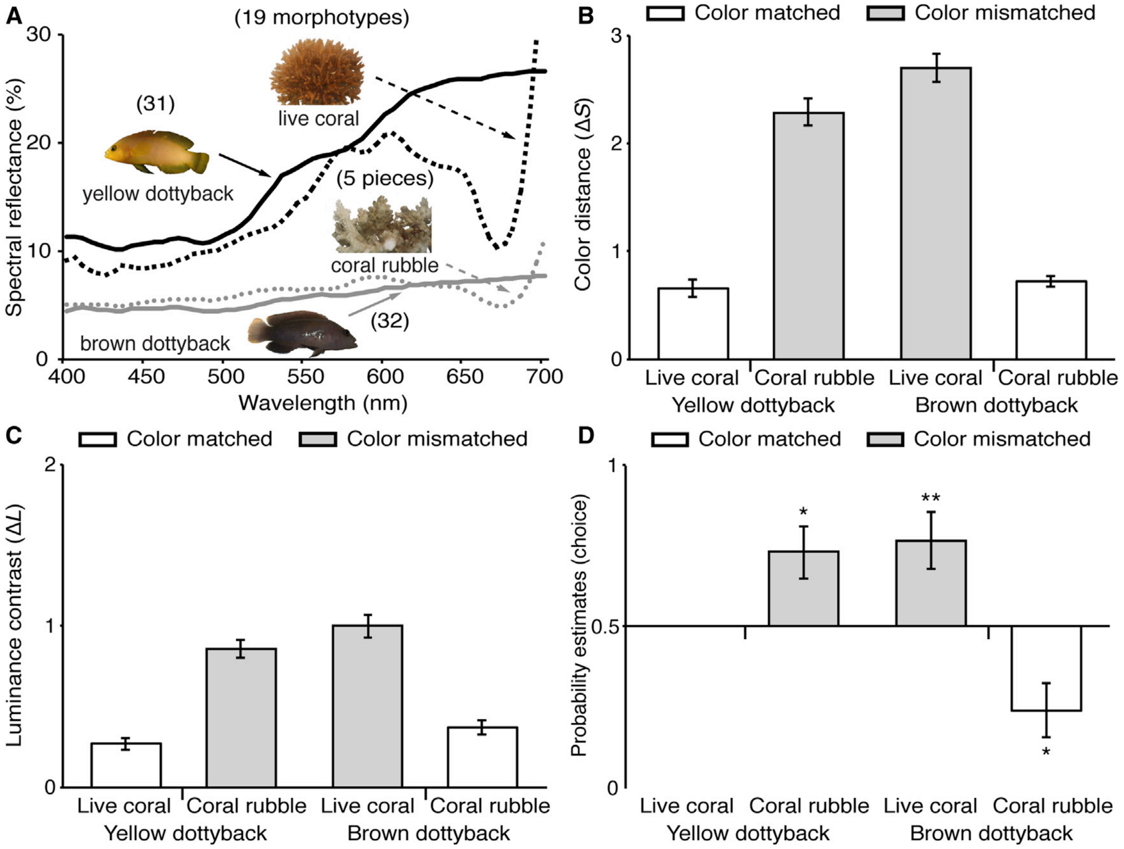

Figure 2. Cryptic Benefits of Color Change

(A) Mean spectral reflectance measurements used to assess the conspicuousness of dottybacks (yellow and brown) when perceived on model-associated habitat types (live coral and coral rubble) by the predatory coral trout. Numbers in parentheses denote sample size. Images by F.C.

(B and C) Color distance (B) (ΔS, mean ± SEM), and luminance contrast (C) (ΔL, mean ± SEM) between dottyback morphs and different habitat types.

(D) Probability estimates (mean ± SEM) of coral trout striking at yellow and brown dottyback morphs when placed against different habitat backgrounds (see also Movie S1). Yellow dottyback on live coral was used as the baseline treatment against which the other treatments were compared. The 0.5 line indicates equal choice between treatments and the baseline (significant difference from baseline, $^{*}z \leq -2.51$ or ≥ 2.35, $p < 0.05$; $^{**}z \geq 2.43$, $p < 0.01$).

comprising primarily live coral (60%–70% cover, light green to yellow background coloration; Figure 2A) or coral rubble (80%–90% cover, darker brown background coloration; Figure 2A) and stocked them with yellow (Ambon and lemon) or brown (whitetail) adult damselfish (n = 15 per patch reef). We then added a single yellow or brown dottyback (individually marked with elastomer tags) and assessed whether they changed color after two weeks. Our setup was equivalent to a 2 × 2 × 2 experimental design (dottyback color × damselfish color × habitat type, each with two levels: yellow/brown dottyback, yellow/brown damselfish, live coral/coral rubble) (Table 1). To quantify color change, we measured the spectral reflectance of each dottyback in the laboratory prior to their release and again after recapture (n = 36; Figures 1C and 1D; Table 1). Yellow dottyback morphs were defined as those that exhibited spectral reflectance curves with a cut-on step around 500 nm, reaching a plateau around 625 nm, whereas brown dottyback morphs were defined as those that showed a low overall reflectance with a gradual rise after 500 nm (for a framework of color categorizations, see [14]) (Figures 1C, 1D, and 2A). Next, we used the Vorobyev-Osorio theoretical vision model [15, 16] to quantify changes in body coloration using color distance (ΔS). ΔS was modeled using visual templates of a common predator of dottybacks and damselfishes, the coral trout, *Plectropomus leopardus* [17], and a prey item of dottybacks, juvenile Ambon damselfish [18]. Theoretical fish visual models were used to assure that color change was assessed from the point of view of the relevant signal receivers and independently of human perception. Because it is currently unknown whether these fishes use three or four distinct visual receptors to perceive color, we modeled color change from the perspective of both potentially trichromatic and tetrachromatic visual systems. We found using both models (Figures 1E, 1F, and S2) that independent of habitat type (all interactions involving habitat as a factor were nonsignificant; Table S1), dottyback morphs changed color (from yellow to brown and vice versa) in treatments where dottybacks were released onto patch reefs with damselfishes of a coloration mismatched to their own (potentially tetrachromatic visual system, coral trout: linear model [LM], dottyback color × damselfish color: $F_{1,31} = 34.59$, $p < 0.001$; Ambon damselfish: LM, dottyback color × damselfish color: $F_{1,31} = 60.39$, $p < 0.001$; Figures 1E and 1F; for potentially trichromatic visual systems, see Figure S2

Table 1. Variables Used to Examine the Cues for Color Change in Dottybacks

Treatment	Dottyback Color at Release	Habitat	Damselfish Color (Model) n = 15/Reef	Dottyback n = Release, Recapture	Dottyback Color at Recapture
1	yellow	live coral	brown	6, 5	brown*
2	yellow	live coral	yellow	12, 4	yellow
3	yellow	coral rubble	brown	7, 6	brown*
4	yellow	coral rubble	yellow	9, 4	yellow
5	brown	live coral	brown	8, 3	brown
6	brown	live coral	yellow	9, 6	yellow*
7	brown	coral rubble	brown	5, 4	brown
8	brown	coral rubble	yellow	11, 4	yellow*

A 2 × 2 × 2 translocation experiment (dottyback color × damselfish color × habitat type, each with two levels: yellow/brown dottyback, yellow/brown damselfish, live coral/coral rubble) was used to examine whether habitat or mimicry would induce color change in dottybacks. Note that dottybacks changed color only when mismatched to the color of the damselfish, independent of habitat type (indicated by asterisk). Therefore, dottybacks change color to mimic the local damselfish community. (See also Figures 1 and S2.)

and Table 1). This demonstrates that dottybacks can change their body coloration to match the color of the resident damselfish community.

Subsequent histological examination of skin sections from yellow and brown dottybacks (n = 8 each) revealed that, although morphs did not change the overall number of chromatophores within their skin (number of chromatophores per 0.1 mm^2: yellow dottyback 73.4 ± 4.1, brown dottyback 83.9 ± 4.0; independent t test, $t_{14} = 1.83$, p = 0.09), color change was achieved by an alteration in the relative proportion of xanthophores (yellow pigment cells) compared to melanophores (black pigment cells) (percentage of xanthophores: yellow dottyback 71.6% ± 0.7%, brown dottyback 52.1% ± 1.4%; independent t test, $t_{14} = -11.09$, $p < 0.001$; Figure S3). This change in the relative proportion of chromatophore types appears to be different from other reported cases of color change in fishes, which usually occur as a result of changes in the number of a single chromatophore type (mostly melanophores; “slow” morphological changes) [19] or dispersion and aggregation of pigments inside chromatophores (“fast” physiological changes) [20].

As a second step, we investigated whether dottybacks gain a fitness benefit in terms of increased capture success of juvenile damselfish prey when matching the color of adult damselfish. To examine this, we conducted laboratory predation experiments, in which dottybacks (n = 10 of each color morph per treatment) were placed in a tank with five adult damselfish (TL 45–57 mm, either color matched or mismatched) and ten juvenile brown damselfish (TL < 14.5 mm) for 24 hr. We found that dottybacks were significantly more successful at capturing juvenile damselfish when their color matched that of adult damselfish (generalized linear mixed model [GLMM; binomial], color of dottyback × color of damselfish: $\chi^2_1 = 57.92$, $p < 0.001$; Figure 3), suggesting that by flexibly matching the coloration of adult damselfishes, dottybacks facilitate predation by increased deception of juvenile damselfish prey. This is probably due to the prey exhibiting reduced anti-predator vigilance when unable to detect differences between harmless models (adult damselfishes) and predatory mimics (dottybacks).

In the field, dottyback predation rates are very high (up to ~30 prey fish per day [21]), forcing juvenile fish to learn quickly about the risk that dottybacks impose (either through direct experience or socially) in order to survive [22]. Therefore, similar to the benefits gained from polymorphic adaptations [6] or the deployment of facultative mimetic signals [1, 7], the flexible imitation of multiple models might enable dottybacks to continuously dupe signal receivers by limiting learning in juvenile fish prey. Alternatively, phenotypic plasticity may also enable dottybacks to expand their niche by moving to novel locations devoid of experienced receivers, which may occur both within home ranges and by relocating across reef habitats.

Interestingly, although there was no difference in predatory success when dottyback morphs were matching the color of adult damselfish (prey survival, matched colors: yellow dottyback 5.0 ± 0.7, brown dottyback 3.4 ± 0.9; pairwise post hoc Tukey contrast, $p > 0.05$), brown dottybacks were significantly more successful at capturing prey compared to yellow dottybacks when mismatched in color to the damselfish (prey survival, mismatched colors: yellow dottyback 9.2 ± 0.3, brown dottyback 6.2 ± 1.1; pairwise post hoc Tukey contrast, $p < 0.05$; Figure 3). However, we found no difference in the number of strikes against prey between yellow or brown dottybacks (number of strikes within the first 60 min: yellow dottyback 9.2 ± 3.3, brown dottyback 8.9 ± 3.0; W = 178, p = 0.56). Hence, when mismatched to the color of the adult damselfish, the probability of capturing a prey item per strike was lower in yellow dottybacks, which may be due to an innate higher level of vigilance in juvenile fish prey toward dottybacks of a different color to their own (and the use of only juvenile brown prey during our experiment).

To investigate this, we conducted an additional experiment without adult damselfish, and we found that when given the choice between a juvenile brown or yellow prey, dottybacks more frequently directed their first strike at prey fish that matched their own body coloration (GLMM; binomial: $\chi^2_1 = 17.97$, $p < 0.001$). Dottybacks could exhibit a preference for prey that match their own coloration, but in this scenario, we would expect that yellow dottybacks would strike less frequently at brown prey, which was not observed in the experiment above. Instead, our results suggest that predator avoidance behavior in juvenile prey fish is enhanced when dottybacks are of a different coloration from their own and that, by changing color to imitate

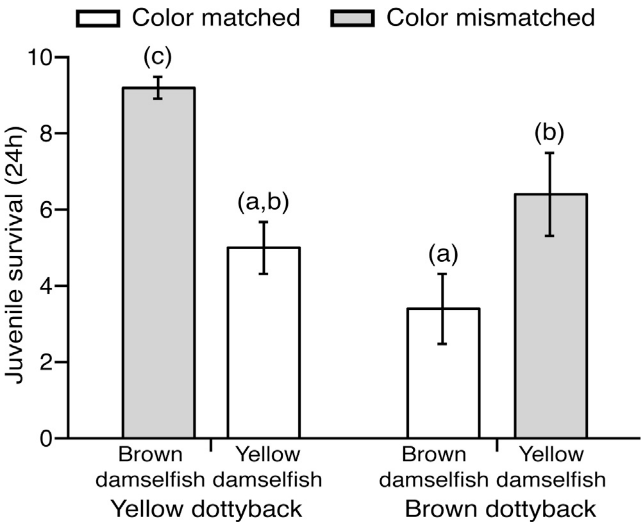

Figure 3. Aggressive Mimicry Benefits of Color Change
Juvenile damselfish prey survival (mean ± SEM, out of 10) after 24 hr when exposed to dottybacks that were matched or mismatched in color to adult damselfish coloration (n = 10 per treatment). Letters above bars denote significant differences between treatments (pairwise post hoc Tukey contrast, $p < 0.05$).

the local damselfish community, dottybacks are able to overcome this innate vigilance. This is comparable to a “wolf in a sheep’s clothing” scenario where distinguishing the predator from harmless heterospecifics becomes increasingly difficult when the predator and the heterospecific look alike, regardless of whether or not the model species matches the appearance of the prey.

Finally, although changes in dottyback coloration were not driven by habitat variables (see the translocation experiment in Figures 1E and 1F), damselfish models match the color of the different habitat types they are naturally found upon (i.e., yellow damselfish on live coral; brown damselfish on coral rubble [23]), which is likely to reduce predation pressure due to cryptic benefits [23]. To investigate whether dottybacks experience similar benefits when matching the color of their habitat, we used the coral trout theoretical vision model to assess dottyback conspicuousness against the different habitat types (Figure 2A). We found that, similar to the damselfish they imitate, dottyback morphs also match the habitat they are commonly found upon, in terms of both color distance (ΔS, linear mixed model [LMM], dottyback color × habitat type: $\chi^2_1 = 171{,}41$, $p < 0.001$; Figure 2B) and luminance contrast (ΔL, LMM, dottyback color × habitat type: $\chi^2_1 = 90.05$, $p < 0.001$; Figure 2C). Next, to test the predictions of the visual model, we conducted a predator choice experiment in the laboratory. Coral trout (n = 5) were trained to strike at laminated images of yellow or brown dottybacks placed against an image of live coral or coral rubble background to receive a food reward. Images were adjusted in Adobe Photoshop CS4 v11.0.2 to ensure that their spectral reflectance matched the predicted coral trout visual receptor response (in ΔS and ΔL) from the visual model. In each trial, coral trout were given the choice between two randomly allocated backgrounds with either a yellow or brown dottyback image placed in front of them. A third background without a dottyback image in front of it was used as a distractor to ensure that trout would not strike haphazardly at backgrounds to elicit the food reward (Movie S1). Coral trout struck significantly more often at dottybacks that were color mismatched with the background (110 trials; 22 ± 4.1 trials per trout; Bradley-Terry model for paired choices, GLMM, yellow dottyback on coral rubble: $z = 2.35$, $p < 0.05$; brown dottyback on live coral: $z = 2.43$, $p < 0.01$) compared to dottybacks that were color matched with the background (Figure 2D). Therefore, while dottybacks change color to aggressively mimic damselfish models, they may also gain a secondary benefit of reduced predation risk when matching the color of model-associated habitat types. Moreover, although not specifically tested in our study, predation risk to dottybacks may be further reduced through dilution when they are associated with a school of similarly colored damselfish models (social mimicry [24]).

Our findings demonstrate that phenotypic plasticity facilitates aggressive mimicry of multiple models in our study system. Dottybacks can change their body coloration depending on the availability of suitable models to gain fitness benefits in terms of increasing access to food. Furthermore, our results highlight that phenotypic plasticity may inherently confer secondary benefits to mimics when mimics and models share ecological pressures: dottybacks benefit from reduced predation risk when living on model-associated habitat. Therefore, phenotypic plasticity may offer a solution to reduce the constraints of deceptive signaling, and dottybacks provide a good example of this adaptive ingenuity.

SUPPLEMENTAL INFORMATION

Supplemental Information includes three figures, one table, Supplemental Experimental Procedures, and one movie and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.02.013.

AUTHOR CONTRIBUTIONS

F.C. conceived the study and designed the experiments together with K.L.C., N.J.M., W.S., and M.C.O.F. F.C., W.E.F., P.A.W., G.A.C.P., E.C.M., and M.C.O.F. performed the experiments. F.C., W.E.F., G.A.C.P., H.N.S., and K.L.C. analyzed the data. F.C., W.E.F., and K.L.C. wrote the initial manuscript. All authors reviewed and approved the final version of the manuscript.

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