ZOOL 567

Annotated bibliography

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My bibliography is ordered chronologically as the information provided in each subsequent article builds on the previous findings. It transitions from findings when cuttlefish camouflage was just beginning to be studied and builds from how camouflage was originally perceived to how it is neutrally controlled.

**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. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1516), 429–437.** [**https://doi.org/10.1098/rstb.2008.0270**](https://doi.org/10.1098/rstb.2008.0270)

**Summary:** This review explores the versatility of cuttlefish camouflage and the various ways their environment impacts the patterns they display. It is well known that these critters exhibit complex visual systems vital to determining the body color pattern and recent papers have narrowed down the numerous numbers of patterns to fit into one of three pattern types: uniform, mottle, and disruptive. This review focused on how the cuttlefish’ environment induces one of these three patterns with an overarching question of how disruptive coloration is distinguished from background matching (a.k.a. uniform and mottle). Uniform is when there is little contrast present within the pattern and is most observed in homogenous rocks or sand. Mottle is when there are evenly spread patches of light and dark with moderate contrast and is the most common pattern seen due to the required environment being most typical. Disruptive coloration is characterized by high contrast between large light and dark patches that exhibit varying shapes and orientations. Quantitative analysis was completed by looking at the granularity of skin coloration when placed in various environments and the observations may suggest that contrast, substrate size and substrate intensity all play a role in which pattern is displayed. Further, a hybrid pattern was observed in which both disruptive coloration and mottle was seen and is suggested to occur in order to take the best of both patterns. Therefore, the link between background matching and disruptive coloration is still under study but this review suggests that contrast and edges of background are key in determining which one is utilized, if not both. With the work completed on how to quantify camouflage, there can be new insights on how to concretely determine camouflage patterns and what environments align with these patterns.

**Contribution:** This review manages to compile research results from many different papers on cuttlefish camouflage and create an informed estimate of where to go next. With the description of different color patterns and what environments these patterns occur in, research can begin to focus more on other factors influencing camouflage. For example, there may be occasions where mottle would suffice but disruptive coloration is chosen due to unknown pressures. The presentation of the hybrid is also a launching-off point for future research and the environment’s role in this pattern. This review was included for its in depth analysis of camouflage patterns.

**Zylinski, S., Osorio, D., & Shohet, A. J. (2009). 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*(1516), 439–448.** [**https://doi.org/10.1098/rstb.2008.0264**](https://doi.org/10.1098/rstb.2008.0264)

**Summary:** This study was interested in exploring the importance of edge perception and texture in cuttlefish camouflage. The objective was first to determine what role substrate edge information has in the cuttlefish’ choice of pattern display and secondly, to see how texture impacted camouflage when luminescence of the substrate is identical to the background. Two smaller cuttlefish were used in experiment one while two larger were used in experiment two. The cuttlefish were recorded and scored on a four-point scale in terms of how much expression of disruptive pattern was observed in both of the experiments. Experiment one was concerned with only using high contrast edges while experiment two maintained identical luminescence between the substrate and the environment and only varied in texture. Experiment one discovered that solely edge information is enough to stimulate a disruptive pattern. Experiment two instead found that when brightness is consistent with the surroundings, the texture of the substrate plays a key role in stimulating an appropriate pattern. Together these results are significant as they suggest that the cuttlefish visual system uses multiple factors to determine their best camouflage pattern. They respond to intensity first but will also integrate other features of texture when intensity does not give enough information. This suggests that cuttlefish actually have the ability to distinguish objects of identical luminescence of the background. Further, this finding stresses the highly impressive vision of cuttlefish to the extent of sharing similarities with vertebrate vision. This leads to possible assumptions that cuttlefish have evolved along with their predators in a visual arms-race type relationship. Understanding what their predators see has likely influenced their decisions of how to camouflage.

**Contribution:** This study is an essential piece to the puzzle of cuttlefish camouflage as it fills in the gap of how cuttlefish observe their environment to such a degree that they can disappear into it. It supports previous finding of how cuttlefish are solely visual animals when it comes to camouflage but expands this understanding further than it has been before. It also allows for future research to be better conducted on how predators may view the underwater world. I included this in my literature review because it suggested a new perspective on what cuttlefish perceive to camouflage effectively.

**Allen, J. J., Mäthger, L. M., Barbosa, A., & Hanlon, R. T. (2009). Cuttlefish use visual cues to control three-dimensional skin papillae for camouflage. *Journal of Comparative Physiology A*, *195*(6), 547–555.** [**https://doi.org/10.1007/s00359-009-0430-y**](https://doi.org/10.1007/s00359-009-0430-y)

**Summary:** This article investigates textural camouflage in cuttlefish with a focus on whether tactile or visual stimulation drives textural response. Papillae, the main organs responsible for this textural camouflage, have been found in previous studies to be expressed from visual cues alone however, this study is the first to compare papillae expression when both visual and tactile stimulus is applied. In addition, the study was also interested in determining how papillae are expressed differently between the various known body patterns (uniform, mottle, disruptive). In pursuit of these objectives, thirty cuttlefish were tested on three separate substrates with each substrate having three variations: actual substrate (to fulfil the tactile stimulus), actual substrate covered with pane of glass (visual of tactile stimulus) and a picture of the substrate (to fulfil the visual stimulus). The substrates consisted of sand, gravel, and rocks in order to induce the uniform, mottle, and disruptive body patterns, respectively. Once cuttlefish were settled in each trial, a photograph was taken and papillae were counted to determine expression. The results showed the cuttlefish matched the expected body pattern for all substrates regardless of there being tactile stimulus. This suggests that cuttlefish do not use tactile feedback to camouflage and instead use visual cues, two or three-dimensional, to control papillae expression. Further, different types of papillae were found to be expressed in the various body patterns with small dorsal papillae being expressed at higher rates in the uniform and mottle patterns than in the disruptive body patterns. This finding, along with the fact that other types of papillae were expressed in all three patterns, suggest that papillae around the body have different roles in contributing to successful camouflage. Therefore, visual reception is crucial to the camouflage ability of cuttlefish and plays a direct role in determining which papillae will be expressed.

**Contribution:** This study uncovered the key elements of cuttlefish camouflage by discovering that papillae expression is controlled by visual stimulus. With this knowledge, more research can be done on the different types of papillae as knowing what induces their expression creates new opportunities to study their control. Determining which papillae are expressed in various color patterns reinforces the patterns previously described and sparks new questions about the neural control that may be involved in creating different patterns. This article was included in my literature review as it offered information as to how cuttlefish perceive their environment to camouflage.

**Allen, J. J., Bell, G. R. R., Kuzirian, A. M., & Hanlon, R. T. (2013). Cuttlefish skin papilla morphology suggests a muscular hydrostatic function for rapid changeability. *Journal of Morphology*, *274*(6), 645–656.** [**https://doi.org/10.1002/jmor.20121**](https://doi.org/10.1002/jmor.20121)

**Summary:** This article investigates the morphology of skin papilla in cuttlefish and their role in textural camouflage. With previous knowledge that papillae are responsible for textural changes in cuttlefish, Allen et al. (2013) aimed to determine if small dorsal papilla acted in a muscular hydrostatic manner by analyzing their morphology and the mechanisms behind papilla extension. To investigate these concepts, three methods of microscopy were used; brightfield, confocal, and scanning electron microscopy (SEM). The skin of seven *Sepia officinalis* cuttlefish was removed, stretched and given an electrical stimulus to extend the papillae. The papillae were cut into two microscopy views; cross-section orientation and an orientation termed *en face* in which they were cut in half horizontally. The core of the papillae exhibited dense bundles of dermal erector muscles (DEM’s), concentrically organized at the basal end and horizontally stretched out to surrounding connective tissue at the apex. During extension, an increase in pressure was also discovered due to interstitial fluid being trapped between muscle fibers. Therefore, both the DEM’s and the pressure created by the interstitial fluid confinement were determined to induce extension and provide the hydrostatic support to maintain shape of the papilla. Therefore, this study was significant as it determined that muscular hydrostatic function is prevalent in cuttlefish’ ability to camouflage. As papilla extension was the main focus of this study, future studies could look into the mechanism of papilla retraction and what antagonistic muscle bundles are responsible for this retraction. Further, this research was only conducted for a specific species of cuttlefish so future studies could look into other species of cuttlefish as well as octopus to see if similar mechanisms are used in camouflage.

**Contribution:** This article provides new understanding of to how textural camouflage occurs in cuttlefish and opens doors to determining if other cephalopods exhibit similar morphological features. The study advances knowledge of muscular hydrostatic function as it is one of the first discoveries of thousands of hydrostats working together to create an overall appearance instead of a single hydrostat working by itself, for example a tongue. I included this article in my review as it offered an in-depth analysis of skin papilla, the main organ in textural camouflage.

**Allen, J. J., Bell, G. R. R., Kuzirian, A. M., Velankar, S. S., & Hanlon, R. T. (2014). Comparative morphology of changeable skin papillae in octopus and cuttlefish. *Journal of Morphology*, *275*(4), 371–390.** [**https://doi.org/10.1002/jmor.20221**](https://doi.org/10.1002/jmor.20221)

**Summary:** This article investigates the structure of papillae in both cuttlefish and octopuses with the goal of determining how papillae differ across multiple species. Papillae are components of the skin that play key roles in textural camouflage. Prior to this study, little research had been done on comparative analysis of papillae and although papillae extension was well studied, mechanisms of retraction were still undetermined. To do a comparative analysis, two species of cuttlefish (*S. officinalis*, *S. apama*) and four species of octopus (*O. vulgaris, M. defilippi, A. aculeatus, O. bimaculoides*) were used to harvest papillae. Papillae chosen exhibited a wide range of locations on the animals to study if papillae composition were location-dependent. Papillae were viewed via both brightfield and scanning electron microscopy (SEM) with staining methods used to visualize the various tissues involved in extension and retraction. The results from the microscopy supported previous findings of both a circular organization of extending muscles near the base of the papillae and horizontal extending muscles in the surrounding connective tissue. However, the results also gave rise to the presence of two key elements responsible for retraction: carbohydrate-rich connective tissue and retractor muscles. This discovery aided in determining that retraction is not completely elastic and is instead coordinated. Further, it explained that support of the papillae is not solely aided by the dermal extending muscles but by a combination of collagen and connective tissue. Although the various papillae studied had varying organizations of internal morphology based on where they were located on the body, they all were built upon the same components. Therefore, the comparative analysis determined that papillae of the studied species share very similar composition in musculature and connective tissue as well as the extension and retraction muscles necessary for function.

**Contribution:** The findings determined in this article are essential in moving forward with cuttlefish textural camouflage as now both extension and retraction mechanism have been uncovered. This article was able to build on past studies that discovered the morphology of extension and supported the previous finding of the role of dermal erector muscles. Moving forward, research in this field can explore deeper the elements necessary for retraction as well the role of collagen and carbohydrate-rich connective tissues. I included this article due to its primitive discovery of how papillae retraction occurs.

**Chiao, C.-C., Chubb, C., & Hanlon, R. T. (2015). A review of visual perception mechanisms that regulate rapid adaptive camouflage in cuttlefish. *Journal of Comparative Physiology A*, *201*(9), 933–945.** [**https://doi.org/10.1007/s00359-015-0988-5**](https://doi.org/10.1007/s00359-015-0988-5)

**Summary:** In the ten years prior to this review, plenty of research had been done on cuttlefish visual perception and its role in camouflage but there was still a gap in understanding as to how cuttlefish interpreted the features of their environment to create the best camouflage pattern. Therefore, this review investigates these previous findings and combines their efforts with an objective to create a better understanding of the environmental features responsible for specific pattern types and the visual perception involved. Many methods were used in these previous studies but a common approach was taking photos and looking at the granularity of the pattern to deduce whether uniform, mottle or disruptive patterns were being displayed. The review combined the findings of these experiments to determine the six background features responsible for inducing specific patterns: spatial scale, background intensity, background luminance contrast, object edges, object contrast polarity, and object depth. In response to these features, cuttlefish will utilize both their skin and the position of their arms to best fit into the environment. Therefore, the visual system of cuttlefish must be able to perceive the texture and orientation of objects to direct the expression of their skin and the positionality of their arms. The swift camouflage of cuttlefish is due to integration of perception by the optic lobe and subsequent excitation of papillae which directly targets the skin and the arm muscles. Thus, these findings are significant as they highlight that the combination of an adept visual system with rapid neural control of skin is what allows cuttlefish to pick the best pattern for their survival and continue to monitor it accordingly. There is still plenty of research to be done including deep analysis of the optic lobe anatomy and how camouflage can occur in a color-blind organism.

**Contribution:** This review manages to combine essential findings of cuttlefish camouflage discovered in the past ten years with the main objective of discerning what features of the environment are essential to camouflage decision. It supports each finding over the decade and sets up future questions of how the neural side of camouflage supports visual perception. It also creates a solid base for research to be conducted on predator perception, particularly in regards to object texture and edge distinction. I included this study in my review as it combined many of the recent findings of cuttlefish camouflage.

**Buresch, K. C., Ulmer, K. M., Akkaynak, D., Allen, J. J., Mäthger, L. M., Nakamura, M., & Hanlon, R. T. (2015). Cuttlefish adjust body pattern intensity with respect to substrate intensity to aid camouflage, but do not camouflage in extremely low light. *Journal of Experimental Marine Biology and Ecology*, *462*, 121–126.** [**https://doi.org/10.1016/j.jembe.2014.10.017**](https://doi.org/10.1016/j.jembe.2014.10.017)

**Summary:** This article investigated the relationship between luminescence and the intensity of the pattern displayed by a camouflaging cuttlefish. The object of this study was to determine how well cuttlefish match the intensity of a substrate in varying amounts of light as no previous study had examined this relationship in a lab. Two experiments were completed with ten adult cuttlefish used in each one. Experiment one involved four computer generated substrates varying in brightness (black and white checkerboard, light gray, medium gray, and dark gray) and each substrate was tested in four varying amounts of light for a total of sixteen trials. Experiment two was the same except the substrates were natural (dark sand, light sand, and white sand) for a total of twelve trials. In each trial a flash photograph was taken and then analyzed for intensity. In both experiments, the pattern of the cuttlefish displayed the substrate intensity in bright and moderate light but did not do as well in low or extremely low light. Instead, the cuttlefish took on a mottle pattern in low light and a pale uniform pattern in extremely low light. Therefore, it was determined that cuttlefish likely adjust their intensity to match the substrate when they have efficient light to do so. Without efficient light, they cannot observe their environment properly and resort to what they think would be the safest display. This finding is significant as it suggests that intensity matching is a key factor for successful camouflage in cuttlefish. In deeper environments, intensity becomes even more important than color as color vision is less helpful for predators and will rely more on intensity differences in the environment.

**Contribution:** This was the first study to look into the importance of intensity in cuttlefish camouflage and not only uncovered new ideas but questioned previous findings. For example, previous studies have found that cuttlefish can camouflage their patterns at night when light levels are extremely low, conflicting with this study’s findings. Therefore, more research could be carried out on this topic to narrow down exactly what kinds of light are essential for cuttlefish camouflage. I included this study in my literature review because it offered great insight into yet another component of camouflage.

**Panetta, D., Buresch, K., & Hanlon, R. T. (2017). Dynamic masquerade with morphing three-dimensional skin in cuttlefish. *Biology Letters*, *13*(3), 20170070.** [**https://doi.org/10.1098/rsbl.2017.0070**](https://doi.org/10.1098/rsbl.2017.0070)

**Summary:** Dynamic masquerade is a method of camouflage in which organisms aim to resemble an item expected to be found in an environment instead of the background itself. It was previously discovered that cuttlefish only need a visual stimulus to camouflage however, a gap in understanding exists in what features the visual object portrays in order to produce this masquerade pattern. Therefore, the object of this study was to determine the process to assessing an object as well as the features of that object that induce pattern and textural responses in cuttlefish. Fifteen cuttlefish were used in three sequential experiments occurring in seawater tanks. Experiment one was to determine which rocks induced the desired patterns and texture while experiments two and three placed these rocks at varying distances in each tank to test whether or not the cuttlefish would choose to move and camouflage or remain where it was at the other end of the empty tank. The results showed that cuttlefish chose to move towards the rocks and would express papillae to appropriately match the rock’s texture. This suggests that cuttlefish follow a two-step process when pursuing dynamic masquerade, first by visually detecting the three-dimensional item and then evaluating its texture to reflect on its own skin. The textural change exhibited in each scenario occurred extremely fast and demonstrated easy reversibility when switching from a textured rock to a smooth rock. By having this ability to quickly change texture, cuttlefish are better selected for a wide range of habitats and can respond quickly to danger by either increasing hydrodynamic shape when fleeing or blending into the surrounding background. The findings of this study allow for future research to explore the specific features of the environment that cuttlefish perceive to texturally camouflage as well explore predator cognition in response to camouflage.

**Contribution:** This study offers clearer understanding of cuttlefish visual perception, particularly in regards to seeing possible opportunities to camouflage and choosing to do so. As this study was built upon the past findings that cuttlefish mainly use visual stimuli, not textural stimuli, when camouflaging, it managed to support and further this understanding of visual perception. This work also projects new questions such as if visual perception is the same across benthic cephalopod species. This study was included in my review as it is very recent in terms of cuttlefish textural camouflage research and focuses on cuttlefish visual perception.

**Josef, N., Berenshtein, I., Rousseau, M., Scata, G., Fiorito, G., & Shashar, N. (2017). Size matters: Observed and modeled camouflage response of European cuttlefish (*Sepia officinalis*) to different substrate patch sizes during movement. *Frontiers in Physiology*, *7*.** [**https://doi.org/10.3389/fphys.2016.00671**](https://doi.org/10.3389/fphys.2016.00671)

**Summary:** This article was interested in exploring the characteristics of camouflage in moving cuttlefish with the objective of determining how large a substrate patch has to be to provoke a pattern change. Plenty is known about how cuttlefish determine which pattern to choose when immobile but how they stay inconspicuous when moving is a problem yet to be uncovered about their visual system perception. Eight young cuttlefish were subject to an elongated grey tank with six black patches of varying lengths; the varying length were between 10 and 16 cm with the goal of seeing the minimum size that would induce a camouflage response. Cuttlefish were recorded as they swam the length of the tank from a top down view and the footage was analyzed. After analysis, they determined the cuttlefish display changes in pattern and an increase in intensity when swimming over the longer black patches. Therefore, the larger the patch size, the more rapidly the cuttlefish would respond. The smallest patches that induced a pattern change were deemed Camouflage Eliciting Patch Size (CEPS). Changes in pattern were seen in between these 10 and 16 cm long patches suggesting that there is a CEPS threshold within these two lengths. As the mantle of the cuttlefish used averaged in length within this range, it is likely that a cuttlefish’ minimum patch size to stimulate camouflage is only slightly larger than its mantle. They further discovered cuttlefish are continuously scanning their environment for patch sizes and gauging whether or not their pattern is acceptable for the surroundings. Therefore, the ultimate discovery is that they have self-awareness which is significant as it is the first evidence in determining how cuttlefish increase their survival during locomotion.

**Contribution:** This study has offered the first evidence of understanding how cuttlefish remain camouflaged during locomotion as all previous studies have only considered stationary camouflage. It advances knowledge of cuttlefish camouflage by uncovering the locomotory side of it. It supports previous findings of the pattern’s cuttlefish display and creates new concepts that future research can analyze. For example, future studies can combine cuttlefish camouflage with biomimicry and utilize these findings to solve problems faced in society. I included this study in my literature review because it contributed findings not explored in any other article I could find.

**Gonzalez-Bellido, P. T., Scaros, A. T., Hanlon, R. T., & Wardill, T. J. (2018). Neural control of dynamic 3-dimensional skin papillae for cuttlefish camouflage. *IScience*, *1*, 24–34.** [**https://doi.org/10.1016/j.isci.2018.01.001**](https://doi.org/10.1016/j.isci.2018.01.001)

**Summary:** This study was interested in uncovering the neural control behind cuttlefish camouflage with emphasis on determining three objectives: 1) the pathway of neural signals when contracting and relaxing papillae, 2) how the papillae are able to be expressed and retracted so quickly, and 3) how papillae can continue to be expressed on a long-term basis without constant neural input. Chromatophores and papillae both play a key role in camouflage, the former in regards to colour change and the latter to textural change. Although they work together to create the correct pattern, they are innervated, activated and controlled independently. 18 juvenile cuttlefish were used in the various experiments within the study and were anaesthetised before any internal or external manipulations occurred. By severing various nerves and observing how the chromatophores and papillae responded, they determined that neural control of papillae runs through the stellate ganglion. This finding is significant as no previous study had explicitly found this neural pathway. To study the second objective, various neurotransmitters were injected under the skin and the textural response was recorded. This process determined that FMRFamide, acetylcholine, and L-glutamate are likely the primary neurotransmitters responsible for the fast contraction and relaxation of papillae, again being a significant finding in regards to the neural pathway. Lastly, objective three was investigated by severing the key nerve responsible for all neural signals shared from the brain to the mantle and fins. Even though this nerve was severed, papillae expression was still observed which is likely due to a catch mechanism that allows very slow relaxation of the papillae after an initial neural stimulus. This catch mechanism is essential to maintaining the energy of a cuttlefish during camouflage as, without it, the organism would have to continuously be sending signals requiring energy to stimulate the papillae.

**Contribution:** This article is extremely significant as very little is known about the neural control involved in cuttlefish camouflage. This article supports the previous findings of papillae morphology and adds to scientists’ understanding of cuttlefish camouflage. The findings described here offer a firm base for future research on neural control to launch off of and propose many future questions to be studied. For example, understanding regarding the evolution of neural control and skin morphology in cuttlefish is still elusive. I included this article in my literature review as it offered recent findings of neural control in cuttlefish camouflage.