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Interactive effects of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish

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Abstract

Disruptive body coloration is a primary camouflage tactic of cuttlefish. Because rapid changeable coloration of cephalopods is guided visually, we can present different visual backgrounds (e.g., computer-generated, two-dimensional prints) and video record the animal's response by describing and grading its body pattern. We showed previously that strength of cuttlefish disruptive patterning depends on the size, contrast, and density of discrete light elements on a homogeneous dark background. Here we report five experiments on the interactions of these and other features. Results show that Weber contrast of light background elements is—in combination with element size—a powerful determinant of disruptive response strength. Furthermore, the strength of disruptive patterning decreases with increasing mean substrate intensity (with other factors held constant). Interestingly, when element size, Weber contrast and mean substrate intensity are kept constant, strength of disruptive patterning depends on the configuration of clusters of small light elements. This study highlights the interactions of multiple features of natural microhabitats that directly influence which camouflage pattern a cuttlefish will choose.

Keywords: Color pattern; Body pattern; Disruptive coloration; *Sepia officinalis*; Defense; Crypsis

1. Introduction

Our quest is to understand how the camouflaged body patterns of cephalopods are influenced by properties of the visual background. It is known that this behavior is guided visually (e.g., Hanlon & Messenger, 1988, 1996; Holmes, 1940; Packard, 1972) and Boycott (1961) demonstrated with neurophysiological methods that the pathway is: visual input → eyes → optical lobes → lateral basal lobes → chromatophore lobes → skin patterning. This last step is accomplished by motoneurons that travel without synapse to radial muscles that control pigmented chromatophores in the skin. Thus, rapid adaptive coloration in cephalopods can be described as a visual sensorimotor system in which visual input is processed by the CNS and the motor output is expressed as the neurally controlled body pattern. Despite knowledge of many aspects of cephalopod vision (Messenger, 1991; Muntz, 1999), little is known about specific visual features of the substrate that cephalopods use selectively to produce adaptive camouflage. To test this, we have developed a non-invasive behavioral assay that is based on the fact that camouflage is the primary defense of most cephalopods (Hanlon & Messenger, 1996). Camouflage in benthic, shallow-water cephalopods such as cuttlefish and octopus is so remarkably robust a behavior that cephalopods will attempt to camouflage themselves on any natural substrate on which they are placed, and even on very unnatural backgrounds such as we present in this and recent papers (e.g., Barbosa et al., 2007; Chiao & Hanlon, 2001a).

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Cephalopods use diverse appearances for camouflage on benthic substrates, yet the body patterning repertoire can be grouped into three general categories: uniform (or finely stippled), mottled, and disruptive (Hanlon & Messenger, 1988). Crypsis through disruptive coloration has been shown in squid (Hanlon, Maxwell, Shashar, Loew, & Boyle, 1999) and octopus (Hanlon, Forsythe, & Joneschild, 1999) but is particularly common and highly developed in cuttlefish (Hanlon & Messenger, 1988; Holmes, 1940) as illustrated in Fig. 1a. Disruptive coloration is common in the animal kingdom, for example in isopods (Merilaita, 1998), moths (Cuthill et al., 2005), and many other species, both large and small (Cott, 1940; Edmunds, 1974). Disruptive coloration is a complex form of camouflage whose exact mechanisms and functions are not fully known, but are receiving long-overdue attention recently (e.g., Endler, 1991, 2006; Merilaita & Lind, 2005). It is generally recognized that disruptive patterns help break up the recognizable body outline into large-scale light and dark mosaics in different orientations, and that certain components of the patterns also help achieve general background resemblance (e.g., Cott, 1940; Cuthill et al., 2005).

Cephalopod body patterns are made up of neurophysiological "building blocks" in the skin called "chromatic components" (e.g., Hanlon, 1982; Packard, 1982; Packard & Hochberg, 1977; Roper & Hochberg, 1988). There are 34 discrete chromatic components in *Sepia officinalis* (Hanlon & Messenger, 1988). Eleven of these chromatic components—used in different combinations—constitute different variations of disruptive body patterns. In our earlier studies, we used only one disruptive component (White Square) to indicate the degree of disruptive body patterns for simplifying the quantification (Chiao & Hanlon, 2001a, 2001b). However, many of the 11 disruptive components are involved in generating the integrated appearance of disruptive camouflage patterns. Therefore, in recent studies, we (Chiao, Kelman, & Hanlon, 2005; Mäthger, Barbosa, Miner, & Hanlon, 2006) and others (Poirier, Chichery, & Dickel, 2005) have adopted a grading scheme that includes most or all of the 13 disruptive skin components. This expanded grading scheme provides more data for objectively evaluating the strength of disruptive body patterning on different substrates, and provides more detailed clues about the visual perception and neural processing of body patterning.

There are few experimental systems in which rapidly changing sensory input can be assayed quantitatively by a fine tuned motor output (Marshall & Messenger, 1996; Mast, 1916; Saidel, 1988). Several lines of statistical and computational approaches have been developed to describe and analyze skin patterns of cuttlefish and flatfish (Anderson et al., 2003; Crook, Baddeley, & Osorio, 2002; Ramachandran et al., 1996), but we have opted to grade the precise skin components that, when expressed neurophysiologically, produce the disruptive body pattern. This approach enables a non-invasive manner of studying visual perception that guides body patterning for camouflage in a freely behaving animal.

Previously we determined that certain visual features (i.e., size, contrast, and density of light squares on a black background) were influential in controlling disruptive skin patterns produced by cuttlefish (Chiao & Hanlon, 2001a). Subsequently, we showed that cuttlefish cue visually on area—not shape or aspect ratio—of light objects in the substrate to produce disruptive body patterns (Chiao & Hanlon, 2001b). We applied this robust behavioral assay to show that cuttlefish perceive polarized and non-polarized signals differently (Grable, Shashar, Gilles, Chiao, & Hanlon, 2002). Recently, the same checkerboard method was used to confirm color blindness in *Sepia officinalis* (Mäthger et al., 2006), which had been demonstrated in a different manner by Marshall and Messenger (1996). In addition to these simple checkerboard stimuli, we used pictures of natural gravel to show that disruptive body patterning requires information regarding edges and contrast of background objects (Chiao et al., 2005).

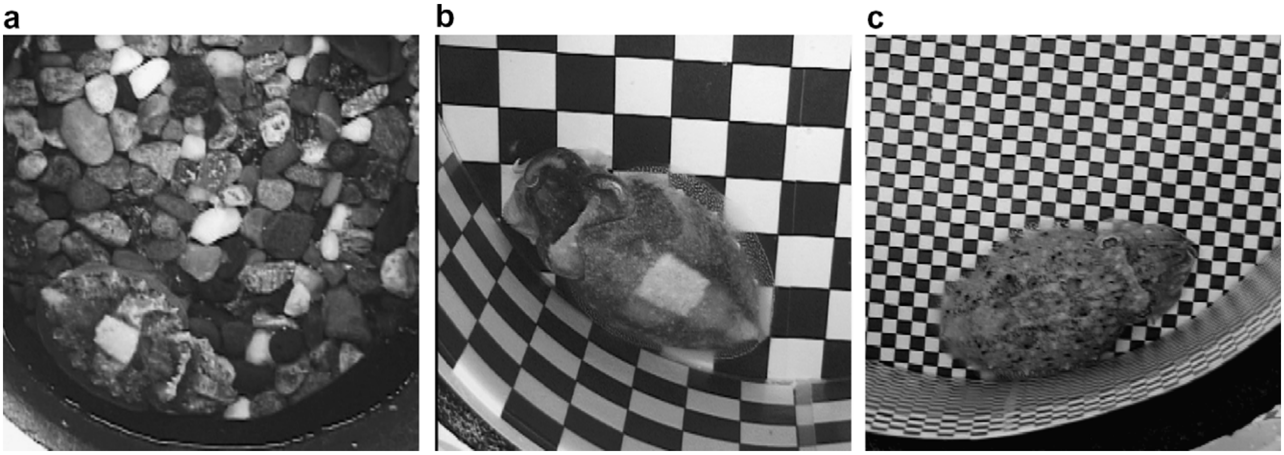

Fig. 1. Camouflage body patterns of *Sepia officinalis* on natural and artificial substrates. (a) A cuttlefish in disruptive coloration on a stone substrate (animal is at the bottom-left corner). (b) A cuttlefish showing a strong disruptive body pattern on a black/white checkerboard with 100%-WS-size. (c) A cuttlefish expressing a mottle body pattern on a black/white checkerboard with 12%-WS-size.