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### Permalink

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### Journal

Journal of Experimental Biology, 213(2)

### ISSN

0022-0949

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### Publication Date

2010-01-15

### DOI

10.1242/jeb.030247

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## Mottle camouflage patterns in cuttlefish: quantitative characterization and visual background stimuli that evoke them

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Accepted 14 October 2009

### SUMMARY

**Cuttlefish and other cephalopods achieve dynamic background matching with two general classes of body patterns: uniform (or uniformly stippled) patterns and mottle patterns. Both pattern types have been described chiefly by the size scale and contrast of their skin components. Mottle body patterns in cephalopods have been characterized previously as small-to-moderate-scale light and dark skin patches (i.e. mottles) distributed somewhat evenly across the body surface. Here we move beyond this commonly accepted qualitative description by quantitatively measuring the scale and contrast of mottled skin components and relating these statistics to specific visual background stimuli (psychophysics approach) that evoke this type of background-matching pattern. Cuttlefish were tested on artificial and natural substrates to experimentally determine some primary visual background cues that evoke mottle patterns. Randomly distributed small-scale light and dark objects (or with some repetition of small-scale shapes/sizes) on a lighter substrate with moderate contrast are essential visual cues to elicit mottle camouflage patterns in cuttlefish. Lowering the mean luminance of the substrate without changing its spatial properties can modulate the mottle pattern toward disruptive patterns, which are of larger scale, different shape and higher contrast. Backgrounds throughout nature consist of a continuous range of spatial scales; backgrounds with medium-sized light/dark patches of moderate contrast are those in which cuttlefish Mottle patterns appear to be the most frequently observed.**

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/213/2/187/DC1>

Key words: crypsis, body pattern, mottle coloration, *Sepia officinalis*, defense.

### INTRODUCTION

Cephalopod adaptive coloration is among the most sophisticated in the animal kingdom because the neurally controlled chromatophore system permits a diverse repertoire of body patterning (Messenger, 2001) for a broad range of communication and camouflage (Hanlon and Messenger, 1996). The present study concerns visual perception of diverse backgrounds by cephalopods, which are able to rapidly assess surrounding visual information and immediately camouflage themselves effectively (<1 s) on nearly any background they encounter in complex visual environments (cf. Hanlon and Messenger, 1996; Holmes, 1940; Marshall and Messenger, 1996). Our extensive field and laboratory observations of cuttlefish camouflage [beginning with Hanlon and Messenger (Hanlon and Messenger, 1988)] begged a basic question: how many camouflage patterns does any individual have? Surprisingly, and counter-intuitively, our morphological analyses of body patterns uncovered only three basic patterning templates among thousands of cuttlefish images: Uniform, Mottle and Disruptive; many other cephalopods (squid, octopus, etc.) show these three types of camouflage patterns as well [summarized in Hanlon and Messenger (Hanlon and Messenger, 1996)]. This comparative morphological trend enabled us to develop a working hypothesis to account for the remarkable speed of visual assessment and subsequent body pattern change. We reasoned that cephalopods were using only selected visual stimuli to enact their extremely rapid body pattern change. Our overall hypothesis, based upon the concept of parsimony, is that

there is a relatively simple ‘visual sampling rule’ for each of the basic camouflage pattern types of uniform, mottle and disruptive [summarized in Hanlon (Hanlon, 2007; Hanlon et al., 2009)]. Such a rule set would represent the simplest, fastest neural pathway that begins with visual input at the retina, progresses to central nervous system (CNS) processing and proceeds to motor output *via* direct neuro-muscular control of the skin chromatophores to produce the camouflage pattern (Messenger, 2001).

The initial morphological approach, which is based on the appearance of the animal, is not incompatible with a functional approach that emphasizes the visual mechanism of how different patterns deceive predator vision. The functional approach has recently stimulated a new classification of the terms and definitions of camouflage (Stevens and Merilaita, 2009a); these will undoubtedly change as experimentation and other approaches help refine them. There is general agreement, however, that background matching [‘where the appearance generally matches the color, lightness and pattern of one (specialist) or several (compromise) background types’ *op. cit.*] is one of the most common mechanisms of crypsis, which functions initially by preventing detection by the predator (Cott, 1940; Edmunds, 1974; Endler, 2006; Stevens and Merilaita, 2009a; Thayer, 1909). For background matching to be effective, the light and dark patches of the body pattern (regardless of the type of animal) need to generally resemble the size scale and contrast of light and dark background patches (of course, color and physical texture have to generally match as well but here we

emphasize the pattern components). In cephalopods, the Uniform and Mottle pattern components of light and dark achieve background matching by controlling the scale and contrast of their skin components. Such classification into named categories of ‘uniform’ or ‘mottle’ is partly descriptive but the quantitative method described below shows that these pattern categories are based on statistical properties and have the future advantage of being compared with the visual surroundings with a common terminology. In the present study, which is about visual perception, we focus on which specific statistical properties of reduced and defined backgrounds (the psychophysics methodology) influence the production of the light and dark components of cuttlefish body patterns. Eventually, the same statistical properties of the animal body pattern can be correlated to natural background statistics to address questions related to visual camouflage mechanisms that deceive predators. We acknowledge and appreciate (Hanlon et al., 2009) that the full repertoire of camouflage patterns of cuttlefish are more like a continuum of sorts, in which there is considerable variation in the basic pattern types of uniform, mottle and disruptive. Yet this pattern-type categorization (which is both descriptive and quantitative) facilitates terminology and hypothesis testing. Moreover, it begins to uncover some of the conserved features of mottle in cuttlefish and other cephalopods. We point out that there are morphological and physiological limitations to the scaling of individual mottle components in cephalopod skin (Hanlon and Messenger, 1988), i.e. cuttlefish and octopus only have two or perhaps three mottle sizes in their skin repertoires, so that they cannot produce a truly continuum scale for background matching. Finally, the quantitative method used here to define mottle provides some

complementary features (and perhaps some advantages) to independent or principal component characterization of patterns (e.g. Anderson et al., 2003; Kelman et al., 2007).

Mottle has been defined generally as an irregular arrangement of spots or patches of color on a surface (Cott, 1940; Edmunds, 1974). Other synonyms of mottle include splotched, dappled, spotted, blotchy and speckled. However, the broad class of mottle body patterns as described here for cuttlefish [and based on classic definitions (Cott, 1940; Edmunds, 1974)] is characterized by small-to-moderate-scale light and dark patches that are distributed somewhat evenly across the body surface (Hanlon and Messenger, 1988). Importantly, the scale aspect of this characterization is based on the size of the light and dark patches relative to the size of the animal. Often, there is some repetition of the patches within the pattern. The light or dark patches can vary mildly in shape (ovoid or streaky) and size, yet when a cuttlefish deploys a mottle pattern, it does so when those skin patches are generally similar in size, shape and contrast to some adjacent background objects. Fig. 1A1–A6, illustrate examples of mottle patterns in cuttlefish. In higher magnification (Fig. 2), it can be seen that the same skin patch can vary in size, shape and contrast of the patterns because the skin is organized into ‘physiological units’ of chromatophores (Packard, 1982) that are under direct neural control by the CNS (cf. Boycott, 1961; Dubas et al., 1986). Indeed, the mottle body pattern works by the principle of background matching, one of the commonest animal camouflage tactics (Stevens and Merilaita, 2009a). There is no dispute that the mottled appearance in animal coloration thus should be emphasized in terms of its role in camouflage function (i.e. background matching).

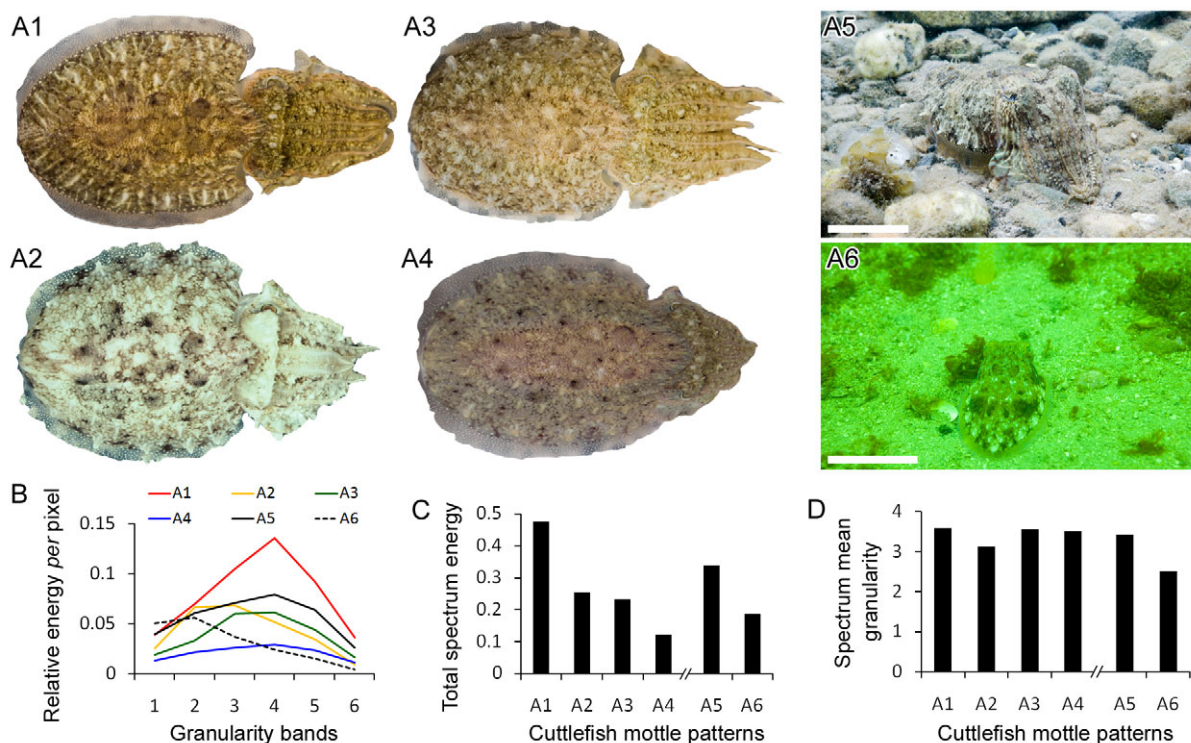


Fig. 1. Diverse mottle body patterns of cuttlefish (*Sepia officinalis*). (A) Selected images of various mottle pattern types in cuttlefish. (A1–A4) Cut-outs of animals from images taken in the laboratory. (A5, A6) Field images taken in Turkey and Spain, respectively. Scale bars, 10 cm. (B) Granularity spectra of all six cuttlefish shown in A1–A6. The amplitude and shape of these curves reflect high/low contrast and coarse/fine scale of the mottle body patterns, respectively (see Fig. 3 for details). In *S. officinalis*, mottle patterns have different appearances. (C) Total energies (TEs) of granularity spectra for the animals in A1–A6 (see text for TE definition). A1 had the highest contrast mottle pattern and A4 had the lowest contrast mottle pattern. (D) Mean granularities (MGs) of granularity spectra for the animals in A1–A6 (see text for MG definition). Animals in A1, A3, A4 and A5 showed finer scale of mottle patterns whereas A2 showed medium scale and A6 showed relatively large scale mottle body pattern.

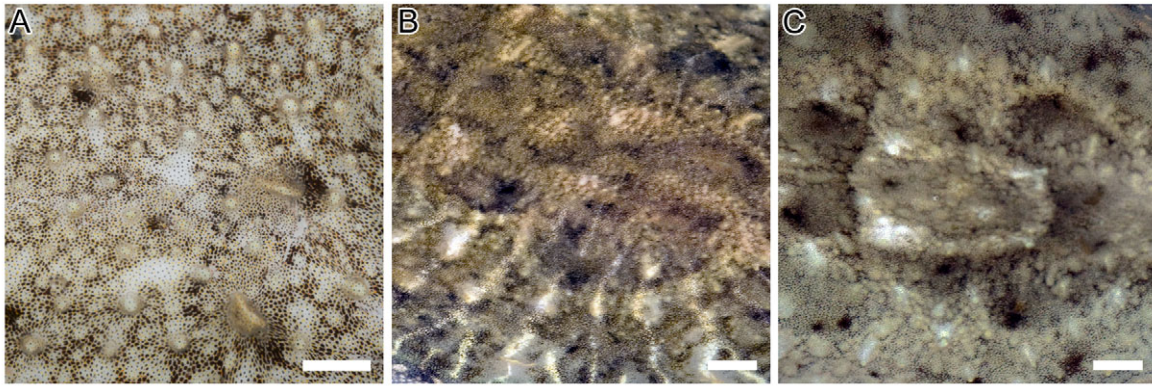


Fig. 2. Variations in the composition of mottle patterns. (A) Small splotches of expanded dark chromatophores; in these patterns the number and size of light and dark splotches are roughly equal. (B) Medium-sized splotches of mottle in which the dark patches are more irregular and larger; note that there can be a 'streaky' appearance to some mottles when the white leucophores on the mantle stripes are shown. (C) Large splotches of mottle in which distinctive dark patches are shown. In this photograph, the four sets of Paired mantle spots (Hanlon and Messenger, 1988) that surround the White square are expressed. Scale bars, 5 mm.

To quantify the degree of 'mottledness' or 'granularity' of the light and dark skin patches expressed by a cuttlefish, we developed an automated method (Barbosa et al., 2008b) (see details in Materials and methods below) to statistically characterize mottle patterns by analyzing the image of the animal in different spatial frequency bands (or granularity bands) accomplished with a fast Fourier transform of the image. This tool essentially provides the size of the light and dark patches in the skin as well as a measure of their contrast, and it is the resultant curve shape in the granularity statistical output that distinguishes Uniform from Mottle from disruptive body patterns (Fig. 3) with considerable precision (see Results below). By quantifying the mottle in body patterns, we can then seek correlations with the visual background cues that elicit mottle patterns in cuttlefish.

We and others have published multiple papers on specific visual cues that elicit Disruptive body patterns in cuttlefish coloration (Barbosa et al., 2008a; Barbosa et al., 2008b; Chiao and Hanlon, 2001a; Chiao and Hanlon, 2001b; Chiao et al., 2005; Chiao et al., 2007; Chiao et al., 2009; Kelman et al., 2007; Kelman et al., 2008; Mäthger et al., 2007; Shohet et al., 2007; Zylinski et al., 2009). We have also elicited Uniform patterns on uniform backgrounds (Allen et al., 2009; Barbosa et al., 2007; Chiao and Hanlon, 2001a; Mäthger et al., 2007). However, it has proved difficult to find the specific background features that elicit mottle patterns. In particular, it has been challenging in psychophysical experiments (using artificial, computer-generated backgrounds) to elicit 'pure' mottle patterns, i.e. mottle patterns that do not have one or several large, high-contrast light disruptive components in them. Various studies have provided clues for some of the background features that evoke mottle patterns in cuttlefish (Barbosa et al., 2004; Barbosa et al., 2008b; Kelman et al., 2007; Shohet et al., 2007; Zylinski et al., 2009). In the present study, we report extensive experimentation with both natural and artificial backgrounds that demonstrates the primary background features that elicit mottle camouflage patterning in the cuttlefish *Sepia officinalis*.

## MATERIALS AND METHODS

### Animals and experimental setup

Young cuttlefish (*Sepia officinalis* L.) ranging in size from 3.3 to 4.9 cm mantle length (ML) were used in experiments 1–3, and cuttlefish ranging from 2.0 to 3.7 cm (ML) were used in experiment

4 (see below). All animals were hatched, reared and maintained at the MBL Marine Resources Center (Woods Hole, MA, USA). To provide a stable visual environment and minimize stress to the animals, the experimental trials were conducted inside a tent made of black plastic sheeting. Each animal was placed in a tank (55 cm × 40 cm × 15 cm) with flowing seawater and restricted to a cylindrical arena (25 cm diameter and 11 cm height for experiments 1–3; 15 cm diameter and 7.5 cm height for experiment 4) where various computer-generated artificial substrates (laminated to be waterproof) or natural substrates were presented on both the floor and wall (in experiments with natural substrates, the wall was uniform gray). A circular 40 W fluorescent light source (Phillips CoolWhite, Andover, MA, USA) was used to reduce the effect of shadow. A light meter (Extech EasyView EA30, Waltham, MA,

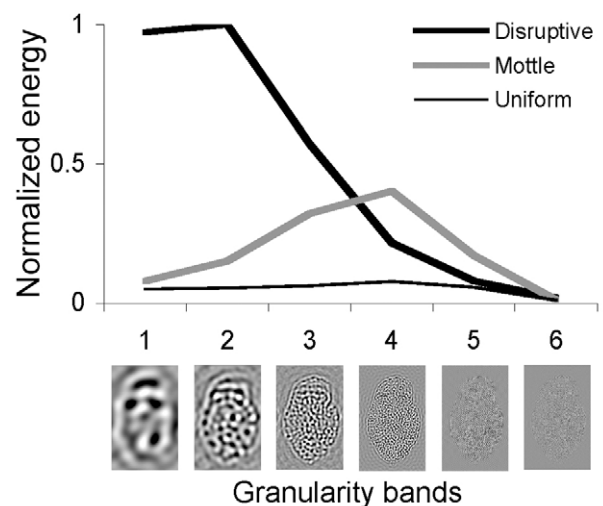


Fig. 3. Granularity analysis. Each image of cuttlefish (*Sepia officinalis*) is band-pass filtered into six images corresponding to those shown on the horizontal axis. From each of the six images the sum of squared pixel values is extracted; this is the total energy contributed to the original image by the spatial frequencies isolated in the filtered image. These six band-specific energies are referred as the 'granularity spectrum' of the image. The scale is normalized for readability. The three spectra shown are typical of uniform/stipple, mottled and disruptive patterns [modified from Fig. 4 in Barbosa et al. (Barbosa et al., 2008b)]. See Materials and methods for details.

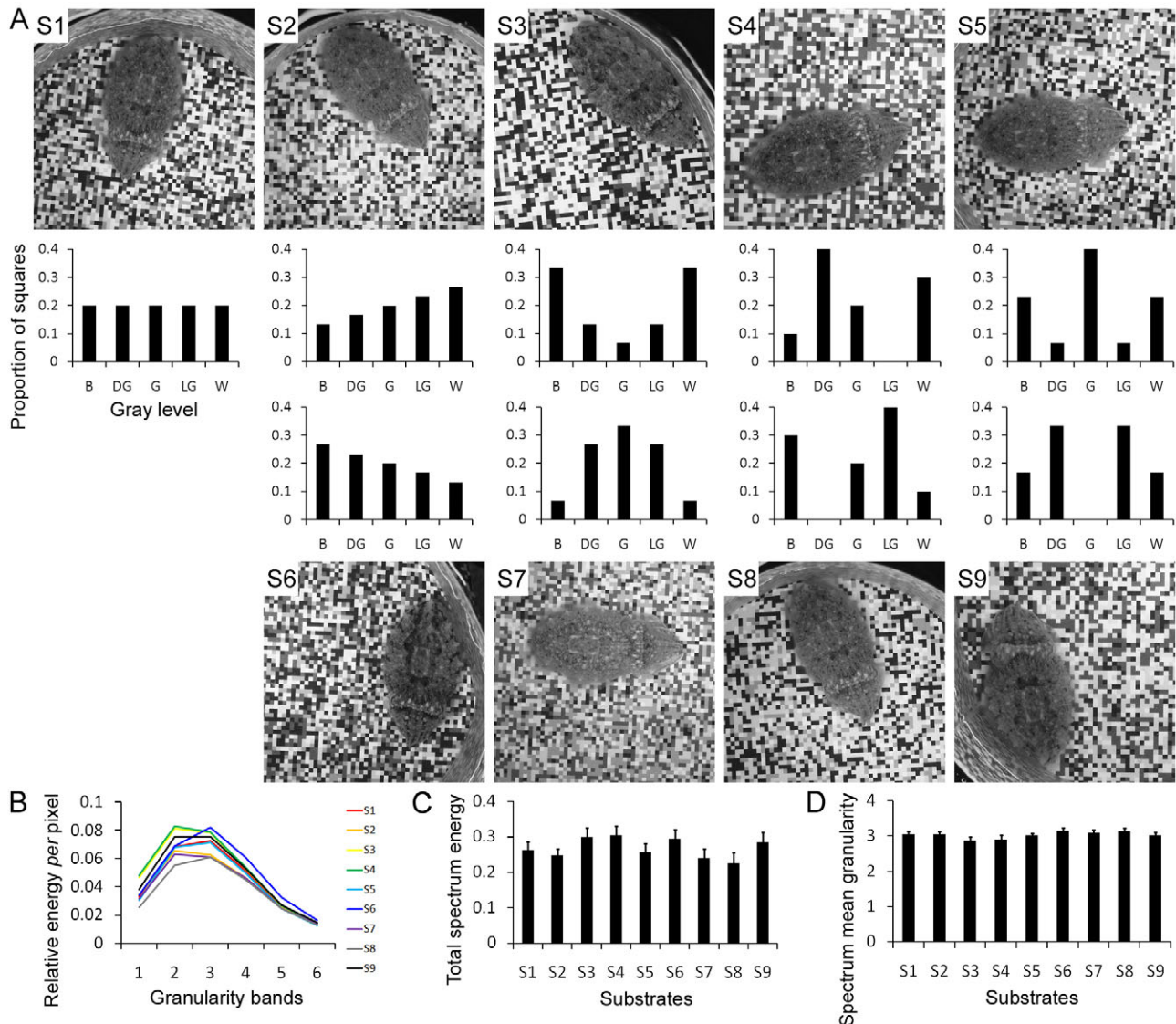


Fig. 4. Cuttlefish showed mottle patterns on nine scramble substrates of different histograms. (A) Each scramble substrate was composed of small squares (equivalent to 3% White square component area) of five gray levels (B, black; DG, dark gray; G, gray; LG, light gray; W, white). These nine scramble substrates were designed to have different gray level distributions. Except for S1 (even distribution of all gray levels), all of the other eight substrates were designed to form four complementary pairs (S2/S6, S3/S7, S4/S8 and S5/S9), so that each pair of substrates has opposite histograms. Regardless of different gray level distributions of the nine scramble substrates, cuttlefish showed distinct mottle body patterns on all backgrounds. (B) Average granularity spectra of 10 animals on nine scramble substrates. The shapes of these spectra were similar across different backgrounds, indicating similar mottle body patterns. The error bars were omitted for clarity. (C) Average total energies (TEs) of granularity spectra of all animals on nine substrates. There were significant differences among TEs of cuttlefish's mottle patterns on these backgrounds ( $F_{8,72}=8.637$ ,  $P=0.015$ ), suggesting that different contrast level expression of the mottle colorations depends on scramble substrate histograms. (D) Average mean granularities (MGs) of all animals on nine substrates. There was no significant difference in MGs of all cuttlefish across various substrate types ( $F_{8,72}=3.085$ ,  $P=0.115$ ), showing that the expression of mottle body patterns is not affected by scramble substrate histograms. The error bars in C and D represent s.e.m.s.

USA) was used to take readings around the perimeter and near the center of the arena (center 1.07 klx; perimeter 1.03 klx), showing that the arena was lit relatively evenly. Once the animal had acclimated (i.e. ceased swimming and hovering movements and expressed a stable body pattern), three still images were taken at 4 min intervals using a digital video or still image camera (Panasonic PVGS400, Secaucus, NJ, USA, or Nikon Coolpix 5400, Melville, NY, USA) mounted 60 cm above the arena and connected to an external monitor so that the animal's movements could be followed from outside the chamber without disturbing it. The three images per animal per substrate in each trial were used to quantify

the animal's response (see below on the automated methods for quantification of body patterns). In experiment 3 (see below), after the animal had acclimated, one second of video (30 frames  $s^{-1}$ ) was recorded at 30-second intervals for 20 min using a different digital video camera (SONY HDV1080i, Tokyo, Japan). Ten images per animal per substrate in each trial were extracted from the total 40 s video images at 4-second intervals, and were used to quantify the animal's response. There were 10 animals used in experiment 1, 14 in experiment 2, six animals in experiment 3 and 40 animals in experiment 4. Except in experiment 4, animals were repeatedly used for different substrates.

### Substrates

#### Experiment 1 (scramble substrates)

Nine scramble substrates (Fig. 4) were generated by randomly placing small squares of five different gray levels with specifically designed histograms [gray level distributions (for details, see Chubb et al., 1994)]. The size of each small square was equivalent to 3% White square (WS) component area. Previous studies showed that cuttlefish express mottle body patterns on black/white checkerboards with check sizes within 3–12% of the WS area (Barbosa et al., 2004; Barbosa et al., 2008b). Five equally spaced gray levels (B, black; DG, dark gray; G, gray; LG, light gray; W, white) were used in this study. All nine scramble substrates (S1–S9) were designed to have different gray level distributions. Except for S1 (even distribution of all gray levels), all of the eight substrates were systematically created to have four complementary pairs (S2/S6, S3/S7, S4/S8 and S5/S9) with opposite histograms. For example, S2 and S6 have identical overall contrast but different background intensity. On the contrary, S3 and S7 have identical background intensity but different overall contrast. Furthermore, the pairs S4/S8 and S5/S9 both have equal background intensity and contrast but different gray level distributions. The design of these scramble substrates tests whether the elicited mottle body pattern is differentially influenced by different gray levels of these backgrounds. By presenting animals with scramble substrates of opposite histograms, we can systematically examine the influence of each different texture element on modulating the mottle patterns.

#### Experiment 2 (texture substrates)

Two sets of texture substrates (Figs 5 and 6) were generated by band-pass filtering spatial white noise and then thresholding the resulting filtered noise images at zero. The bandwidth of this filter (impulse

responses were 0-mean, differences-of-circular-Gaussians) was designed to match the spatial scale of the mottle components of cuttlefish. Note that the 0-mean and differences-of-circular-Gaussians are a balanced design of the band-pass filters, in which the summation of the impulse response is zero. This yielded a texture substrate with roughly equal numbers of black and white pixels. To test the contrast effect on mottle body patterning, three such texture substrates with different contrasts (Michelson contrast 0.76, 0.59 and 0.23) were applied. The contrast was determined by calculating the quantum flux of a cuttlefish's photoreceptor (Bellingham et al., 1998; Brown and Brown, 1958) using the reflectance spectra of the laminated surfaces measured by a spectrometer [USB2000, Ocean Optics, Dunedin, FL, USA (for details, see Chiao et al., 2007)]. Note that the Michelson contrast is defined as  $(B_{\max} - B_{\min}) / (B_{\max} + B_{\min})$ , where  $B_{\max}$  is the greater of the quantum catches produced by the lights reflected from the two areas and  $B_{\min}$  is the lesser. To test whether the black/white ratio of substrates (i.e. the mean intensity of backgrounds) plays a role in determining mottle body patterning, three texture substrates with different black/white ratios (1:3, 1:1 and 3:1) were used. These texture substrates were produced by thresholding the filtered noise images at different intensity levels. This design examines whether background contrast and mean luminance (known to influence variations in disruptive body patterns) are also the key visual cues for modulating the mottle body patterning.

#### Experiment 3 (checkerboard substrates)

A black/white checkerboard with check size equivalent to 10% cuttlefish WS area was generated as a control substrate for evoking mottle body patterns because previous studies showed that this substrate consistently evoked a mottle body pattern (Barbosa et al.,

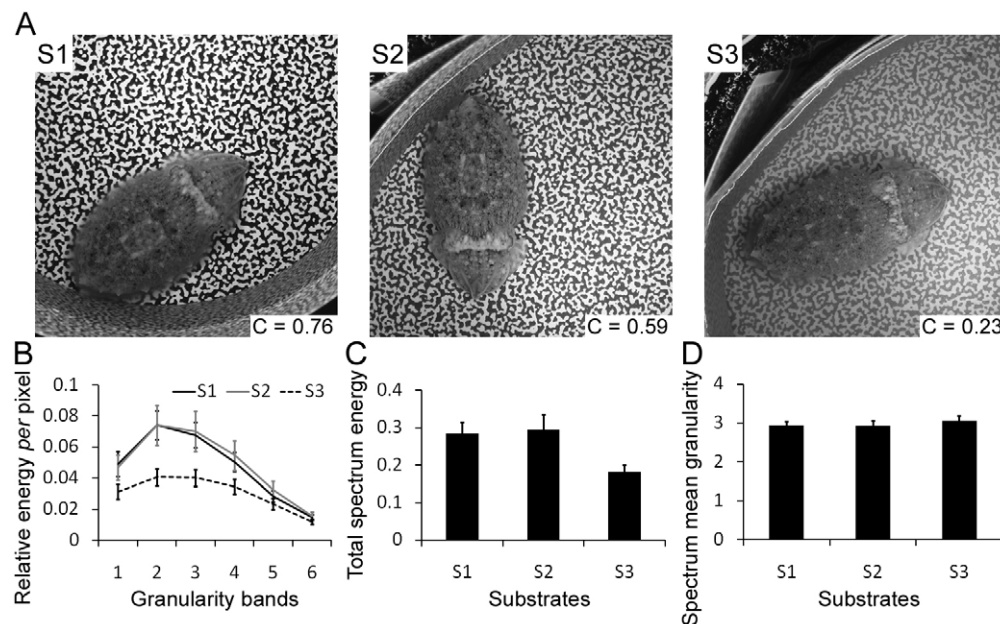


Fig. 5. Contrast of random-texture substrates modulates the strength of mottle body patterning in cuttlefish. (A) Three different substrates (S1–S3) were generated by band-pass filtering white noise images and binarizing the outputs. The bandwidth of this filter was designed to match the spatial scale of mottle components of cuttlefish. Three different Michelson contrasts (S1, 0.76; S2, 0.59; S3, 0.23) were chosen to examine their effects on mottle body patterning. Animals appeared to reduce the strength of mottle body patterns when contrast is low. (B) Average granularity spectra of 14 cuttlefish on random-texture substrates of three contrast levels. (C) Average total energies (TEs) of granularity spectra of all animals on three substrates. The average TE of animals on S3 was significantly different from the ones on S1 and S2 ( $F_{2,26}=8.608$ ,  $P=0.044$  and  $0.022$ , respectively; adjustment for multiple comparisons, Bonferroni), which indicates that substrate contrast modulates the contrast level expression of mottle body patterning. (D) Average mean granularities (MGs) of all animals on three substrates. There was no significant difference in MGs of all cuttlefish across various substrate types ( $F_{2,26}=3.847$ ,  $P=0.051$ ), suggesting that the overall mottle body pattern is independent of substrate contrast. The error bars in B–D represent s.e.m.

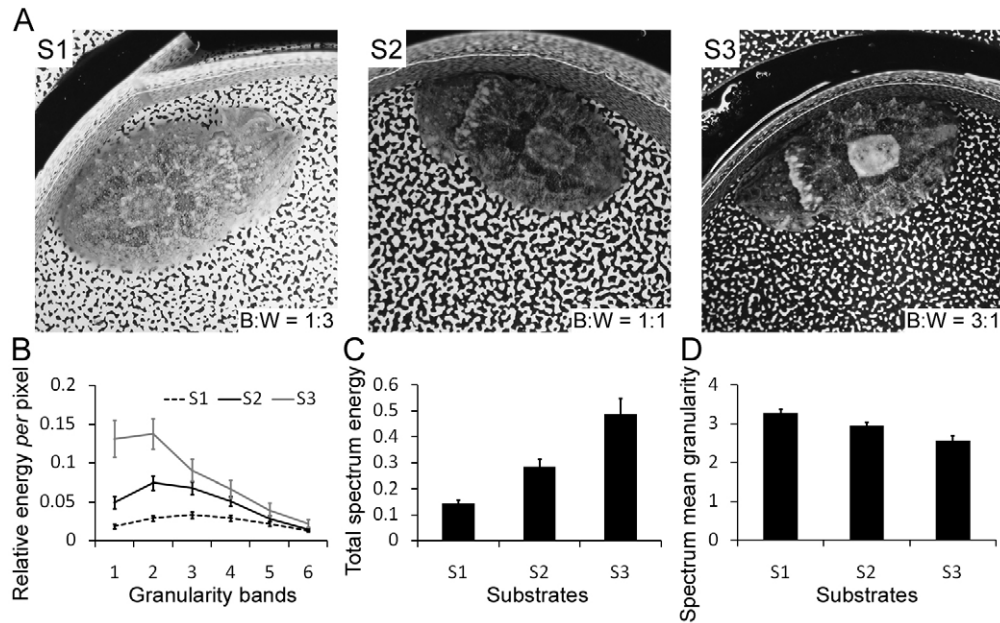


Fig. 6. Black/white ratio (B:W) of random-texture substrates affects mottle body patterning of cuttlefish. (A) Three different substrates (S1–S3) were generated as in Fig. 5, except the binarized thresholds were set 75%, 50% and 25% for S1, S2 and S3, respectively, which resulted the black/white ratio of 1:3, 1:1 and 3:1 for S1, S2 and S3. The Michelson contrast was 0.76 for all 3 substrates (i.e. S2 is identical to S1 shown in Fig. 5). Animals showed a few salient disruptive components on S3, indicating that darkening the background could change cuttlefish body patterns from mottle to disruptive. (B) Average granularity spectra of 14 cuttlefish on random-texture substrates of three black/white ratios. The average curve of animals on S3 showed a typical granularity spectrum of the disruptive body pattern. (C) Average total energies (TEs) of granularity spectra of all animals on three substrates. The average TEs of animals on all substrates were significantly different from one another ( $F_{2,26}=44.586$ ,  $P<0.001$ ), suggesting that the black/white ratio of substrates (i.e. mean background intensity) affects overall contrast of cuttlefish body patterns. (D) The average MGs of animals on all substrates were also significantly different from one another ( $F_{2,26}=28.512$ ,  $P<0.001$ ), which indicates that the mean background intensity is a key visual feature for cuttlefish to switch from mottle body patterns to disruptive body patterns. The error bars in B–D represent s.e.m.

2008b). To examine the role of different spatial frequency contents of the substrate in affecting mottle body patterning, a plaid pattern with only the fundamental frequency of the checkerboard (similar to low-pass filtering) and a substrate lacking the fundamental frequency of the checkerboard (similar to high-pass filtering) were generated (Fig. 7). To examine the contrast effect of these filtered substrates on mottle body patterning, a reduced contrast checkerboard (unfiltered dark-gray/light-gray checkerboard) was used as a comparison. This design tests whether high and low spatial frequency contents of the background (known to affect the disruptive body patterns) are also key visual cues for influencing mottle patterns.

#### Experiment 4 (natural substrates)

Four natural substrates (Fig. 8) were chosen to test if mottle body patterns can be evoked on these backgrounds: (i) small gravel, (ii) medium gravel, (iii) Kona Coast (Tidal Marine Substrates by Seachem, Madison, GA, USA; ‘Kona Coast Aragonite’), and (iv) Sieved Dark Gray Coralline [CaribSea Coraline Marine Aquarium Gravel (Fort Pierce, FL, USA) sieved through a mesh net for size]. Both small and medium gravels [reflectance spectra were reported in Mäthger et al. (Mäthger et al., 2007)] were collected locally and dried before being sieved at the Sedimentation Laboratory of the United States Geological Survey (Coastal and Marine Geology Program, Woods Hole Science Center, MA, USA). The small gravel was a mixture of low contrast, small–medium brown colored stones [size= $2.7\pm 1.2\text{ mm}^2$ ; root mean square (r.m.s.) contrast=0.19] whereas the medium gravel was a slightly larger version of the small gravel (size= $10.1\pm 4.6\text{ mm}^2$ ; r.m.s. contrast=0.19). The Kona Coast was a low contrast substrate of small gray and yellow shells

(size= $5.3\pm 2.4\text{ mm}^2$ ; r.m.s. contrast=0.17), and the Sieved Dark Gray Coralline was a low contrast substrate of small gray shells [size= $3.3\pm 1.1\text{ mm}^2$ ; r.m.s. contrast=0.18; reflectance spectra of both substrates were reported in Mäthger et al. (Mäthger et al., 2008)]. Although the choice of these natural substrates was somewhat arbitrary, the criteria for selection were based on the designed visual features of artificial substrates in aforementioned experiments. Thus, these natural substrates were intended to confirm the results of experiments 1–3.

#### Quantification of body patterns

An automated method for characterizing the body pattern produced by an animal was used here to enable us to discriminate between uniform/stipple, mottle and disruptive patterns (Fig. 3) (for details, see Barbosa et al., 2008b). Disruptive patterns are marked by large-scale, light and dark components of multiple shapes and orientations whereas mottle patterns are marked by fine-grained light/dark variations, and uniform/stipple patterns are even finer in texture, having an overall uniform appearance. In other words, these three pattern types differ in granularity (or spatial scales). We can capture such differences by analyzing the image of the animal in different spatial frequency bands. Each animal image was cut out from its context and warped to conform in size and shape to a standard cuttlefish template. Six octave-wide isotropic ideal filters were used for this granularity analysis. Applying these six filters to the warped cuttlefish image yields six images that partition the information in the original image into different ‘granularity bands’. This procedure is similar to the two-dimensional Fourier analysis of the cuttlefish images, and six discrete energy bands were assigned to capture the relative contribution in different spatial frequency (i.e. granularity).

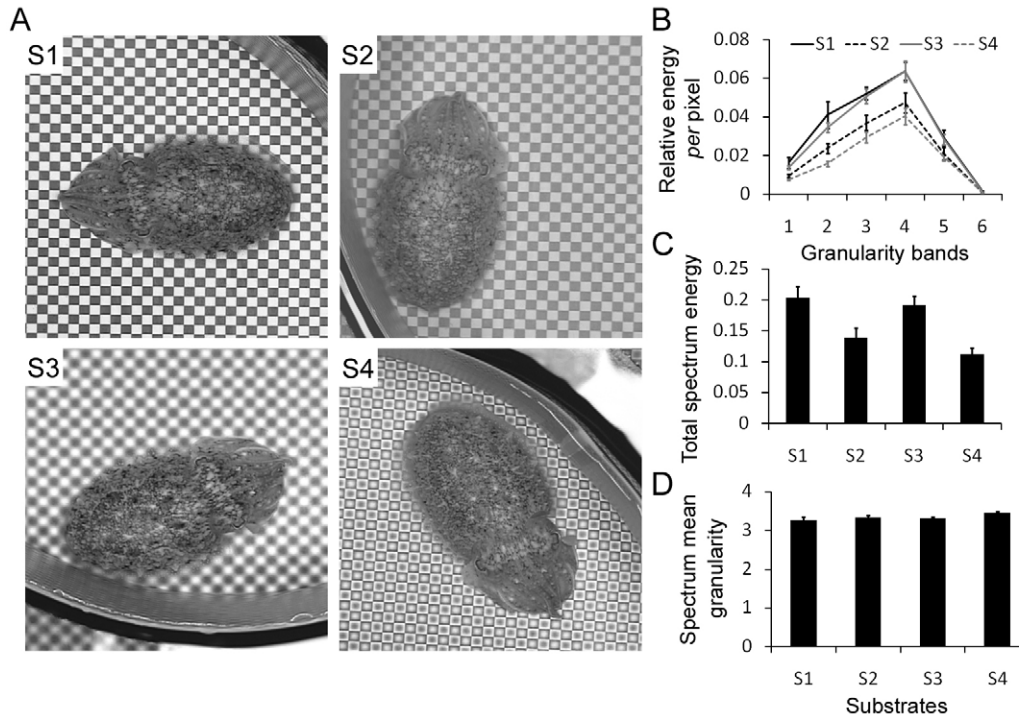


Fig. 7. Low spatial frequency content of checkerboard substrates is required for mottle body patterns in cuttlefish. (A) Four variations of checkerboard substrates were presented to examine the role of different spatial frequency contents in affecting mottle body patterning. Substrate S1 was a black/white checkerboard with its check size equivalent to 10% White square (WS) whereas S2 was a reduced contrast version of S1. S3 and S4 were the complementary pair, in which S3 contained only the fundamental frequency of S1 (ca. low-pass version of S1), and S4 was a substrate lacking the fundamental frequency of S1 (ca. high-pass version of S1). Animals showed nearly equivalent mottle body patterns on S1 and S3, suggesting the importance of low spatial frequency information. (B) Average granularity spectra of six cuttlefish on four variations of checkerboard substrates. These average curves were similar in shape but differed in amplitude. (C) Average total energies (TEs) of granularity spectra of all animals on four substrates were significantly different ( $F_{3,15}=42.411$ ,  $P=0.006$ ), indicating that both spatial frequency content and contrast of substrates affects overall strength of mottle body patterns. (D) The average MGs of animals on all substrates were not significantly different from one another ( $F_{3,15}=2.165$ ,  $P=0.271$ ), which suggests that mottle pattern of cuttlefish on a given substrate scale is independent of spatial frequency content and contrast of substrates. The error bars in B–D represent s.e.m.

From each of the six band-pass filtered images we extracted one number: the sum of the squared pixel values in that image. This is the total energy of the original, standardized image in the given spatial frequency band. We refer to these six energies as the ‘granularity spectrum’ of the image. The scale of these numbers is arbitrary. We use a scheme in which energy is expressed as a mean quantity per pixel and is normalized so as to reflect a proportion of the maximum possible energy that could exist in any image. This energy measurement is closely related to the r.m.s. contrast typically used in characterizing the contrast of complex scenes (Bex and Makous, 2002); specifically, the square root of the sum of the granularity spectrum values would closely approximate the r.m.s. energy in the image. This modification of the Fourier analysis allows us to quantify the granularity of body patterns in a discrete spatial scale. Based on the shape of this granularity spectrum, three major body patterns (uniform/stipple, mottle and disruptive patterns) can be easily distinguished. Typically, the spectrum of the uniform/stipple pattern has low energy in all six granularity bands, which corresponds to low contrast in overall appearance. The mottle pattern yields a spectrum with more total energy than the uniform pattern, and the spectral curve typically has highest energy in granularity bands 3 and 4, which indicates that the mottle body patterns have moderate contrast with the presence of medium-spatial-scale light/dark components. Finally, the disruptive pattern evokes a spectrum with more total energy than either the

uniform/stipple or mottle patterns, and most of this energy is in the two coarsest granularity bands 1 and 2.

#### Data analyses

To further characterize the granularity spectrum of each body pattern described above, two additional statistics [total spectrum energy (TE) and spectrum mean granularity (MG)] were derived to quantify the magnitude and shape, respectively, of the granularity spectrum (Barbosa et al., 2008b). The TE was computed by adding together the six granularity spectrum values. This reflects the overall amplitude of the spectrum. This statistic essentially gauges the overall contrast of the pattern expressed by the animal. The MG, however, was defined as:

$$MG = \frac{\sum_{g=1}^6 gS(g)}{TE}$$

where  $g$  is the energy band number in the granularity spectrum, and  $S(g)$  is the strength in each granularity band (i.e. the granularity spectrum value). This measurement is likely to reveal systematic changes in spectrum shape. The higher the MG, the finer the corresponding cuttlefish body pattern will tend to appear. Thus, this statistic essentially gauges the overall granularity of the body pattern expressed by the animal.



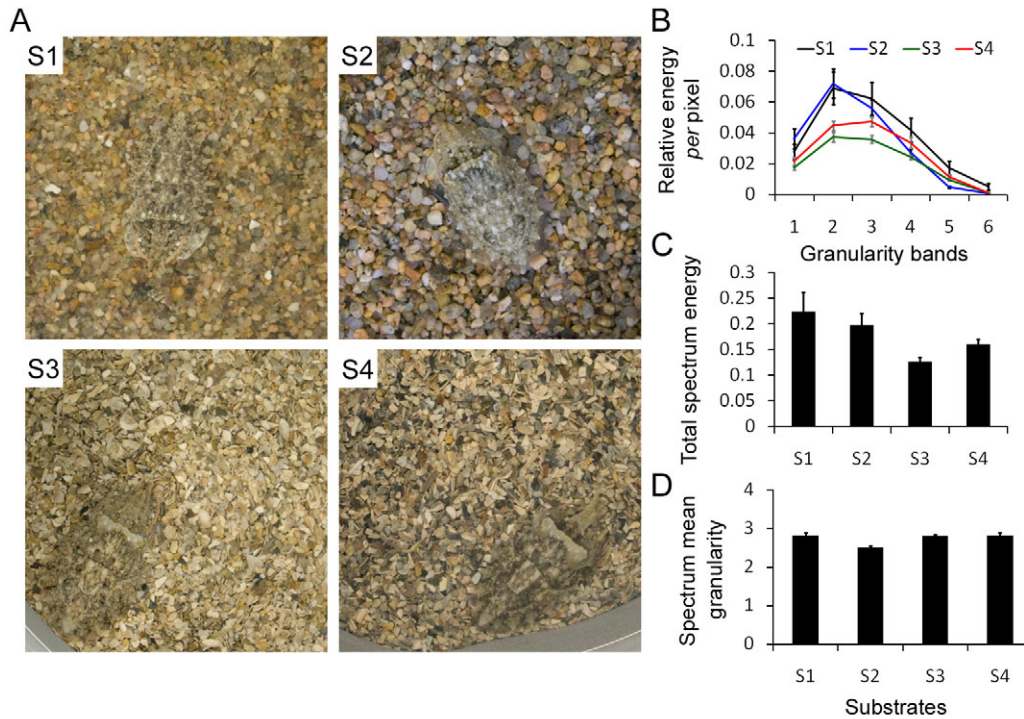


Fig. 8. Natural substrates that evoke mottle body patterns. (A) Cuttlefish showed mottle colorations on all four natural substrates. S1: small gravel; S2: medium gravel; S3: Kona Coast; S4: Sieved Dark Gray Coralline (see text for details). (B) Average granularity spectra of 10 cuttlefish on each of the four types of natural substrates. Animals showed typical curves of mottle body patterns. (C) Average total energies (TEs) of granularity spectra of all of the animals on the four substrates were significantly different ( $F_{3,36}=3.569$ ,  $P=0.023$ ), indicating that the strength of mottle patterning depends on spatial properties of natural substrates. (D) The average MG of animals on S2 was significantly lower than the one on the other three substrates ( $F_{3,36}=7.386$ ,  $P=0.002$ ,  $0.003$ ,  $0.003$  for S1, S3, S4, respectively; adjustment for multiple comparisons, Bonferroni), which suggests that the spatial scale of natural substrates plays an important role in determining mottle patterns of cuttlefish. The error bars in B–D represent s.e.m.

A within-subjects one-way repeated-measures analysis of variance (ANOVA) was used to evaluate the response difference throughout this study, except for experiment 4, where the typical one-way ANOVA was applied. A *post hoc* (Bonferroni/Dunn) test was also used to determine the difference among various conditions. All statistical analyses were performed using SPSS 13 (SPSS Inc., Chicago, IL, USA).

## RESULTS

Mottle body patterns in cuttlefish (*S. officinalis*) show variations in shape, contrast and scale. First, a selection of lab and field images was quantified. Then, characterizations of background visual features for eliciting mottle patterns using a series of systematically designed artificial substrates were obtained. Finally, several natural substrates whose properties are similar to the background visual features of the artificial substrates were applied to confirm these findings.

### Quantification of various mottle body pattern types in cuttlefish

Although the mottle pattern of an animal is commonly described as having small-to-moderate-scale light and dark patches distributed somewhat evenly across the body surface, the mottle body pattern in cuttlefish has a wide range of variations (images A1–A6 in Fig. 1). In Fig. 3, we described a typical granularity spectrum that depicts the mottle pattern, in which the curve tends to peak (i.e. has highest energy, which is a measurement of contrast) in granularity bands 3 and 4. Bands 1–6 represent the size scales of the patches of light and dark in the animal's body pattern: bands 3 and 4 are moderately

sized patches of light and dark whereas bands 1 and 2 are larger patches and bands 5 and 6 are more fine-grained. Some mottle body patterns can deviate from this norm of having peaks in granularity bands 3 and 4, and still be considered mottle patterns (e.g. A2, A4 and A6, respectively, in Fig. 1B). This deviation in amplitude of the granularity spectra indicates the contrast strength variations (e.g. light and dark patches) in mottle coloration (Fig. 1C) whereas the difference in shape of the granularity spectra reflects the spatial scale variations (i.e. small-to-moderate-scale) in mottle patterns (Fig. 1D).

### Cuttlefish show mottle patterns on scramble substrates

Previous studies showed that cuttlefish express mottle body patterns on the black/white checkerboard with its checker size equivalent to 3–12% WS area (Barbosa et al., 2004; Barbosa et al., 2008b). To extend this restricted spatial property of the checkerboard (i.e. regularly spaced binary squares), and systematically examine the effects of background intensity, contrast and texture on mottle body patterning, we generated nine scramble substrates (Fig. 4A) by randomly placing small squares of five gray levels with specifically chosen histograms [gray level distributions (for details, see Chubb et al., 1994)]. If cuttlefish are sensitive to the histogram of scramble substrates, one might expect to find different body patterns on some of these complementary pairs of substrates. Our results showed that cuttlefish expressed mottle patterns on all nine scramble substrates (Fig. 4A). The nine average granularity spectra from 10 animals appeared very similar in shape and slightly different in amplitude (Fig. 4B). The TE and MG statistics confirmed this observation (Fig. 4C,D). Particularly, the TE of S6 was slightly larger than that of S2, suggesting that lowering background intensity tends to



Fig. 9. Mottle coloration for background matching is widespread in the animal kingdom. (A) Owlet moth (*Leuconycta lepidula*; common in N. America). (B) Flowerly cod (*Epinephelus fuscoguttatus*; Great Barrier Reef). (C) Toad (northern New Hampshire, USA). (D) Owl (Copyright Art Wolfe /www.artwolfe.com from the book *Vanishing Act*).

increase the mottle contrast. Similarly, the TE of S3 was slightly larger than that of S7, suggesting that increased background contrast also tends to enhance the mottle contrast. Furthermore, the TE of S4 was significantly larger than that of S8 ( $P=0.033$ ), indicating that the proportion of small dark objects in the scene has an important role in modulating the mottle contrast.

#### Effect of texture substrate contrast on the strength of mottle body patterning

It was known previously that checkerboard contrast can influence cuttlefish body patterning (Barbosa et al., 2008b; Chiao and Hanlon, 2001a; Kelman et al., 2007; Kelman et al., 2008; Mäthger et al., 2006). However, checkerboards are a very restricted class of substrates, and thus it might be a special case for cuttlefish. To further examine whether the contrast dependency of the cuttlefish patterning responses previously observed with checkerboards and scramble backgrounds (described above) can be generalized to other substrates, we generated a set of substrates (Fig. 5A) whose spatial scale was matched closely to that of cuttlefish's mottle components (Fig. 2) with different Michelson contrasts (0.76, 0.59 and 0.23). Not surprisingly, cuttlefish appeared to show reduced strength of mottle body patterns when the substrate contrast was low (S3 in Fig. 5A). The three average granularity spectra from 14 animals showed that mottle body patterning of cuttlefish on S1 and S2 were quite similar whereas the response amplitude on S3 was much lower (Fig. 5B). The TE measurement suggests that average TE of animals on S3 was significantly different from the ones on S1 and S2 ( $P=0.044$  and  $0.022$ , respectively), which indicates that substrate contrast indeed modulates the strength of mottle body patterning but only in lower background contrast range (Fig. 5C). Interestingly, the average MGs of all animals on three substrates were not significantly different from one another ( $P=0.051$ ), suggesting that mottle body patterns are shown on a range of contrasts provided that the small spatial scale criteria are met (Fig. 5D).

#### Effect of the black/white ratio of texture substrates on mottle body coloration

In disruptive body patterns of cuttlefish, it is known that cuttlefish visually cue on light objects and not dark objects on the background

(Kelman et al., 2007; Mäthger et al., 2007; Zylinski et al., 2009). In the experiment described above (Fig. 4), the strength of cuttlefish mottle patterns seemed to be determined by the proportion of dark objects in the scene. To test whether the black/white ratio of substrates plays a role in determining mottle body patterning [see also Barbosa et al. (Barbosa et al., 2004)], three texture substrates with different black/white ratios (1:3, 1:1 and 3:1) were used (Fig. 6A). Note that the texture substrate with a black/white ratio of 1:1 (S2 in Fig. 6A) is identical to the substrate shown in the previous experiment (S1 in Fig. 5A). Inevitably, changing this ratio also changes the mean intensity of background. Thus, this experiment was also intended to examine the effect of background intensity on mottle body patterning. Noticeably, animals showed a few salient disruptive components on S3 (e.g. the White square and the White head bar), indicating that darkening the background could substantially change cuttlefish body patterns from mottle to moderate disruptive (S3 in Fig. 6A). However, animals retained mottle body patterns on S1, although the overall contrast was lower than on S2. This result is consistent with our previous finding that decreasing background intensity tends to evoke the expression of disruptive components and increasing background intensity tends to eliminate it (Chiao et al., 2007). The three average granularity spectra from 14 animals showed differences in both shape and amplitude (Fig. 6B). Particularly, the average curve of animals on S3 resembled a typical granularity spectrum of the disruptive body pattern (Fig. 3). The average TEs of animals on all substrates were significantly different from one another ( $P<0.001$ ), which suggests that the black/white ratio of substrates (i.e. mean background intensity) affects overall contrast of cuttlefish body patterns significantly (Fig. 6C). Furthermore, the average MGs of animals on all substrates were also significantly different from one another ( $P<0.001$ ; Fig. 6D). This indicates that the mean background intensity plays an important role for cuttlefish to modulate the expression of mottle and disruptive body patterns.

#### Low spatial frequency of substrates is required for mottle body patterns

Earlier studies have shown that both low and high spatial frequency contents of backgrounds are required for evoking disruptive body

patterns (Chiao et al., 2005; Kelman et al., 2007). However, little is known about whether low or high spatial frequency information of substrates is sufficient for eliciting mottle body patterns. To address this, we turned to the checkerboard, because it contains a fundamental frequency that defines the check size and it is easy to separate from other spatial frequency contents. Four variations of checkerboard substrates were used (Fig. 7A). Substrate S1 was a small black/white checkerboard, S2 was a reduced contrast version of S1, and S3 and S4 were substrates containing only the fundamental frequency of S1 (a plaid pattern, *ca.* low-pass version of S1) and lacking the fundamental frequency of the S1 (*ca.* high-pass version of S1), respectively. Consistent with previous findings, animals on S1 showed mottle body patterns (Barbosa et al., 2004), and the mottle strength was slightly reduced on S2 (Barbosa et al., 2008b). However, cuttlefish showed nearly equivalent mottle body patterns on S1 and S3, which suggest the importance of low spatial frequency information for mottle patterning (Fig. 7A). Surprisingly, animals showed weak mottle patterns on S4, indicating that high spatial frequency information is not sufficient to drive the expression of strong mottle patterns (Fig. 7A). The four average granularity spectra from six animals showed similar trends with different amplitudes (Fig. 7B). The average TEs of all animals (Fig. 7C) on four substrates were significantly different ( $P=0.006$ ), which supports the notion that both substrate contrast (S1 vs S2) and spatial frequency content (S1 vs S4) affect the strength of mottle body patterning. Furthermore, the average MGs of animals (Fig. 7D) on all substrates were not significantly different from one another ( $P=0.271$ ). This suggests that mottle patterning of cuttlefish on a given spatial scale background is independent of spatial frequency content and substrate contrast.

#### Natural substrates that evoke mottle patterns

Although the early attempts (Barbosa et al., 2004; Barbosa et al., 2008b; Kelman et al., 2007) and the experiments reported here have demonstrated that various artificial substrates with small-scale light and dark objects of moderate contrast tend to elicit mottle body patterns, and some field images also show distinct mottle body pattern in the cuttlefish's natural environments (A5 and A6 in Fig. 1), the type of natural substrates that can evoke mottle patterns has not been empirically tested in the laboratory. We chose four natural substrates (Fig. 8A) with spatial properties similar to the artificial substrates known to evoke mottle patterns (see Materials and methods for spatial property details). Cuttlefish deployed mottle patterns on all of the four natural substrates, although the mottle strength appeared to be different on these backgrounds (Fig. 8A). The four average granularity spectra from a total of 40 cuttlefish (10 on each substrate) showed typical curves of mottle body patterns, except that animals on S2 had a slightly different curve shape with fewer small-scale mottle splotches (Fig. 8B). The average TEs of all animals on four substrates were significantly different ( $P=0.023$ ; Fig. 8C). These different mottle contrasts of cuttlefish on four natural substrates appear to be consistent with the difference in background contrast and size distribution. Furthermore, the average MG of animals on S2 was significantly lower than on the other three substrates ( $P=0.002, 0.003, 0.003$  for S1, S3, S4, respectively; Fig. 8D). This may be explained by the spatial scale difference between S2 and the other substrates (*i.e.* the medium gravel had particles about twice the size of the other natural substrates), and suggests that background spatial scale could play an important role in affecting mottle patterning of cuttlefish on natural substrates.

## DISCUSSION

Animals achieve camouflage using a variety of body patterns, colors, contrasts, etc. (Cott, 1940; Edmunds, 1974; Poulton, 1890; Ruxton et al., 2004; Thayer, 1909). We propose that mottle (according to the definition presented in this paper) is a widespread form of body pattern for background matching in the animal kingdom (see Fig. 9 for examples of non-cephalopods). Cuttlefish, and cephalopods in general, provide a unique system to study visual background features responsible for camouflage because of their ability to adapt their appearance in response to different visual backgrounds (Hanlon and Messenger, 1996). In this set of experiments, we varied the spatial properties of visual backgrounds to reveal the background statistics that cuttlefish perceive and use to deploy mottled camouflage patterns.

#### Multiple scales of background-matching body patterns in cuttlefish

Although the mottle body pattern is generally described as the mixture of light and dark patches across the body surface, the scale of these light/dark patches varies depending on background features (Fig. 1A). The skin of cuttlefish is composed of millions of chromatophore organs, and each of them receives direct excitatory input from the chromatophore lobes in the brain (Messenger, 2001). However, the splotches seen in the skin of cuttlefish (Fig. 2) are aggregations of chromatophores, which form so-called 'physiological units' of chromatophore patterns (Packard, 1982). These physiological units have been shown to represent neurally controlled components of body patterns (Packard, 1995). In *S. officinalis*, the large-scale mottle component is mainly composed of four sets of Paired mantle spots (Hanlon and Messenger, 1988) that surround the White square (Fig. 2C) whereas the small-scale mottle component is represented by dark splotches of chromatophore aggregations, interspersed with light patches throughout the mantle and arms (resulting from the retraction of chromatophores) (Fig. 2A). By varying the expression strength and frequency of these large- and small-scale mottle components, cuttlefish are able to produce a variety of mottle patterns. Importantly, however, the size scale is somewhat limited because they basically have only two sizes of dark mottle patches: small and large. Because the background commonly contains a mixture of various scales of light and dark objects, the flexibility of expressing multiple scales of mottle body patterns in cuttlefish is advantageous for achieving general background matching in different environments.

#### Multiple visual stimuli that evoke mottle coloration

It is well known that cephalopods with their single-lens eyes have keen vision, and may even exceed their vertebrate counterpart, fish eyes (Land and Nilsson, 2002; Messenger, 1991). Cuttlefish, with a peculiar W-shaped pupil, have been shown to have high spatial acuity (Groeger et al., 2005; Messenger, 1991; Muntz, 1999; Watanuki et al., 2000). Therefore, it is likely that cuttlefish can resolve fine details in the surroundings and perhaps perceive many visual features except color (Mäthger et al., 2006; Marshall and Messenger, 1996), although little is known about visual processing beyond the retina. Because mottle body patterning is so commonly used to achieve background matching (often referred to as general background resemblance), for changeable cuttlefish it is crucial to assess the visual features of substrates and control the expression of those mottle components to resemble the background. In the present study, we have revealed that cuttlefish cue on spatial scale (or granularity), contrast of backgrounds and overall brightness of the scene to evoke mottle body patterning.

In general, these three cues are essential for texture match between animal and background. On an artificial substrate, earlier and present studies indicated that the spatial scale of a background must be within 3–12% of WS area to evoke mottle body patterns (Barbosa et al., 2004; Barbosa et al., 2008b; Shohet et al., 2007). This size range is consistent with the smaller scale of mottle components on the skin of cuttlefish. Because animals showed similar mottle responses to lower spatial frequency content of checkerboard as to the unfiltered black/white checkerboard (Fig. 7), it is likely that this low spatial frequency information is used to extract granularity information from the background. From previous studies, it is known that cuttlefish have good contrast sensitivity (Barbosa et al., 2008b; Chiao et al., 2007; Chiao and Hanlon, 2001a; Kelman et al., 2007; Kelman et al., 2008; Mähger et al., 2006). Thus, it is not surprising that these animals can modulate their mottle strength to generally match the background contrast.

In addition to spatial scale and contrast, cuttlefish seem to be sensitive to the mean intensity of the background, i.e. lowering the overall brightness of substrates tends to evoke disruptive components even on small-scale textures (Fig. 6). This is consistent with our previous finding that changing the mean intensity of the background (inevitably changing the Weber contrast) affects body patterning (Chiao et al., 2007). Note that the Weber contrast is defined as the normalized deviation of intensity from the mean intensity of the substrate. When the Weber contrast is extremely high (by lowering brightness), it may be that the contrast match between animal and background for mottle body patterns is unlikely (or impossible); thus, cuttlefish switch to a different crypsis tactic (i.e. disruptive coloration). Note that when cuttlefish switch to a disruptive body pattern in such cases, there is no longer a match in scale between animal and background.

Although all four natural substrates used in this study successfully evoked mottle body patterns, animals on S2 showed a slightly different granularity spectrum (Fig. 8). The main difference between S2 and the other three substrates is the gravel size (contrast and brightness are similar). This suggests that the spatial scale of natural substrates may play a crucial role in eliciting mottle colorations.

### Background matching and mottle camouflage patterns

Camouflage definitions and quantification have so far been difficult (e.g. Cott, 1940; Edmunds, 1974; Endler, 1978; Endler, 1984; Thayer, 1909). Recently, the crypsis tactic of disruptive coloration has received attention and some empirical support (Cuthill et al., 2005; Cuthill et al., 2006; Fraser et al., 2007; Merilaita, 1998; Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Stevens et al., 2006b; Stobbe and Schaefer, 2008). For a disruptive pattern to be effective, the highly contrasting markings on the body are used to break up the animal's outline; thus, the appearance of the animal shape is difficult to detect or recognize by the predators (Stevens, 2007; Stevens et al., 2006a; Stevens and Merilaita, 2009b); there is little argument that disruptive patterns also achieve some measure of background matching (Hanlon et al., 2009). While disruptive coloration as a distinct crypsis tactic may be context-dependent and is currently under lively debate (Endler, 2006; Sherratt et al., 2005), background matching is an accepted mechanism of crypsis, and mottle body patterns as described and quantified herein represent a common form of background matching. For simplicity, we have assigned two body pattern types that function by background matching in cuttlefish (Uniform and Mottle), where these two pattern types are examples on the continuum of background matching patterns that these animals can show. Although in the present study we are only addressing the visual cues that elicit mottle patterns,

the other body patterns (e.g. uniform and stipple and perhaps more fine-tuned patterns) that are on this continuum of background matching patterns will be addressed in the future.

Although background matching is common among animals, only in certain cases will animals be able to achieve a 'high fidelity' specific background match on natural substrates. In uniform body patterning, specific resemblance may be more readily possible, where an animal is able to match the intensity, contrast, color and pattern scale of the few truly uniform backgrounds that exist in nature. However, in complex visual backgrounds (i.e. non-uniform backgrounds), a high-fidelity match will nearly always be impossible due to the enormous visual diversity of natural backgrounds (such as coral reefs, kelp forests, rain forests, etc. where biodiversity is great). Under these conditions, animals with mottle body patterns are possibly the best adapted to achieve camouflage *via* a general background resemblance where the match is not perfect in all respects. We have explored this idea recently with respect to cephalopods (Hanlon et al., 2009). It has been hypothesized that the evolution of camouflage is facilitated by visual background complexity (Merilaita, 2003; Merilaita et al., 2001). Mottle body patterns are certainly advantageous in visually complex environments; thus, the different scales of mottle patterning seen in cuttlefish may be the result of their diverse habitats. Further empirical investigations are required to verify these concepts.

Although the present study is about visual perception of cuttlefish, as a first attempt to examine background matching by comparing spatial properties of the animal's mottle body pattern and its immediate surroundings, we applied the same granularity analysis method to a cuttlefish-sized area of the background within the image. The granularity spectra of the cuttlefish-shaped background areas from all natural and artificial substrates used in the present study are shown in supplementary material Fig. S1. It is apparent that the overall shape of the granularity spectrum of the backgrounds is similar to that of the animals. However, close examination of these curves reveals that the magnitude and the peak of the backgrounds do not exactly match that of the animals, even in the case of natural substrates. This observation supports the notion that cuttlefish's mottle body pattern works as general background resemblance to conceal themselves on a variety of substrates, a point we introduced earlier (Hanlon et al., 2009).

In addition to background matching [(which is considered by Stevens and Merilaita, as one of the six types of crypsis to defeat detection (Stevens and Merilaita, 2009a)], there is another common mechanism of camouflage called masquerade (Cott, 1940; Stevens and Merilaita, 2009a). Cuttlefish and octopus often perform a type of masquerade in which they do not generally resemble or match the substrate they are sitting on (or surrounded by) but rather they generally resemble rocks, algae or corals (i.e. three-dimensional objects) in the vicinity (e.g. Fig. 1A6). Because dapples or splotches are common surface characters on those objects that cuttlefish try to resemble, it renders the mottle body pattern an effective means of avoiding detection and/or recognition, i.e. in Fig. 1A6, the cuttlefish could be explained as background matching to the nearby rock with algae to avoid detection (because it is a random sample of other similar sized/patterned objects on the sand plain) or as masquerade to resemble an uninteresting object to defeat recognition. From the viewpoint of cephalopod visual perception, this raises the question of when, how and why cuttlefish or octopus choose masquerade of distant or specific objects rather than the commonest visual surrounds, which is what they usually do as judged by our underwater *in situ* photographs.

Marine visual backgrounds consist of many small-to-moderate objects of moderate contrast; thus, mottle camouflage is common in benthic cephalopods such as cuttlefish, octopus and some squids (Hanlon et al., 1999a; Hanlon et al., 1999b; Hanlon and Messenger, 1996) as well as many animals, both aquatic and terrestrial (Brunberg et al., 2006; Graf and Nentwig, 2001; Purcell and Tekanene, 2006; Sazima et al., 2006). Mottle body patterns that achieve some degree of background matching are expected to be among the most prevalent form of body patterning coloration throughout the animal kingdom but a great deal of research is required before such assertions can be backed up with quantitative assessments.

### ACKNOWLEDGEMENTS

We are grateful to the Sholley Foundation and ONR grant N000140610202 for partial support of this project. We also thank Justin Marshall for identifying the species of flowery cod, and Art Wolffe for allowing use of the owl photo in Fig. 9. Special thanks to the Animal Care Staff of the Marine Resources Center of the MBL. C.-C.C. was supported by the MBL summer research fellowship, and the National Science Council of Taiwan (NSC-97-2918-I-007-004).

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