The Chameleon of the Sea: *Sepia officinalis*:

Endowed with an uncanny ability to alter its appearance within seconds of stimulation, the cuttlefish (*Sepia officinalis)* indisputably deserves its reputation as the chameleon of the sea. The cuttlefish is a member of the phylum Mollusca and resides in both tropical and temperate waters including the eastern Atlantic Ocean and the Mediterranean Sea (Gofas 2014). Despite its own colorblindness, the cuttlefish uses a complex system of neuromuscular signals and epidermal arrangements to respond to visual cues. Predation, a primary ecological pressure, prompted the evolution of the trait in diverse environments (Messenger 2001). However, cuttlefish also use camouflage as a tool for communicating and capturing prey. In conjunction with the camouflage mechanism, polarized sensitivity evolved in cuttlefish and presents intriguing implications for concealment and communication (Mathgar et al. 2009). A comprehensive analysis of the neuromuscular adaptations that cuttlefish possess reveals a compelling link between ecological factors and evolution.

Ecological pressures for camouflage: predation and abiotic factors

The complex system of neuromuscular control primarily evolved through efforts to evade predators including toothed whales and pinnipeds (Messenger 2001). During the late Triassic and early Cretaceous periods, evidence suggests that predatory vertebrates possessed acute optic systems, so phenotypes that promoted concealment increased fitness. Common camouflage responses directly reflect selection from predation. For instance, fish use a “centre-surround” system to perceive their surroundings, so cephalopods mimic ringed patterns to evade perception. Furthermore, while studying the orientation of visual stimuli, Barbosa *et al.* discovered that, though the intensity of responses increases when cuttlefish receive both horizontal and vertical cues, vertical information most strongly determines pattern (2008). In uncontrolled environments, bottom-dwelling predators often approach from lateral directions, so reliance on vertical cues for camouflage information is advantageous.

The patterns derived from both vertical and horizontal stimuli fit into four survival strategies that directly minimize detection. Through “general resemblance,” cephalopods sense brightness, color, and other defining characteristics to imitate their general environment (Messenger 2001). Cephalopods also possess a “countershading reflex” that automatically sustains a disguise in dangerous situations. Additionally, cephalopods employ “disrupted coloration” to visually separate their bodies from physical surroundings to confuse predators. Finally, some cephalopods practice “deceptive resemblance” to mimic inanimate objects. The vast variation of responses signifies adaptive efforts to prevent predators from using a single phenotypic profile to detect cuttlefish (Hanlon and Messenger 1988).

In addition to predation, diverse abiotic pressures shaped camouflage responses. Developmental studies reveal that idiosyncrasies exist among individual cephalopods depending on their specific habitats (Hanlon and Messenger 1988). For instance, if cephalopods possess few chromatophores, which are specialized pigment-producing organs, they typically dwell nocturnally or live in uniform environments. In contrast, complex epidermal systems enable survival in ecosystems of greater variability. In general, the spectral range of chromatophores directly corresponds to the range of natural substrates, which indicates positive selection for relevant pigments (Mathgar et al. 2008). However, despite phenotypic flexibility, extreme abiotic factors impose limits on success. Buresch *et al*. tested camouflage reactions to various lighting scenarios and showed that the clarity of patterns positively relates to the intensity of substrates in highly lit conditions (2015). Cuttlefish do not match against substrates in poorly illuminated environments and rather revert to pale uniform hues. The results indicate that, while cuttlefish are able to gauge their surroundings in settings of high and moderate light, the reactions fail with minimal illumination. Buresch *et al*. conjectured that this default setting could be an evolved choice to conserve energy in the absence of adequate cues. However, another plausible explanation simply recognizes that physical limitations exist within the optic system. Regardless of its limitations, the camouflage mechanism illustrates the ability of a single system to adjust to various abiotic and biotic pressures.

Additional function of camouflage: communication

Though camouflage evolved to minimize the risk of predation, evidence suggests that cuttlefish use pigmentation for both interspecific and intraspecific communication. Cuttlefish are well adapted for such communication since neural connections to the chromatophores create quick, independent signals, and specific patterns relate to conflict, predation and reproductive interactions (Messenger 2001). For instance, dark hues radiate in the "Passing Cloud" display to distract potential prey while the cuttlefish prepares an attack. Likewise, the cuttlefish uses a different interspecific pattern, known as a deimatic display, to deter predators by compressing itself and adopting a pale hue with dark accents around its eyes. Interestingly, the cuttlefish employs similar black and white shades in the "Intense Zebra," a pattern used to signal mating interest and express hostility towards other cuttlefish. The countless patterns further illustrate the adaptive versatility of cuttlefish that enables survival in diverse ecosystems.

Supplementary optic adaptation: polarized sensitivity

In addition to their central camouflage mechanism, recent research suggests that cuttlefish use polarized light as a tool for communication and predation. Unlike their vertebrate counterparts, cuttlefish possess microvilli and photoreceptors on their retina that allow them to perceive linearly polarized light (Mathgar et al. 2009). Chromatophores extend over underlying reflective cells, or iridophores, and the relative conformational changes that occur while cuttlefish modify pigment also produce light. The adjustable nature of the cells suggests a mode of secret signaling, or the production of undetectable stimuli, yet speculation exists as to whether reflectance is simply a consequence of camouflage efforts (Brandley et al. 2013). Despite this uncertainty, the polarized sensitivity that could allow interspecific communication also increases the predatory effectiveness of cuttlefish (Mathgar et al. 2009). Polarized light appears on translucent fish when they intentionally reflect light in an evasive strategy known as radiance matching (Shashar et al. 2000). Shashar *et al.* demonstrated that cuttlefish preferentially prey on fish that employ radiance matching because they are able to see through the façade. Thus, the emerging understanding of polarized sensitivity adds a dimension to the adaptive value of the neuromuscular optic system that cuttlefish possess.

The structural mechanism for camouflage

How do cuttlefish effectively camouflage themselves if they cannot detect color? Though the ecological pressures associated with the mechanism are fairly clear, the structural system behind the trait is complex. Recent studies refute hypotheses that cuttlefish rely on physical sensations to gauge their surrounds and show that neuromuscular signals depend almost entirely on visual cues. A study by Allen *et al.* confirmed that the physical dimensions of substrates do not play a role in perception (2009). The experiment manipulated external cues by systematically exposing cuttlefish to a substrate, the substrate covered with glass, and a photograph of the substrate. Observations of papillae, or muscular projections that mimic texture to supplement chromatophore-facilitated coloration changes, revealed that responses remained consistent throughout the three scenarios. Thus, cuttlefish only requires two-dimensional information to create an appropriately patterned response. The optic lobe registers these visual cues and subsequently conveys relevant signals to the specialized chromatophore lobe *(Fig. 1)* (Barbosa et al. 2008). From the chromatophore lobe, a series of complex nerve branches deliver information to the chromatophores, which ultimately determine color based on their expansion level, light reception, and orientation with inner reflecting cells (Messenger 2001). The self-organized neurological mechanism functions separately from other motor controls to promote energetic efficiency (Hochner et al. 2013).

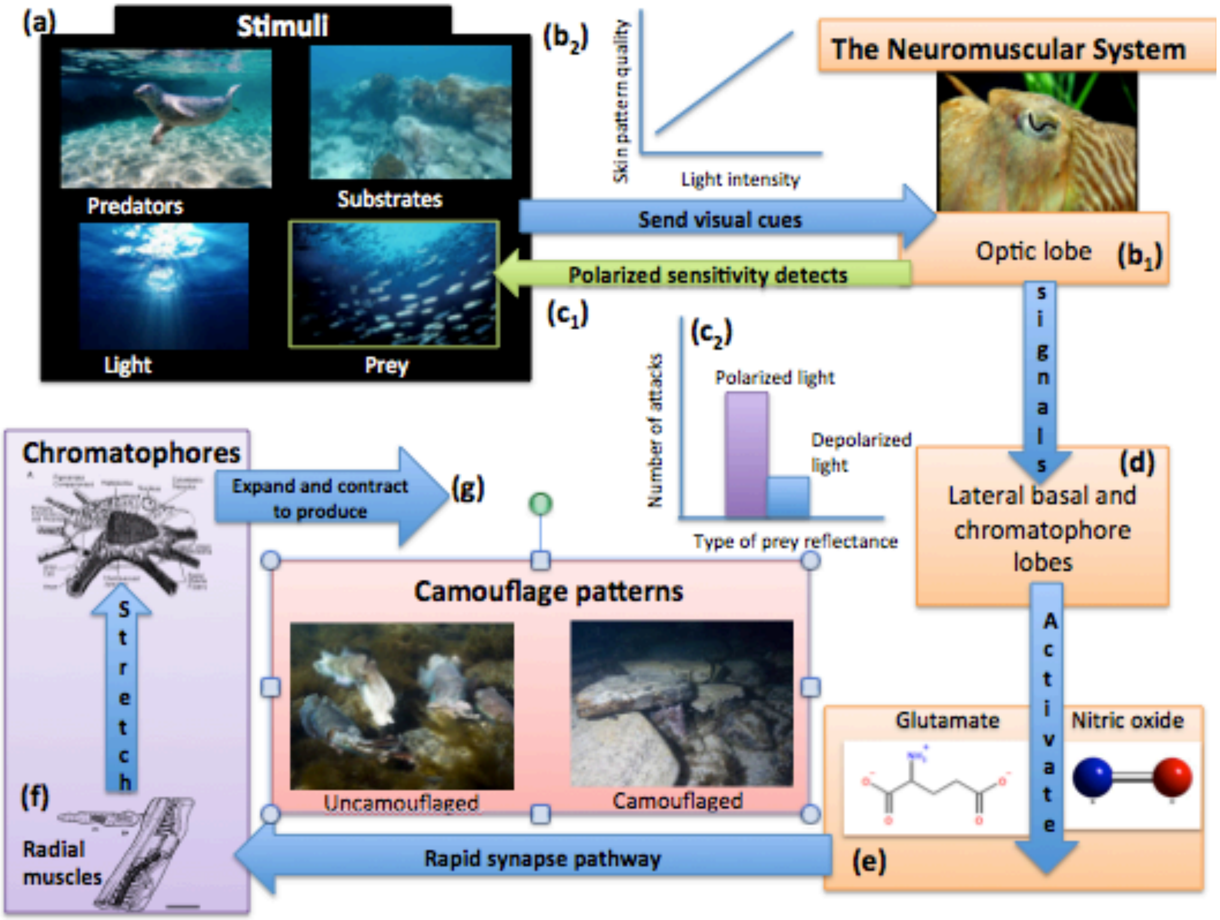
Impact of adaptations on the ecosystem

The adaptations of cuttlefish significantly impact interactions with the ecosystem from a young age (Hanlon and Messenger 1988). Cuttlefish hatchlings are born with the correct tools to react to visual stimuli as aptly as adult organisms. Since inherited instincts act without any acquired skills, genetics, rather than learning, appear to define the camouflage behavior. The ability of infant cuttlefish to survive in a diverse environment affects ecological balances since effectiveness of nascent evasive skills forces predators to supplement their diet with other resources. Moreover, in a developmental analysis, Darmaillacq et al. demonstrated that young cuttlefish visually imprint on prey depending on exposure (2006). Despite initial interest in shrimp, cuttlefish changed their preferences without reinforcement when presented with crab during a critical period. The ability to alter predatory priorities based on resource availability expands the potential impact that cuttlefish could have on their surroundings. Additionally, adaptations that promote predation directly affect other organisms. Polarized sensitivity improves the predatory competence of the cuttlefish and requires at-risk prey such as radiance matching fish to adjust their own camouflage mechanisms. As phenotypes evolve in both cuttlefish and their interspecific counterparts, the effects radiate throughout the ecosystem.

Future direction

With its complex neuromuscular system and direct developmental patterns, scientists assert that the cuttlefish is a promising model for "eco-evo-devo" research (Bassaglia 2013). Though information has accumulated over the past few decades, numerous avenues exist for future exploration. For instance, the field lacks concrete evidence for the true significance of polarized light. In an experiment analyzing the concurrent manifestation of color and light on the wings of the *Heliconius cydno* butterfly species, Brandley *et al.* tested the conjecture that butterflies use polarized light to prevent "eavesdropping" predators (2013). To evaluate the significance of polarization, the level of distinction for three categories, coloration, polarization, and luminance, was analyzed. The results indicated that polarization patterns do not differ significantly from other factors, and hence butterflies do not likely use polarization for communication. Since cuttlefish emit similar visual cues, an observational analysis could weigh the significance of polarized light patterns relative to color to assess the possibility of signaling. Other opportunities for future research lie in the nascent efforts to apply biomechanical elements of camouflage to human technology. Detailed analyses of the way that chromatophores create pigment suggest that synthetic replicas of the organs could be used in artificial camouflage and photonic systems (Deravi 2014). The development of the complex mechanism in nature can thus be applied directly to modern technology. Overall, the neuromuscular system of the cuttlefish does indeed illustrate the direct relationship between ecological pressures and adaptive development that fosters a complex mechanism of concealment and communication. Further exploration of the relationship between camouflage and behavioral traits will reveal complexities that are waiting to be discovered.

Figure 1: Structural Mechanism for Camouflage



(a) Abiotic and biotic stimuli send visual cues to the optic system of the cuttlefish. (b) The optic system passes information to other lobes of the brain while also allowing the cuttlefish to perceive polarized light. (b_2) The light intensity of specific cues directly corresponds to the quality of resulting skin patterns. (c_1) The cuttlefish uses polarized sensitivity to detect prey. (c_2) The cuttlefish thus preferentially attacks fish that reflect polarized light. (d) Visual information passes through the lateral basal lobe to the chromatophore lobe. The chromatophore lobe contains closely linked motorneurons that cause distinct reactions in the body in response to stimulation in different areas of the brain. It activates neurological chemicals including glutamate and nitric oxide, a messenger molecule frequently involved in biological signaling. (e) The neurotransmitters send signals down a synapse pathway to radial muscles that surround the chromatophore. Structurally, the chromatophore is made up of five different cells, one of which contains an elastic compartment known as the cytoelastic sacculus. The cytoelastic sacculus encases pigment granules that range in color from yellow, brown, black, red, and orange and is attached to the cell membrane of the chromatophore by muscular filaments. (f) Radial muscles that expand and contract in response to neurological signals. (g) The conformational changes of the pigment-containing chromatophore produces patterns that promote camouflage.

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