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The use of background matching vs. masquerade for camouflage in cuttlefish *Sepia officinalis*

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ABSTRACT

Cuttlefish, *Sepia officinalis*, commonly use their visually-guided, rapid adaptive camouflage for multiple tactics to avoid detection or recognition by predators. Two common tactics are background matching and resembling an object (masquerade) in the immediate area. This laboratory study investigated whether cuttlefish preferentially camouflage themselves to resemble a three-dimensional (3D) object in the immediate visual field (via the mechanism of masquerade/deceptive resemblance) rather than the 2D benthic substrate surrounding them (via the mechanisms of background matching or disruptive coloration). Cuttlefish were presented with a combination of benthic substrates (natural rocks or artificial checkerboard and grey printouts) and 3D objects (natural rocks or cylinders with artificial checkerboards and grey printouts glued to the outside) with visual features known to elicit each of three camouflage body pattern types (Uniform, Mottle and Disruptive). Animals were tested for a preference to show a body pattern appropriate for the 3D object or the benthic substrate. Cuttlefish responded by masquerading as the 3D object, rather than resembling the benthic substrate, only when presented with a high-contrast object on a substrate of lower contrast. Contrast is, therefore, one important cue in the cuttlefish's preference to resemble 3D objects rather than the benthic substrate.

1. Introduction

Cuttlefish are one of few animal groups with the ability to camouflage themselves on a wide variety of backgrounds, from open sandy plains to complex coral and rock reef habitats (e.g., Barbosa, Litman, & Hanlon, 2008; Hanlon & Messenger, 1988). Because the color, contrast, patterning and physical texture of their skin are under direct neural control, camouflage is almost instantaneous (Hanlon, 2007; Messenger, 2001). They change their body pattern and physical skin texture using two main tactics to achieve camouflage: background matching (resembling the color, contrast and pattern of the background) to hinder detection; and disruption (breaking up the body outline) to impede recognition (e.g., Cott, 1940; Hanlon & Messenger, 1988; Hanlon et al., 2009; Stevens & Merilaita, 2009).

Alternatively, cuttlefish may choose to resemble an inanimate object such as seaweed or a rock (Hanlon & Messenger, 1988; Hanlon et al., 2009), a tactic known as deceptive resemblance (Cott, 1940) or masquerade (Stevens & Merilaita, 2009). For example, in an open area such as a sandy plain a cuttlefish may choose to look like nearby objects to masquerade its true identity (such as depicted in Fig. 1). This requires assessment of the visual background on the substrate, as well as 3D objects in the immediate vicinity.

The driving force for having a choice of camouflage tactics is that predators view cuttlefish from many angles: swimming predators (fish, dolphins, etc.) view them vertically down against the substrate while benthic predators view them horizontally against vertical 3D objects on the substrate. A key conceptual question arises for masquerade as a camouflage tactic: is the prey organism using masquerade to avoid visual recognition (as posited by Endler (1981) and Stevens and Merilaita (2009)) or visual detection? Recent experimental papers using chicks preying on moth caterpillars argue that both mechanisms are at play in masquerade (Skelhorn, Rowland, & Ruxton, 2010; Skelhorn, Rowland, Speed, De Wert, et al., 2010; Skelhorn, Rowland et al., 2010; Skelhorn & Ruxton, 2010, 2011a, 2011b; Skelhorn et al., 2011). In this paper, we concentrate on the perceptual capabilities of the prey (cuttlefish) that enable this choice, although this may eventually shed light on the predator's visual cues as well.

Sepia officinalis occurs in the Mediterranean and Eastern North Atlantic where they live predominately in muddy and sandy/seagrass habitats (Jereb & Roper, 2005) that often have 3D features such as rocks and algae; we have recorded many field

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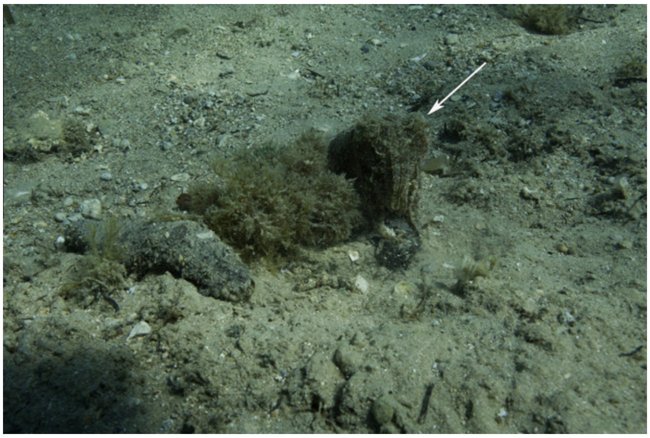

Fig. 1. *Sepia officinalis* masquerading as a clump of seaweed. The cuttlefish is indicated by the arrow. Photograph taken by R.T. Hanlon.

images of cuttlefish apparently resembling nearby rocks and algae to camouflage themselves (Fig. 1). In the laboratory, cuttlefish have been shown to respond preferentially to 2D vertical stimuli presented on the wall of an arena rather than the 2D pattern presented on the substrate (Barbosa, Litman, & Hanlon, 2008). However, their response to 3D objects has not been studied thus far, and we do not know if cuttlefish preferentially respond to 3D objects or to the substrate.

There are three basic body pattern types that cuttlefish use for camouflage (Hanlon, 2007); each body pattern is made up of light and dark splotches that range along a continuum (Hanlon et al., 2009), yet can be placed into the categories of Uniform (very small to small splotches), Mottle (medium-sized splotches) and Disruptive body patterns (large splotches but also bars, stripes, etc.; Hanlon & Messenger, 1988). Uniform and Mottle body patterns both function by "background matching" (although we prefer Cott's term "general background resemblance" because no statistical matches have been shown between animal and background; Hanlon et al., 2009), whereas the Disruptive body pattern can act either through background matching (i.e., when the animal is in an environment that consists of large-scale light and dark objects) or disruption (i.e., when the animal uses the large-scale markings of different orientations, shape and contrast on its body to break up its recognizable body outline rather than resembling the substrate (Hanlon et al., 2009).

In the laboratory, we can control the visual features of substrates and 3D objects presented to cuttlefish. Uniform body patterns can be elicited on fine-grained sand or uniformly-colored artificial backgrounds (Chiao & Hanlon, 2001; Chiao et al., 2010; Hanlon & Messenger, 1988; Kelman et al., 2007; Langridge, 2006; Mäthger et al., 2006); Mottle body patterns can be elicited on black and white checkerboards with a check size of 4–12% of the animal's White square or with a roughly equal size of light and dark gravel (Barbosa et al., 2007; Mäthger et al., 2007); and Disruptive body patterns can be elicited by presenting a black and white checkerboard with checks approximately 40–120% of the animal's White square or the equivalent sized rocks, shells or gravel (Barbosa et al., 2007; Mäthger et al., 2007). By using our knowledge of which body pattern various substrates elicit, we presented cuttlefish with both natural and artificial materials to test whether they prefer to resemble a 3D object (masquerade), or if they prefer to camouflage to the substrate (background matching).

2. Materials and methods

Three separate sets of experiments were performed: (1) natural substrates with natural 3D objects (real rocks and shells), (2) artificial substrates with artificial 3D objects (cylinders made of petri dishes covered with artificial substrates) and (3) artificial substrates with 2D rock-sized patches (designed to compare with the effects of the 3D artificial rocks). The substrates and rocks used in each experiment are described in detail below.

2.1. Animals

European cuttlefish (*S. officinalis*) were hatched, reared and maintained at the MBL in Woods Hole, Massachusetts. Fourteen cuttlefish (3.5–5.5 cm mantle length; ML) were used in the natural substrates experiment, 13 cuttlefish (2.12–4.31 cm ML) were used in the artificial substrates experiment, and five animals were used in the 2D experiment.

2.2. Natural substrate experiments

2.2.1. Benthic substrates

Three natural substrates were selected to elicit Uniform, Mottle and Disruptive body patterns: (1) A substrate was made from fine sand glued to a Plexiglas sheet to evoke Uniform. (2) Gravel/small pebbles sieved from local beach sand were used to evoke Mottle. (3) A substrate was made of larger grey and white shells to evoke Disruptive (see images for approximate substrate size relative to cuttlefish).

2.2.2. 3-D rocks

A single uniformly-colored, tan rock was used to evoke Uniform, a single rock with small white and black splotches (similar to the size of the small gravel used as a benthic substrate) was used to evoke Mottle, and a single rock with large areas of white and black (similar to the size of the grey and white shells used as a benthic substrate) was used to evoke Disruptive. All rocks were approximately 4 cm in diameter and about equal to one body length of the mean size of the animals. Since individual cuttlefish show some variation within each major body pattern (Uniform, Mottle and Disruptive) in the presence of the same visual stimulus (i.e., a single rock), we exposed each cuttlefish to the same 3D object to minimize variance when evoking different body patterns.

Animals were tested on each of the natural substrates as a control, and then on each substrate along with a natural rock that evoked either Uniform, Mottle or Disruptive (for a total of 12 trials per animal; e.g., sand that evoked Uniform with the rock that evoked Disruptive, large grey and white shells that evoked Disruptive with the rock that evoked Uniform, etc.).

2.3. Artificial substrate experiments

2.3.1. Benthic substrates

Three artificial substrates were made: (1) uniform grey (50% grey) designed to evoke Uniform, (2) small black and white checks designed to evoke Mottle (2.63 mm square size – 8% of area of animal's white square), and (3) large black and white checks designed to evoke Disruptive (9.31 mm square size – 100% of area of animal's White square area). Substrates were computer generated, laminated to be waterproof and placed on the floor of the experimental arena.

3. 3D rocks

Artificial rocks were made by gluing two small petri dishes together. Petri dishes were 3.5 cm diameter and 2.5 cm tall, which equaled approximately one cuttlefish ML and two times the dorsoventral height of the cuttlefish. These "rocks" were covered with the grey or checked substrates that were used to make the floor substrates. Animals were presented with each of the artificial