Active background choice facilitates crypsis in a tropical crab

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ABSTRACT

Animals can evade predators in multiple ways, one of the most effective of which is to avoid detection in the first place. We know much about the evolution of color patterns that match the visual background to avoid detection (*i.e.*, crypsis), yet we know surprisingly less about the specific behaviors that have co-evolved with these morphological traits to enhance or maintain crypsis. We here explore whether the match between body color and background in a seemingly well-camouflaged tropical shore crab is a result of active background choice. Taking advantage of a coastal area in the Solomon Islands with variable sand color and a population of the pallid ghost crab *Ocypode pallidula* with varying carapace color, we experimentally tested whether individuals actively choose specific substrate that best matches their color patterns. We found that individuals taken from extreme sand colors chose substrate that maintained crypsis, with relatively darker crabs typically choosing dark sand and lighter crabs choosing light sand. Crabs of intermediate color pattern, in contrast, showed no clear preference for dark or light sand. Our results suggest that potential prey can actively choose specific backgrounds to enhance and maintain crypsis, providing insights into how behavior interacts with morphological traits to avoid predator detection.

Key words: background matching; camouflage; crypsis; ghost crab; *Ocypode pallidula*.

PREDATION IS ONE OF THE MOST SIGNIFICANT SELECTIVE PRESSURES IN NATURE (Endler 1981, Stevens & Merilaita 2009), especially in the tropics where biotic interactions are more intricate than in temperate regions (Jeanne 1979, Bertness *et al.* 1981, Schemske *et al.* 2009). As such, many animals have evolved a diverse set of adaptations to avoid becoming prey (Cott 1940, Magurran 1990, Caro 2005, Rowland *et al.* 2008, Vignieri *et al.* 2010). Generally, potential prey can prevent predation by first avoiding detection and then escaping if they are detected and pursued by predators (Lima & Dill 1990). Avoiding detection is therefore one of the best ways to avoid predation, and one way to do so is through crypsis such as background matching (Endler 1978, Ruxton *et al.* 2004, Rowland *et al.* 2008, Stevens & Merilaita 2011, Stevens *et al.* 2015). In fact, some of the classic examples of natural selection operating in the wild are from animals that have evolved color patterns that match their background to avoid predator detection (Dice & Blossom 1937, Kettlewell 1955). This observed match between animal color patterns and their visual background, in turn, could result from (1) individuals actively changing their color to match distinct backgrounds (Allen *et al.* 2010); (2) predators selectively taking prey that fail to match their background (Bishop 1972); and/or (3) individuals actively choosing particular backgrounds that best match their own color pattern (Sargent 1966, Gillis 1982).

In a few predator and prey species, individuals can dynamically change their color to match the visual background (Kang *et al.* 2016), the most famous examples of which include chameleons (Stuart-Fox *et al.* 2008) and cephalopods (Allen *et al.* 2010). For animals that cannot quickly change their color, individuals could instead actively choose specific backgrounds that match their own color pattern to maintain camouflage. This ability to choose matching background has been shown in a wide range of taxa, which include several species of insects (Kettlewell & Conn 1977, Grant & Howlett 1988, Kang *et al.* 2012), fish (Kjernsmo & Merilaita 2012, Tyrie *et al.* 2015), reptiles (Nafus *et al.* 2015, Marshall *et al.* 2016) and birds (Lovell *et al.* 2013). However, the ability to choose matching backgrounds varies across species and between individuals within species. For instance, in nocturnal moths found within the same habitats, some species actively choose roosting substrate to match their own color patterns, whereas other species do not (Sargent 1966, Steward 1985). Likewise, in Aegean wall lizards, males and females vary in dorsal coloration, with females having stronger preferences for background that enhance crypsis (Marshall *et al.* 2016). Given that background matching is common in many species and that species, as well as individuals within a single species, vary in their ability to choose matching substrates, it is critical to determine how behavioral traits interact with morphological adaptations to better understand the evolution of crypsis (Stevens 2015, Skelhorn & Rowe 2016). We here explore active background choice in the pallid ghost crab *Ocypode pallidula*, an Indo-Pacific shore crab

species with carapace color patterns that match their substrate (Fig. 1A), to determine whether individuals actively choose specific substrate to enhance background matching.

Crabs are known for evolving color patterns that match their visual background (Todd *et al.* 2006, Stevens *et al.* 2014a, Vermeiren & Sheaves 2014). One of the most direct mechanisms for background matching in crabs is through the active change of carapace color (Hultgren & Stachowicz 2007, Stevens *et al.* 2013) or by incorporating materials from the environment onto their carapace (Thanh *et al.* 2003). However, color change of the carapace can take hours (Stevens *et al.* 2013, 2014b) or even months (Hultgren & Stachowicz 2007) to complete. As such, if an individual is trying to avoid detection, it could, instead, choose specific substrate that matches its current color pattern. Therefore, could the commonly observed pattern of background matching in shore crabs result from active background choice? We take advantage of a tropical, coastal habitat with varying sand color to experimentally test the hypothesis that pallid ghost crabs actively choose specific backgrounds to enhance and maintain crypsis. We discuss our results in light of the growing number of studies that show the important role of behavioral adaptations in the evolution of crypsis.

METHODS

STUDY SITE.—The study was conducted during June of 2015, along the coast of the Namare Community on Makira Island, Solomon Islands (S 10° 45.635, E 162° 16.787; Fig. 1B). In this habitat, sand and gravel of different color and brightness are exposed as the tide recedes. Typically, the highest points along the beach are lighter with fine and dry sand, while those at lower points are darker with wet, algae-coated sand and gravel (Fig. 1C). The area between the two is intermediate in brightness, with fine but compact and wet sand (Fig. 1C). Pallid ghost crabs *O. pallidula* were commonly observed to forage and build burrows in all three substrate types. We therefore collected crabs and conducted field experiments during low tide, when much of the shore was exposed, and predators such as shorebirds (*e.g.*, Lesser Sand-Plover *Charadrius mongolus,* Whimbrel *Numenius phaeopus,* Gray-tailed Tattler *Tringa brevipes*) were abundant and actively hunting for crabs and other invertebrates (J.A.C Uy, pers. obs.). In a follow-up study in 2016, we explored the validity of the subjective classification of substrate types by quantifying substrate brightness of light, intermediate, and dark sand using a portable spectrophotometer at the same locality. We found that the three substrate types indeed varied significantly in brightness, as predicted by our initial classification (quantified by the area under a reflectance curve; Fig. S1).

CRAB SAMPLING.—Our preliminary observations suggest that individual crabs found along the beach varied in color patterns (*e.g.*, amount of dark pigments), and that they generally matched their visual background (Fig. 1A). To more directly quantify background matching, we caught and photographed 15, 11, and 16 ghost crabs collected from dark, intermediate, and light sand, respectively (Fig. 1C). Images were taken with a Canon EOS 5D Mark 3 and a Tamron 28–300 mm telephoto lens at the field site under bright and open (no canopy) conditions. The ISO was set at automatic, and images were saved as CR2 (Canon Raw) files at 5760 × 3840 pixel resolution. Because crabs seem to vary in the
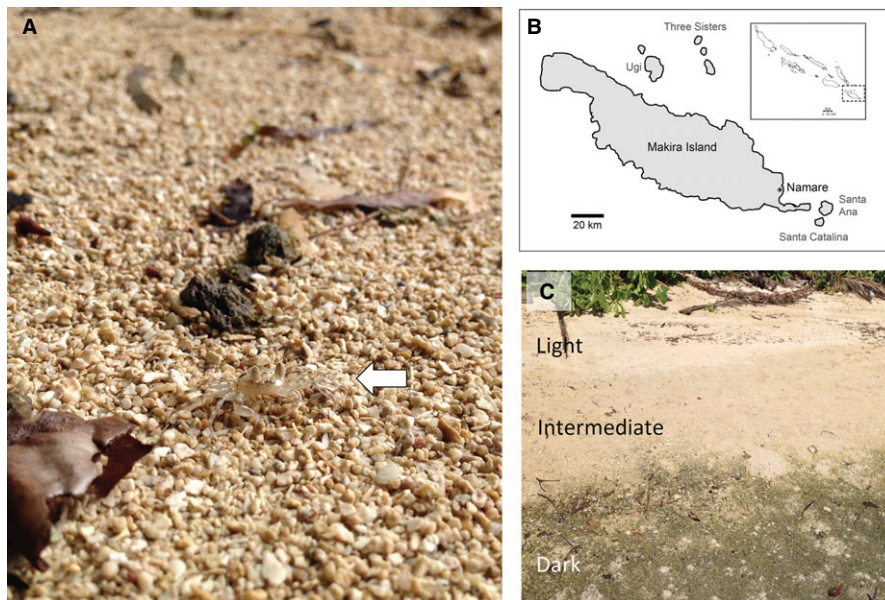

FIGURE 1. (A) A well-camouflaged pallid ghost crab (indicated by the arrow) on an intermediate substrate. (B) Map of Makira Island showing the Namare Community coastline. (C) Qualitative variation of sand color and brightness, showing the dark, intermediate, and light sand (see Fig. S2 for validation of the subjective classification of substrate types).

amount of dark pigments on their carapace, we used the relative area of dark pigments as an index of overall brightness for each crab. Relative area of dark pigments was calculated as the total area of dark pigment (mm^2) divided by the total carapace size (mm^2). Total area of dark pigments and of carapace was measured with ImageJ 1.31 (Rasband 1997). We used ImageJ's automated method of area measurement via 'automatic thresholding', which creates a distinction between an object (*i.e.*, pigment spots) and its background (*i.e.*, remainder of the carapace) based on differences in brightness intensity, and then calculates the area of the specified objects (Baviskar 2011). An observer, without prior knowledge of where each crab was collected, conducted the measurements.

A recent study by Troscianko and Stevens (2015) indicated that the brightness of an image can affect the estimate of a color patch's overall brightness, and so each image needs to be calibrated to allow for comparisons across images. Although we were unable to calibrate our images, we argue that our method of deriving an index of carapace brightness is robust to variable camera settings and natural ambient light for several reasons. First, we did not measure the brightness of the carapace but rather the area of dark pigmentation as a proxy for overall brightness. Given that we are comparing patches with or without dark pigments, our results are likely robust to the ambient light conditions in the field (open and extremely bright). Second, automatic thresholding in ImageJ converts our color images to black and white, and then uses an automatic threshold to bin each pixel as black or white. Although the absolute brightness of the image could influence whether a pixel is classified as black or white, the difference between pixels with or without pigments is very distinct, especially since all our images were taken under bright ambient light conditions. Finally, in a follow-up study in 2016, we validated the utility of using relative area of dark pigments as an index of brightness by collecting 17 ghost crabs from the same locality and additionally measuring carapace brightness with a portable spectrophotometer (see Appendix S1). We found that carapace brightness, quantified as the area under a reflectance curve, strongly correlated with the relative area of dark pigments, as quantified by automatic thresholding in ImageJ using unstandardized images (Spearman correlation: $r_s = -0.620$, $N = 17$, $P \ll 0.001$; Fig. S2).

To test whether specific substrate color ('source substrate') predicted carapace brightness, we ran a one-way analysis of variance (ANOVA), with source substrate as the predictor (dark, intermediate, or light sand) and relative area of dark pigments as the dependent variable. Relative area of dark pigments was arcsine transformed to meet the assumptions of ANOVA (Sokal & Rohlf 1995). We also ran corrected *post hoc* pairwise comparisons to test for differences in relative area of dark pigments between crabs collected from dark, intermediate, and light sand (see below for details on the method of correction for multiple comparisons).

SUBSTRATE CHOICE EXPERIMENT.—Although ghost crabs can alter the brightness of their carapace in a few hours (Stevens *et al.*

2013), including in our study species (K.S. Patel, J.A.C. Uy & F.M.K. Uy, unpubl. data), the observed association between carapace, and substrate color and brightness could also be due to active background choice. To test this hypothesis, we constructed arenas that allowed test individuals collected from light, intermediate, and dark sand to freely choose between light and dark sand ($N = 4$ arenas; see Fig. S3). Each choice arena measured 1 m × 1 m, and was divided into two equal parts of light and dark sand collected from a beach adjacent to our experimental site (*ca* 10–20 m away). For each arena, the line that separated the dark and light sand was perpendicular to the shore, insuring that neither dark nor light sand was closer to the ocean (*i.e.,* crabs attracted to the water will not bias the results). At the start of each experiment, a focal crab was placed in the center of the arena and inside an opaque, bamboo cylinder, with a leaf acting as substrate (neutral substrate). After 5 min of acclimation, the bamboo cylinder was gently lifted and the crab was observed for an additional 5 min, recording the time the focal crab spent on either light or dark sand. Observations were conducted 10 m away using binoculars to minimize disturbance. Experiments were conducted between 0700 and 1130, with the start depending on the onset of low tide. A total of 60 crabs were tested, with 19, 20 and 21 crabs collected from dark, intermediate, and light sand, respectively. Each crab was collected immediately before running each trial.

To statistically test whether crabs preferentially chose dark or light sand, we analyzed our data set for comparisons within- and between treatment groups (*i.e.,* light, intermediate, and dark sand). First, we tested whether the relative amount of time spent on light sand (*i.e.,* active time spent on light sand divided by active time spent on both light and dark sand) deviated from chance (*i.e.*, 0.5 on light sand). Relative amount of time spent on light sand was arcsine transformed to meet the assumptions of ANOVA (Sokal & Rohlf 1995). Three separate one-sample *t*-tests were run for crabs collected from light, intermediate, and dark sand. Second, we ran a one-way ANOVA to compare time spent in each substrate among our three treatments, with the relative amount of time spent on light sand (arcsine transformed) as the dependent variable and the source substrate (dark, intermediate, or light sand) as a predictor. In addition, because the orientation of the focal individual could influence their ultimate substrate choice, we included orientation at the start of the experiment (*i.e.*, facing the dark or light sand, or neutral) as a second predictor in the model. Corrected *post hoc* pairwise comparisons were conducted to test for differences in substrate preference between crabs collected from dark, intermediate, and light sand (see below for details on the method of correction for multiple comparisons). All tests of hypotheses are two-tailed, and all statistical analyses were performed using SPSS 21.0 (IBM Corp, Armonk, NY, U.S.A.).

CONTROLLING FOR TYPE-1 ERROR.—Given that we conducted multiple tests on our single data set, including *post hoc* pairwise comparisons, the chance of type-1 errors is elevated. As such, we controlled for family-wise error rate using Benjamini and

Hochberg's (1995) False Discovery Rate (FDR) correction approach, with the FDR set at 5%. Corrected P values were calculated for the combined main analyses and *post hoc* pairwise comparisons, adjusting for a total of 14 statistical tests.

RESULTS

Individuals varied in the relative area of dark pigments on their carapace, and this variation was predicted by the brightness of the substrate from which they were collected (Fig. 2). The relative area of dark pigments was greatest in crabs collected from dark sand, intermediate for crabs collected in intermediate-colored sand, and least for crabs collected in light sand (ANOVA, $F_{3,39} = 217.54$, Type III SS = 10.53, $P \ll 0.001$, adjusted $R^2 = 0.94$; Fig. 2).

In the substrate choice experiment, crabs collected from light sand proportionally spent more time on light than dark sand ($t = 4.425$, df = 20, $P \ll 0.001$), whereas crabs collected from dark sand proportionally spent more time on the dark than light sand ($t = -2.662$, df = 18, $P = 0.016$; Fig. 3). Intermediate crabs did not spend more time on light versus dark sand ($t = -1.256$, df = 19, $P = 0.224$; Fig. 3). Similarly, comparing across groups, crabs varied in the amount of time spent on light or dark sand depending on their source substrate ($F_{2,52} = 10.69$, Type III SS = 8.09, $P < 0.001$), with crabs collected from light sand spending more time on light sand than crabs collected from dark sand (Fig. 3). Crabs collected from intermediate sand were intermediate to crabs from dark and light sand in the relative amount of time spent on light sand (Fig. 3). Orientation at the start of

the experiment was not a significant predictor of time spent on light sand ($F_{2,52} = 1.78$, Type III SS = 1.35, $P = 0.178$), and there was no significant interaction between orientation at the start of the experiment and source substrate ($F_{3,52} = 1.48$, Type III SS = 1.68, $P = 0.232$). Source substrate was the only significant predictor in the final full model ($F_{8,52} = 15.13$, Type III SS = 45.84, $P < 0.001$), which explained 65% of variance in time spent on light sand.

DISCUSSION

BACKGROUND MATCHING.—We found that individual crabs varied in the relative amount of dark pigments on their carapace, and this variation was associated with the substrate color on which each crab was collected. Crabs collected from dark sand had more dark pigment spots than those collected from intermediate and light sand. This observation is consistent with the hypothesis that individual prey species are less conspicuous against their own visual background to avoid predator detection (Stevens & Merilaita 2011). Given this observation, we asked whether the association between crab and substrate color is a product of active background choice by each individual. Our substrate choice experiment indicated that indeed crabs from the dark and light sand, the two extreme substrate types in the Namare coastline, chose backgrounds that generally matched the brightness of their carapace. That is, crabs collected from dark sand, which typically have more dark spots, choosing dark substrate, and crabs collected from light sand, which have fewer dark spots, choosing light substrate. Crabs collected from intermediate sand did not
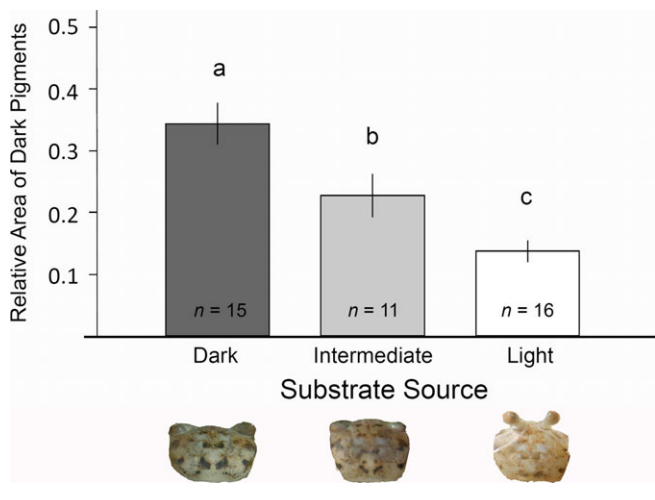

FIGURE 2. Mean ± SE relative area of dark pigments (total area of dark pigments/total area of carapace) and substrate from where individual crabs were collected ('substrate source'). Relative area of dark pigments was arcsine transformed prior to data analysis. We present raw data for illustrative purposes. Different letters above each bar indicate statistical differences between groups (FDR-corrected *post hoc* tests: dark vs. light, $P < 0.001$; dark vs. intermediate, $P = 0.011$; light vs. intermediate, $P = 0.025$). [Color figure can be viewed at wileyonlinelibrary.com]
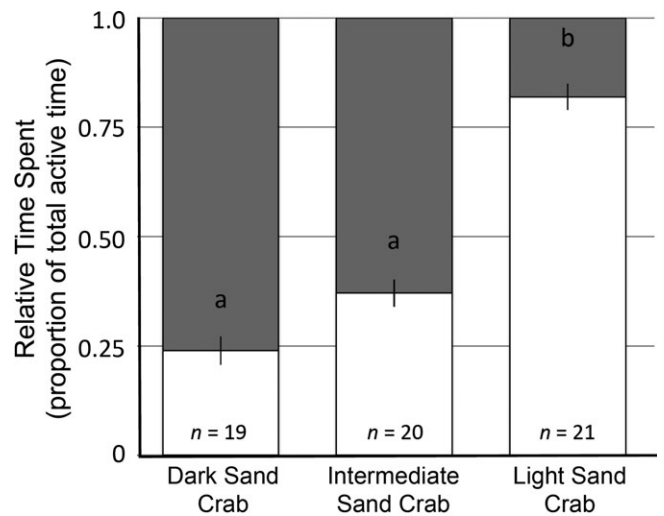

FIGURE 3. Mean ± SE relative time spent on dark versus light sand (proportion of total active time) for crabs collected from dark, intermediate, and light sand. Proportion time spent on light sand was arcsine transformed prior to data analysis, but we present raw data for illustrative purposes. Different letters above each bar indicate statistical differences between groups (FDR-corrected *post hoc* tests: dark vs. light, $P < 0.001$; dark vs. intermediate, $P = 0.288$; light vs. intermediate, $P = 0.001$).

show a clear preference, and were intermediate to dark and light crabs in substrate preference. Our inability to detect substrate choice in intermediate crabs may be due to our exclusion of intermediate-colored sand in our choice trials. Perhaps intermediate crabs would have settled on intermediate-colored sand if given the opportunity to do so. Overall, however, the observed active choice by dark and light crabs of background that maintains crypsis suggests important implications for the evolution of anti-predator adaptive strategies. We discuss these implications below.

BEHAVIORAL AND MORPHOLOGICAL ADAPTATIONS FOR CRYPSIS.—Textbook cases of natural selection operating in the wild involve examples of prey species matching their substrate to avoid predation, which include melanism in the peppered moth *Biston betularia* (Kettlewell 1955, Kettlewell & Conn 1977) and pocket mice of the genus *Chaetodipus* and *Perognathus* (Dice & Blossom 1937). In addition, some species can alter their color to match their background either immediately, as in the cuttlefish *Sepia officinalis* (Allen *et al.* 2010), within a few hours, as in the horned ghost crab *Ocypode ceratophthalmus* (Stevens *et al.* 2013) or after a few days, as in the fiddler crab *Uca vomeris* (Hemmi *et al.* 2006). Therefore, several studies have shown that specific behaviors interact with such morphological and physiological adaptations, especially for species that cannot quickly change their color patterns. For example, peppered moths *Biston betularia,* Peacock flounders *Bothus mancus*, desert tortoises *Gopherus agassizii*, and wall lizards *Podarcis erhardii* actively choose microhabitats that best maintain camouflage (Nafus *et al.* 2015, Tyrie *et al.* 2015, Marshall *et al.* 2016). Similarly, in the Japanese quail *Coturnix japonica,* females actively choose to lay their eggs on substrate that augment the camouflage of their mottled eggs (Lovell *et al.* 2013). Ghost crabs have the ability to change the brightness of their carapace within a few hours in response to ambient light, and thus this ability to change color could enhance background matching (Stevens *et al.* 2013). However, in our study in pallid ghost crabs, we also found that active substrate choice enhances the match between carapace color and the background during the time period when predators are actively searching for prey. Therefore, our results, along with Stevens *et al.*'s (2013) previous study on a congeneric ghost crab, highlight the importance of explicitly considering the interaction between behavior, physiology, and morphology when exploring the evolution of crypsis. The evolution of these multifaceted anti-predator defense may be especially important in regions like the Tropics where predation is particularly intense (Jeanne 1979, Bertness *et al.* 1981, Schemske *et al.* 2009).

MECHANISM OF BACKGROUND CHOICE.—The mechanism underlying active background choice remains little understood (reviewed by Skelhorn & Rowe 2016). Substrate choice could be achieved by a simple rule of thumb or perhaps more advanced cognitive abilities. For instance, individuals could simply scan the substrate to decide on color or brightness suitability, as in the color polymorphic grasshopper, *Circotettix rabula*, which achieves background matching by comparing the color of its own body against the visual background (Gillis 1982). Because terrestrial crabs have well-developed color vision (Zeil & Hemmi 2006) and can alter their color patterns in response to ambient light (Stevens *et al.* 2013), visual cues from the environment can allow individuals to actively choose a substrate that best suit their current carapace color. Alternatively, individuals may rely on additional cues, such as moisture, temperature, or olfactory cues, to decide on the appropriate background. In fiddler crabs, for instance, temperature affects color change (Silbiger & Munguia 2008). In our study species, ghost crabs that have spent the night on dark substrate may simply cue on the algae present on sand and gravel. As we collected sand from the natural environment for our experiments, olfactory cues were not removed and thus we cannot exclude the possibility that chemical cues are being used for substrate choice. Overall, more work is needed to uncover the mechanisms that facilitate active background choice, and this will involve understanding the physiology and perhaps cognitive abilities of potential prey (Skelhorn & Rowe 2016).

CONCLUSION

Potential prey species have evolved a diverse set of morphological adaptations to avoid being detected by predators (Cott 1940, Endler 1978, Caro 2005). These adaptations range from color patterns that match the visual background to more complex physical structures that mimic the shape of objects in the background (reviewed by Stevens & Merilaita 2009, 2011, Skelhorn & Rowe 2016). Additionally, but less understood, potential prey have evolved behaviors that enhance their morphological adaptations, and these include mimicking the movement of the physical background (*e.g.,* moving leaves; see Bian *et al.* 2016) or postures that enhance camouflage (Webster *et al.* 2009, Wang & Schaefer 2012). More simply, potential prey can evolve the ability to choose background that enhances or maintains crypsis (Kettlewell & Conn 1977, Lovell *et al.* 2013, Tyrie *et al.* 2015, Marshall *et al.* 2016). Given growing evidence for the interaction between behavior and visual traits, future studies need to explicitly explore how behavioral traits co-evolve with morphological and physiological traits to better understand the ecology and evolution of anti-predator adaptations (Stevens & Merilaita 2009, 2011, Stevens 2013).

ACKNOWLEDGMENTS

DATA AVAILABILITY

Data deposited in the Dryad Repository: http://doi.org/10.5061/dryad.2h914 (Uy *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Spectrophotometry methods.
FIGURE S1. Direct quantification of substrate brightness.
FIGURE S2. Correlation between area of pigments and carapace brightness.
FIGURE S3. Substrate choice arena in the field.

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