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Towards an Integrated Study of Camouflage and Cognition in Cephalopods

Willa M. Lane and Nicola S. Clayton

Department of Psychology, University of Cambridge, Cambridge, UK

Abstract

The coleoid cephalopods (i.e., octopus, squid, and cuttlefish) are notable for their complex cognition and dynamic camouflage, but the two processes have rarely been considered in conjunction. Here, we argue that camouflage and cognition likely coevolved and should therefore be studied as linked processes, which we term the “camocognitive hypothesis”. We suggest that camouflage serves as a “self-report” measure of a cephalopod’s subjective inner world, and is therefore a critical innate tool for studying complex cognition in cephalopods. We draw a comparison between camouflage in cephalopods and food caching in corvids, suggesting that camouflaging cephalopods may “cache” themselves in the environment; in doing so, they may draw upon complex cognitive processes similar to those used by caching corvids. With a focus on cuttlefish of genus *Sepia*, we briefly review knowledge arising from the interaction of camouflage and cognition, including visual perception, amodal completion, visual perspective taking, and flexible control of camouflage. Moving beyond the widespread view that camouflage is a reflexive behaviour based solely on visual input, we suggest that it may be subject to cognitive control in certain contexts, much like mammalian breathing is largely automatic but subject to volitional control. Finally, we discuss barriers to using camouflage as a method to study cognition and provide two hypothetical paradigms using camouflage to study object permanence and predator deception.

Keywords: cephalopods, comparative cognition, dynamic camouflage, caching, camocognitive hypothesis

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Willa M. Lane https://orcid.org/0000-0002-1784-3501
Nicola S. Clayton https://orcid.org/0000-0003-1835-423X

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✉ Willa M. Lane and Nicola S. Clayton, Department of Psychology, University of Cambridge, UK. E-mails: *wl442@cam.ac.uk, nsc22@cam.ac.uk*

Towards an Integrated Study of Camouflage and Cognition in Cephalopods

The coleoid cephalopods (i.e., octopus, squid, and cuttlefish; hereafter cephalopods) are increasingly used as model organisms in the study of comparative cognition. This is because vertebrates and cephalopods possess similarly complex cognition (Schnell, Amodio, et al., 2021; Schnell et al., 2022), despite their evolutionary divergence 530 million years ago (Kröger et al., 2011). While certain aspects of cephalopod cognition remain untested or have only been studied superficially, similarities between vertebrates and cephalopods are particularly notable because of the different selection pressures for intelligence experienced by each group (Amodio et al., 2019a; Schnell et al., 2023). Moreover, cephalopods have remarkably complex and highly distributed nervous systems with up to 500 million neurons (Hochner, 2004) – on par with corvids and small mammals – and a higher brain-to-body size ratio than many fish and reptiles, a measure widely hypothesised to be an estimate of intelligence (Nixon & Young, 2003; Packard, 1972).

In common with primates and birds, cephalopods are considered cognitive generalists because they possess diverse, flexible, and domain-general intelligences (Vitti, 2013). As reviewed by various authors (e.g., Hanlon & Messenger, 2018; Mather & Dickel, 2017; Schnell, Amodio, et al., 2021; Schnell et al., 2023), cephalopods are widely accepted as demonstrating several cognitive skills considered pre-requisites for more complex cognition. They are capable of learning (including associative learning, discrimination and reversal learning, and spatial learning), mental time travel (including short- and long-term memory, as well as episodic-like memory in certain species), self-control, concept formation, quantity discrimination, and problem solving. Claims that cephalopods demonstrate social learning, tool use, play, causal reasoning, future planning, and theory of mind (including visual perspective taking) are heavily debated; all current evidence of these skills can be explained through simpler mechanisms, such as associative learning or behavioural reading accounts. While such assertions have given rise to suggestions of consciousness, sentience, or a cephalopod "mind" (e.g., Mather, 2008, 2019), researchers have been cautioned against making definitive claims about high-level cognitive capabilities when alternative explanations are possible (Amodio, 2019; Schnell & Vallortigara, 2019). This approach follows an 1894 principle still used in animal cognition today: the simplest explanation that accounts for an animal's success is all that can be accepted without further testing (Morgan, 1894).

In addition to complex cognition, cephalopods are perhaps most widely noted for their so-called rapid neural polyphenism, which is the unique ability to rapidly change appearance including skin colour, pattern, and texture (Hanlon & Messenger, 2018). Changes in skin colour and pattern are achieved through pigment-filled muscular sacs called chromatophores, which densely cover the skin (with up to 230 per square millimetre) and expand or contract to create tiny "pixels" (Hanlon & Messenger, 2018; Shook et al., 2024). Reflecting cells (iridophores and leucophores) create additional structural colours, while dermal muscles (papillae) modify the physical texture of the skin. The chromatophores are directly innervated by the nervous system, allowing body patterning to shift in as little as 100 milliseconds (Montague, 2023). This direct innervation allows changes orders of magnitude faster than known in all other actively camouflaging taxa, such as reptiles and fish (Stevens & Merilaita, 2008). Chromatophores can be individually controlled but are often activated in groups to create pattern components such as stripes and spots (Shook et al., 2024; Woo et al., 2023). When considered in entirety, changes in appearance in cephalopods combine chromatic (i.e., skin colour and pattern), textural, postural, and locomotor elements, with several dozen known elements combined flexibly (Hanlon & Messenger, 2018). These changes in appearance can also be broadly categorised according to their apparent goal, although many cannot be sorted neatly. As reviewed by Hanlon and Messenger (2018), crypsis makes detection difficult, and includes background matching patterns, disruptive patterns (which break up the animal's outline), and distractive markings (which distract from traits that would "give away" the animal, such as its outline). Mimicry is resemblance to another animal, while masquerade is resemblance to anything that is not an animal, including rocks and seaweed. Finally, a cephalopod's appearance may be changed for the purpose of communication, also called signalling. However, these are not discrete categories, and there is often overlap: for example, the female mimicry described later in this paper is both mimicry and communicative signalling.

The way we describe the term "camouflage" in this publication only partially overlaps with the meaning most widely used in cephalopod research. Most authors (e.g., Hanlon & Messenger, 2018; Shook et al., 2024) draw a distinction between camouflage — a primary defence with the function of concealment — and changes in appearance instead used for communication, or as a secondary defence. The label rapid neural polyphenism (Hanlon & Messenger, 2018) was likely coined to create an umbrella term which refers to both functions. We agree that an umbrella term is needed, especially because both functions rely on the same effectors. However, we dislike rapid neural polyphenism because it is a highly technical term that requires considerable explaining to non-specialists, and because it implicitly suggests that these behaviours are based *solely* on visual inputs (i.e., neurally controlled, with no room for the possibility of cognitive control). The term also has yet to be widely adopted by other authors, with many recent publications instead referring to both functions together as "dynamic skin behaviour" or "skin patterning" (e.g., Jaitly et al., 2022; Shook et al., 2024). But unless specifically talking *only* about the skin, this is not quite right either, because both functions encompass postural and locomotor elements in addition to chromatic and textural elements (Hanlon & Messenger, 2018). Although not a long-term solution, for the purposes of this publication, our answer is to refer to both functions as "camouflage", especially based on the term's colloquial familiarity, with the inclusion of this caveat and a request for the reader's understanding and leniency.

Historically, camouflage in cephalopods has been considered a passive, neurally controlled process: an automatic response to visual stimuli. This view has merit, as a significant amount of space and energy is dedicated to visual processing in the cephalopod nervous system. In cuttlefish, the optic lobes comprise up to 75% of the total brain volume. The visual environment is somehow represented and transformed in the brain to create camouflage; information from the optic lobes passes to the motor control system, including the median and lateral basal lobes (implicated in this representation/transformation) and the dedicated chromatophore lobes (Montague et al., 2023). Precisely *what* visual information is encoded by the cephalopod brain, and how, is an area of active research, with proposed models including approximation of broad visual texture statistics, encoding of finer-scale specific visual features, a combination of these models, or a yet unknown process (Montague, 2023; Osorio et al., 2022; Pungor & Niell, 2023; Woo et al., 2023). Complicating matters is a debate about how many camouflage patterns exist and the best scale at which to define them. Some researchers adhere to the three historically used “templates” of uniform, mottle, and disruptive camouflage patterns (e.g., Hanlon & Messenger, 1988, 2018). Using an estimate from recent machine learning analyses attempting to capture the dimensionality of camouflage causes the number of potential patterns rises to more than sixty, including permutations not distinguishable to the human eye (Woo et al., 2023). Assuming that each camouflage component, such as stripes and spots, is under independent control (Osorio et al., 2022), more than a billion patterns are possible. This question will likely remain unresolved until we have a better understanding of the neural basis of camouflage. Here, we introduce another wrinkle: what if camouflage can also be controlled cognitively?

A small amount of evidence suggests that cephalopod camouflage is not solely dependent on external visual stimuli, and is perhaps subject to some higher-level, “top-down” control. Cohen-Bodénès and Neri (2024) have demonstrated that cuttlefish can alter their camouflage in the absence of external stimulation based on internal states, such as satiety, and Hough et al. (2016) have shown that cuttlefish can learn to change their body patterning for a reward. Camouflage allows cephalopods to “wear” their thoughts on their skin, directly “self-reporting” their perceptions, experiences, and even beliefs about the surrounding world. Camouflage can therefore be considered an explicit representation of a cephalopod’s perceptual state (Montague et al., 2023; Reiter et al., 2018), internal state (Cohen-Bodénès & Neri, 2024; Shook et al., 2024), and subjective inner world (Montague et al., 2023; Schnell et al., 2023): in essence, a “self-report” measure rarely encountered in animal cognition. This remains true even if camouflage is a passive, non-cognitive process, which we know may not be the case (Hough et al., 2016). Accordingly, we argue that camouflage is a critical tool for studying complex cognition in cephalopods. In support of this point, we examine three areas: first, we discuss the shared evolutionary history and likely coevolution of dynamic camouflage and complex cognition in cephalopods; second, we draw an analogy between cephalopod camouflage and corvid caching to highlight the rich cognitive processes that may underpin both behaviours; and third, we provide examples of how cognition has already been used as a method for studying cephalopod cognition. Finally, we turn to future directions, including challenges in using camouflage to study cognition as well as two hypothetical experimental paradigms that leverage camouflage to study poorly understood aspects of cephalopod cognition.

Cognition, Camouflage, and Evolution

The evolutionary pressures selecting for complex cognition in vertebrates and cephalopods, though overlapping, are distinct. As reviewed by Amodio et al. (2019a), the evolution of cognition in vertebrates is attributed to three main theories, either independently or in combination. The first is the Ecological Intelligence Hypothesis, according to which intelligence has evolved to enable foraging and, more generally, to support navigation in complex environments (e.g., Gibson, 1986; Milton, 1981). The second is the Social Intelligence Hypothesis, which states that intelligence has evolved as a result of competition and cooperation with conspecifics (e.g., Dunbar, 1998). A third theory posits that intelligence arises due to a coevolutionary relationship between these socioecological pressures and slow life histories (Amodio et al., 2019a; Barton & Capellini, 2011; Rosati, 2017; Street et al., 2017).

In cephalopods, as in most groups, the Ecological Intelligence Hypothesis remains relevant: all life needs nourishment. However, although some squid species are gregarious, most cephalopods lead solitary lives except during reproduction, and most have fast life histories, living only a few years (Hanlon & Messenger, 2018).[1] Through this lens, the Social Intelligence Hypothesis is therefore not generally applicable. However, some social interactions such as "challenging" mating scenarios, including terminal reproduction and a risk of cannibalism in certain species (Ibáñez & Keyl, 2010), may have served as additional drivers for the evolution of complex cognition (Amodio et al., 2020). But the most important evolutionary driver of complex cognition in cephalopods is likely predation, closely followed by competition with teleost fish (Amodio et al., 2019a, 2020; Aronson, 1991; Grasso & Basil, 2009; Jaitly et al., 2022; Packard, 1972). The modern coleoid cephalopods evolved from shelled ancestors, with the shell internalised or lost during evolution. At some point either before (Mollo et al., 2019) or following (Amodio et al., 2019a, 2019b) the loss of this physical defence, cephalopods evolved complex cognition. This new intelligence was likely supported by co-evolving sensory capacities; the "sudden wealth" of visual information due to cephalopods' evolution of camera-type eyes (Vitti, 2013) would have necessitated development of new cognitive pathways.

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[1] Although also note reports of densely aggregated octopus throughout the year in some locations (e.g., Scheel et al., 2017) and shoaling cuttlefish outside of mating season (Drerup & Cooke, 2021).

Emphasising that sensation and cognition are tightly coupled processes, some authors have further proposed that cognition in cephalopods may be considered embodied, based on principles of embodied organisation from robotics (Cheng, 2018; Chiao et al., 2015; Hochner, 2012). In this view, adaptive behaviour (including arm movement and camouflage) emerges from dynamic interactions between the sensorimotor systems and surrounding environment, leading to the evolutionary endpoint of coevolving sensation and cognition. Consequently, certain aspects of cognition occur outside of the central brain. In octopus, where 350 million of the total 500 million nervous system cells are located in the peripheral nervous system (Hochner, 2004), goal-directed arm extension is not reliant on the central brain (Sumbre et al., 2001), and the arms may communicate directly via a nerve ring, without sending signals through the central brain (Chang & Hale, 2023). In cuttlefish, beyond the highly developed optic lobes and directly innervated chromatophores, there is some evidence of dermal extraocular photoreception (Kingston et al., 2015), which Cheng (2018) cites in support of a theoretical “photomuscular loop in the skin” used to refine camouflage (although acknowledging that such a view is far-fetched based on current evidence). Even with our present knowledge, it is not unreasonable to consider camouflage a fundamentally embodied aspect of cognition, because it *is* an embodied representation of perception and “thought”: the most highly elaborated sensory transform in existence.

Considering camouflage as an embodied aspect of cognition, we further theorise that camouflage and cognition coevolved in response to the same evolutionary pressures, becoming intrinsically intertwined in a positive feedback loop that allowed for increasing complexity of each process. We term this the “camocognitive hypothesis”. Just as the pressures described previously are hypothesised to have contributed to the evolution of cephalopod cognition, they too may have contributed to the evolution of camouflage. Foraging and predation pressures drove a need to remain hidden from prey and predators. Reproductive pressure drove a need to navigate complex mating scenarios (including the ability to adopt opposite-sex mimicry to “cheat” during mating, discussed later). Finally, there was a need to process and use newly available visual information to increase success in other domains, which is most visibly demonstrated in background-matching camouflage. In their discussion of camouflage and cognition as evolutionary endpoints for predator avoidance in cephalopods, Jaitly et al. (2022) touch upon the idea of camocognitive coevolution with the observation that sophisticated camouflage may have become possible as brains became larger and more complex. Similarly, as part of a broader discussion about how predator and prey cognition have likely influenced the evolution of animal camouflage, Skelhorn and Rowe (2016) suggest that the ability to dynamically alter camouflage may be linked to cognitive abilities in cephalopods. While other taxa are able to increase the efficacy of concealment behaviourally (Skelhorn & Rowe, 2016), no other animal can change camouflage as rapidly as cephalopods do. We argue that it is this dynamism that indicates that beyond simple mechanisms of perception, there may be rich cognitive processes underpinning cephalopod camouflage, potentially including cognitive control.

Camouflage as Caching

We find it useful to metaphorically compare two flexible, dynamic hiding behaviours – cephalopod camouflage and corvid caching – as a starting point for further discussion about the theory that rich cognitive processes may be correlated with, or even underpin, dynamic camouflage. Caching is the act of hiding food items for future consumption, while pilfering occurs when competitors steal stored food. Widespread among vertebrates, in some groups caching is regarded as a compulsive and stereotyped behaviour (Vander Wall, 1980). However, caching strategy complexity increases with brain size in mammals (Mahoney & Pasch, 2024), and caching specialisation is positively correlated with both hippocampal size and overall brain size in birds (Garamszegi & Eens, 2004; Lucas et al., 2004). In corvids, caching is considered complex cognition because of the flexibility with which it is performed (Grodzinski & Clayton, 2010), e.g., first, the fact that their ability to remember the 'what, where and when' of past events can be updated after the time of caching should additional information be presented about the perishability rates of certain food items (Clayton, Bussey, & Dickinson, 2003); second, that they can use past experiences to plan for future caching events (Raby et al., 2007); and third, that their cache protection tactics can also be adjusted flexibly depending on experience (Emery & Clayton, 2001) and which individuals are watching when (Dally et al., 2006). Cognitive skills, including mental time travel, self-control, and mental attribution, are linked to both caching and overall intelligence in corvids (Grodzinski & Clayton, 2010; Schnell et al., 2022).

We suggest that camouflage in cephalopods can be figuratively considered a strategy for individual animals to "cache" themselves in their environment, so that they are protected from predators (avoiding being "pilfered"), hidden from prey, or able to "pilfer" resources from conspecifics (as may be the case when male cuttlefish adopt female mimicry to approach females in the presence of rival males, as discussed later). Before elaborating further, it is important to note that caching in corvids relies on episodic-like memory for spatiotemporal maps of food locations, and it is unlikely that cephalopod camouflage involves an analogous spatiotemporal component.[2] Therefore, rather than considering camouflage and caching as direct behavioural parallels, we draw the analogy to highlight both the inherent flexibility

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[2] While the use of spatiotemporal maps to determine camouflage is *unlikely* (especially given the modelled finding by Woo et al. (2023) that camouflage may rely on continual updates via visual feedback instead of memory), it is not *impossible*. Cephalopods possess advanced spatial learning (as reviewed by Schnell, Amodio, et al., 2021, and Jozet-Alves et al., 2023), along with anticipatory memory for upcoming environmental features, which, theoretically, could factor into decisions about what camouflage to adopt if camouflage is controlled cognitively. A method for studying this could combine spatial memory, camouflage, and expectancy violation.

of each behaviour and the potential cognitive underpinnings of camouflage. Some of the same cognitive skills supporting caching behaviour in corvids are also present in cephalopods and may similarly support successful camouflage. At present, there is limited evidence that camouflage can be cognitively controlled, let alone that it is correlated with other cognitive abilities or a putative "overall intelligence". However, the only way to empirically determine whether such correlations exist is to integrate research on camouflage and cognition, which is what we argue for throughout this paper. With this in mind, we discuss evidence for specific cognitive skills known to underpin caching in corvids, which are also documented in cuttlefish, as well as how these skills may support dynamic camouflage.

Mental time travel is the ability to remember the past or imagine the future, and can enable remarkable behavioural flexibility (Clayton, Yu, & Dickinson, 2003). Episodic-like memory (Clayton & Dickinson, 1998) and future planning, the main components of mental time travel, are instrumental for successful food caching because these skills allow animals to recall what they cached, where they cached it, and when, as well as how this information can fulfil anticipated needs (Clayton, Yu, & Dickinson, 2003). Mental time travel, especially future planning based on prior experience, could play an instrumental role in allowing cephalopods to make decisions about what camouflage is best to adopt in various contexts. In corvids, episodic-like memory is known from studies looking at perishable and non-perishable food caching, where birds will alter their recovery behaviour based on previous knowledge about the degradation rates of perishable food (e.g., Clayton & Dickinson, 1998). Future planning requires that prospective decisions must be independent of current need, following the Bischof–Köhler hypothesis (Clayton, Yu, & Dickinson, 2003; Suddendorf & Corballis, 1997). On the other hand, future planning in corvids from research showing that scrub jays and Eurasian jays adjust caching based on anticipated future needs (e.g., Cheke & Clayton, 2011) and can plan for tomorrow's breakfast (Raby et al., 2007). Cuttlefish similarly demonstrate some elements of mental time travel in the context of predation, including episodic-like memory (Jozet-Alves et al., 2013) and retrieval of associated sensory features, such as whether they saw or smelled prey (Billard, Clayton, & Jozet-Alves, 2020). At present, however, there is no concrete evidence of future planning in cuttlefish. They are known to adjust foraging behaviour in anticipation of future preferred prey availability (Billard, Schnell et al., 2020), but this may not be independent of current needs. Cuttlefish will also prioritize a current need to hide over a future need for food (Poncet et al., 2025). An example of potential future planning in cephalopods unrelated to food comes from the observation that veined octopuses transport coconut shells, potentially as tools to reduce predation (Finn et al., 2009), but without further study, we cannot rule out alternative explanations such as associative learning.

Self-control does not necessarily involve mental time travel (as present actions do not necessitate past or future considerations), but it is a valuable cognitive skill implicated in executive functioning in humans (Diamond, 2013) and linked to general intelligence in both humans and animals, including cuttlefish and corvids (reviewed by Schnell et al., 2022). Critically important for decision making and future planning, self-control allows caching corvids to supress immediate gratification in favour of planning for future meals, as well as to act to reduce the chance of pilfering by waiting to cache until conspecifics are out of sight and earshot (Dally et al., 2010; Shaw & Clayton, 2013; Stulp et al., 2009). The maximum amount of time Eurasian jays delay gratification is also significantly correlated with performance on a five-task battery assessing physical cognition, including spatial memory, object permanence, generalisation learning, discrimination learning, and reversal learning (Schnell et al., 2022). Conversely, in cuttlefish, mean abandon time in a delayed gratification task is significantly correlated with the number of trials required to reach learning criterion in two phases of a reversal-learning task (Schnell, Boeckle et al., 2021). If cephalopods are capable of cognitive camouflage control, self-control may be critically important in deciding which camouflage to adopt when, as it affords temporal latitude for decision-making across contexts. For example, as we propose in a hypothetical experimental paradigm later in this paper, self-control might allow a hungry cuttlefish to maintain masquerade or mimicry when hunting (rather than adopting stereotypical hunting camouflage) if faced simultaneously with a threat from a predator and a predation opportunity. Moreover, because self-control is tentatively linked to general intelligence in cuttlefish, “smarter” individuals may be better at factoring self-control into decision-making about camouflage.

A key difference between corvids and cephalopods is the complexity of their social interactions and ability to perform mental attribution, which is the understanding that perceptual or attentional mental states of others are distinct from those of the self. There is strong evidence that corvids demonstrate Theory of Mind, including desire-state attribution, as shown through specific satiety partner-feeding experiments (e.g., Ostojić et al., 2013). Other evidence, reviewed by Dally et al. (2010), suggests that corvids are also capable of visual perspective-taking and factor this information into cache protection strategies. Evidence is more limited for mental attribution in cephalopods (Schnell et al., 2023), but some aspects, such as visual perspective-taking, could aid camouflage by allowing cephalopods to understand who can see what and how to adjust their camouflage accordingly. Evidence used to support mental attribution in cephalopods includes observations of different predators provoking different camouflage responses in squid (Mather & Dickel, 2017), and examples of octopus and fish hunting collaboratively (Schnell et al., 2023). However, no firm conclusion can be drawn from these observations because they may be explained by alternative cognitive processes. While the same is true for putative evidence of visual perspective-taking based on cuttlefish camouflage during mating (to be reviewed shortly), we believe that conspecific mating interactions provide the strongest case for potential mental attribution in cephalopods and offer a good starting point for future research into this topic.

Using Camouflage to Study Cognition

Almost all research into cephalopod camouflage is predicated on the assumption that the process is purely reflexively controlled (e.g., Hanlon & Messenger, 2018). Taking this reflexive view, many studies have provided valuable insight into cephalopod visual perception based on camouflage expression and are important examples of how we can leverage camouflage as a method to study cognition. However, other innovative work provides potential evidence for how cognition may influence camouflage in addition to reflexive control (Figure 1). For example, studies of intraspecific signalling and communication demonstrate that in multiple cuttlefish species, non-dominant males "cheat" during mating via camouflage, which may be indicative of visual perspective-taking. Moreover, in laboratory settings, common European cuttlefish (*Sepia officinalis*) are capable of learning to control camouflage (Hough et al., 2016). While it is difficult to rule out explanations simpler than cognitive camouflage control in each case, the absence of definitive evidence is not evidence of absence.

Perhaps camouflage is akin to mammalian breathing: predominantly an automatic, neurally controlled process that does not require conscious thought or action, but still a process that is subject to volitional, cognitive control in certain contexts. An analogous example in humans is the conscious control of breathing during meditation. We urge that future research profits from the opportunity to use camouflage to learn about cognition, especially given tentative evidence of cognitive camouflage control and a coevolutionary relationship between camouflage and cognition.

Visual Perception

Most work examining the intersection of cognition and camouflage has been concerned with visual perception in cuttlefish. As described previously, several theories exist about the mechanistic underpinnings of camouflage at the neural level, with no resolution reached yet. However, these theories are heavily informed by work about how cuttlefish camouflage draws on "image parameters" related to the visual environment, as reviewed by Josef and Shashar (2014) and Hanlon and Messenger (2018). The "image parameters" influencing body patterning include contrast, brightness, granularity, depth, and coarseness (spatial frequency), as well as pattern size and scale (relative size in comparison to own body size). Also important are edges, edge completion, and localised visual edges. Small light pattern elements influence camouflage based on their size, area, number, contrast, and intensity. As camouflage is not limited to body patterning alone, the orientation of vertical background stimuli aids in determining dynamic arm posture. Other visual cues are relevant for skin texture, although *which* visual cues influence skin texture is unresolved (see Allen et al., 2009). We note that the majority of work aiming to understand visual perception via camouflage has used artificial backgrounds for testing, such as the ubiquitous checkerboard; we encourage the replication and extension of this work using ecologically-relevant natural or naturalistic backgrounds and arenas to confirm that these findings extend beyond the laboratory. Additional research using both camouflage (Kelman et al., 2008; Zylinski et al., 2016) and other methods (Feord et al., 2020; Josef et al., 2014) has demonstrated that cuttlefish have depth perception. We also know that cuttlefish see linearly (but not circularly) polarised light and can adopt polarised camouflage for intraspecific recognition and communication (Marshall et al., 2019; Shashar, 2014). This is partly known due to experiments leveraging camouflage, in which cuttlefish shown a looming stimulus only visible with polarization vision adopt antipredatory deimatic body patterning, indicating that the stimulus was visible (Temple et al., 2012). Somewhat surprisingly, cuttlefish are colourblind: they have only one visual pigment and fail to differentiate colours of the same greyscale contrast intensity in camouflage experiments (e.g., Mäthger et al., 2006). Despite this, modelling suggests that colourful background-matching camouflage is successful enough to fool predators with both di- and trichromatic colour vision (Chiao et al., 2011). While unresolved, several hypotheses for colour-match camouflage have been proposed, including iridophore reflection of ambient light (Hanlon, 2007), extraocular photoreception (Pungor & Niell, 2023), compensation through polarisation vision (Temple et al., 2012), RNA editing in the opsin gene (Montague, 2023), and spectral discrimination via diffraction as a result of chromatic aberration and pupil shape (Stubbs & Stubbs, 2016). Given this lack of theoretical resolution, and the knowledge that colourful camouflage may serve as an antipredation strategy, it is unfortunate that most cutting-edge methods of computational camouflage analysis transform RGB images to greyscale ahead of data processing (e.g., Cohen-Bodénès & Neri, 2024; Woo et al., 2023). This may result in these analyses missing subtle but significant aspects of camouflage. We therefore recommend that moving forward, camouflage analyses include a comparison of RGB colour and greyscale results and preferentially report the colour results if there are significant differences.[3]

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[3] A similar argument can be made about the importance of testing for, and analysing, polarised camouflage. However, because most cephalopod predators do not see polarised light, the use of polarised camouflage appears to be primarily limited to intraspecific communication (and therefore only important to consider in this context). Additionally, the equipment necessary to capture polarised camouflage in living animals, such as polarimeters, is expensive and specialised (for a comprehensive review of major experimental work, see Mäthger et al., 2009). A change from analysing only greyscale images to analysing and comparing greyscale and RGB colour images is simple and easy to implement within existing methodologies.

Amodal Completion

A special subcategory of visual perception and cognition deals with the ability to “fill in” missing visual information: amodal completion (also called contour completion or visual interpolation), which is the recognition of partial objects as components of a unified whole. As described in Gestalt psychology, it is a higher-level cognitive process than simple perception of visual input because it relies on organising principles such as closure and contiguity (Gregory, 1997; Gunnars & Bruck, 2022). Amodal completion in cephalopods is known from two studies on common European cuttlefish (*S. officinalis*), the first using discrimination training (Lin & Chiao, 2017) and the second using camouflage (Zylinski et al., 2012). In Lin and Chiao (2017), amodal completion is suggested based on the results of a transfer test following discrimination training using pictures of fish and shrimp; however, a lower-level alternative explanation based on recognition of specific prey body features instead of amodal completion is also possible. Conversely, in Zylinski et al. (2012), cuttlefish were shown to adopt disruptive camouflage on backgrounds of repeating circles, fragmented circles made of eighth-circle fragments, and quarter circles, suggesting that these backgrounds are treated as equivalent; the subjects adopted mottle camouflage on backgrounds of eighth circles and rotated eighth-circle fragments (positive control), and uniform camouflage on a plain grey background (Figure 1A). Importantly, the eighth-circle fragments elicited disruptive camouflage when presented as a fragmented circle, but not when presented alone or randomly scattered. This indicates that when arranged as a fragmented whole, cuttlefish respond to fragments below the size threshold needed to elicit disruptive camouflage as if they are a unified whole; in other words, amodal completion. Moreover, because camouflage is an innate behaviour, it avoids the alternative explanations of amodal completion that are difficult to rule out in training and discrimination tasks. Using camouflage to investigate other cognitive abilities primarily known from training and discrimination tasks could provide similarly definitive evidence of these abilities in cephalopods.

Visual Perspective Taking

Visual perspective taking is the ability to make assumptions about what others can and cannot see and is part of a suite of cognitive skills related to mental attribution (Boeckle & Clayton, 2018; Schnell, Amodio, et al., 2021). As previously highlighted in our comparison of mental attribution in cephalopods and corvids, all potential evidence of visual perspective taking in cephalopods can be explained by simpler mechanisms. Of the available evidence, however, we believe the strongest case for visual perspective taking (and by extension, mental attribution) comes from mating interactions in cuttlefish. In these encounters, non-dominant males (so-called sneaker males) engage in female mimicry, adopting stereotypically “female” courtship patterns as a dishonest signal to “cheat” their way to females in the presence of dominant or rival males. In giant Australian cuttlefish (*S. apama*), sneaker males adopt full-body female courtship patterns in the presence of mate-guarding males (Hanlon et al., 2005; Norman et al., 1999), while in mourning cuttlefish (*S. plangon*) and common European cuttlefish (*S. officinalis*), sneaker males unilaterally display male courtship patterns towards females on one side of the body and female courtship patterns to rival males on the other side of the body (Figure 1B) (Brown et al., 2012; Cooke et al., 2017).

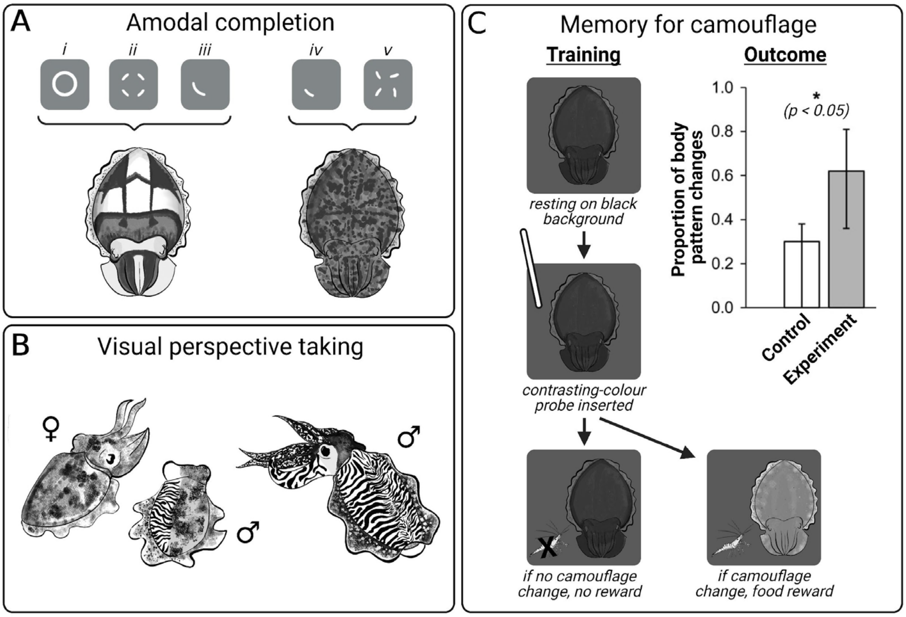
If this female mimicry is a result of visual perspective taking, unilateral courtship patterning indicates that certain species of cuttlefish may have an awareness of their own body and its position in the environment, are capable of visual perspective taking for multiple conspecifics simultaneously and possess the cognitive camouflage control to alter their body patterning based on this information. Of course, this female mimicry could also be explained by a much simpler behavioural reading account where sneaker males are responding to observable cues (e.g., about the presence and relative positions of females and rival males) rather than using complex cognition. While it will be difficult to empirically demonstrate the intentionality of female mimicry (which underpins the visual perspective taking account), understanding what others can see and altering camouflage accordingly would have extreme adaptive significance for interactions with predators, prey, conspecifics, and competitors.

Flexible Control of Camouflage

The most important evidence suggesting that camouflage may be subject to cognitive control comes from an experiment where common European cuttlefish (*S. officinalis*) learned to break cryptic camouflage for a food reward via associative conditioning, as shown in Figure 1C (Hough et al., 2016). In this experiment, contrastingly coloured probes were inserted into black or white experimental arenas following acclimatisation, and cuttlefish were rewarded if their body pattern changed within 15 seconds. Over one month, learning was statistically significant for the black background group (graph in Figure 1C), but habituation explained changes in the white background and control groups. It is unclear why the white background group demonstrated habituation instead of learning, although the authors note that it may be because this group rarely responded when the probe was inserted: a reaction was elicited in only 33% of trials. Still, the finding that cuttlefish are capable of learning to change their body patterning in response to an external stimulus for a food reward – even in just one experimental condition – indicates that cephalopods are capable of *some* level of cognitive, motivationally-based camouflage control. Moving forward, it will be necessary to test whether camouflage can be remembered (and beyond that, whether there is innate memory rather than just learned or trained memory for camouflage), because this study only demonstrates that cuttlefish can learn to change their body patterning, not that they remember and return to specific body patterns. Still, the ability to anticipate upcoming environmental cues and remember relevant camouflage would be adaptively valuable for animals that devote so much time and energy to staying hidden.

Figure 1

Camouflage Has Informed Knowledge of Cognitive Processes in Cuttlefish



Note. **A)** Cuttlefish have amodal completion, as demonstrated by the adoption of disruptive camouflage on backgrounds with (i) full circles, (ii) fragmented circles, and (iii) quarter circle arcs, but not (iv) eighth circle arcs or (v) rotated fragments (redrawn with permission from Zylinski et al., 2012). **B)** Male cuttlefish may engage in visual perspective taking, as evidenced by unilateral signalling displays during courtship where "sneaker" males (centre) display male patterning to a female on one side of the body and female patterning to a rival male on the other side of the body (Brown et al., 2012; Cooke et al., 2017). **C)** Cephalopods may be capable of cognitive camouflage control, as shown by cuttlefish learning to break camouflage for a food reward following insertion of a probe into a black experimental arena (although note that habituation occurred instead of learning when the experimental arena was white) (redrawn with permission from Hough et al., 2016). Artwork by Peiru Chen.[4]

Future Directions

In closing, we find it important to briefly discuss challenges with studying cognition using camouflage. The most obvious difficulty, historically, is the time it takes to manually code the camouflage components present in pictures or videos of camouflage. Much of the research discussed in this review has been concerned with common European cuttlefish (*S. officinalis*), and as such, has relied heavily on

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[4] Created in BioRender. Lane, W. (2024). https://BioRender.com/a20b839

qualitative assessments of the body pattern elements described in Hanlon and Messenger (1988), with occasional modifications (e.g., Osorio et al., 2022). Alternatively, many studies have attempted to classify camouflage into one of the three major "templates" suggested for *S. officinalis* (uniform, mottle, and disruptive), likely to facilitate comparison. As partially reviewed by Josef and Shashar (2014), beginning in the early 2000s, a number of studies have used computationally driven image analysis methods with the goal of analysing camouflage more objectively; these methods include measures of contrast, reflectance, granularity, and pixel intensity variance as well as Fourier transforms as "pattern descriptors". In the decade since this publication, a veritable explosion of image analysis methods has been reported, and an updated review is long overdue.

Importantly, in 2018, Reiter et al. published the first method for tracking camouflage at the individual-chromatophore resolution, although this is likely excessive for studies examining cognition with camouflage. The same group recently published a lower-resolution method for tracking camouflage, which leverages the feature maps of deep convolutional neural networks to produce a vectorised quantification of skin patterning in a given image or video frame (Woo et al., 2023). While groundbreaking, these and other quantitative approaches have their own drawbacks. They require vast amounts of computing power to run, they can involve questionable pre-processing steps (such as conversion to greyscale as well as histogram equalisation within a single image rather than relative to a standard or the full dataset, important for accurate comparison), and they have only been superficially compared with other quantitative methods (let alone qualitative methods). Analysis also frequently takes the form of dimensionality reduction methods such as Principal Components Analysis (PCA) or Uniform Manifold Approximation and Projection (UMAP), but little effort is made to provide relevant ecological grounding for the resulting dimensions. We recommend that future work building on these methods works to link the presence/absence of individual pattern components, such as spots and stripes, to aspects of vectorised skin pattern quantifications. This will help bridge the gap between present and past studies, increase our ability to understand the ecological relevance of different camouflage patterns, and broaden accessibility of these methods for researchers unfamiliar with machine learning.

Object Permanence

Object permanence (OP) is the ability to understand that objects continue existing even when they are not visible and requires foundational cognitive skills including representation and potentially symbolic thought (as reviewed by Jaakkola, 2014). Because of the mental representation required by OP, it is also considered a precursor for higher-level cognitive abilities, such as mental attribution (Call & Tomasello, 1999). Known or suggested in most major vertebrate groups, OP also has major adaptive significance for key survival behaviours – including navigating, foraging, avoiding predators, and acting socially – as it affords the subject an understanding of agents and objects that are not immediately perceivable (Zewald & Jacobs, 2022). Additionally, Stage 3 of Piagetian OP, "retrieving partially hidden objects" (as reviewed by Zewald & Jacobs, 2022), incorporates amodal completion, already known in cephalopods. Given this information, it could be expected that OP exists in cephalopods, and indeed, this has been suggested (as in Schnell & Clayton, 2021). However, this claim is based on two inconclusive observations from experiments not explicitly seeking to test OP.

The first observation is a report of cuttlefish following a prawn attached to a string during hunting, even after the prawn is drawn out of the visual field (Sanders & Young, 1940). It is possible that cuttlefish followed the prawn based on OP, but also possible that they responded to non-visual cues, such as smell or water movement, or a learned association about where the prawn was moved, as the location never varied. The latter final strategy is most likely, because following removal of the vertical lobe (implicated primarily in learning and memory, as reviewed by Montague et al., 2023), cuttlefish continued to hunt visible prey but ignored prey that moved out of sight. The second observation claimed to support OP in cephalopods comes from research examining the problem-solving abilities of octopus tasked with removing prey from a transparent, plugged jar (Fiorito et al., 1990). Trained octopus later attacked and explored an empty, opaque jar introduced to their tank. It is possible that the trained individuals generalised knowledge from the baited transparent jars, and anticipated that prey, while not visible, would also be present in the unbaited opaque jars: OP based on a learned contingency. It is equally possible, however, that introducing any object into the tank could act as a stimulus for attack in trained individuals. Without further work ruling out alternative possibilities, such as associative learning, it is therefore impossible to conclude based on current evidence that OP exists in cephalopods.

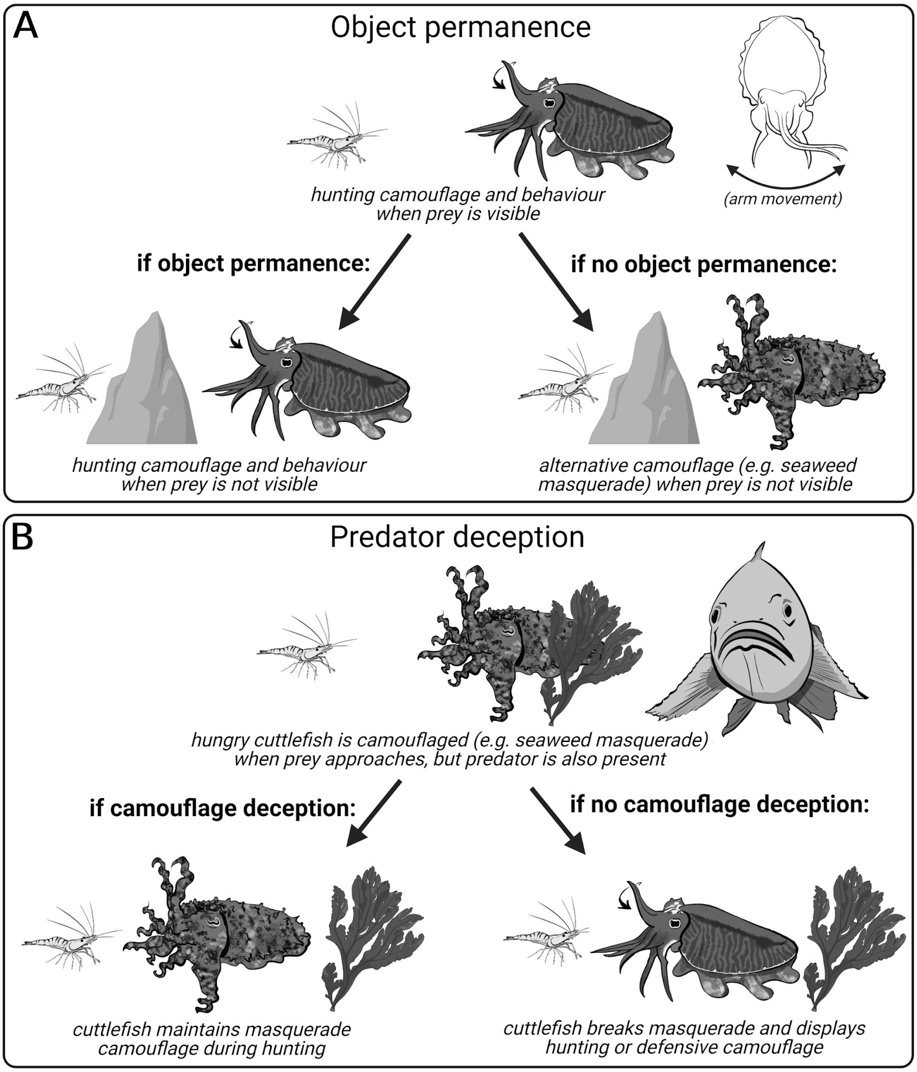
Work seeking to establish the presence of OP in cephalopods must be careful to avoid widespread methodological issues with testing OP in animals, many of which enable simpler, non-OP strategies to be used when solving tasks. As reviewed by Jaakkola (2014), many studies fail to control for nonvisual sensory cues, social cues from the experimenter, or associative learning strategies that may be used to "solve" OP tasks. Additionally, studying OP in cephalopods may prove challenging because most species are primarily visually driven ambush predators (Villanueva et al., 2017). We therefore suggest an experimental paradigm using camouflage as an innate behaviour to test for OP in cuttlefish, which can provide evidence of OP even if subjects refuse to engage with or manipulate experimental materials (Figure 2A). Cuttlefish display highly specific and stereotyped hunting camouflage and behaviour. If this hunting camouflage and behaviour is directed at a barrier blocking prey from view when alternative strategies are controlled for, even in the absence of attempts to remove or otherwise interact with the barrier, OP will conclusively be demonstrated for the first time in cephalopods.

Predator Deception

In contrast to the proposed experiment studying object permanence, cognitive control of camouflage may be implicated (but not definitively involved) in the second experiment we propose on predator deception. As previously discussed, mental attribution in cephalopods is a contentious subject, and this experiment would not empirically demonstrate its existence without careful controls for associative learning and other alternative strategies. However, it may be possible that cephalopods use camouflage for flexible predator deception during foraging. This could be the case if they maintain cryptic camouflage (including masquerade or mimicry) when hunting instead of adopting stereotyped hunting camouflage and behaviour (Figure 2B). In this paradigm, a hungry cuttlefish is hiding when prey becomes available, but a predator is also present. The cuttlefish must address simultaneous current needs: eating and avoiding being eaten. It may be possible to satisfy both needs at once if the cuttlefish can maintain cryptic camouflage while approaching and attacking prey, rather than engaging in stereotypical hunting camouflage and behaviour. This would allow the cuttlefish to capture its prey while reducing the likelihood that it will be seen by the predator due to conspicuous hunting camouflage. A series of modifications to this paradigm would be necessary to determine what underlying cognitive strategies are involved, which may include cognitive control of camouflage, self-control, mental attribution (including visual perspective taking and theory of mind), goal-directed behaviour, inferential reasoning, and associative learning. However, we believe this paradigm may provide a useful starting point for work attempting to integrate camouflage and cognition to investigate the potential drivers of antipredatory camouflage.

Figure 2

Camouflage Can Inform New Knowledge of Cognitive Processes in Cuttlefish



Note. **A)** If cuttlefish have object permanence, then we expect hungry cuttlefish to continue demonstrating hunting camouflage towards visually occluded prey. **B)** Hungry cuttlefish still need to hunt when their own predators are present. If they display camouflage-based predator deception during hunting, then we expect cuttlefish to maintain cryptic camouflage (e.g., by seaweed masquerade) during prey approach rather than adopting hunting or antipredatory camouflage. Animal artwork by Peiru Chen.[5]

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[5] Created in BioRender. Lane, W. (2024). https://BioRender.com/c03k884

Author Contribution Statement

W. M. L. and N. S. C. conceived the presented ideas. W. M. L. wrote the initial manuscript draft with support and supervision from N. S. C. Both authors contributed to the final version of the manuscript.

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