I organized my entries first by secondary vs primary literature; secondary articles that provided overall context for the mechanism and structure of cuttlefish (cephalopod) camouflage/dynamic coloration and mimicry behaviour. I then separated the primary articles into either dynamic coloration/camouflage or mimicry behaviour and within each of these three larger headings, the entries have been organized from oldest to newest publication date.

Secondary articles outlining the overall context for cuttlefish camouflage/dynamic coloration and mimicry behaviour

Messenger, J.B. (2001). Cephalopod chromatophores: Neurobiology and natural history. *Biological Reviews of the Cambridge Philosophical Society, 76,* 473-528. https://doi.org/10.1017/S1464793101005772

Summary: Previous research has found that cephalopod chromatophores are unlike those of other animals, which are hormonally controlled. In cephalopods, chromatophores are neuromuscular organs which allow them to alter their body pattern and texture instantaneously. This review elaborates on the identification of chromatophores as neuromuscular organs by summarizing research conducted on neurobiology, the building blocks of chromatophore structure and their contribution to the dynamic coloration/texture behaviours of cephalopods. Cephalopods utilize their dynamic coloration for behaviours such as camouflage and communication. These behaviours are controlled by the “brain” of the cephalopod. Their brain functions unlike a human, that is without visual or proprioceptive feedback. Considering that cephalopods are invertebrates, their brain structure is highly developed; with several lobes surrounding ganglia. They rely on their high visual acuity (despite being color blind) to relay a message to the chromatophores, which elicits a colorful response. The neuromuscular control of chromatophores produces several dynamic coloration behaviours. The first one being concealment, which is the most well-recognized camouflage behaviour. Concealment can however be broken down into many types: background resemblance, countershading, disruptive coloration, deceptive resemblance. Background resemblance entails the cephalopod blending into their surroundings, countershading occurs when their dorsal and ventral surface have chromatophores expanded differing amounts, disruptive coloration is defined as displays put on by the cuttlefish that would startle a predator and deceptive resemblance is taking on the appearance of an inanimate object. Communication, both interspecific to predators by putting on a display that lessens their chances of being eaten or intraspecific where a sexually mature male demonstrates the “Intense Zebra”, an alternating light/dark striped pattern display in agonistic interactions with other males. This review is significant in that it addresses and explains the complexity of chromatophore structure and neuromuscular function within cephalopods, which are responsible for their ability to alter their appearance.

Contribution: This review article summarizes important background knowledge on the mechanisms responsible for cephalopod’s ability to employ dynamic coloration. Although the fitness advantages provided by altering their body pattern are not directly addressed, this review provides an excellent summary of the understanding of cephalopod neurobiology. It is evident that with such sophisticated internal mechanisms, cephalopods are able to generate several different coloration behaviours. It also reinforces the idea that cephalopods, despite being invertebrates, possess a highly complex brain that functions in ways not yet well understood.

Evidently, much more research is required to fully comprehend this incredible ability of cephalopods.

Morris, J., Harley, R., & Tsoutas, N. (2014). Mimicking the masters: a new age for camouflage design. In A. Elias (Ed.), *Camouflage cultures: Beyond the art of disappearance,* (pp. 65-76). Sydney University Press.

Summary: This book chapter reviews research that has been conducted on cephalopods (squid, octopus and cuttlefish) in order to better understand the nature of and mechanisms behind their ability to mimic other organisms and blend into their surroundings using camouflage. When cephalopods encounter a predator, they analyze the surroundings and within 7/10ths of a second, they are able to essentially "disappear". Cephalopods have evolved acute vision (despite being color blind) and "dynamic neural control" of their skin. This means that with a combination of structural and pigmentary color, 3D shape, contrast and the ability to alter patterns, cephalopods are able to consciously alter their physical appearance. Delving deeper into the structure of cephalopod skin, there are both muscles and light that interact across three layers of pigment cells and reflectors. The three different cells (from outer to innermost) are the chromatophores or pigment cells, iridophores and leucophores. When a cephalopod wants to change its appearance, they release a protein called reflectin into the skin layer of iridophore cells which alters the reflectance of the jewel-like nanoscale structures found within the iridophores. The passive structures within the leucophore cells reflect ambient light which illuminates the pattern effects created by the layers above. Cephalopods, having been coined as the most intelligent invertebrate, are able to consciously send neural impulses from the brain to the muscles in order to carry out the physical movements necessary to camouflage. It is hypothesized that this behaviour of cephalopods provides many fitness advantages; predator-avoidance, hunting and reproduction.

Contribution: This book chapter summarizes the understanding of the science behind camouflage behaviour of cephalopods. It provided a detailed description of each key element involved and the neurobiological, chemical and physical mechanisms responsible for their color-changing ability. It also identified that despite this behaviour being well understood by researchers, there are still many questions regarding the neuroscience and consciousness of cephalopods that is highly involved in this behaviour. As a secondary source, this book chapter served as a great resource to obtain pertinent primary literature related to cephalopod's ability to change their physical appearance both to mimic organisms and the environment.

Deravi, L.F. (2021). Compositional similarities that link the eyes and the skin of cephalopods: Implications in optical sensing and signaling during camouflage. *Integrative and Comparative Biology, 1*(1). https://doi.org/10.1093/icb/icab143

Summary: This review investigated all components that contribute to cephalopod's ability to color adapt and camouflage. It is mentioned throughout the article that the mechanisms by which all structural elements of cephalopod skin work together cooperatively are not yet well understood, however this review analyzes research from different scientists that are contributing to the evolving pool of knowledge. What is known is that cephalopods are capable of absorbing, scattering and refracting light using their pigmentary chromatophores. Chromatophores are situated above light reflecting and scattering iridocytes, which generate iridescence and below are leucocytes which diffusely scatter white light. With these three components working together, cephalopods can display all wavelengths of visible light. This facilitates communication, protection and recruitment efforts within their environment. It is a combination of biochemical, electrical and mechanical input signals that induce the colored and textured patterns. However, how these signals work in conjunction with one another is poorly understood. Researchers are certain that the nanostructures and proteins found within the three pigment cells along with signaling cascades (i.e. acetylcholine) that originate from the eyes and central nervous system (CNS) render cephalopods capable of altering their body pattern and texture. The reviews states that researchers have discovered that cephalopods possess extraocular photoreceptor organs that contain rhodopsin and retinochrome, which function in helping the cephalopod to perceive and control incoming light. The research stated in this review is significant as it reinforces the complexity of the proteins and skin cell structure themselves, not to mention the sophisticated signals and pathways that link it all together. This reiterates that their ability to employ camouflage and mimicry behaviour is elaborate and the science responsible for the signaling pathways remains unknown.

Contribution: This review article summarizes research on the relationship between the different pigment cells within the skin and cephalopod's ability to coordinate these pigments cells with activity of the central nervous system to display different body patterns. Although this article does not directly discuss the fitness advantage(s) provided by the use of camouflage for cuttlefish specifically, it helps in understanding the neurological, biochemical and physical mechanisms behind the dynamic coloration behaviour. It also identifies that despite cephalopod camouflage behaviour being a highly researched topic, many questions remain regarding the mechanistic details of how cephalopods are able to actually produce the behaviour.

Primary articles outlining research on cuttlefish mimicry behaviour

Norman, M. D., Finn, J., & Tregenza, T. (1999). Female impersonation as an alternative reproductive strategy in giant cuttlefish. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1426), 1347–1349. https://doi.org/10.1098/rspb.1999.0786

Summary: This article investigated *Sepia apama* male-mating strategies, specifically female impersonation by non-dominant, "satellite" males. Alternative male mating strategies have been well documented throughout the animal kingdom and previous work shows that smaller male animals are able to escape detection by larger males by impersonating a female. This provides evidence that impersonating a female is used for both reproduction and predator avoidance. *Sepia apama* is a sexually dimorphic species with males having longer arms than females and females displaying a mottled body pattern consisting of dark blotches on a white background. Thus, female-impersonation behaviour is described as the male taking on a female appearance. The researchers conducted this study by observation of *S. apama* mating and copulation in the shallow waters of southern Australia. They found that male-female pairs were often shadowed by a smaller "satellite" male that impersonated a female (mottled body pattern and short arms). This "satellite" male would go undetected by the larger male and thus would attempt to copulate with the female while the larger mate-guarding male was actively fighting or putting on a display for other large males. In mating with the female, the "satellite" male either presented colorful male displays or remaining disguised as a female. Interestingly, when the larger male returned, two responses were observed, either; he aggressively separated the pair, or he ignored the mating couple. In the absence of rivals, males who previously impersonated females instead displayed typical male body patterns and courted females in the same fashion as larger males. These findings suggest that dynamic female mimicry is a behaviour used by male *S. apama* cuttlefish to both deceive other males and copulate with females. Future studies could explore whether the females respond differently to an attempted mating from a smaller female-impersonating male versus an attempted mating from a larger male.

Contribution: This article provides insight into male *S. apama* 's ability to impersonate females, showcasing an evident fitness advantage provided by dynamic coloration behaviour. The higher reproductive fitness that results from male cuttlefish employing this behaviour reinforces the multi-purpose function of cuttlefish's ability to alter their body color/pattern. This research advances the field of knowledge regarding the breadth of functions of dynamic coloration in cuttlefish. It also formulates a series of follow-up questions regarding whether females preferentially choose to mate with the larger male over the female-impersonating male or if they are indifferent.

Okamoto, K., Yasumuro, H., Mori, A., & Ikeda, Y. (2017). Unique arm-flapping behaviour of the pharaoh cuttlefish, *Sepia pharaonis*: Putative mimicry of a hermit crab. *Journal of Ethology*, *35*(3), 307–311. https://doi.org/10.1007/s10164-017-0519-7

Summary: The article investigated the motivation and function of a specific arm-flapping behaviour of *Sepia pharaonis.* This behaviour was described as *S. pharaonis* raising its front arms, darkening and wrinkling the distal ends while simultaneously bending the back arms as if they were jointed and then flapping the distal ends. Prior studies have observed this same behaviour when *S. pharaonis* was introduced into large, unfamiliar spaces or during hunting. It is known that cuttlefish manoeuvre their arms in highly sophisticated ways and that they do this in order to camouflage themselves while hunting prey, to startle predators or by males during courtship. In this study, researchers submerged a video camera in a large tank containing eight cuttlefish in hopes of capturing the arm-flapping behaviour to investigate its function. They observed that *S. pharaonis* would display this behaviour while actively approaching prey. It was determined that cuttlefish that displayed the arm-flapping behaviour captured a significantly higher number of preys compared to those cuttlefish that did not. The researchers concluded that this behaviour was different than previously described arm-spreading behaviours because the cuttlefish flapped their arms with intentional aggression. The authors were unable to determine definitively the motivation and function behind this behaviour however hypothesized that the likely function was either in luring prey or as mimicry of a gastropod. Unfortunately, very few field studies have been conducted on *S. pharaonis* and thus their behaviour in the wild is not well understood. Future studies of *S. pharaonis* in the wild are needed to confirm the hypothesis for the behaviour described above.

Contribution: This article is important because it contributes to our understanding of cuttlefish mimicry behaviour in the wild. The research in this study provides additional insight into the motivation and function behind this strange, complex and highly specific decapod-mimicry behaviour that many researchers have observed. It is significant that the researchers were unable to draw definitive conclusions from this study because it demonstrates that full comprehension of this cuttlefish behaviour requires a different study approach.

Van Elden, S., & Meeuwig, J.J. (2020). Wild observation of putative dynamic decapod mimicry by a cuttlefish (*Sepia cf. smithi). Marine Biodiversity, 50*(93), 1-6. https://doi.org/10.1007/s12526-020-01117-0

Summary: This article investigated the motivation behind 'crustacean-like aggressive' mimicry behaviour of *Sepia smithi* cuttlefish. Previous studies described this behaviour as the tentacles being bent and raised laterally, as if imitating a hermit crab; this was performed aggressively as if charging towards a predator or prey. Prior research found that cuttlefish are one of few organisms that perform dynamic mimicry by rapidly changing their appearance. This is contrasted with static mimicry, where the animal is in a permanent state of mimicry. Van Elden et al. (2020) investigated motivation behind dynamic mimicry by observing *Sepia smithi* in the wild. To explore their question, Stereo baited remote underwater video systems (BRUVS) was used to observe live footage of *Sepia smithi*. In watching a sample of underwater footage, the cuttlefish approached the bait bag (hidden camera) raising its dorsal pair of arms vertically, the distal ends began to darken and resemble eyestalks, while at the same time, the second and third pairs of arms were bent, appearing jointed and used to "walk". The fourth, ventral pair of arms were used to raise all the arms and head of the cuttlefish off the sand; this was done to have the head higher than the mantle while hiding the tentacles. This body pattern was identical to the 'crustacean-like aggressive mimicry' behaviour as described previously. The researchers were unable to determine a definitive motivation however hypothesized either predator avoidance or aggression towards prey. Although researchers were unable to draw a definitive conclusion regarding motivation, they were able to narrow it down to two plausible hypotheses. These findings suggest that future studies are required, perhaps in a lab setting where controlled experiments could be performed to determine the definitive motivation behind this behaviour.

Contribution: This article provides insight into dynamic mimicry behaviour of cuttlefish. It has been selected for my review as it adds to the effort to understand motivation behind cuttlefish's use of mimicry. Although researchers were unable to determine why the 'crustacean-like aggressive' behaviour was observed, they had two strong hypotheses. Their hypotheses could be tested in future experiments to answer follow-up questions regarding the definitive motivation behind this mimicry behaviour and other interesting cuttlefish behaviours. It is significant that researchers were unable to draw conclusions because it demonstrates that alternate study techniques are required.

Primary articles outlining research on cuttlefish camouflage and dynamic coloration behaviour

Boal, J. G. (1997). Female choice of males in cuttlefish (Mollusca: Cephalopoda). *Behaviour*, *134*(13/14), 975–988. https://doi.org/10.1163/156853997x00340

Summary: This article explored the influencing factors and role of female choice within cuttlefish (*Sepia officinalis*) reproductive behaviour. Previous research shows that larger, dominant males obtain more copulations than smaller, subordinate males. Researchers hypothesize that this is because dominant males are larger and produce more conspicuous visual displays. Boal (1997) was interested in determining if females receive an 'honest signal' of a male's fitness based on their ability to produce colorful displays. In the laboratory, researchers reared twenty *S. officinalis* females and ten males. One female and two males were placed in a tank, separated by a partition which was overlain by an opaque sheet. The opaque sheet was raised so that the female could view both of the males. The movement of the female was observed over several hours and whichever male's 'side of the tank' she frequented most was concluded as her "choice" of male. The activity of each male was then analyzed, and the researchers concluded that females did not base their choice on characteristics known to be associated with dominance, such as body size or displays. Instead, they chose males that were more likely to mate. Through chemical signals released by the males, females could determine which males had previously mated and how recently, and they preferentially migrated towards males that had more recently mated. The researchers believed that a pheromonal signal was released by the males as an indication of their mating history. This study was significant as it uncovered that a male's ability to produce dramatic displays is not always an accurate indication of their fitness. Future studies in *S. officinalis'* natural environment are required to determine the strength of the relationship between male social dominance and reproductive success as well as the mechanisms that allow males to communicate their mating history to nearby females.

Contribution: This article provides insight into factors influencing a female *S. officinalis'* mate selection. The research in this study offers an evolutionary perspective on *S. officinalis* fitness by identifying female choice as a strong selective pressure on male traits, thus determining traits will be passed down. These findings provide an interesting addition to my research as they disprove the theory that male color display is an important factor influencing female choice. A male's copulation frequency is the most 'honest signal' of his fitness, however questions remain as to whether male's color displays influence female choice in their natural environment.

Zylinski, S., Osorio, D., & Shohet, A. J. (2009). Cuttlefish camouflage: Context-dependent body pattern use during motion. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1675), 3963–3969. https://doi.org/10.1098/rspb.2009.1083

Summary: This article explored cuttlefishes' (*Sepia officinalis*) body pattern during movement versus when static. *S. officinalis* body pattern throughout movement, was compared to predictions made by the model of motion camouflage. Previous studies on motion camouflage predict that when animals are presented with a fine-scale checkerboard background, they display a pattern called "mottle"; characterized by random, alternating patches of light and dark skin, allowing them to blend into the background. When presented with a coarse-scale checkerboard, animals display a "disruptive" pattern which breaks up the body outline. The researchers wanted to investigate whether the body patterns of *S. officinalis* changed during movement and upon exposure to different backgrounds. The researchers designed an experiment comprised of the two different background types described above; known to promote either the "mottle" or the "disruptive" body pattern. These backgrounds were artificial simulations of what would be found in *S. officinalis'* natural environment. Printouts of each checkerboard pattern were placed on the floor and walls of tanks which housed *S. officinalis*. *S. officinalis* was exposed to each background for ten minutes, then a photograph of their body pattern was taken and each body pattern was assigned a number. The numbers were entered into a principal component analysis and resulting coefficients were used to test for differences amongst them. The researchers observed that if *S. officinalis* displayed a high-contrast disruptive pattern while static, it would reduce the disruptive characteristics of the pattern while moving. If *S. officinalis* displayed the "mottle" pattern, this was retained while moving. These findings suggest that cuttlefish are extremely aware of their coloration relative to that of their surroundings and will adjust their coloration accordingly to reduce susceptibility to predators. Future studies are required to address the mechanisms of adaptive coloration over a natural stimulus or in the presence of a threat.

Contribution: This article outlines research which advances knowledge of *S. officinalis'* awareness of their coloration and the coloration of the surroundings and ability to make adjustments as needed. Observing the specific body patterns in response to artificial substrates aids in understanding how *S. officinalis* is able to survive in its environment. This is one of few studies that explored the specific body patterns during cuttlefish movement, which formulates a series of follow-up questions regarding if these same body patterns during movement would be observed in the wild and in the presence of a predator.

Buresch, K. C., Mäthger, L. M., Allen, J. J., Bennice, C., Smith, N., Schram, J., Chiao, C.C., Chubb, C., & Hanlon, R. T. (2011). The use of background matching vs. masquerade for camouflage in cuttlefish *Sepia officinalis*. *Vision Research*, *51*(23), 2362–2368. https://doi.org/10.1016/j.visres.2011.09.009

Summary: This study explored the ability of cuttlefish (*Sepia officinalis*) to survive and thrive in their environment through both background matching and resembling an object (masquerade). Previous research shows that *S. officinalis* utilized either of the above-mentioned camouflage behaviours to avoid predation. The researchers in this study selected the natural substrates used in their experiment on the basis that each elicited a different known body pattern. A substrate made of fine sand evoked ‘Uniform’ – very small to small splotches, a second substrate made of gravel and small pebbles evoked ‘Mottle’ -medium sized splotches and a single rock with large white and black areas evoked ‘Disruptive’ – large splotches, bars, stripes. Researchers tested to confirm whether the substrates elicited the expected body patterns and investigated whether *S. officinalis* preferentially selected to camouflage to a substrate or to resemble a 3D object. Three experiments were performed with *S. officinalis* in a tank that was housed within an enclosed tent: The first consisted of natural substrates with natural 3D objects, the second was artificial substrates (artificial checkerboard) with artificial 3D objects (cylinders with grey printouts glued on) and third was artificial substrates with 2D rock-sized patches. *S. officinalis* preferentially chose to resemble a 3D object (masquerade) over displaying a body pattern that would result in camouflage, however this was dependent on the contrast between the object and the substrate it was present on. The presence of contrast is an important cue for the *S. officinalis* to preferentially employ masquerade behaviour and resemble 3D objects. The researchers hypothesized that this masquerade behaviour allows *S. officinalis* to escape recognition by the predator once they have already been detected. Future studies would be required to address the frequency of camouflage versus masquerade behaviour in the presence of predators.

Contribution: This article contributes to understanding *S. officinalis’* ability to select one coloration behaviour over another to maximize its fitness. Altering their body pattern dependent on the substrate reinforces the idea that throughout evolution, *S. officinalis* that were able to alter their body pattern to match the substrate or background, were able to better survive and therefore reproduce. It is significant that researchers were able to elicit these behaviours in *S. officinalis* in a laboratory setting in the absence of predators, as this leaves a gap in knowledge regarding whether similar behaviours would be observed when cuttlefish are under predation pressure.

Hanlon, R.T., & McManus, G. (2020). Flamboyant cuttlefish behaviour: Camouflage tactics and complex colorful reproductive behaviour assessed during field studies at Lembeh Strait, Indonesia. *Journal of Experimental Marine Biology and Ecology, 529*(1), 1-9. https://doi.org/10.1016/j.jembe.2020.151397

Summary: This article attempted to answer the question: how does a small, solitary cuttlefish survive, hunt and reproduce? Previous research found that both sexes of cuttlefish utilize a form of dynamic coloration or camouflage behaviour for each of the following activities: hunting, courtship and predator avoidance. In courtship for example, it has been determined that females remain camouflaged, whereas males attempt to mate with females by displaying a conspicuous, "Flamboyant Display"; described as bright, neon coloration and waving of the arms up and down. To explore their question, the researchers studied cuttlefish at Lembeh Strait, Indonesia using focal animal sampling, photography and videography. In watching the underwater footage, both male and female cuttlefish appeared to employ camouflage behaviour as their primary defense and avoidance of predator behaviour. This camouflage behaviour was divided into two categories; background matching and masquerade, the former delayed detection and the latter delayed recognition. Background matching involved altering the body pattern to blend into the background whereas masquerade entailed resembling an object, both of which were employed to avoid predation. The secondary predator defense behaviour observed was referred to as a "Deimatic predator response" where the cuttlefish switched from camouflage to Flamboyant in 700 milliseconds when a predator was approaching. They determined that the "Flamboyant Display" is observed in both males and females, however females use it as an additional predator defense as well as hunting behaviour whereas males use it for courtship. This study was significant as it reinforced that the color-changing ability of cuttlefish is responsible for their ability to survive and thrive in their environment. It is used in hunting, predator avoidance and courtship. Future studies are required to determine how the difference in internal signaling between males and females leads to each sex utilizing different camouflage behaviours for different purposes.

Contribution: This article provided new insight into the breadth of cuttlefish's use of dynamic coloration. The research within this article advances knowledge of what was previously thought to be the only function of cuttlefish camouflage behaviour; predator-avoidance. With these researchers determining that between background matching, masquerade and Flamboyant display, cuttlefish are effectively permanently camouflaged, it is evident that camouflage behaviour is employed persistently throughout the life of a cuttlefish. This work provides a series of follow up questions regarding whether this behaviour could be produced to the same extent in the controlled setting of a laboratory as in the wild.