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Cuttlefish adjust body pattern intensity with respect to substrate intensity to aid camouflage, but do not camouflage in extremely low light

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ABSTRACT

Cuttlefish are able to camouflage to a wide variety of natural backgrounds that contain varying colors, intensities and patterns. Numerous studies have investigated the visual cues that influence cuttlefish body pattern expression, yet none have addressed experimentally how well overall intensity is matched between animal and substrate. Here, cuttlefish were tested on artificial and natural substrates that varied in intensity and were illuminated by different light levels; calibrated grayscale photographs were used to analyze the intensity of cuttlefish and their surrounding substrates. We found that cuttlefish scaled their body pattern intensity with respect to substrate intensity under bright and moderate lighting conditions, but not under low or extremely low lighting conditions. Surprisingly, in extremely low light (<0.0001 lux), cuttlefish did not camouflage to the substrate, but instead retracted most of their dermal chromatophores, assuming a pale appearance. This closed chromatophore body pattern may represent a low-energy choice when cuttlefish have extremely limited visual input. Overall, these results suggest that at light levels most often encountered in the wild, cuttlefish may achieve resemblance to the background by matching the intensity of the substrates on which they are settled, but they do not camouflage in low or extremely low lighting conditions. In addition, our results suggest the possibility that cuttlefish may be able to detect light at an order of magnitude darker than starlight (<0.0001 lux), as evidenced by the expansion of their chromatophores when exposed to this low light level; however, these cuttlefish did not appear to be able to distinguish patterns since they did not camouflage themselves with respect to the substrate.

1. Introduction

Cephalopods, like *Sepia officinalis*, are able to rapidly adapt their body pattern, color and intensity to camouflage on backgrounds that they encounter in the wild (Akkaynak et al., 2013; Hanlon, 2007; Hanlon and Messenger, 1988; Hanlon et al., 2011, 2013); this ability appears to be largely under visual control (Hanlon and Messenger, 1988; Marshall and Messenger, 1996). Cuttlefish are also capable of adjusting their body patterns to camouflage at night (Allen et al., 2010; Hanlon et al., 2007), and their night vision must be well developed to detect prey, as well as avoid predation. In fact, one experimental study has shown that *S. officinalis* are capable of dynamically camouflaging in very dim lighting conditions (the equivalent of starlight levels on land; Allen et al., 2010), suggesting that their vision is indeed especially sensitive in low light.

Although they are colorblind (Marshall and Messenger, 1996; Mäthger et al., 2006), cuttlefish are able to produce a wide variety of colors and intensities using their sophisticated skin (e.g., Mäthger et al., 2008, 2009; Wardill et al., 2012). A cuttlefish's appearance depends on which combinations of skin elements are expressed at any given time; light is reflected by pigmented chromatophores, structural reflectors (iridophores and leucophores), or both at the same time (Mäthger and Hanlon, 2007). The interaction between chromatophores and structural reflectors produces colors that encompass the whole visible spectrum (400–700 nm; Mäthger and Hanlon, 2007), allowing these animals to produce the abundance of colors and intensities that enable them to camouflage themselves to their natural surroundings.

Several recent studies have investigated the color- and luminance-matching capabilities of cuttlefish in the laboratory and in the wild, and have found that the spectral properties of cuttlefish and their surroundings (nearby objects and substrates) were closely related

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(e.g., Akkaynak et al., 2013; Chiao et al., 2011; Hanlon et al., 2013; Mäthger et al., 2008; Zylinski et al., 2011). Akkaynak et al. (2013) also showed that, in general, *S. officinalis* matched the luminance spectra of their surrounding substrates more closely than they matched color; the authors suggested that intensity-matching may be more important than color-matching for cuttlefish since most objects tend to appear blue–green underwater due to attenuation of longer wavelengths.

While the color- and luminance-matching capabilities of cuttlefish have been investigated, no study has addressed experimentally how well overall intensity is matched between animal and substrate. In addition, although cuttlefish have been shown to camouflage at night (Allen et al., 2010; Hanlon et al., 2007), their ability to intensity-match under low light conditions has not been examined previously. We tested whether cuttlefish scale their body pattern intensity with respect to the intensity of surrounding artificial or natural substrates under different lighting conditions that were close to what they may encounter in the shallow water they inhabit in the wild: daylight (2000 lux—typical overcast day), crepuscular conditions (56 lux—sunrise/sunset), and a moonless overcast night (<0.0001 lux; Johnsen, 2012). We used calibrated grayscale photographs to compare cuttlefish body intensity to the intensity of their surrounding benthic substrate (we use the term *intensity* to refer to the values recorded in the pixels of an image taken by a camera).

2. Materials and methods

2.1. Animals and experimental setup

Ten adult *S. officinalis* were used for each set of experiments. Animals were reared from wild-collected eggs and ranged in size from 6.8 cm–8.7 cm in mantle length. To minimize stress to the animals, no more than three trials per day were performed with a single cuttlefish. Experiments were performed in a black tent inside of a light-occluding galvanized steel box (2.0 mm thick). A circular arena (15 cm diameter) was placed inside of a tank with running seawater to confine the animals to the substrates. The arena was illuminated with a ring of broad-spectrum white LED lights (high brightness daylight white, Environmental Lights, San Diego, CA; spectral distribution shown in Supplementary Fig. S1). Cuttlefish were tested at four light levels: 1) bright (LED ring illuminated without any filters), 2) moderate (LED ring with two neutral density filters (LEE Filters #211, Burbank, CA, USA)), 3) low (inside of closed black tent inside of a galvanized steel box with steel door slid open 10 cm) and 4) extremely low (inside of closed black tent inside of a galvanized steel box with steel door closed completely). Light levels were measured inside the arena using a hand-held Field Max II radiometer with an OP-2VIS sensor (Coherent, Inc, Santa Clara, CA) to produce a measurement in watts/cm^2 and with an International Light Technologies Research radiometer with a SED033/Y sensor (International Light Technologies, Peabody, MA) to produce a measurement in lux. Cuttlefish behavior was monitored via a television screen outside of the steel box and photographs were taken remotely with a Canon Rebel XS digital camera with a Canon Speedlite 580EX flash. A white and black standard was placed on the outside of the arena—inside the field of view of the camera, but outside the view of the cuttlefish—to standardize the intensity in each photograph.

2.2. Experiment 1: artificial substrates

We tested cuttlefish on four computer-generated substrates that were placed on the floor and the walls of the arena (Fig. 1A): dark gray (RGB 61), medium gray (RGB 122), light gray (RGB183), and black and white checkerboard (known to evoke a Disruptive body pattern) at four light levels (bright: 408 μW/cm^2, 2100 lux; moderate: 40.1 μW/cm^2, 56 lux; low: 2.04 nW/cm^2, <0.0001 lux; extremely low: 1.02 nW/cm^2, <0.0001 lux) to determine whether light intensity affected cuttlefish body intensity and/or body pattern. The substrate and light intensity combinations were presented to cuttlefish in a randomized order. At the beginning of each trial, cuttlefish were placed inside of the experimental arena and allowed to acclimate to extremely low light for 20 min. After acclimation, a flash photograph was taken of the cuttlefish using a remote trigger (modified optical interrupter, Mumford Microsystems, Santa Barbara, CA). Then, a second photograph was taken using the following procedure: The lights inside of the experimental arena were turned on to the setting to be tested in that trial and the cuttlefish were allowed to acclimate to the experimental light setting for 20 min. After 20 min, the lights inside of the experimental arena were turned off, which immediately (i.e., 5 μsec) triggered the camera to take a flash photograph; this speed is faster than cephalopods are known to respond with a change in body pattern (e.g., in *Hapalochlaena lunulata*, the blue-ring flashes can be shown in as little as 0.3 s (Mäthger et al., 2012)). All photographs were taken under identical conditions (using an external camera flash in the dark), regardless of the experimental light setting. This procedure allowed the photographs to record any differences in cuttlefish body pattern intensity according to the experimental light levels without affecting the overall intensity of the images.

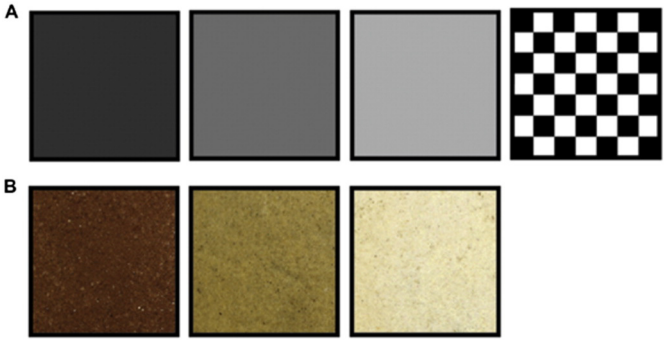

Fig. 1. Experimental substrates used to test for scaling of body pattern intensity with respect to substrate intensity in *Sepia officinalis*. A) Artificial gray substrates: dark gray (RGB = 61), medium gray (RGB = 122), light gray (RGB = 183) and black (RGB = 0) and white (RGB = 255) checkerboard. B) Natural sand substrates: dark brown sand, light brown sand and white sand.

2.3. Experiment 2: natural substrates

We tested whether cuttlefish scale their body intensity on natural substrates that were glued to the floor and the walls of the experimental arena: dark brown sand, light brown sand and white sand (Fig. 1B) at four light levels (bright: 408 μW/cm^2, 2100 lux; moderate: 40.1 μW/cm^2, 56 lux; low: 2.04 nW/cm^2, <0.0001 lux; extremely low: 1.02 nW/cm^2, <0.0001 lux). Photographs were taken using the same method and time intervals as in Experiment 1. Since substrates were made from natural sand that was not homogeneous, there was some natural variation in the intensity of each substrate.

2.4. Image analysis

Images were captured in camera raw format and were manually processed in MATLAB (Mathworks, Inc. Natick MA) as described in Akkaynak et al. (2014). White and black photographic calibration targets were placed outside of the arena—inside the field of view of the camera, but outside the view of the cuttlefish—to standardize the intensity in each photograph. Demosaicing was done with the default algorithm used by Adobe DNG converter (Adobe, Inc., version

6.3.0.79). Following demosaicing, camera raw (linear RGB) values were white balanced using the calibration targets in the scene. These targets were always placed in the same location in the photographic setup in order to achieve consistency throughout the data set. Since all photographs in the dataset were obtained with the same camera, we omitted step 4 in (Akkaynak et al., 2014) and

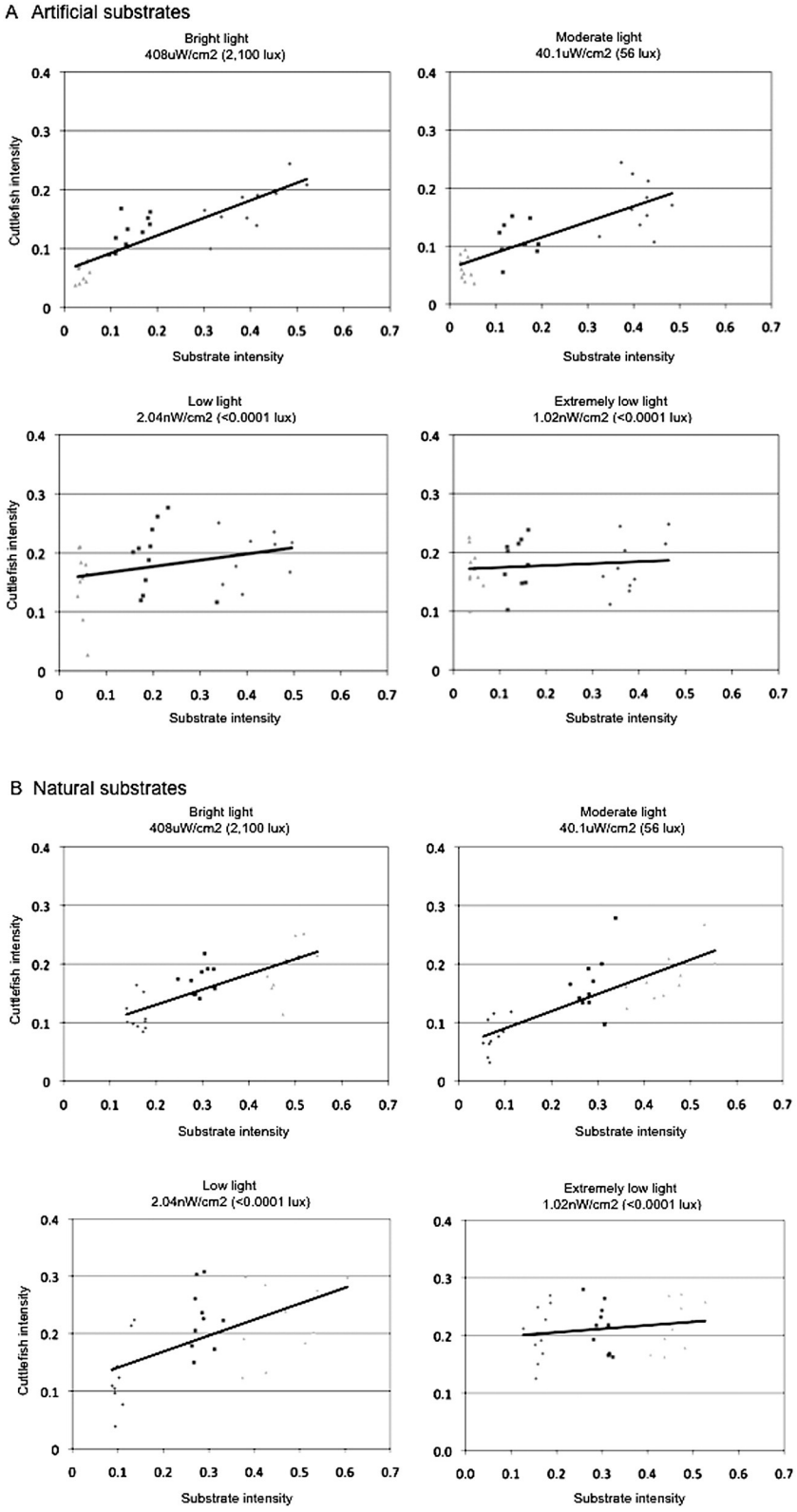

Fig. 2. Cuttlefish scale their body pattern intensity with respect to substrate intensity under bright and moderate lighting conditions, but not under low or extremely low light. A) Cuttlefish body pattern intensity versus substrate intensity on artificial gray: bright light, $\rho = 0.76$, $p = 3.13 \times 10^{-6}$; moderate light, $\rho = 0.79$, $p = 1.52 \times 10^{-6}$; low light, $\rho = 0.58$, $p = 6.06 \times 10^{-4}$; extremely low light, $\rho = 0.17$, $p = 0.37$ and B) cuttlefish body pattern intensity versus substrate intensity on natural sand substrates at four light levels: bright light, $\rho = 0.90$, $p = 2.34 \times 10^{-7}$; moderate light, $\rho = 0.80$, $p = 1.26 \times 10^{-6}$; low light, $\rho = 0.36$, $p = 0.05$; extremely low light, $\rho = 0.17$, $p = 0.21$).

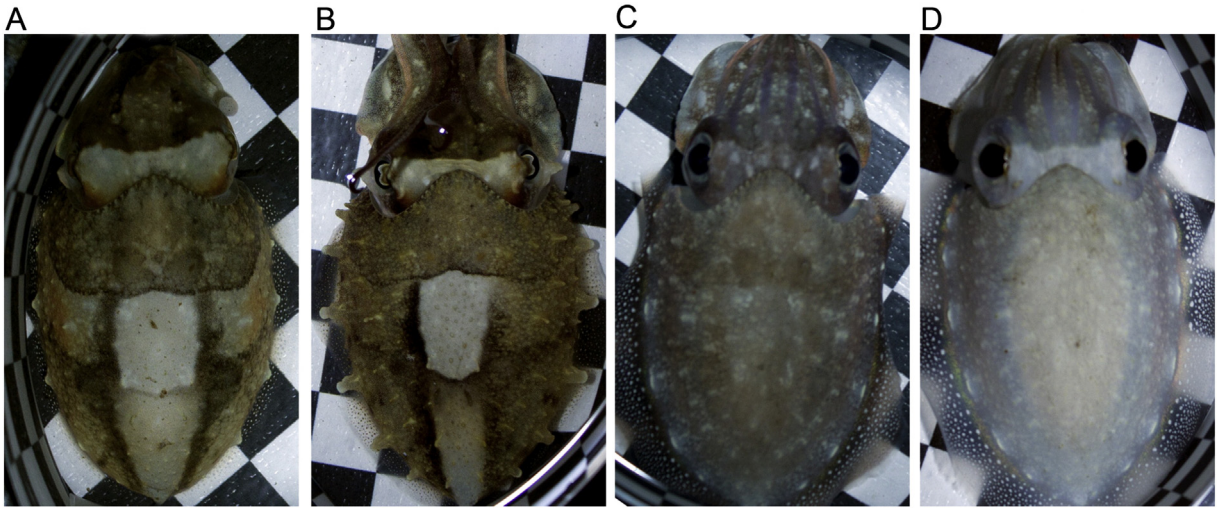

Fig. 3. Images of cuttlefish on a black and white checkerboard in A) bright, B) moderate, C) low and D) extremely low light. Cuttlefish showed a disruptive body pattern on the black and white checkerboard substrate when tested under bright and moderate lighting levels. In low light, cuttlefish responded with mixed, blotchy body patterning. In extremely low light, cuttlefish showed a closed chromatophore body pattern (most chromatophores punctate).

no color profile was applied. To obtain a grayscale image I_g, the linearized RGB image was converted via a linear transformation as follows:

$$I_g = W_R R + W_G G + W_B B$$

R, G and B represent the red, green and blue channels of the image respectively, multiplied by weights W_R, W_G and W_B that sum up to 1($W_R = 0.2989$, $W_G = 0.5870$ and $W_B = 0.1140$). This transformation is equivalent to obtaining the Commission on Illumination (CIE) luminance for each pixel (commonly denoted Y). Consumer cameras, as the one used for this study, are optimized for the tri-chromatic and metameric nature of the human visual system and instead of recording colors by sampling the visible spectrum, they capture RGB metamers instead (Akkaynak et al., 2014). Therefore, our analysis in this work is inevitably through the visual system of a human observer. Thus, we have chosen the relative values of W to be representative of the sensitivity of the human visual system to different channels. These are the standard values used in many RGB color spaces and display devices (Reinhard, 2008) and also form the basis of the RGB-to-grayscale transformation functions in computational programs such as MATLAB.

The regions that represented the cuttlefish body and the background substrate in each grayscale photograph were manually marked because the cuttlefish were not always in the same location for each photograph; this created some variation in measured substrate intensity. Intensity values in these pixels were averaged to smooth out noise, and variations due to lighting (some areas of the arena had more shadow than others due to the positioning of the arena wall), to obtain the mean cuttlefish and background intensity; μ_c and μ_b respectively. For each substrate and light level, the correlation between μ_c and μ_b was computed using Spearman's linear correlation coefficient (ρ) using the statistics toolbox in MATLAB.

3. Results

3.1. Experiment 1: artificial substrates

Cuttlefish body pattern intensity was strongly correlated with substrate intensity under bright (408 μW/cm^2, 2100 lux) and moderate light (40.1 μW/cm^2, 56 lux) (Fig. 2A; bright, $\rho = 0.76$, $p = 3.13 \times 10^{-6}$; moderate, $\rho = 0.79$, $p = 1.52 \times 10^{-6}$), moderately correlated in low (2.04 nW/cm^2, <0.0001 lux) light (Fig. 2A; $\rho = 0.58$, $p = 6.06 \times 10^{-4}$) and weakly correlated in extremely low (1.02 nW/cm^2, <0.0001 lux) light (Fig. 2A; $\rho = 0.17$, $p = 0.37$). Cuttlefish were best able to match the intensity of the dark gray substrate (mean difference (md) = 0.05), less capable of matching the medium gray substrate (md = 0.12), and least able to match the light gray substrate (md = 0.23). Cuttlefish had similar body pattern intensity on the medium (mean intensity = 0.42) and light gray substrates (mean intensity = 0.44); a Kruskal–Wallis ANOVA showed a significant difference between the dark gray substrate (mean intensity = 0.29) and both the medium and light gray substrates ($X^2 = 16.47$, $p = 0.0003$), but not between the medium and light gray substrates ($p > 0.05$). Supplementary Fig. S2 illustrates examples of body pattern intensities of cuttlefish on artificial gray substrates at all light intensities.

Cuttlefish showed a Disruptive body pattern on the black and white checkerboard substrate when tested under bright and moderate light (Fig. 3A and B). In low light, cuttlefish had a blotchy appearance, and did not camouflage according to the substrate (Fig. 3C). In extremely low light, cuttlefish did not camouflage according to the substrate, but instead had a pale appearance, with most of their chromatophores retracted, few papillae expressed and their pupils fully dilated (Fig. 3d, closed chromatophore body pattern).

3.2. Experiment 2: natural sand substrates

Cuttlefish body pattern intensity was strongly correlated with sand intensity under bright and moderate light (Fig. 2b; bright: $\rho = 0.90$, $p = 2.34 \times 10^{-7}$; moderate: $\rho = 0.80$, $p = 1.26 \times 10^{-6}$), moderately correlated in low light (Fig. 2b; $\rho = 0.36$, $p = 0.05$) and weakly correlated in extremely low light (Fig. 2b; $\rho = 0.17$, $p = 0.21$). Cuttlefish more closely matched the dark and light brown sand substrates (md = 0.02) than the white sand substrate (md = 0.23). Cuttlefish had similar body pattern intensity on the light brown (mean intensity = 0.13) and white sand (mean intensity = 0.17); a Kruskal––Wallis ANOVA showed a significant difference between the dark brown sand (mean intensity = 0.06) and both the light brown and white sand substrates ($X^2 = 22.17$, $p = 1.54 \times 10^{-5}$), but not between the light brown sand and white sand substrates ($p > 0.05$). Supplementary Fig. S3 illustrates examples of body pattern intensities of cuttlefish on natural substrates at all light intensities.

Similar to the artificial substrates, cuttlefish had a blotchy appearance (similar to the Mottle body pattern used for camouflage) in low light, and a closed chromatophore body pattern in extremely low light (Fig. S3).

4. Discussion

Our experiments show that cuttlefish reliably scale their body pattern intensity with respect to changing substrate intensity under bright (2100 lux) and moderate (56 lux) lighting conditions. However, their ability to adjust their body patterns according to the intensity of the surrounding substrates was limited under low lighting conditions (<0.0001 lux) and failed under extremely low light. Furthermore, cuttlefish did not camouflage themselves (i.e., they did not show the typical Disruptive body pattern) on the checkerboard substrate under low or extremely low lighting conditions, suggesting that they were unable to reliably distinguish visual cues when placed in extremely low light levels. In bright and moderate lighting conditions, cuttlefish were best able to match substrates that were closest to the intensity of the substrates/objects commonly found in their natural environment—the artificial dark gray substrate and the dark and light brown sands. *S. officinalis* often occur in areas with a sandy substrate that is similar in intensity to the light brown sand (and medium gray substrate) used in our experiments, and cuttlefish often choose to bury themselves in this type of substrate, while closely resembling the intensity of the sand (Hanlon and Messenger, 1988; Poirier et al., 2004). Our dark substrates (dark gray and dark brown sand) were similar in intensity to many rocks and algae that may be present in the wild; cuttlefish may often resemble these types of objects rather than camouflaging to the substrate (Buresch et al., 2011; Hanlon et al., 2009). In contrast, the lightest substrates (light gray and white) were lighter than most naturally occurring substrates in a cuttlefish's surroundings. Interestingly, the mean body pattern intensity of the cuttlefish in our experiments on light gray and white sand were not significantly different from their body pattern intensity on the medium gray and light brown sand. This suggests that there may be a biological limit to how light a cuttlefish's body pattern intensity will be when camouflaged (it is possible that there may be a similar dark limit).

4.1. Color matching vs. intensity matching

Our experiments were designed to test whether cuttlefish adjust their body intensity to aid in camouflage. While we cannot directly compare our study with previous studies on spectral body pattern/substrate matching (Akkaynak et al., 2013; Chiao et al., 2011; Hanlon et al., 2013; Mäthger et al., 2008), we found that cuttlefish did scale their body intensity according to different substrate intensities in bright and moderate lighting conditions. Although they did not perfectly match substrate intensity, cuttlefish body pattern intensity matching is likely an important component of an effective camouflage body pattern. In fact, several authors have suggested that intensity matching may be an effective camouflage tactic at greater water depths (Akkaynak et al., 2013; Cott, 1940; Denton and Nicol, 1966; Johnsen, 2001; Lythgoe, 1979; Mäthger et al., 2008) since underwater daylight becomes more and more restricted to the blue–green spectrum with increasing depth (Jerlov, 1976; Tyler and Smith, 1970). Under these blue–green light conditions, color vision may not be as useful for a predator searching for camouflaged prey. In that case, matching the general intensity of the environment may be a successful camouflage tactic.

4.2. Camouflage body patterning in the dark

Previous work has shown that *S. officinalis* are capable of dynamically camouflaging in very dim lighting conditions—the equivalent of starlight levels on land (0.003 lux) (Allen et al., 2010). Since cuttlefish are found where light levels in the sea drop to well below this level (Guerra, 2006; Jerlov, 1968; Reid et al., 2005; Warrant and Locket, 2004), it would not be surprising if they were capable of detecting light at even lower light levels than starlight. However, the visual acuity of *S. officinalis* has been shown to decline as light levels decrease (Groeger et al., 2005). Indeed, cuttlefish in our experiments appeared to be able to detect light at an order of magnitude darker than starlight (<0.0001 lux), as evidenced by the expansion of their chromatophores when exposed to this low light level. However, these cuttlefish did not appear to be able to distinguish patterns since they did not camouflage themselves with respect to the substrate.

In our experiments, cuttlefish were exposed to as little light as possible (extremely low light) before being tested on substrates of different intensity, under different lighting conditions. This protocol was used for two reasons: 1) to dark adapt cuttlefish prior to testing them at various light levels, and 2) to see what body pattern would be expressed in an extremely low light environment where vision may not be possible for these animals. Interestingly, at extremely low light levels most cuttlefish did not expand their chromatophores. Photographs of animals taken in extremely low light showed that they produced a pale body pattern in which, few to no expanded chromatophores and few papillae were expressed. A few animals expanded some chromatophores under extremely low light, but these animals were still pale in appearance. In addition, cuttlefish at this light level were never camouflaged on the substrate. This was a surprising result because several studies have shown that cuttlefish are capable of dynamic camouflage at night (Allen et al., 2010; Hanlon et al., 2007); however, the light levels in our experimental setup were arguably darker than what would typically be encountered on a reef at night. This unexpected behavioral response raises the question of whether this closed chromatophore body pattern, produced in response to extremely low light levels, may be a type of "resting state." Expansion of chromatophores in cephalopods presumably requires energy expenditure, since the radial muscles that control the pigment cells have to contract to expand the chromatophores (Bell et al., 2013; Florey and Kriebel, 1969), but the amount of energy required to expand chromatophores from their punctate state has not been well-studied.

Interestingly, the light intensity at which cuttlefish expanded their chromatophores (albeit without achieving the appropriate camouflage body pattern) was not much higher than the low light level that evoked the closed chromatophore body pattern. In low lighting conditions cuttlefish responded with mixed, blotchy body patterning (similar to the Mottle body pattern used for camouflage) rather than camouflage patterns appropriate for the substrate. It seems likely that these cuttlefish were sensing light because they expanded their chromatophores, but that they could not see well enough to distinguish substrate features for body patterning. This low light level (<0.0001 lux) may be close to the absolute visual threshold of cuttlefish.

The low and extremely low light conditions used in our experiments were darker than those this species most frequently experiences in the wild; *S. officinalis* are most often found in shallow coastal waters. However, in autumn and winter, *S. officinalis* migrate to deeper shelf waters that can be as deep as 200 m (Guerra, 2006; Reid et al., 2005). At this depth, light intensity drops to well below our experimental lighting conditions (0.1 nW/cm^2 at 100 m; Jerlov, 1968). While it is most likely that cuttlefish detect low level environmental luminance through their large and sensitive (Groeger et al., 2005) eyes, it is possible that rhodopsin located in the skin (Mäthger et al., 2010), might be employed in light sensing under low lighting conditions.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2014.10.017.

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References

Akkaynak, D., Allen, J.J., Mäthger, L.M., Chiao, C.-C., Hanlon, R.T., 2013. Quantification of cuttlefish (*Sepia officinalis*) camouflage in the eyes of fish predators: a study of color and luminance using *in situ* spectrometry. J. Comp. Physiol. A. 199, 211–225. http://dx.doi.org/10.1007/s00359-012-0785-3.

Akkaynak, D., Treibitz, T., Xiao, B., Gurkan, U.A., Allen, J.J., Demirci, U., Hanlon, R.T., 2014. Use of commercial-off-the-shelf (COTS) digital cameras for scientific data acquisition and scene-specific color calibration. J. Opt. Soc. Am. A 31, 312–321.

Allen, J.A., Mäthger, L.M., Buresch, K.C., Fetchko, T., Gardner, M., Hanlon, R.T., 2010. Night vision by cuttlefish enables changeable camouflage. J. Exp. Biol. 213, 3953–3960. http://dx.doi.org/10.1242/jeb.044750.

Bell, G.R.R., Kuzirian, A.M., Senft, S.L., Mäthger, L.M., Wardill, T.J., Hanlon, R.T., 2013. Chromatophore radial muscle fibers anchor in flexible squid skin. Invertebr. Biol. 132, 120–132. http://dx.doi.org/10.1111/ivb.12016.

Buresch, K.C., Mathger, L.M., Allen, J.J., Bennice, C., Smith, J., Chiao, C.-C., Chubb, C., Hanlon, R.T., 2011. The use of background matching vs. masquerade for camouflage in cuttlefish *Sepia officinalis*. Vis. Res. 51, 2362–2368.

Chiao, C.-C., Wickiser, J.K., Allen, J.J., Genter, B., Hanlon, R.T., 2011. Hyperspectral imaging of cuttlefish camouflage indicates good color match in the eyes of fish predators. Proc. Natl. Acad. Sci. 108, 9148–9153.

Cott, H.B., 1940. Adaptive Coloration in Animals. Methuen and Company Limited, London.

Denton, E.J., Nicol, J.A.C., 1966. A survey of reflectivity in silvery teleosts. J. Mar. Biol. Assoc. U. K. 46, 685–722.

Florey, E., Kriebel, M.E., 1969. Electrical and mechanical responses of chromatophore muscle fibers of the squid, *Loligo opalescens*, to nerve stimulation and drugs. Z. Vergl. Physiol. 65, 98–130.

Groeger, G., Cotton, P.A., Williamson, R., 2005. Ontogenetic changes in the visual acuity of *Sepia officinalis* measured using the optomotor response. Can. J. Zool. 83, 274–279.

Guerra, A., 2006. Ecology of *Sepia officinalis*. Vie Milieu-Life Environ. 56, 97–107.

Hanlon, R.T., 2007. Cephalopod dynamic camouflage. Curr. Biol. 17, 400–404.

Hanlon, R.T., Messenger, J.B., 1988. Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. Phil. Trans. R. Soc. Lond. B 320, 437–487.

Hanlon, R.T., Naud, M.-J., Forsythe, J.W., Hall, K., Watson, A.C., McKechnie, J., 2007. Adaptable night camouflage by cuttlefish. Am. Nat. 169, 543–551.

Hanlon, R.T., Chiao, C.-C., Mäthger, L.M., Barbosa, A., Buresch, K.C., Chubb, C., 2009. Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. Philos. Trans. R. Soc. Lond. B 364, 429–437.

Hanlon, R.T., Chiao, C.-C., Mäthger, L.M., Buresch, K.C., Barbosa, A., Allen, J.J., Siemann, L., Chubb, C., 2011. Rapid adaptive camouflage in cephalopods. In: Stevens, M., Merilaita, S. (Eds.), Animal Camouflage: Mechanisms and Functions. Cambridge University Press, pp. 145–163.

Hanlon, R.T., Chiao, C.-C., Mäthger, L.M., Marshall, N.J., 2013. A fish-eye view of cuttlefish camouflage, using in-situ spectrophotometry. Biol. J. Linn. Soc. 109, 535–551. http://dx.doi.org/10.1111/bij.12071.

Jerlov, N.G., 1968. Optical Oceanography. Elsevier, Amsterdam.

Jerlov, N.G., 1976. Marine Optics. Elsevier, Amsterdam.

Johnsen, S., 2001. Hidden in plain sight: the ecology and physiology of organismal transparency. Biol. Bull. 201, 301–318.

Johnsen, S., 2012. The Optics of Life: A Biologist's Guide to Light in Nature. Princeton University Press, Princeton, NJ.

Lythgoe, J.N., 1979. The Ecology of Vision. Oxford University Press, Oxford.

Marshall, N.J., Messenger, J.B., 1996. Colour-blind camouflage. Nature 382, 408–409.

Mäthger, L.M., Hanlon, R.T., 2007. Malleable skin coloration in cephalopods: selective reflectance, transmission and absorbance of light by chromatophores and iridophores. Cell Tissue Res. 329, 179–186.

Mäthger, L.M., Barbosa, A., Miner, S., Hanlon, R.T., 2006. Color blindness and contrast perception in cuttlefish (*Sepia officinalis*). Vis. Res. 46, 1746–1753.

Mäthger, L.M., Chiao, C.-C., Barbosa, A., Hanlon, R.T., 2008. Color matching on natural substrates in cuttlefish, *Sepia officinalis*. J. Comp. Physiol. A. 194, 577–585.

Mäthger, L.M., Denton, E.J., Marshall, J., Hanlon, R.T., 2009. Mechanisms and behavioral functions of structural coloration in cephalopods. J. R. Soc. Interface 6, S149–S164.

Mäthger, L.M., Roberts, S., Hanlon, R.T., 2010. Evidence for distributed light sensing in the skin of cuttlefish, *Sepia officinalis*. Biol. Lett. 6, 600–603.

Mäthger, L.M., Bell, G.R.R., Kuzirian, A.M., Allen, J.J., Hanlon, R.T., 2012. How does the blue-ringed octopus (*Hapalochlaena lunulata*) flash its blue rings? J. Exp. Biol. 215, 3752–3757.

Poirier, R., Chichery, R., Dickel, L., 2004. Effects of rearing conditions on sand digging efficiency in juvenile cuttlefish. Behav. Process. 67, 273–279.

Reid, A., Jereb, P., Roper, C.F.E., 2005. Family *Sepiidae*. In: Jereb, P., Roper, C.F.E. (Eds.), Cephalopods of the world. An annotated and illustrated catalogue of species known to dateChambered nautiluses and sepioids (*Nautilidae*, *Sepiidae*, *Sepiolidae*, *Sepiadariidae*, *Idiosepiidae* and *Spirulidae*). FAO Species Catalogue for Fishery Purposes. No. 4 vol. 1. FAO, Rome, pp. 57–152.

Reinhard, E., 2008. Color Imaging. A. K. Peters Limited, Natick, MA.

Tyler, J.E., Smith, R.C., 1970. Measurements of Spectral Irradiance Underwater. Gordon and Breach Science Publishers, New York, NY.

Wardill, T.J., Gonzalez-Bellido, P.T., Crook, R.J., Hanlon, R.T., 2012. Neural control of tuneable skin iridescence in squid. Proc. R. Soc. 279, 4243–4252.

Warrant, E.J., Locket, N.A., 2004. Vision in the deep sea. Biol. Rev. 79, 671–712.

Zylinski, S., How, M.J., Osorio, D., Hanlon, R.T., Marshall, N.J., 2011. To be seen or to hide: visual characteristics of body patterns for camouflage and communication in the Australian giant cuttlefish *Sepia apama*. Am. Nat. 177, 681–690.