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To Be Seen or to Hide: Visual Characteristics of Body Patterns for Camouflage and Communication in the Australian Giant Cuttlefish *Sepia apama*

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ABSTRACT: It might seem obvious that a camouflaged animal must generally match its background whereas to be conspicuous an organism must differ from the background. However, the image parameters (or statistics) that evaluate the conspicuousness of patterns and textures are seldom well defined, and animal coloration patterns are rarely compared quantitatively with their respective backgrounds. Here we examine this issue in the Australian giant cuttlefish *Sepia apama*. We confine our analysis to the best-known and simplest image statistic, the correlation in intensity between neighboring pixels. *Sepia apama* can rapidly change their body patterns from assumed conspicuous signaling to assumed camouflage, thus providing an excellent and unique opportunity to investigate how such patterns differ in a single visual habitat. We describe the intensity variance and spatial frequency power spectra of these differing body patterns and compare these patterns with the backgrounds against which they are viewed. The measured image statistics of camouflaged animals closely resemble their backgrounds, while signaling animals differ significantly from their backgrounds. Our findings may provide the basis for a set of general rules for crypsis and signals. Furthermore, our methods may be widely applicable to the quantitative study of animal coloration.

Keywords: camouflage, communication, signaling, image structure, cephalopods, vision.

Introduction

To be camouflaged, an animal must match some aspect of its background, and to be conspicuous, it must differ from that background. Despite the relative simplicity of this notion, comparisons between animals and their backgrounds have rarely been conducted quantitatively. Presently, the relative crypsis or conspicuousness of animal

patterns is commonly assessed using overall (or mean) body coloration (Marshall 2000; Stuart-Fox et al. 2003; Endler and Mielke 2005; Cummings et al. 2008). Also, few systematic studies compare the visual properties of body patterns with their natural visual backgrounds. The problem is that it is difficult to define—and hence measure—the parameters that humans and other animals use to segregate an object from its background (Julesz 1981; Zylinski et al. 2009b). After overall color, the simplest measure of visual appearance is to consider how well defined the spatial pattern of the animal is compared with its background. This comparison can be quantified as the mean difference between neighboring points in the image. A tool to quantify the spatial frequency is a Fourier transform, which is based on the theory that real-world signals—here, images—can be approximated by the sum of sinusoidal waves of certain amplitudes, spatial frequencies, and phases. High frequencies generally represent fine detail, such as edges and visual texture, whereas low frequencies are associated with coarser-scale global attributes (fig. 1; Bruce et al. 2003). The measure of a whole image is commonly given by the spatial frequency power spectrum, which is a representation of the magnitude of the various frequency components of a two-dimensional image.

Natural scenes (in this case, backgrounds) are not random but rather contain a large degree of structure that is reflected in their second-order statistics. The consistent relationship between amplitude and spatial frequency is well documented, with the power spectrum of a given scene falling roughly as the inverse of the square of the spatial frequency (Shapley and Lennie 1985; Bex and Makous 2002; Balboa and Grzywacz 2003). In other words, the amount of visual information that might be classified as fine scale or coarse scale is very similar between scenes regardless of the habitat type and viewing distance, a phenomenon that is probably due to a fractal-like self-simi-

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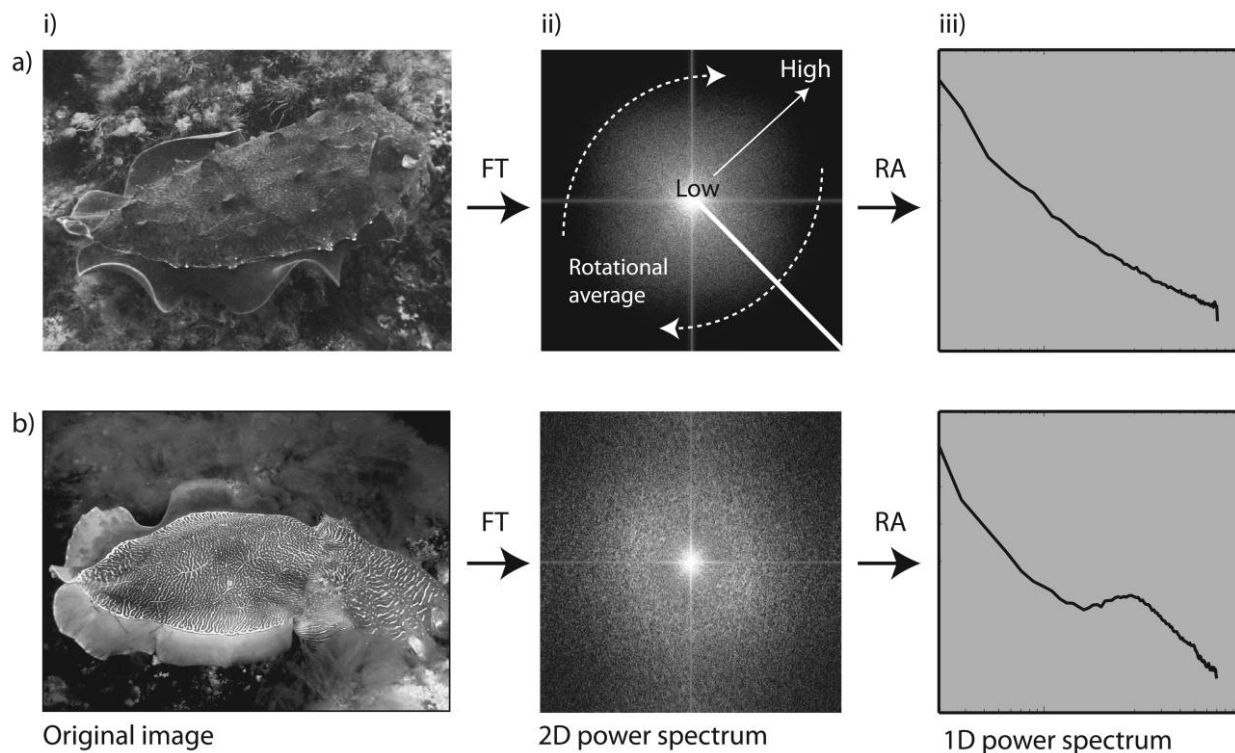


Figure 1: Fourier transform (FT) reveals the spatial distribution encoded in a two-dimensional image, and the resulting power spectra enable us to visualize this information. In two-dimensional power spectra, low-frequency components are in the center of the plot, with increasingly high-frequency components displayed toward the edges (the power at each point is conveyed by the shading, with white being high and black being low). *a*, Original image contains relatively low-frequency information, as is apparent in the two-dimensional power spectrum of the FT (*i*); most of the spatial information is concentrated in the center, with little or no contribution by high frequencies (*ii*). *b*, This original image contains a higher degree of fine detail and edge information (*i*), which can be clearly seen in the two-dimensional power spectrum (*ii*). Two-dimensional spectra are difficult to interpret and compare, so one can take the rotation average (RA) of each point around the center axis to give a single data point for each spatial frequency, resulting in a one-dimensional power spectrum (*iii*). As shown here, one-dimensional power spectra are commonly displayed as log-log plots of power-frequency because the power contained in an image may span several orders of magnitude.

larity, leading to scale invariance across a wide range of natural scene types (Field 1987; Ruderman 1994). The consistent relationship between amplitude and spatial frequency has implications for visual processing because scenes contain the same amount of detail regardless of the scale at which they are viewed. Balboa and Grzywacz (2003) found that underwater images are characterized by a steeper fall in spatial frequency compared with terrestrial ones; this can be attributed to the optics of water, in which light scatter and attenuation act to reduce high-frequency information (Lythgoe 1979).

Given the robustness and consistency of natural scene structure, we hypothesize that patterns used in camouflage will be generally matched to—while signaling patterns will differ from—the measured image statistics of relevant backgrounds. In other words, if an animal is attempting to be camouflaged, then one would expect the second-

order attributes, such as the power spectra, to be similar between the animal and its background. Conversely, if a body pattern is to be conspicuous, then it should diverge from the second-order attributes of the background in a way that maximizes the visibility of the pattern to a target viewer (Endler 1978, 1992; Rosenthal 2007). We are aware of only a single study that attempts to assess animal body patterns in these terms: Fourier transforms of zebra and tiger stripes were used to demonstrate that the former were conspicuous and the latter camouflaged against relevant backgrounds (Godfrey et al. 1987).

The Australian giant cuttlefish (*Sepia apama* Gray, 1849) provides a unique opportunity to test questions regarding crypsis and conspicuousness. These animals can change between signaling and camouflage patterns almost instantaneously, primarily via neurally driven intradermal chromatophores (Messenger 2001; fig. 2). The patterns that

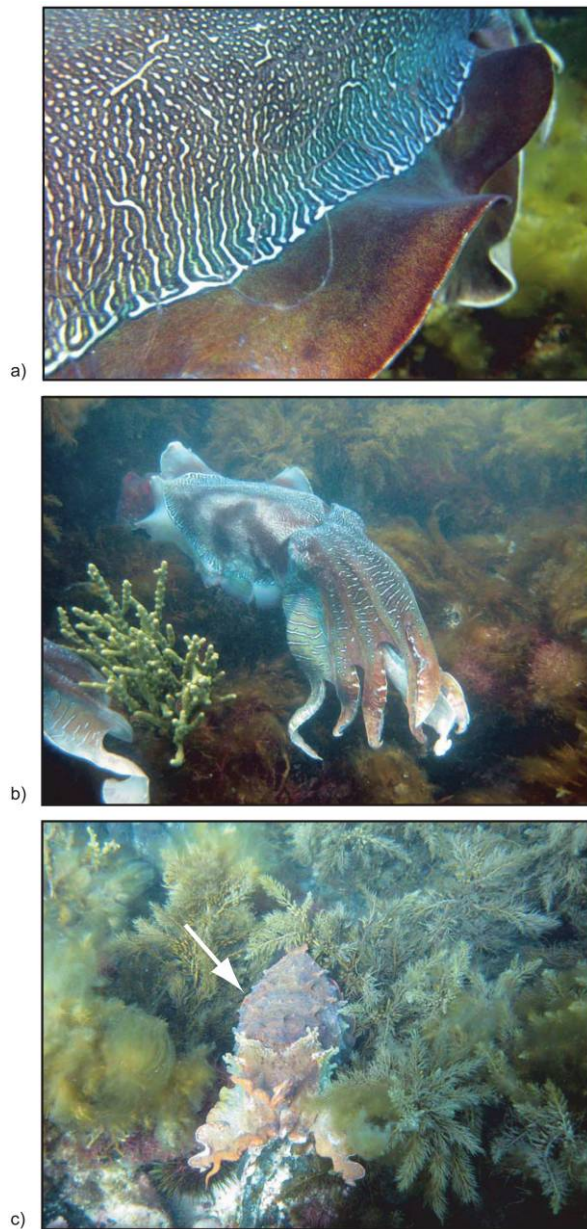


Figure 2: *Sepia apama* signaling and camouflage. *a*, Detail of a conspicuous mantle/fin pattern used by males seeking to mate. *b*, Male engaged in kinetic display to second male (arms visible in lower left of image), passing bands of dark chromatophores over the dorsal mantle. *c*, Individuals not engaged in mate finding resume camouflage (arrow).

cuttlefish produce are used in a range of behaviors, including camouflage, courtship, and threat responses (Hanlon and Messenger 1996; Langridge et al. 2007). *Sepia* camouflage patterns are primarily visually driven. The study of how these animals choose an appropriate body

pattern for a given visual environment has offered much insight into visual perception in a system that has evolved independently of vertebrates (e.g., Chiao et al. 2007; Kelman et al. 2008; Zylinski et al. 2009b).

Large numbers of *S. apama* gather in annual spawning aggregations in the Spencer Gulf, South Australia (Hall and Hanlon 2002). Males outnumber females at a ratio of approximately 4 : 1, and during daylight males compete with each other for access to females via complex visual displays (Hall and Hanlon 2002; but see Norman et al. 1999 and Hanlon et al. 2005 for an alternative strategy of female mimicry). Males often adopt a body pattern of contrasting small-scale “stripes” that are assumed to be a conspicuous display to females and competitor males (fig. 2*a*), which escalates to an elaborate kinetic display during agonistic contests (fig. 2*b*). An individual (female or male) not actively seeking to mate will become camouflaged against the background on which it has settled (fig. 2*c*).

To investigate the relationship between the second-order attributes of background and patterns, we used two measures: (1) the pixel intensity variance (PIV), an estimate of image-region homogeneity (which in turn provides a simple description of how textured the image appears), and (2) the power spectra of the mantle patterns. These two measures were obtained for both signaling and camouflaging cuttlefish and were compared with the values of the backgrounds against which each cuttlefish was photographed in the wild.

Material and Methods

Images of *Sepia apama* were collected in the animals' natural environment using SCUBA over a 2-week period in June 2008 at Stoney Point near Whyalla, South Australia (32°59'44"S, 137°45'04"E; for details of the field site, see Hall and Hanlon 2002), at depths between 2 and 5 m. Animals were photographed from above at a distance of approximately 1 m during daylight hours, generally under clear skies. Camera angle ranged from a 90° viewing angle (directly overhead) to no less than 60°. Individuals were classified as being either in camouflage or in signaling mode on the basis of the presence or absence of conspicuous patterns, as shown in figure 2. Image analysis was carried out in MATLAB (MathWorks, Natick, MA), using the Image Processing Toolbox.

Images were resized to standardize the mantle length of the animals. This resizing was within a narrow range of around 10%, since animal-to-camera distance was similar throughout the data set. The color channels of the images were split, and only the green channel was used in further analysis. This channel contains the most biologically relevant visual information for cuttlefish, with a single peak in color sensitivity around 490 nm for *Sepia officinalis*

(Marshall and Messenger 1996; Mäthger et al. 2006) and their aquatic predators (e.g., peak sensitivity for snappers 489–502 nm; Lythgoe et al. 1994) and 488–524 nm for dolphins (Fasick and Robinson 1998). The mantle pattern of the animal in each image was cropped (average crop area 260×330 pixels, depending on animal orientation) from each image, and three crops of corresponding size were taken from areas of the background (fig. 3).

The PIV of each animal and background crop was obtained by

$$\frac{1}{N-1} \sum_{i=1}^N (x_i - \hat{x}),$$

where N is the length of the data vector, \hat{x} is the mean of the data vector, and x_i is element number i of the data vector. PIVs within crop areas were used as an estimate of image-region homogeneity, which in turn provides a crude description of image “texture.” We used paired two-tailed t -tests to compare animal crops with their respective backgrounds and unpaired t -tests to compare between the signaling and camouflaged classes.

For power spectra comparison, the cropped areas of animals and backgrounds used for PIV were fast Fourier transformed (Bruce et al. 2003). To reduce bordering effects, where image edges cause high-frequency noise, a tapering Gaussian filter frame ($\delta = 5$) was applied to the edges of the cropped areas before Fourier transformation. The power spectrum was then obtained by taking the square of the modulus of the Fourier transform, using code adapted from Kovessi (2000). To enable us to represent the power of a given spatial frequency as a single point, a rotational average was taken across all orientations of

the power spectra (fig. 1). We used 100 frequency bins and ignored the lowest 2% of frequencies to avoid spiking in this region through image artifacts (Kovessi 2000). Because the power contained in an image may span several orders of magnitude, the slopes of log-log power-spatial frequency plots were used to compare the spectra of animal and background in each image, as commonly used in natural scene comparison (Field 1987; Ruderman 1994; Bex and Makous 2002). Linear regression was applied to ascertain how well these data fitted a linear model, and slopes and intercepts obtained from regressions were used to test for differences between the data.

A set of 20 random images was obtained during the period of experimental sampling using the same protocol as for the test images. This image set included scenes at a variety of spatial scales and were processed in the same way as the test images. We compared the PIV and power spectra of our test data to those obtained from these uncropped control images to evaluate their consistency and to ensure that our results were not affected by our cropping method. Data available in Dryad (<http://dx.doi.org/10.5061/dryad.8527>).

Results

Measures of PIV and the power spectra were obtained from images of 32 camouflaged *Sepia apama*, 49 signaling *S. apama*, and their respective backgrounds. Overall, we found the same image structure in both camouflaged animal patterns and their backgrounds, but the intensity of the animals’ patterns was typically lower than that of their backgrounds. The mean PIV of camouflaged animal man-

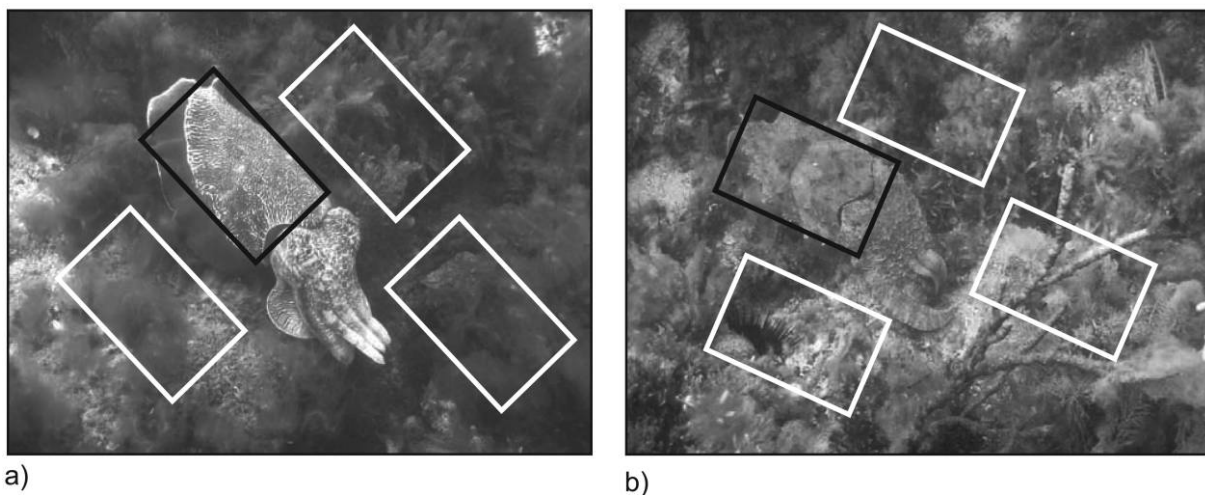


Figure 3: Examples of signaling (a) and camouflaged (b) individuals in the green channel. Black rectangles show cropped region of animals, and white rectangles show the three corresponding background crops used in the analysis.

tle patterns was significantly lower than that of their backgrounds (0.016 ± 0.014 in animals vs. 0.024 ± 0.006 in backgrounds; paired t -test, $t = -9.36$, $df = 31$, $P \leq .01$; fig. 4). The power spectra of camouflaged individuals were well matched to the spectra of their backgrounds (mean slope -2.49 ± 0.36 for animals compared with -2.53 ± 0.27 for backgrounds; linear regression mean $r^2 = 0.97$ for animals, 0.98 for backgrounds; in all cases, $P \ll .05$; fig. 5a). We found no significant difference between power spectra slopes of camouflaging individuals and their backgrounds (t -test, $t = 1.77$, $P = .10$, $df = 31$, $SD = 0.43$).

The PIVs of the mantle patterns of signaling individuals were significantly higher than the PIVs of their backgrounds (0.036 ± 0.009 compared with 0.010 ± 0.007 ; paired t -test, $t = 17.19$, $df = 48$, $P \ll .05$; fig. 4). Furthermore, the power spectra of signaling individuals and their backgrounds showed marked differences: at lower frequencies, signaling individuals and their backgrounds appeared similar, while at higher frequencies, the power spectra of animals and backgrounds deviated noticeably (slope mean -1.89 ± 0.37 for animals compared with -2.45 ± 0.34 for backgrounds; paired t -test, $t = 7.87$, $df = 48$, $P \ll .001$; fig. 5b). This deviation occurred at a characteristic and consistent point of the plot at frequencies above 0.1 times body length, indicating a larger amount of higher frequency information in the body pat-

terns of the animals compared with the backgrounds against which they are displaying. Regression analysis of the power spectra indicated that signaling individuals showed power spectra slopes that were significantly less steep than their backgrounds, which is as expected, given the larger amount of information present at higher spatial frequencies. The mean r^2 value for signaling individuals (0.90) was lower than that of their backgrounds or that of camouflaged individuals (both 0.97), reflecting the non-linear characteristics of the power spectrum coefficients.

We found significant differences between the PIVs for signaling and camouflaged cuttlefish, with the PIVs of signaling patterns higher than the PIVs of camouflaging patterns (0.036 ± 0.010 vs. 0.015 ± 0.006 ; t -test, $t = 11.8$, $df = 78$, $P \leq .01$). We also observed a difference between the backgrounds selected by the two cuttlefish classes, with camouflaging individuals tending to use backgrounds with a higher PIV than the backgrounds of signaling individuals (0.024 ± 0.006 vs. 0.010 ± 0.007 , respectively; t -test, $t = 23.9$, $df = 77$, $P \leq .01$; fig. 4). Control images had a mean PIV of 0.0346 ± 0.012 and a mean power spectrum slope of -2.40 ± 0.41 ($r^2 = 0.98$). Mean power spectra slopes of the control images, test backgrounds (-2.53 and -2.45), and camouflaging individuals (-2.49) were therefore consistent with the mean power spectra slope of -2.5 previously documented from aquatic scenes (Balboa and

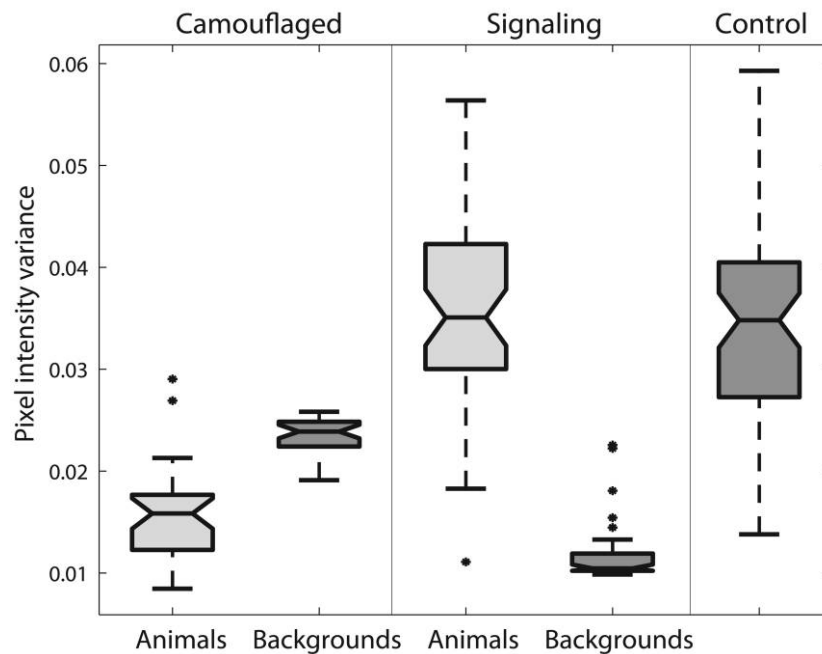


Figure 4: Box plots of pixel intensity variance for camouflaged cuttlefish and their backgrounds (*left*), signaling animals and their backgrounds (*center*), and a set of control backgrounds (*right*; $n = 20$). Light gray, cuttlefish body; dark gray, background. Center bar, median; box width, interquartile range (IQR); notch width, $(1.58 \times \text{IQR})/n^{1/2}$; whiskers, $\pm 1.5 \times \text{IQR}$; asterisk, outliers (Chambers et al. 1983).

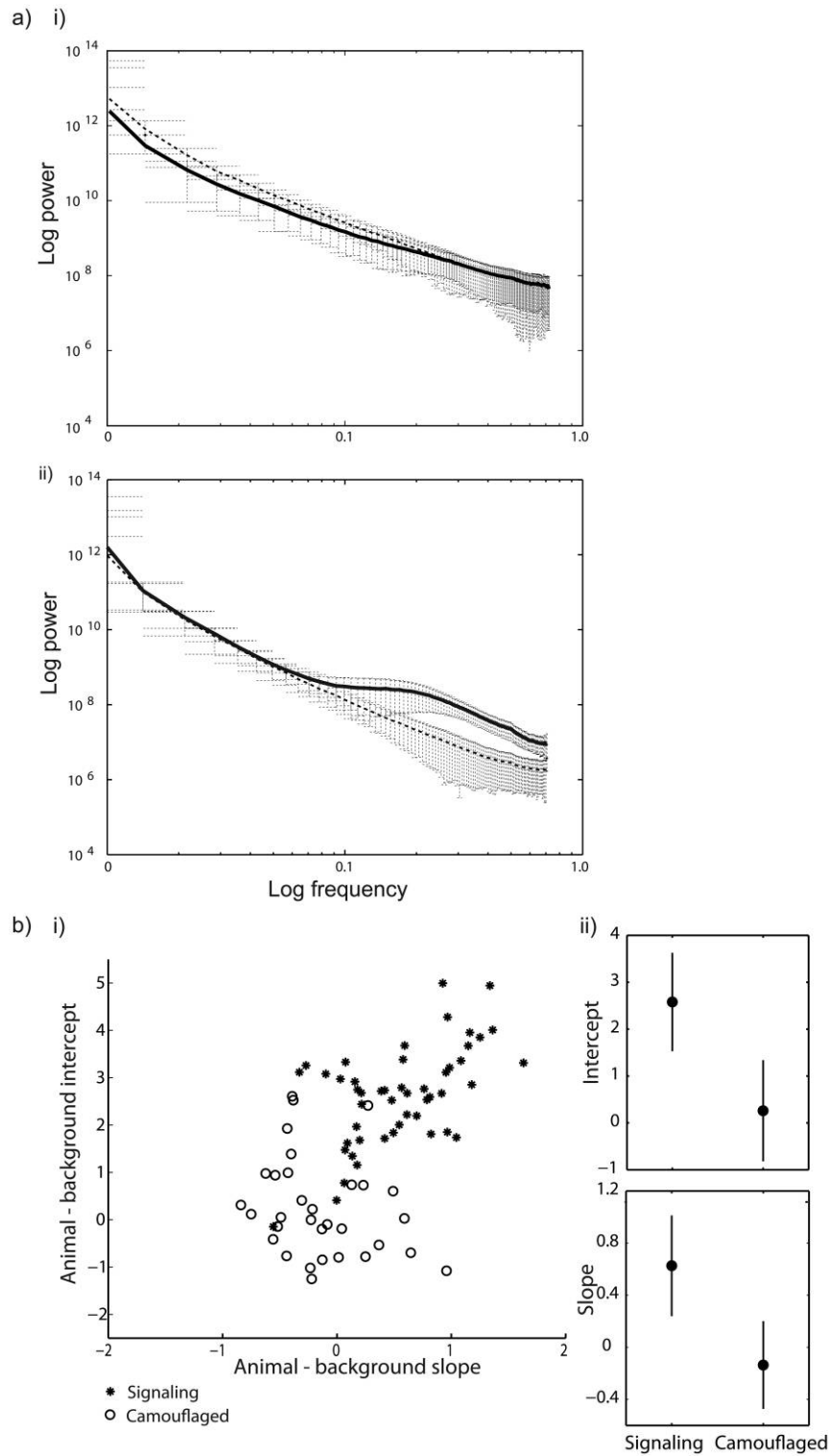


Figure 5: *a*, Mean power spectra \pm SD of cuttlefish (*solid line*) and their backgrounds (*dashed line*) when camouflaged (*i*) and in signaling mode (*ii*). *b*, Difference in slope and intercept of power spectrum fitted lines gained via regression analysis (*i*). Background slopes and intercepts were subtracted from cuttlefish values, so that a value of 0 indicates the best match. *Circles*, camouflaged; *asterisks*, signaling. *ii*, Mean \pm SD for intercept (*top*) and slope (*bottom*).

Grzywacz 2003). This consistency suggests that our image processing methodology did not introduce undesired artifacts to the analysis.

The differences between camouflaged and signaling animal power spectra is well illustrated by the characteristics of their fitted regression lines. By subtracting the slope and intercept values of the fitted lines of animals from those of their backgrounds, we see that the values for camouflaged animals lie close to 0, while background values fall well above this (fig. 5*b*, *ii*). Paired t-tests show that this difference is highly significant ($P \ll .01$ in both cases).

Discussion

Our results clearly demonstrate that in terms of spatial frequency power spectra, camouflaging cuttlefish tend to closely resemble their backgrounds while signaling individuals deviate from theirs. The PIV characteristics of the images used in this study suggest that cuttlefish use, or perhaps choose, visually complex backgrounds when camouflaging but visually less complex, homogeneous backgrounds when signaling. This might be explained by the observation that males often exhibit agonistic displays in the water column. High spatial frequency information, associated with fine visual detail, is rapidly attenuated over distance in the shallow marine environment through optical effects such as scatter and veiling (Lythgoe 1988), so this information may be reduced in the intervening space between the animal and the background. The reduction of complexity, regardless of how it is achieved, will make a scene less busy to the viewer and thus aid signal efficacy (Hailman 1977; Guilford and Dawkins 1991; Endler 2000).

Camouflaging Animals Resemble the Background

Experimental research on camouflage often attempts to assess how well local image parameters (such as color, patch size, local luminance) of a camouflage pattern match a background. Here we show that global spatial characteristics are also important to achieving camouflage. The use of global spatial characteristics may be vital if the structures and features of a potential predator's environment provide background information that can be subtracted from new sensory information with minimal computation (Atick and Redlich 1992). In this respect, a camouflaged animal that matches a simple statistical property of natural scenes (e.g., the scale-invariant power spectrum) might literally blend into the background.

Signalers Maximize Conspicuousness

The differences found between signaling cuttlefish and their backgrounds presumably maximize the conspicu-

ousness of signaling patterns to intended conspecific viewers. Deviating from the natural power law of the surrounding visual environment might be an excellent tactic to improve the efficacy of a signal. However, animal visual systems are expected to be most receptive (or "tuned") to the relevant visual characteristics of their environments (Párraga et al. 2000; Hansen and Essock 2004; Zeil and Hemmi 2006). This differential receptivity means that rare image characteristics that are absent in natural scene structure might be less easily detected and therefore less useful in signaling (Guilford and Dawkins 1991). We propose that a certain degree of novel spatial structure (e.g., perturbation of the power spectrum) at the signaling range of frequencies does not distort the visual information to a point where it becomes unnatural and therefore less easy to see but rather increases signal efficacy by its uniqueness in the visual environment.

Signaling animals often use colors that differ from their visual background in order to enhance detectability (Endler 1992; Osorio and Vorobyev 1997). However, cuttlefish are almost certainly color blind (Marshall and Messenger 1996; Mäthger et al. 2006). The high-contrast repetitive markings of the zebra stripe and passing cloud body patterns are probably a strong high-contrast stimulus to a color-blind receiver. This poses intriguing questions concerning the evolution of a color-blind communication system in the presence of color-receiving eavesdroppers. Attenuation of contrast and high spatial frequencies of the aquatic environment (Lythgoe 1979, 1988), combined with the low resolution typical of fish vision (Douglas and Hawryshyn 1990), means that certain conspicuous markings, particularly those of high spatial frequency, may provide camouflage at distance. Therefore, the apparently conspicuous markings used by *Sepia apama* are consistent with hypotheses that predict that bold markings are optimized to carry over short viewing distances but are rapidly attenuated over larger distances (Hailman 1977; Marshall 2000). The characteristic power spectra of *S. apama* signaling body patterns support this hypothesis: the animal power spectra match the background power spectra at low frequencies but deviate from them at a consistent point at high frequencies. This deviation point may correspond to a viewing distance beyond which signaling information is no longer useful for the intended receiver. Indeed, extensive observations of agonistic displays suggest that they are carried out over relatively short distances (e.g., fig. 2*b*; see also Hall and Hanlon 2002).

Background Differences

We found that the mean PIV of backgrounds used by signaling animals was significantly lower than that of backgrounds used by camouflaging animals. This difference

suggests that signaling animals use less complex backgrounds in order to increase their conspicuousness, while camouflaging animals may benefit from habitat heterogeneity. Of interest is the observation that the PIV of camouflaging animals was lower than that of the immediate surroundings and more closely matched the typical levels of the backgrounds used by signaling animals (fig. 4). Thus, camouflaging animals use body patterns of a lower intensity than the general background, suggesting that reducing overall saliency may be more important than precise background matching. It was observed that, when camouflaging, cuttlefish tended to seek structures such as macroalgae or rocks to rest among (see also Barbosa et al. 2008).

Background complexity is known to reduce target recognition and increase search times for targets in humans and other animals (Wolfe et al. 2002; Bond and Kamil 2006; Bravo and Farid 2008). If we assume similar search and image segregation processes in relevant vertebrate predators, then camouflage is likely to be more effective in heterogeneous environments (Merilaita et al. 1999; Merilaita 2003), particularly in cuttlefish, where adaptive camouflage can be utilized to match microhabitat attributes (e.g., Hanlon et al. 2007, 2009).

Signaling cuttlefish appeared to carry out much of their agonistic displays in more open areas; at our particular field site, displays tended to occur over patches of brown “mung” algae (*Pylaiella* species) or over areas of flat rock that were relatively homogeneous in their visual appearance. In addition, agonistic displays often took place above the substrate in the water column. Such behaviors are reflected in the low pixel variance found for signaling backgrounds. Choosing simple microhabitats against which to display is a behavior that enhances signal quality by reducing background noise (Hailman 1977). Our results suggest that *S. apama* may select appropriate backgrounds, depending on behavioral context (but see also Allen et al. 2010).

We have shown that there are clear differences in the spatial attributes of body patterns used in camouflage and signaling and that these differences relate to some well-documented invariant qualities of natural scenes. Cuttlefish have proven to be a unique and exciting model for investigating nonhuman visual perception (e.g., Chiao and Hanlon 2001; Kelman et al. 2008; Allen et al. 2009; Zylinski et al. 2009a); here we reinforce the potential of this system for understanding animal camouflage and communication. Furthermore, our methods are applicable to the wider study of animal patterning, a subject that has received renewed attention in recent years (e.g., Stevens and Merilaita 2009). The questions regarding camouflage and signaling investigated here hold a particular fascination, bridging the fields of visual ecology, behavior, and image

statistics. Our findings suggest that global image characteristics may be as important as local features in defining and characterizing animal body patterns. These characteristics should not be overlooked in the study of camouflage and communication in the field.

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Literature Cited

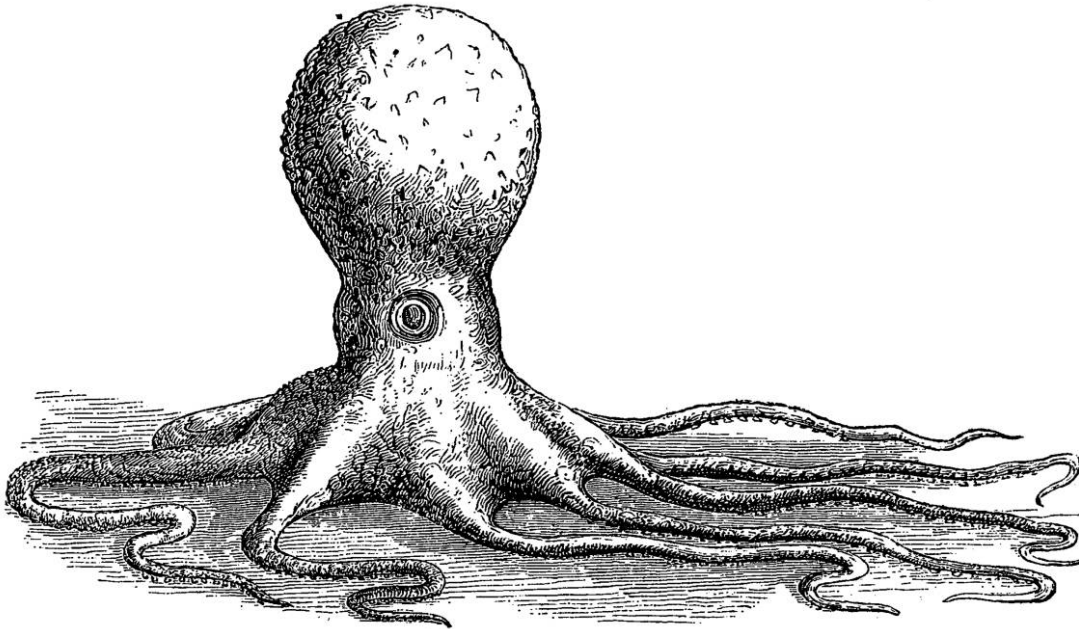
- Allen, J., L. Mähger, A. Barbosa, and R. Hanlon. 2009. Cuttlefish use visual cues to control three-dimensional skin papillae for camouflage. *Journal of Comparative Physiology A* 195:547–555.
- Allen, J. J., L. M. Mähger, A. Barbosa, K. C. Buresch, E. Sogin, J. Schwartz, C. Chubb, and R. T. Hanlon. 2010. Cuttlefish dynamic camouflage: responses to substrate choice and integration of multiple visual cues. *Proceedings of the Royal Society B: Biological Sciences* 277:1031–1039.
- Atick, J. J., and A. N. Redlich. 1992. What does the retina know about natural scenes? *Neural Computation* 4:196–210.
- Balboa, R. M., and N. M. Grzywacz. 2003. Power spectra and distribution of contrasts of natural images from different habitats. *Vision Research* 43:2527–2537.
- Barbosa, A., L. Litman, and R. T. Hanlon. 2008. Changeable cuttlefish camouflage is influenced by the horizontal and vertical aspects of the visual background. *Journal of Comparative Physiology A* 194:405–413.
- Bex, P. J., and W. Makous. 2002. Spatial frequency, phase, and the contrast of natural images. *Journal of the Optical Society of America* 19:1096–1106.
- Bond, A. B., and A. D. Kamil. 2006. Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proceedings of the National Academy of Sciences of the USA* 103:3214–3219.
- Bravo, M. J., and H. Farid. 2008. A scale invariant measure of clutter. *Journal of Vision* 8:1–9.
- Bruce, V., P. R. Green, and M. A. Georgeson. 2003. *Visual perception: physiology, psychology, and ecology*. Psychology, Hove.
- Chambers, J. M., W. S. Cleveland, B. Kleiner, and P. A. Tukey. 1983. *Graphical methods for data analysis*. Wadsworth & Brooks/Cole, Pacific Grove, CA.
- Chiao, C.-C., and R. T. Hanlon. 2001. Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *Journal of Experimental Biology* 204:2119–2125.
- Chiao, C.-C., C. Chubb, and R. T. Hanlon. 2007. Interactive effects

- of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish. *Vision Research* 47: 2223–2235.
- Cummings, M. E., J. M. Jordão, T. W. Cronin, and R. F. Oliveira. 2008. Visual ecology of the fiddler crab, *Uca tangeri*: effects of sex, viewer and background on conspicuousness. *Animal Behaviour* 75:175–188.
- Douglas, R. H., and C. W. Hawryshyn. 1990. Behavioural studies of fish vision: an analysis of visual capabilities. Pages 373–418 in R. H. Douglas and M. B. A. Djamgoz, eds. *The visual system of fish*. Chapman & Hall, London.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evolutionary Biology* 11:319–364.
- . 1992. Signals, signal conditions, and the direction of evolution. *American Naturalist* 139(suppl.):S125–S153.
- . 2000. The evolutionary implications of the interaction between animal signals and the environment. Pages 11–46 in Y. Espmark, T. Amundsen, and G. Rosenqvist, eds. *Animal signals: signalling and signal design in animal communication*. Tapir Academic, Trondheim.
- Endler, J. A., and P. W. Mielke. 2005. Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society* 86:405–431.
- Fasick, J. I., and P. R. Robinson. 1998. Mechanisms of spectral tuning in the dolphin visual pigments. *Biochemistry* 37:433–438.
- Field, D. J. 1987. Relations between the statistics of natural images and the response properties of cortical cells. *Journal of the Optical Society of America* 4:2379–2394.
- Godfrey, D., J. N. Lythgoe, and D. A. Rumball. 1987. Zebra stripes and tiger stripes: the spatial frequency distribution of the pattern compared to that of the background is significant in display and crypsis. *Biological Journal of the Linnean Society* 32:427–433.
- Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42:1–14.
- Hailman, J. P. 1977. *Optical signals: animal communication and light*. Indiana University Press, Bloomington.
- Hall, K. C., and R. T. Hanlon. 2002. Principle features of the mating system of a large spawning aggregation of the giant Australian cuttlefish *Sepia apama* (Mollusca: Cephalopoda). *Marine Biology* 140:533–545.
- Hanlon, R. T., and J. B. Messenger. 1996. *Cephalopod behaviour*. Cambridge University Press, Cambridge.
- Hanlon, R. T., M. J. Naud, P. W. Shaw, and J. N. Havenhand. 2005. Behavioural ecology: transient sexual mimicry leads to fertilization. *Nature* 433:212.
- Hanlon, R. T., M.-J. Naud, J. W. Forsythe, K. Hall, A. C. Watson, and J. McKechnie. 2007. Adaptive night camouflage by cuttlefish. *American Naturalist* 169:543–551.
- Hanlon, R. T., C.-C. Chiao, L. M. Mäthger, A. Barbosa, K. C. Buresch, and C. Chubb. 2009. Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:429–437.
- Hansen, B. C., and E. A. Essock. 2004. A horizontal bias in human visual processing of orientation and its correspondence to the structural components of natural scenes. *Journal of Vision* 4:1044–1060.
- Julesz, B. 1981. Textons, the elements of texture perception, and their interactions. *Nature* 290:91–97.
- Kelman, E. J., D. Osorio, and R. Baddeley. 2008. Review on sensory neuroethology of cuttlefish camouflage and visual object recognition. *Journal of Experimental Biology* 211:1757–1763.
- Kovesi, P. D. 2000. MATLAB and Octave functions for computer vision and image processing. Center for Exploration Targeting, School of Earth and Environment, University of Western Australia, Perth. <http://www.csse.uwa.edu.au/pk/research/matlabfns/>.
- Langridge, K., M. Broom, and D. Osorio. 2007. Selective signalling by cuttlefish to predators. *Current Biology* 17:R1044–R1045.
- Lythgoe, J. N. 1979. *The ecology of vision*. Clarendon, Oxford.
- . 1988. Light and vision in the aquatic environment. Page 75–82 in J. Atema, R. R. Fay, A. N. Popper, and W. N. Tavolga, eds. *Sensory biology of aquatic animals*. Springer, New York.
- Lythgoe, J. N., W. R. A. Muntz, J. C. Partridge, J. Shand, and D. M. Williams. 1994. The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *Journal of Comparative Physiology A* 174:461–467.
- Marshall, N. J. 2000. Communication and camouflage with the same “bright” colours in reef fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 355:1243–1248.
- Marshall, N. J., and J. B. Messenger. 1996. Colour-blind camouflage. *Nature* 382:408–409.
- Mäthger, L. M., A. Barbosa, S. Miner, and R. T. Hanlon. 2006. Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. *Vision Research* 46: 1746–1753.
- Merilaita, S. 2003. Visual background complexity facilitates the evolution of camouflage. *Evolution* 57:1248–1254.
- Merilaita, S., J. Tuomi, and V. Jormalainen. 1999. Optimization of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society* 67:151–161.
- Messenger, J. B. 2001. Cephalopod chromatophores: neurobiology and natural history. *Biological Reviews* 76:473–528.
- Norman, M. D., J. Finn, and T. Tregenza. 1999. Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society B: Biological Sciences* 266:1347–1349.
- Osorio, D., and M. Vorobyev. 1997. *Sepia* tones, stomatopod signals and the uses of colour. *Trends in Ecology & Evolution* 12:167–168.
- Párraga, C. A., T. Troscianko, and D. J. Tolhurst. 2000. The human visual system is optimised for processing the spatial information in natural visual images. *Current Biology* 10:35–38.
- Rosenthal, G. G. 2007. Spatiotemporal dimensions of visual signals in animal communication. *Annual Review of Ecology, Evolution, and Systematics* 38:155–178.
- Ruderman, D. L. 1994. The statistics of natural images. *Network: Computation in Neural Systems* 4:517–548.
- Shapley, R., and P. Lennie. 1985. Spatial frequency analysis in the visual system. *Annual Review in Neuroscience* 8:547–583.
- Stevens, M., and S. Merilaita. 2009. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:423–427.
- Stuart-Fox, D., A. Moussalli, J. Marshall, and I. P. F. Owens. 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. *Animal Behaviour* 66: 541–550.

- Wolfe, J. M., A. Oliva, T. S. Horowitz, S. J. Butcher, and A. Bompas. 2002. Segmentation of objects from backgrounds in visual search tasks. *Vision Research* 42:2985–3004.
- Zeil, J., and J. M. Hemmi. 2006. The visual ecology of fiddler crabs. *Journal of Comparative Physiology A* 192:1–25.
- Zylinski, S., D. Osorio, and A. J. Shohet. 2009a. Edge detection and texture classification by cuttlefish. *Journal of Vision* 9:1–10.

- . 2009b. Perception of edges and visual texture in the camouflage of the common cuttlefish, *Sepia officinalis*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:439–448.

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“I could see nothing but a pair of very bright eyes; but concluding that the eyes had an owner, I determined very rashly to secure him. ... I put my hand down very quietly so as not to ruffle the water, when, suddenly, to my surprise, it was seized with a pressure far too ardent to be agreeable, and I was held fast.” From “A Chapter on Cuttle-Fishes” by Lucie L. Hartt (*American Naturalist*, 1869, 3:257–261).