Annotated Bibliography: An Investigation on the Dynamic Processes of Mimicry in the Mimic Octopus (*Thaumoctopus mimicus*)

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Organisation of Articles: The secondary source is presented first to provide an analysis of mimicry as a behaviour and its role within the animal kingdom. As this is still a relatively new species, the remaining articles are presented chronologically to demonstrate how our understanding of mimicry has evolved with the discovery of the mimic octopus, and how it continues to grow with new information that emerges on this species.

Maran, T. (2017). *Mimicry and meaning: Structure and semiotics of biological mimicry*. Springer International Publishing AG (Chapter 7). https://doi.org/10.1007/978-3-319-50317-2.

Summary: This chapter conducts a review on the dynamic aspects of mimicry, providing a more in-depth understanding of mimicry and how this relates to its use by the mimic octopus (*Thaumoctopus mimicus*). Diverse understandings of mimicry were organised according to the three widely accepted relationships in mimicry: communication between model and receiver, resemblance between model and mimic, and deception between mimic and receiver. Expanding upon the knowledge that a mimic organism utilises properties of the model that offer protection or other advantages to the mimic, Maran (2017) addressed how this behaviour also disrupts the communication flow between the model and the receiver. Exploring the activity and intentionality of mimic's highlighted the remarkable ability of a mimic octopus in that it creates resemblance purely through behavioural activity. This facultative mimicry enables the individual to select an appropriate posture in accordance with a perceived threat. Unlike most mimic organisms, this permits the octopus to expand beyond a limited repertoire that can be recoded and re-established in response to environmental changes. This provides and evolutionary advantage to the octopus that most other mimic species do not benefit from. As the success of a mimic is dependent on both the ability of a receiver to recognise deception and the mimic's ability to be deceiving, it is clear why this species has persisted for so long. Building upon this concept, I would be interested in seeing whether any research is exploring how the mimic octopus incorporates a new mimic into its repertoire. Under what conditions would this phenomenon be triggered?

Contribution: Maran's (2017) work provides a thorough analysis on the role, performance, and significance of mimicry within the animal kingdom. Though only a couple of points explicitly discussed the mimic octopus, information on the dynamic aspects of mimicry as an operational concept provides understanding of its use by this species. Knowledge on the behaviour at a greater scope helps in studying it effectively within a single species.

Hanlon, R. T., Forsythe, J. W., & Joneschild, D. E. (1999). Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society*, *66*(1), 1-22. https://doi.org/10.1111/j.1095-8312.1999.tb01914.x.

Summary: Crypsis, camouflaging to blend in with one's background, was presumed the primary defence mechanism of *Octopus cyanea* against predators when foraging. Hanlon et al. (1999) hypothesized that an octopus would spend most of its time (>80%) inconspicuous within its environment. For a soft-bodied invertebrate, avoidance is likely the most effective method of protection. Four criteria (colour, brightness, shape, and pattern) were used in determining the degree of crypsis of an octopus against their background. Seven-and-a-half-hours of footage was captured of 11 foraging octopuses in the shallow waters (2-25 m) of the Tuamotu and Palau Archipelagos. Individual researchers time sampled each subject through individual scans at 10-second intervals, ranking them according to the number of criteria they met (0-4/4). Results were pooled and averaged to determine the level of crypsis that persisted. Contrary to initial presumptions, subjects were conspicuous (0-1/4) 22-50% of the time away from their den. The researchers posed that a species capable of crypsis would likely opt for low crypsis/conspicuousness, as it enables them to maintain a level of protection whilst minimising their neurophysiological expense in controlling hundreds of thousands of chromatophores (skin organs). First reports were also made of mimicry and deceptive resemblance in octopuses. The subject engaging in deceptive resemblance took form as a rock, using the tips of its arms to traverse the substrate. The mimicry was that of a parrotfish, but this was conjecture. The researchers argued that the high rapidity of pattern change (2.95 times/minute) to appear as anything but an octopus, causes predators to think them 'rare' to the area. More conspicuous individuals were typically larger, suggesting that with greater size comes fewer predators and as such, a lesser need for energetic investment into camouflage. Sexual selection and prey deception were deemed unlikely factors behind crypsis.

Contribution: This study was vital in debunking the preconceived notion that wild octopuses engage predominantly in crypsis predator defence techniques when foraging. These findings offered support to the remarkable claims made by those who first discovered *Thaumoctopus mimicus*, by demonstrating that cephalopods are capable of dynamic mimicry and deceptive resemblance. Suggestions were also made that wave ripples and moving light factor into this behaviour, as they alter a predator's perception of motion within the water. The ability to judge and modify to maintain protection in changing environmental demands, paved the way for further questioning on octopus intelligence and phylogenetic ability.

Norman, M.D., Finn, J.K., & Tregenza, T. (2001). Dynamic mimicry in an Indo-Malayan octopus. *Proceedings of the Royal Society B: Biological Sciences*, *268*(1478), 1755-1758. https://doi.org/10.1098/rspb.2001.1708.

Summary: Norman et al. (2001) performed 24-hour research dives over the course of 16 days to capture footage of the dynamic mimicry behaviour of the newly discovered mimic octopus. Despite camouflage and mimicry being well-documented amongst Cephalopod species, facultative mimicry had never-before been observed. Following their collection of footage on nine adult octopuses off the coasts of Sulawesi and Bali, the authors sought to establish a repertoire of the venomous species that the octopuses modelled after, the behaviours they engaged in for each model and the circumstances that lead to their mimicking. The authors were confident in confirming only three of their five identified mimicries and described each as follows: The first was of a sole (*Zebrias* sp.) and was achieved by the octopus drawing their arms behind them into a leaf-shaped wedge, a central mantle trailing their head and the undulation of their arms to mimic the flatfish's locomotion. The second was of a lionfish (*Pterois* sp.) and its distinctive poisonous spines were replicated by the octopus trailing its arms away from the body with banded colouration. The third was a mimic of a banded sea snake (*Laticauda* sp.) involving the octopus burying its body beneath the sand with two banded arms extended outward in a posture like that of the snake. Following these classifications, the authors speculated on the evolutionary trajectory that would have favoured such behaviour. Though it is likely that selection favoured this behaviour to deceive predators in an open landscape, sexual selection may have played a role and should be further examined (Norman et al., 2001). Additionally, while this behaviour is likely a form of Batesian mimicry, a non-toxic species impersonating a toxic species to appear noxious to predators (Norman et al., 2001), convergent evolution cannot be ignored without first confirming the toxicity of this octopus.

Contribution: As one of the first works to provide a basis for establishing a complete repertoire of the mimic octopus' model species, it serves as an appropriate starting point for a review. Highlighting that no cephalopod species had previously been documented impersonating specific animals in the absence of the model, provided realization of this species' complexity and the need for more research on mimicry in other cephalopods. Most importantly, by demonstrating their ability to decide what mimic is appropriate for each situation, these researchers recognised the need to further explore the cognitive intelligence of the mimic octopus.

Hanlon, R. T., Conroy, L. -A., & Forsythe, J. W. (2008). Mimicry and foraging behaviour of two tropical sand-flat octopus species off North Sulawesi, Indonesia. *Biological Journal of the Linnean Society*, *93*(1), 23-38. https://doi.org/10.1111/j.1095-8312.2007.00948.x.

Summary: Mimicry involves an individual impersonating another species (model) to deceive the receiver, typically a predator (Hanlon et al., 2008). It has long been considered a secondary mode of defence against predation in octopuses, used when the primary mode of crypsis has failed them in evading detection. Hanlon et al. (2008) sought to confirm whether mimicry is in fact a defence mechanism that acts secondary to crypsis in the mimic octopuses, *Thaumoctopus mimicus*. A period of habituation occurred prior to formal observation to ensure reactions of the wild subjects were to their natural environment and not to divers. The foraging habits of four octopuses were recorded in the volcanic sand plains of Aer Perang at a depth of 2-22 m. Over the course of six days, the total diving time was 189 h. Foraging frequencies, successes, time lengths and hours of operation were collected from footage. Subjects showed little to no movement 80% of the time, with their alert eyes scanning for predators. The remaining 20% consisted of noticeable movement while foraging, with 410 occasions of flounder mimicry (Hanlon et al., 2008). Interestingly, they produced a general alikeness to their background for camouflage only 50% of the time. Otherwise, they demonstrated conspicuous colouration with bold disruptive skin patterning (Hanlon et al., 2008). The fact that mimicry was performed on occasions that appeared independent from those of crypsis, suggests that mimicry is a primary mode of defence against predation (Hanlon et al., 2008). Had mimicry displays occurred subsequently to instances of crypsis, it would have been confirmed as a secondary mode of defence. Something that was not observed by these researchers, was an octopus shifted tactics upon predator detection, as there did not appear to be any recorded predator encounters. Observations of such occasions might reveal a previously undocumented secondary defence method.

Contribution: Identifying whether an anti-predator behaviour works as a primary or secondary line of defence, is important in its accurate investigation when in use. Misunderstanding the role that a behaviour serves in protecting a species could lead to misinterpreting a predator encounter instance. Identifying the true purpose of a behaviour to an animal is important in conducting an accurate review on said behaviour. Otherwise, the true meaning behind the behaviour is never fully explored, rendering the review incomplete or incorrect.

Krajewski, J. P., Bonaldo, R. M., Sazima, C., & Sazima, I. (2009). Octopus mimicking its follower reef fish. *Journal of Natural History*, *43*(3-4), 185-190. https://doi.org/10.1080/00222930802450965.

Summary: An octopus species inhabiting a similarly barren landscape as that of the mimic octopus, have been observed displaying advanced mimicry behaviour. *Octopus insularis* was recorded impersonating *Cephalopholis fulva*, small schooling fish that typically tail the octopus. Krajewski et al. (2009) examined whether an association in feeding practises between these two species, promoted the octopus to adopt the fish as a model. Analysis took place at the shallow depths (1-15 m) of the Fernando de Noronha Archipelago. Thirty captured images from 1–10-minute video segments were randomly selected and the colouration of five octopuses were quantified using the crypsis grading scheme developed by Hanlon et al. (1999). Thirty-nine individuals were observed in total, followed by 1-14 *C. fulva* individuals (Krajewski et al., 2009). Octopuses mimicked their followers when swimming more than 40 cm above the substrate. When moving close to the bottom or sedentary, individuals remained highly cryptic 72.1% of the time. Under conspicuous bicolour mimic colouration, the octopus strategically positioned themselves at the centre of the *C. fulva* groups, further accentuating their inconspicuousness to visual predators (Krajewski et al., 2009). Social mimicry, a solitary individual engaging with groups to gain protection, has never been observed in octopus species before (Krajewski et al., 2009). It appears to have originated as a mutually beneficial relationship, as any prey that escapes a foraging octopus is captured by the fish. The opportunistic behaviour of *C. fulva* likely initiated the octopuses' adoption of them as a model. Recognising this as a potential origin of advanced mimicry raises the question of whether any such instances occurred within the evolutionary history of the mimic octopus. Or perhaps, whether any such instances exist presently. Study into a mimic's relationship with their model may provide information on how they incorporate a species into their repertoire.

Contribution: Krajewski et al. (2009) explored whether a feeding association with *C. fulva* factored into *O. insularis'* adoption of social mimicry. This extends beyond other octopus mimicking records, as these instances highlight an engagement with the model that has never been previously observed. It demonstrates how octopus mimicry behaviour involves behavioural manipulation as well as visual, making their efforts more effective. It begs the question of whether the barren substrate of mimic octopus species environments acts secondary or in conjunction with shared diet in promoting this behaviour.

Hanlon, R. T., Watson, A. C., & Barbosa, A. (2010). A “mimic octopus” in the Atlantic: flatfish mimicry and camouflage by *Macrotritopus defilippi*. *The Biological Bulletin*, *218*(1), 15-24. https://doi.org/10.1086/BBLv218n1p15.

Summary: Previous recordings of mimicry behaviour in octopuses, were of three tropical species from Indonesia. Hanlon et al. (2010) reported the first evidence of an Atlantic Ocean resident octopus, *Macroptritopus defilippi*, mimicking a local flatfish species, *Bothus lunatus*. These researchers aimed to confirm the type of mimicry this new species engaged in and whether the practise was one that was inherent or learned. Fieldwork consisted of 51 hours of wild observation, diving at 10-15 m depth in the Netherlands Antilles. Records of swimming practise were kept for both octopus and flatfish subjects on criteria of duration, speed, and style. Additional notes were made on their colouration and posture when stationary versus swimming. Swimming style and posture were most distinctive in their similarities, with both species performing a “contour” locomotory method by undulating their bodies along the natural ripples of the substrate (Hanlon et al., 2010). Performed in bouts of stop-and-start, the timings of which were similar between the two species. The most notable difference came from swimming speed, where *B. lunatus* were typically faster (12-15 cm/s) than *M. defilippi* (9 cm/s). The researchers also reported that *B. lunatus* was determined as non-toxic, suggesting that *M. defilippi* performed neither Batesian (i.e., the imitation of a toxic species by a non-toxic species to appear noxious to predators) nor Müllerian (i.e., the convergent evolution of similar honest signalling by two unrelated species, to warn a shared predator) (Hanlon et al., 2010). Mention was made of a lab-reared octopus who, without prior flatfish exposure, performed a flatfish mimicry (Hanlon et al., 2010). Demonstrating that there is an evolutionary factor behind these behaviours, as they are clearly innate rather than learned. Determining whether these findings extend to other mimicking octopuses could help in establishing whether their shared mimicry tactics are convergent or derived behaviours.

Contribution: As *B. lunatus* was confirmed a non-toxic species in this paper, Batesian and Müllerian mimicry can be ruled out as modes of mimicry for *M. defilippi*. This statement raises questions on whether this also applies to the mimic octopus. According to the criteria used in grading mimicry performance, *T. mimicus* falls within the “poor-mimic” range, as they display conspicuous colouration in around 50% of their flatfish mimics. Are they poor mimics, or is it possible that they incorporate honest signalling into their mimics? Development of the mimic octopus’ toxic profile is necessary in confirming this.

Huffard, C. L., Saarman, N., Hamilton, H., & Simison, W. B. (2010). The evolution of conspicuous facultative mimicry in octopuses: an example of secondary adaptation? *Biological Journal of the Linnean Society*, *101*(1), 68-77. https://doi.org/10.1111/j.1095-8312.2010.01484.x.

Summary: The persistence of conspicuousness as a predator avoidance tactic in soft-bodied octopods is something that evolutionary biologists have long sought the understanding of. The mimic octopus, *Thaumoctopus mimicus*, further complicated this by incorporating diverse morphological and behavioural alterations in each of their mimics. The neural, rather than anatomical, control of these modifications suggests that this species can anticipate how the recipient (i.e., a predator) will interpret their mimic. This paper sought to understand whether these behavioural traits emerged as adaptations or exaptations. Flatfish mimicry was of particular focus. Ancestral states were reconstructed, and the distribution pattern of these traits were tracked throughout octopod evolutionary history. The results produced a clade that the researchers termed the "Long-Armed Sand Octopus" (LASO). This included *Thaumoctopus*, *Wunderpus photogenicus* and *Blandopus*. All three of these are diurnal species that reside in overlapping geographic ranges in habitats that include relatively barren substrate. The most significant shared feature though, is disproportionately long arms relative to the body. From this, Huffard et al. (2010) deduced that the similarities in morphological features, ecological habitats, and behaviours of LASO members indicate that convergent evolution gave rise to these traits. Further, dorsoventrally compressed swimming (DVC) and relatively long arms likely emerged as concurrent adaptations with flatfish mimicry swimming arising as a secondary adaptation. This also reveals an apparent shift in defence mechanisms against predators from crypsis promoting avoidance to conspicuousness works to avoid detection as an octopus. These changes throughout evolutionary history have clearly been successful though, as they are observed in three extant species. A conclusive flatfish model has yet to be identified as a model for the mimic. It would be interesting to see whether discovery of this would alter these conclusions, as the researchers worked on the assumption that this mimic is an imperfect combination of multiple models.

Contribution: This study provided a thorough investigation into the evolutionary history of the mimic octopus. Exploring the rise of such complex morphological and behavioural traits is a difficult feat to accomplish, especially in marine invertebrate species. The reported findings offer background knowledge on the rise of mimicry and what factors could potentially have contributed to its emergence. The historical context of a behaviour aids in understanding its use in present individuals of a species. This will help offer supporting information on what the evolutionary context of mimicry was, when discussing its use by living individuals.

Ureña Gómez-Moreno, J. M. (2019). The 'mimic' or 'mimetic' octopus? A cognitive-semiotic study of mimicry and deception in *Thaumoctopus mimicus*. *Biosemiotics*, *12*, 441-467. https://doi.org/10.1007/s12304-019-09362-y.

Summary: Gómez-Moreno (2019) highlighted that in some instances of mimicry, altering one's appearance to impersonate another species for fitness benefits, *Thaumoctopus mimicus* will engage only in partial mimicry. Recognising this performance inconsistency led the author to question what benefits a partial mimicry could provide, compared to a full one. The focus was predominantly on banded sea-snake mimicry, which is used solely in meetings with territorial damselfish. Complete impersonation involves banded colouration, two arms projected as the head and tail, with the remaining arms and body tucked away in a burrow. Further details include tapering of the "head" arm and dark dots at the distal-most portion to capture the head curvature and eyes of the sea-snake (Gómez-Moreno, 2019). A partial mimic involves the use of only one arm, and the failure to burrow the body or perform the finite details (Gómez-Moreno, 2019). Theoretical and analytic frameworks were used to investigate the possible reasoning behind a partial mimic in performances in live footage. From this, two potential theories arose. The simpler argument suggests that mimicry responses in this species are simply adaptive and therefore, they lack cognitive control over their reaction (Gómez-Moreno, 2019). As such, those observed to perform partial mimics are simply poor at mimicking. The second, and the one supported by the author, suggests that the octopus has a level of self- and bodily-awareness relative to its surrounding space. As such, the octopus can judge the level of energetic investment required for success in any given situation. This is significant, as it demonstrates their ability to anticipate the reaction of their recipient (i.e., damselfish), pre-determine the outcome of the interaction and calculate what is required of them to achieve their desired goal. Further analysis is required to confirm the true extent of these mental mapping abilities.

Contribution: The more complex proposition expands understanding of the mimic octopus' cognitive awareness, sentience, and deceptive abilities. This supports the notion that it's practises of facultative mimicry demonstrate problem-solving and choice of model depending on context. This creates a realm of research to be explored on the mimic octopus, to understand the degree to which it is conscious. In terms of this review, it offers an interesting point of discussion on what the octopus perceives of its own actions.

Sajikumar, K. K., Jeyabaskaran, R., Binesh, C. P., & Mohamed, K. S. (2020). First record of the mimic octopus *Thaumoctopus mimicus* (Cephalopoda: Octopodidae) from the Arabian Sea: range extension and genotyping. *Malacologia*, *63*(1), 115-122. https://doi.org/10.4002/040.063.0111.

Summary: The Arabian Sea is speculated to house the richest collection of cephalopods on Earth, yet it remains one of the most understudied areas. In 1998, the first cephalopod species to display dynamic mimicry was identified and named the mimic octopus. It was presumed to reside solely within the Indo-Malayan archipelago, though Sjikumar et al. (2020) reported first sightings of this species in the Arabian Sea. Morphological and molecular analyses were employed to confirm the identification of two specimens collected as bycatch from a trawler. Morphometric measurements in mantle width, mantle length, and arm length were taken from the subjects, along with additional beak measurements. Mitochondrial DNA was extracted, amplified through PCR, then sequenced. Morphology of both individuals was consistent with that of *T. mimicus*, and genetic profiling confirmed a 99.66-99.67% sequence match with a tropical member of the species. This confirms that the geographic distribution of the mimic octopus extends around 1,400 nautical miles beyond the previously documented range. Habitat is consistent with those recorded; shallow waters (0.5-37 m) with a sandy substrate. While the death of these individuals was unintended and unfortunate, it provided a rare opportunity for conducting more exact morphological analyses. Something interesting, that the researchers made little comment on, was both subjects displayed dark colouration with white marks on their bodies and banding down their legs. This form of bold colouration is typically associated with noxious species truthfully conveying their danger to predators. Unfortunately, toxicity was not tested in these individuals and so, it remains a prominent mystery of the mimic octopus. Another factor worthy of consideration is that the intended fishing target was a flatfish species, *Cynoglossus macrostomus*. This reveals yet another potential flatfish model for the octopus. Future study is required to confirm whether mimicry of this flatfish has been observed within the octopus.

Contribution: Only first discovered in 1998, 23 years later, another significant discovery is made regarding the mimic octopus. These delayed findings further accentuate the effectiveness of this species' ability to evade detection. It begs the question as to whether we have in fact discovered their full geographic range. It also makes one wonder whether other cephalopod mimic species, that are even more effective at evading detection than *T. mimicus*, have yet to be discovered.