DECORATING BEHAVIOR OF MAJOID CRAB, *CAMPOSCIA RETUSA*, DOES NOT FACILITATE THE VISUALLY CRYPTIC CAMOUFLAGE STRATEGY OF BACKGROUND COLOR MATCHING

by

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ABSTRACT

Camouflage conceals an organism through the prevention of detection and/or recognition; and understanding the mechanisms behind various camouflage strategies is vital. As camouflage strategies target the perception of a specific predator or prey species, strategies need to be defined with these intended targets in mind. A species' inherent coloring or markings, habitat choice, and/or decorating behavior could facilitate a specific camouflage strategy. A species exhibiting decorating behavior deliberately accumulates and retains environmental material on the exterior of its body. Some of the most well-known decorators in the animal kingdom are the spider crabs of the Majoidea superfamily. *Camposcia retusa* is a coral reef-dwelling Majoid species that exhibits decorating behavior. However, the sensory modalities utilized by this species in the selection of decoration material remains unknown. It was hypothesized that *C. retusa's* decorating behavior facilitates the cryptic camouflage strategy of background color matching. If so, *C. retusa* should be able to (1) select decoration materials that match the color of its background, and (2) detect the color of its previously attached decorations and choose a habitat in a similar background color. Through a set of laboratory-based behavioral choice experiments, I show that *C. retusa's* decorating behavior does not facilitate background color matching. When placed in a consistent background (either black or white), no statistical difference was found in the color of craft pompoms selected. Additionally, when pre-decorated with craft pompoms of a specific color, crabs did not select a habitat to match the pompoms previously attached to their exterior. Further, no statistical difference was found in the pompom color selection when crabs were allowed to decorate in the absence of light compared to when light was present. While this study focused on one camouflage

strategy, background color matching, *C. retusa* may be utilizing a number of other camouflage and non-camouflage strategies aimed at impacting the visual or non-visual sensory systems of its predators.

Chapter 1

INTRODUCTION

One of the largest selection pressures an organism can face is predation (Stevens & Merilaita 2009a). Camouflage is an essential defense mechanism to many organisms because the efficacy of a species' concealment strategy impacts the survival of that species. The large array of camouflage strategies that have evolved in the animal kingdom indicates the importance of concealment (Stevens & Merilaita 2009a). Camouflage refers to all strategies involved in concealment, including the prevention of detection and/or recognition, and should be defined with the perceptual mechanism of the target organism in mind (Table 1; Stevens & Merilaita 2009a). The definitions of *detection* and *recognition* can be difficult to parse out and sometimes intermingle (Cronin et al. 2014). *Detection* is an organism establishing another organism as an individual entity separate from the background, while *recognition* refers to an organism establishing another organism as a predator or viable prey (Table 1). These two processes may occur simultaneously or separately depending on the sensory modalities involved in the predator's prey-finding strategy. Prey camouflage strategies may aim to avoid one or both of these identification processes.

Table 1. Important definitions commonly used in camouflage literature and research.

term	definition
camouflage	anti-predator strategies involved in concealment, including prevention of detection and recognition (Stevens & Merilaita 2009a)
identification	when an organism detects and recognizes another organism as predator or prey
detection	one of the two processes involved in identification where an organism establishes another organism as an individual entity separate from the background
recognition	one of the two processes involved in identifiction where an organism establishes another organism as a predator or viable prey
cryptic	describes camouflage strategies that have an impact on the target's senses while simultaneously preventing the organism from being detected, but not necessarily from being recognized (Ruxton 2009)
background matching	a cryptic camouflage strategy where the visual appearance of the organism generally matches the color or pattern of one or several background types (Stevens & Merilaita 2009a)
disruptive coloration	a cryptic camouflage strategy in which a set of markings creates the appearance of false edges and boundaries, and hinders the detection or recognition of an organism's true outline and shape (Stevens & Merilaita 2009a)
distractive markings	a cryptic camouflage strategy in which markings direct the attention or gaze of the target from traits that would give away the organism (Stevens & Merilaita 2009a)
marking	a two-dimensional feature on an organism's exterior surface
decorating	a cryptic antipredator behavior where an organism deliberately accumulates and retains environmental material on the exterior of the body (modified from Ruxton & Stevens 2015, Wicksten 1993)
aposematism	an anti-predator strategy where an organism uses a signal, especially a visual signal of conspicuous markings or bright colors, to warn predators that it is unpalatable or poisonous ("aposematism" 2020)
masquerade	a camouflage strategy where recognition is prevented by resembling an uninteresting object (Stevens & Merilaita 2009a)

Predators and prey are often described as being in an arms race, where the evolution of new strategies to hunt or hide are constantly changing. Camouflage can help prey remain undetected or unrecognized by a predator or help facilitate predation by keeping a predator undetected or unrecognized by prey (Stevens & Ruxton 2019). Research investigating camouflage has primarily focused on the visual aspect, specifically an organism's inherent coloration (Stevens & Merilaita 2009a), likely a result of the human reliance on the visual field. However, a camouflage strategy refers to how camouflage functions for an organism and how the organism using the strategy is perceived by the target, not how the organism appears the human eye (Stevens & Merilaita 2009a). It is therefore important to recognize that in order for the function of a specific camouflage strategy to be fully and correctly understood, it needs to be researched through the perception of the intended target.

Cryptic camouflage strategies help the organism go undetected and not necessarily unrecognized, but certain cryptic strategies can do both (Table 1; Ruxton 2009). For a trait or behavior to be cryptic, it must have an impact on the target's senses while simultaneously preventing the organism from being detected and located (Ruxton 2009). Crypsis is essentially hiding in plain sight with the primary aim to avoid detection, and if that does not work, then recognition. A variety of cryptic camouflage strategies can be used to impede visual detection. Here, only three cryptic camouflage strategies are discussed extensively, as they most accurately pertain to the study behavior and study species. Background matching occurs when the organism generally matches the color or pattern of one or several background types (Table 1; Stevens & Merilaita 2009a). More specifically, organisms can background *color* match and background *pattern* match. Second, disruptive coloration occurs when an organism possesses a set of markings that creates the appearance of false edges and boundaries, and hinders the detection or recognition of the organism's true outline and shape (Table 1; Stevens & Merilaita 2009a). Lastly, distractive markings occur when the organism possesses patterns or markings that direct the attention or gaze of the target from traits that would give away the organism (Table 1; Stevens & Merilaita 2009a).

One unique form of crypsis that has evolved multiple times in the animal kingdom is decorating, a process of deliberately accumulating and retaining environmental material on the exterior of the body (Table 1; Ruxton & Stevens 2015, Wicksten 1993). Decorating is found most often in insects and aquatic species, and occurs in approximately 25% of all major metazoan phyla (Berke et al. 2006, Ruxton & Stevens 2015). Decorated organisms must locate decorations, prepare the materials for attachment, attach the items, and carry a heavier-than-normal load. Decorating is energetically costly, and its repeated evolution indicates that benefits are provided to the decorator (Brooker et al. 2018). Many researchers have hypothesized that the benefit is anti-predatory in nature, meaning decorating facilitates camouflage to avoid detection or recognition, or both, by predators.

Spider crabs of the superfamily Majoidea are one of the most well-known decorators in the animal kingdom. Majoid spider crabs have round bodies with four pairs of walking legs and a pair of chelipeds (chelae or pincers) and are covered in specialized hooked setae (Wicksten 1993). Setae are small, hair-like structures that the crabs use to attach materials to their bodies. Majoids decorate by picking up material from their surroundings with their chelipeds, moving the material to their mouth parts where they orient the item and roughen the edges, and then attaching the item to their carapace and legs by rubbing it on hooked setae (Wicksten 1980, Wicksten 1993). The hooked setae are the only setae that hold decorations (Wicksten 1980). Other types of setae may serve other purposes. Spider crabs may determine their extent of decoration via visual inspection of their carapace and legs, but it is also thought that their setae may possess mechanosensory properties that could provide information about the location of decorations on the crab (Wicksten, 1980, Wicksten 1993).

Majoid spider crabs eat carrion, sea urchins, sand dollars, sea stars, mollusks, worms, algae, and ascidians, all slow moving or stationary organisms, however their predators include lobsters, sea otters, fishes, sea stars, and other crabs (Wicksten 1980), indicating that their decorating behavior is aimed at concealing themselves from their predators rather than from their prey. The Majoids' decorating behavior likely evolved from feeding behavior, since the decorations are conveyed to the mouth area before attachment, and food storage behavior, since a few Majoid species today eat the materials after they have decorated with them (Wicksten 1980).

Camposcia retusa (Figure 1), the spider decorator crab, is a coral reef organism native to the Indo-Pacific and is commonly found in hobby aquariums due to its ability to live in captivity. As with other Majoid crabs, *C. retusa* decorates its carapace and legs with items found on the coral reef floor, including sponges, corals, rubble, etc., throughout its life. Although the benefits of decorating are debated, evidence that *C. retusa* decorates to avoid predation has been documented (Brooker et al. 2018). *Camposcia retusa* decorates more and faster when shelter is not available, and when a shelter is present *C. retusa* decorates its exposed legs first (Brooker et al. 2018).

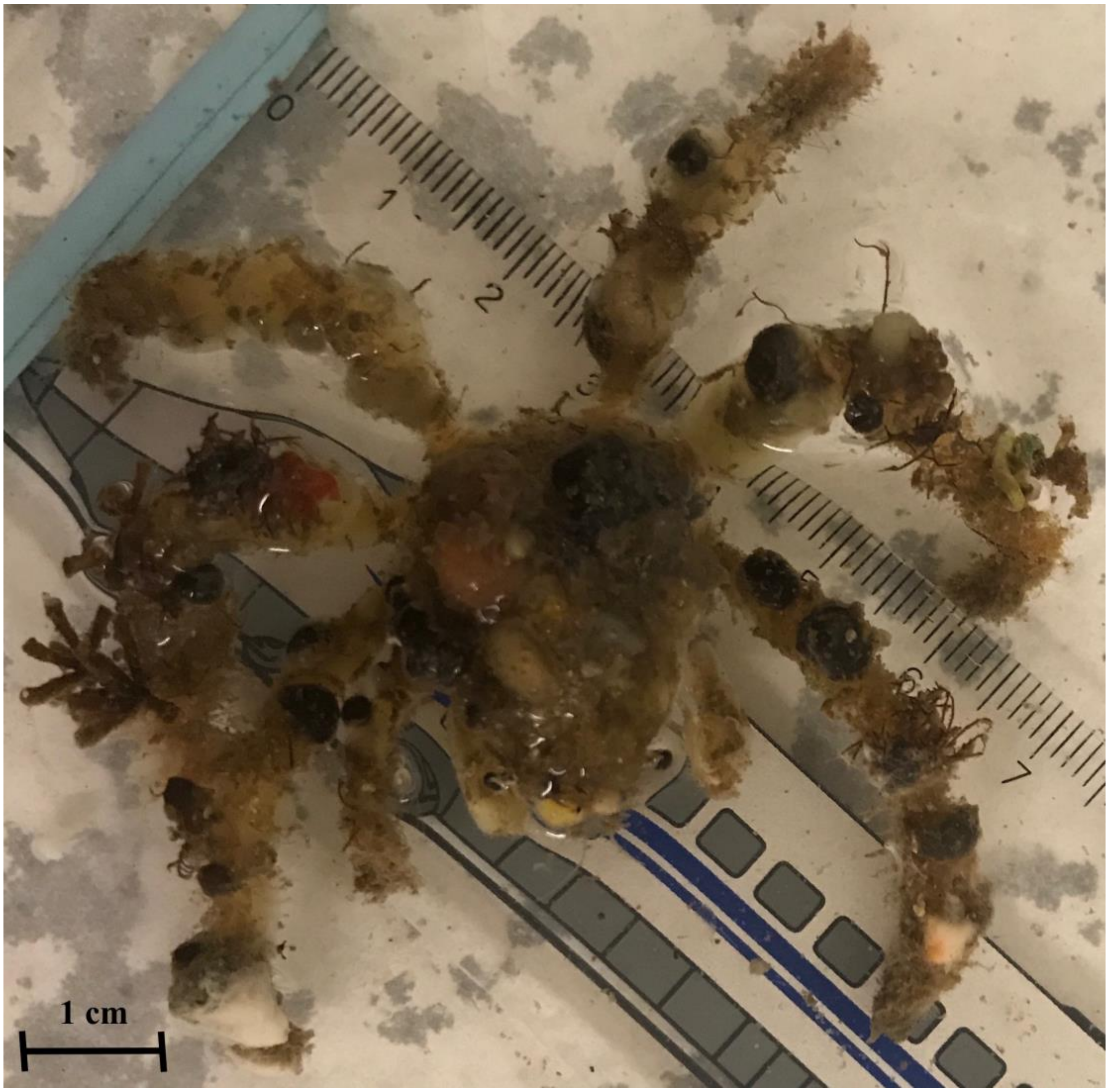

Figure 1. *Camposcia retusa*.

Decorating has been studied in many species, both terrestrial and aquatic, yet there is still a lack in understanding of the benefits of the behavior and the camouflage strategies it facilitates (Ruxton & Stevens 2015). The aim of this study was to determine if *C. retusa* utilizes background color matching as a cryptic camouflage strategy to explain the decorating behavior. Enhancing camouflage via behavior is most easily accomplished by choosing to rest on a background that most closely matches the organism's visual appearance (Stevens & Ruxton 2019). It was hypothesized that if *C. retusa* was aiming to background color match through decorating, it would be able to (1) select decoration materials that match the color of its background, and (2) detect the color of its previously attached decorations and choose a habitat in a background color that matched. Research investigating predator-prey dynamics seeks to understand a foundational question of ecological research. A greater understanding of camouflage provides important information on one aspect of how both predators and prey conceal themselves from each other.

Chapter 2

METHODS

2.1 Animal Husbandry

Adult *C. retusa*, sourced from Bohol Sea, Philippines (LiveAquaria) were held in individual 7.5-L plastic aquaria, each containing one two-inch white PVC elbow shelter from August-November 2018 (Experiments A-E) and September-December 2019 (Experiment F). Aquaria were maintained within an 800-L semi-recirculating seawater system at the University of Delaware's Lewes Campus. Individual crabs were fed pieces of shrimp or squid on alternating days to satiation. No food was provided on the day trials were conducted.

2.2 Experimental Setup

All trials were conducted in a covered area underneath a paper-covered LED light to ensure a uniform overhead light field. Multiple experimental trials were run using two different setups. First, a black and white experimental setup was conducted in four rectangular, 15.2-L flow-through PVC aquaria. Half of each aquarium, walls and floor, was white while the other half was black. Aquaria were arranged to ensure two had the white side on the right while the remaining two had the black side on the right, a measure to ensure a side preference was not being displayed. Individual crabs were placed in the center of the aquarium in a mesh tube for 30 minutes, allowing them to habituate to the experimental environment while receiving sensory cues but unable to access the aquarium. After 30 minutes, the mesh tubing was gently raised and the five-hour trial began. The crab's location was recorded every 15 minutes by briefly opening the cover and photographing the crab from above.

The second experimental setup was constructed from the same flat PVC material however, aquaria were square, 7.6-L containers made of either black or white. As outlined above, identical experimental methods regarding the habituation period and data collection were followed, except photographs were taken every 30 minutes for 10 hours.

2.3 Experimental Trials

2.3.1 Experiment A – Background Color Preference

To determine if *C. retusa* had a preference for either a dark or light background, in the absence of decoration, individual crabs were placed in the black and white experimental setup (n=23; Figure 2A). No shelter or decorations were provided to the crab. The location of each crab was recorded every 15 minutes for five hours. A Nominal Logistic Regression was used to determine if the crabs chose to sit on a specific side more often and if that choice was impacted by the length of the trial, where the crab individual and time were used to construct the model effects, and the side the crab was recorded on was used as the response variable.

2.3.2 Experiment B – Decorating Based on Background Color

To determine if *C. retusa* decorated more when against a light or dark background, individual crabs were placed in either the black or white experimental setup with five 10-mm arts-and-crafts pompoms as items for decoration (Figure 2B). Crabs placed in the white experimental setup were run through the experimental protocol twice, once with matching white pompoms (n=11) and again with mismatching black pompoms (n=11). Crabs placed in the black experimental setup were run through the experimental protocol twice, once with matching black pompoms (n=12) and again with mismatching white pompoms (n=11). A pompom was considered decorated when it was attached to the crab's carapace or legs and had to be removed through gentle pulling and rolling. The number of pompoms each crab used to decorate was recorded every 30 minutes for 10 hours. Ten hours was provided to ensure plenty of time for the crabs to complete decorating. Only the data from the final time point were analyzed. A Nominal Logistic Regression was used to determine if the color of the background had an effect on the number of pompoms the crab used to decorate, where the crab individual, shade of the aquarium (black or white), and the shade of the pompom were used to construct the model effects, and the number of pompoms was used as the response variable.

2.3.3 Experiment C – Decorating Based on Decorations Matching or Mismatching Background

Data collected in Experiment B were analyzed to determine if *C. retusa* decorated more if the provided decorations matched the color of the background (Figure 2C). Again, a Nominal Logistic Regression was used, where the four treatment options (white background, white pompoms; white background, black pompoms; black background, black pompoms; and black background, black pompoms) was used to construct the model effect, and the number of pompoms was used as the response variable.

2.3.4 Experiment D – Background Color Preference After Decoration

To determine if *C. retusa* selected the background that matched the color of its decorations, experiments were conducted in the black and white aquarium setup (n=32; Figure 2D). Ten pompoms were provided to each crab in their individual holding aquaria 24 hours prior to the start of the trial. Individuals were only run through the trial if they were sufficiently pre-decorated with pompoms, having placed three or more pompoms on their bodies. All crabs were run through the trial twice, once pre-decorated with black pompoms (n=18) and once pre-decorated with white pompoms (n=14). Again, the location of each crabs was recorded every 15 minutes for five hours. A Generalized Linear Model (GLM) was used to determine if the crab selected a specific shade of the aquarium more often and if that choice was impacted by the length of the trial, with the crabs' location as the response variable and time, aquarium shade, pompom shade, and the interaction between pompom shade and aquarium shade used to construct the model.

2.3.5 Experiment E – Decorating Based on Background Color

To determine if, when presented with both black and white pompoms simultaneously, *C. retusa* chose to decorate with the color that matched that of its aquarium background, individual crabs were placed in the single-color setup (n=35) and provided with three white pompoms and three black pompoms (Figure 2E). Crabs were run through the experiment twice, once in a black aquarium (n=17) and once in a white aquarium (n=18). The number of each color pompom each crab used to decorate was recorded every 30 minutes for 10 hours. Ten hours was provided to ensure plenty of time for the crabs to complete decorating. Only the data from the final time point were analyzed in order to compare with Experiment F (see below). An analysis of variance (ANOVA) was used to determine if there were differences in decorating behavior where the number of pompoms was selected as the response variable. A Fisher's LSD test was used to determine if the differences in decorating behavior were due to the color of the pompoms, the color of the aquaria, or the behavior of individual crabs.

2.3.6 Experiment F – Decorating Behavior with Visual Cues Removed

The use of visual cues for decoration requires light, therefore to determine how/if *C. retusa* decorated in the absence of visual stimuli (0.08 μ mol photons m^{-2} s^{-1}), 17 individual crabs were placed in the single-color setup (white n=9; black n=8) with three black and three white pompoms available for decoration (Figure 2F). Individuals in this experiment were not monitored throughout the study in an effort to ensure light was not provided to the crab. Photographs were taken at the conclusion of the 10-hour trial. The number of each color pompom each crab used to decorate was recorded every 30 minutes for 10 hours. Ten hours was provided to ensure plenty of time for the crabs to complete decorating. Only the data from the final time point were analyzed in order to compare with Experiment E (see above). An ANOVA was used to determine if there were differences in decorating behavior where the number of pompoms was selected as the response variable. A Fisher's LSD test was used to determine if the differences in decorating behavior were due to the color of the pompoms, the color of the aquaria, or the behavior of individual crabs.

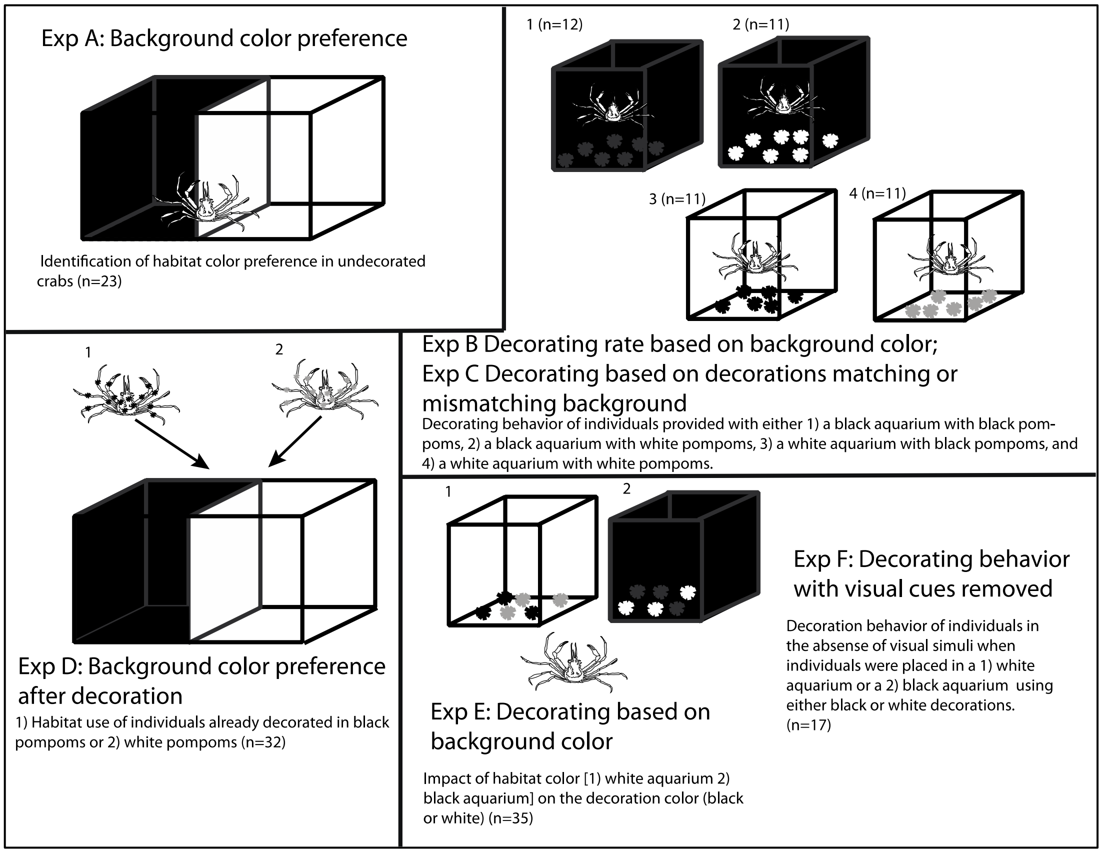

Figure 2. Experimental design used to determine: A) background preference; B) decoration based on background color; C) decoration when material matched or mismatched the background; D) if *C. retusa* selects the background that matches the color of its decorations; E) the decoration color selected when both colored pompoms were presented; F) the decoration rate and colors selected in the absence of visual stimuli.

Chapter 3

RESULTS

3.1 Experiment A – Background Color Preference

Camposcia retusa preferentially selected the black side of the aquarium over the white, indicating a strong preference for a dark habitat or background (Nominal Logistic Regression $p<0.0001$; Table 2; Figure 3). Observations of individual crabs were recorded every 15 minutes for five hours however, time did not significantly impact the background choice ($p=0.9586$; Table 2). Of the 23 crabs that were tested, 18 were found on the black side during 100% of the observations, two during 85%, one during 75%, one during 20%, and one during 5%. The majority of the crabs (70%) were found on the black side of the aquarium during all 20 observations, indicating a strong preference for dark habitat.

Table 2. Experiment A Statistics.

Model	Log Likelihood	DF	χ^2	$p>\chi^2$
Difference	111.31360	41	222.6272	**<0.0001**
Full	36.01518			
Reduced	147.32879			
Effect Likelihood Ratio Test				
Source	**Nparm**	**DF**	**L-R χ^2**	**$p>\chi^2$**
Crab	22	22	219.73975	**<0.0001**
Time	19	19	9.75916234	0.9586

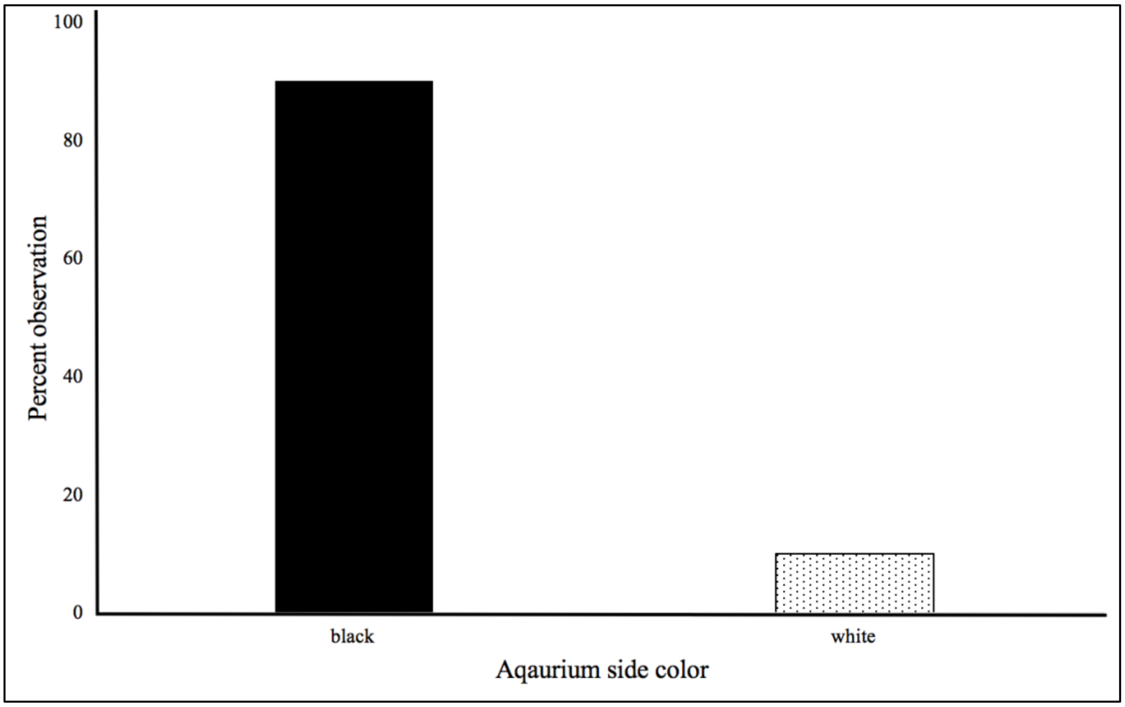

Figure 3. Background Color Preference. Percent of observations on the black side and white side of the aquarium during the five-hour collection time, data recorded every 15 min (20 observations per crab).

3.2 Experiment B – Decorating Based on Background Color

No significant difference was detected in the number of pompoms crabs used to decorate when placed in either a white or black aquarium ($p=0.2341$; Table 3; Figure 4). When in a black aquarium, crabs decorated with a mean of 2.3 ±1.8 SD pompoms. When in a white aquarium, crabs decorated with a mean of 2.0 ±2.0 SD pompoms.

Table 3. Experiment B Statistics.

Model	Log Likelihood	DF	χ^2	$p>\chi^2$
Difference	62.826133	115	125.6523	0.2341
Full	14.425037			
Reduced	77.251170			
Effect Likelihood Ratio Test				
Source	**Nparm**	**DF**	**L-R χ^2**	**$p>\chi^2$**
Crab	110	110	122.43605	0.1967
Aquarium	5	0	0	
Pompom	5	5	9.9661701	0.0762

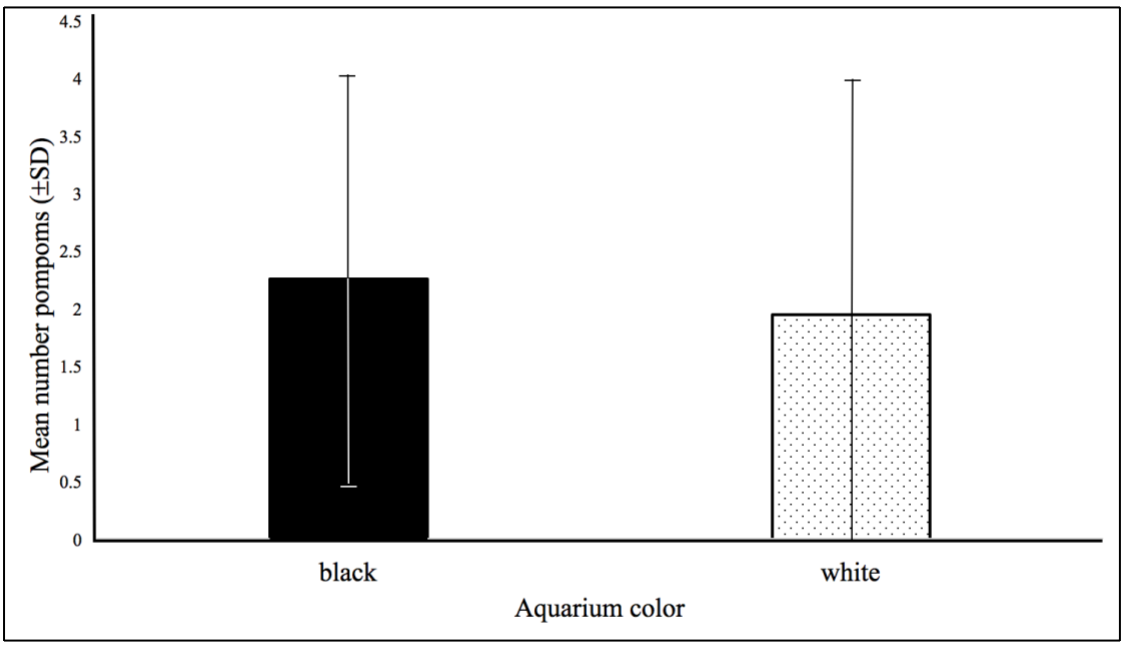

Figure 4. Decorating Based on Background Color. Mean number of pompoms crabs used to decorate in either a black or white aquarium.

3.3 Experiment C – Decorating Based on Decorations Matching or Mismatching Background

The matching treatment (black background with black pompoms or white background with white pompoms) or mismatching treatment (black background with white pompoms or white background with black pompoms) did not significantly impact the number of pompoms the crabs used to decorated after 10 hours ($\chi 2$= 16.01627, p=0.3810; Table 4; Figure 5). In the match treatment, crabs decorated with an average of 2.1 ±1.7 SD pompoms, while similarly in the mismatch treatment, crabs decorated with an average of 2.1 ±2.1 SD pompoms.

Table 4. Experiment C Statistics.

Model	Log Likelihood	DF	χ^2	$p>\chi^2$
Difference	8.008136	15	16.01627	0.3810
Full	69.243034			
Reduced	77.251170			
Effect Likelihood Ratio Test				
Source	Nparm	DF	L-R χ^2	$p>\chi^2$
Treatment	15	15	16.0162729	0.3810

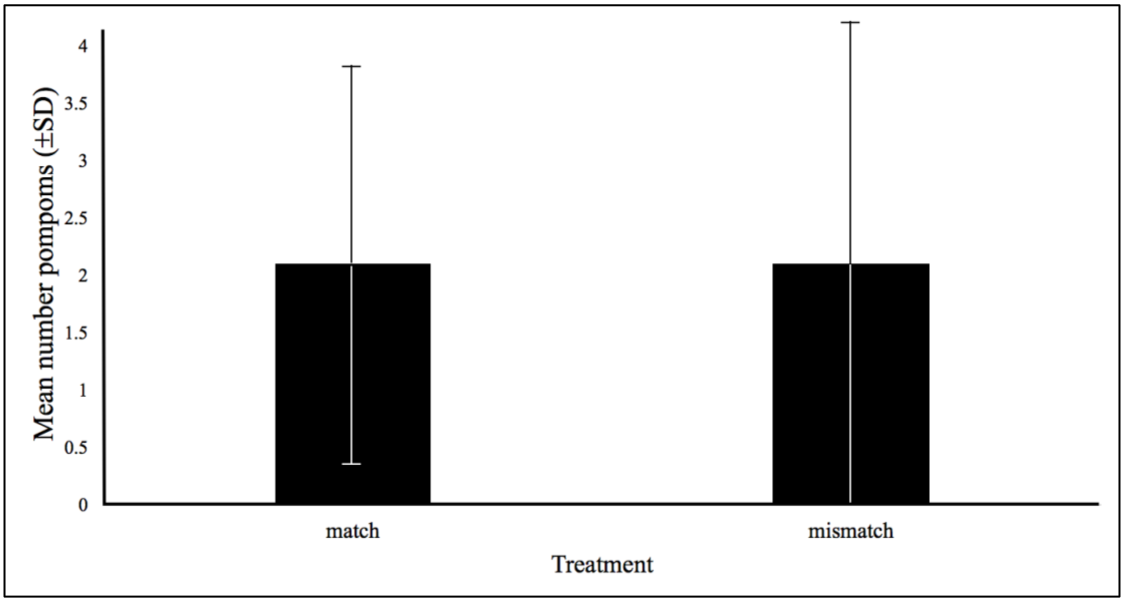

Figure 5. Decorating Based on Decorations Matching or Mismatching Background. Mean number of pompoms crabs used to decorate in either a match treatment – black background with black pompoms or white background with white pompoms – or a mismatch treatment – black background with white pompoms or white background with black pompoms – at the end of 10 hours.

3.4 Experiment D – Background Color Preference After Decoration

The color of *C. retusa's* pre-decorated pompoms did not significantly impact the background color it selected. As seen in Experiment A, *C. retusa* individuals overwhelmingly selected to be on the black side of the aquarium (GLM p=0.9932), regardless of the time the observations were made (GLM p=1) or the color of the pompoms (GLM p=0.9951; Table 5; Figure 6). The crabs were found on the black side during 90.3% of the observations, similar to Experiment A, when background preference was determined in the absence of decoration, where the crabs were found on the black side during 90% of the observations. When 14 crabs were pre-decorated with white, 13 were found on the black side during all of the observations, i.e. the crabs did not choose to rest on the side that matched the color of their decorations.

Table 5. Experiment D Statistics.

Model	Log Likelihood	L-R χ^2	DF	p>χ^2
Difference	14.0604983	28.1210	22	0.1717
Full	74.9384127			
Reduced	89.998911			
Goodness of Fit Satistic		χ^2	DF	p>χ^2
Pearson		322.0000	617	1.000
Deviance		149.8768	617	1.000
Effect Test				
Source		DF	L-R χ^2	p>χ^2
Time		19	0.0071608	1.0000
Pompom Shade		1	3.8039 e^{-5}	0.9951
Aquarium Shade		1	0.0000723	0.9932
Pompom Shade * Aquarium Shade		1	6.7249 e^{-5}	0.9935

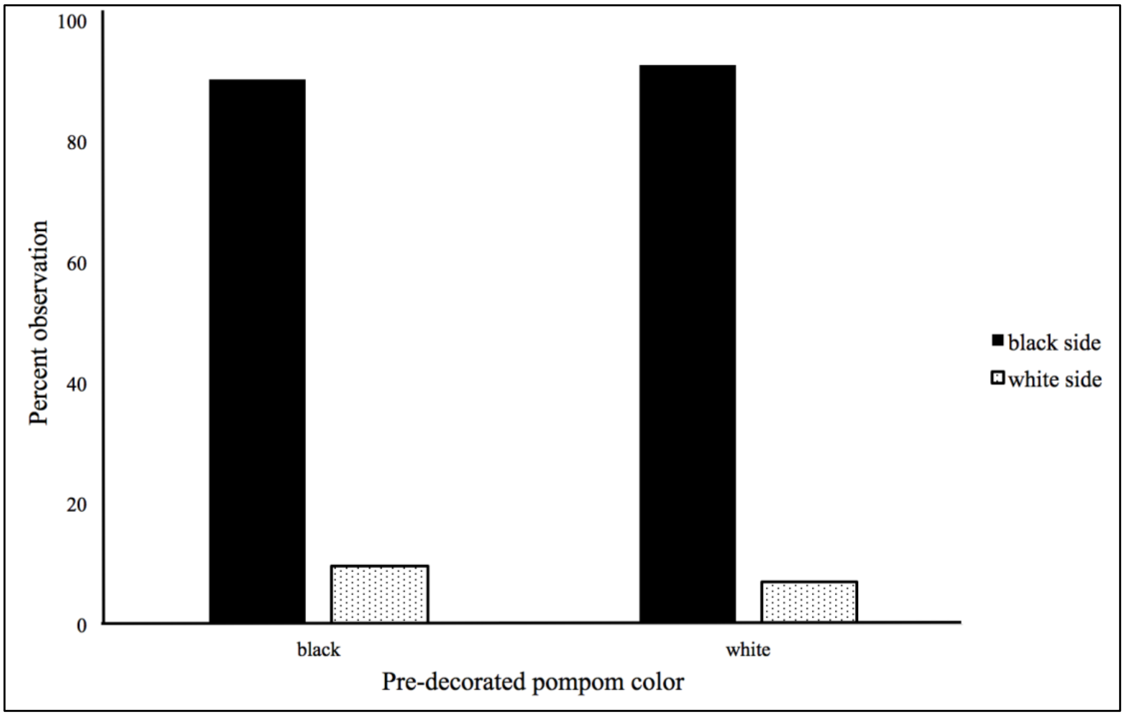

Figure 6. Background Color Preference After Decoration. Percent of observations of crabs with either black or white decorations on either side of the aquarium over five hours; black pre-decorated pompoms on black side, black pre-decorated pompoms on white side, white pre-decorated pompoms on black side, and white pre-decorated pompoms on white side.

3.5 Experiment E – Decorating Based on Background Color

Data were collected every 30 minutes for 10 hours, however for the purpose of comparing with Experiment F (see below), only the data from the final observation were analyzed using an ANOVA. Significant differences were found in the decoration behavior of the individual crabs (ANOVA F= 3.0279, p=0.0008), however neither the color of the pompoms selected (Fisher's LSD p=0.3771) nor the color of the aquarium in which the crabs were held (Fisher's LSD p=0.7036) drove the significant result. Instead, individual crabs drove the significant result, with three individuals decorating significantly more and three individuals decorating significantly less than the other individuals tested (p=0.0003; Figure 7). After 10 hours, the crabs matched more than half of their decorations to their background only 28.6% of the time. On average, individuals decorated with 1.5 ±1.2 SD black pompoms while in a black aquarium, 1.4 ±1.1 SD white pompoms while in a white aquarium, 1.6 ±1.3 SD black pompoms while in a white aquarium, and 1.2 ±1.2 SD white pompoms while in a black aquarium.

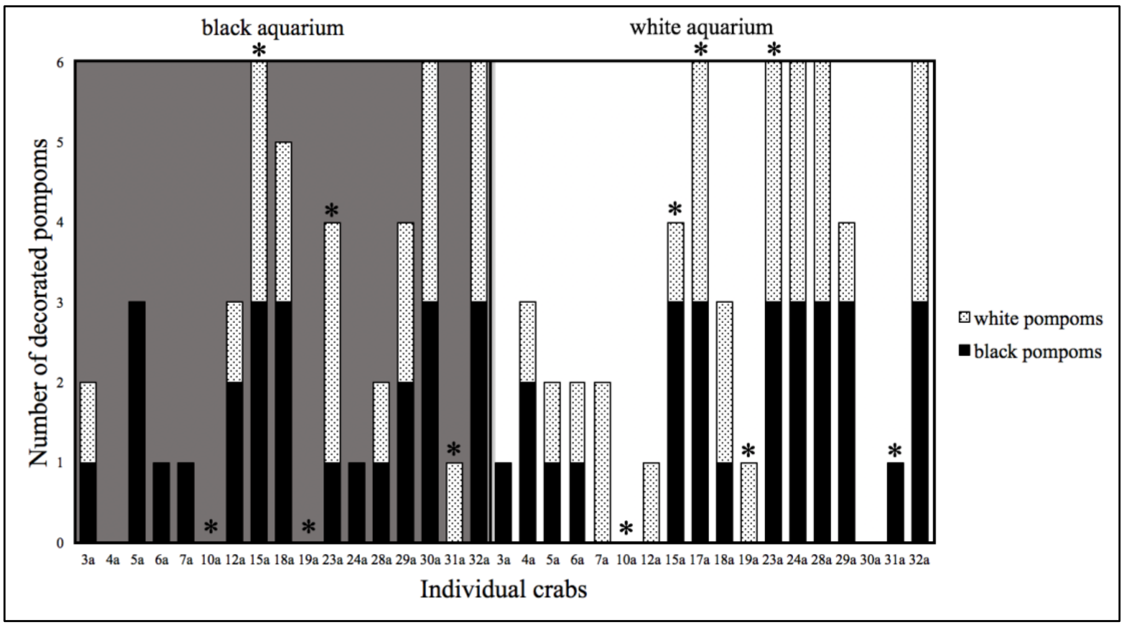

Figure 7. Decorating Based on Background Color. Number of each color pompom individual crabs used to decorate in different color aquaria after 10 hours; * indicates significantly different decorating behaviors (α=0.05).

3.6 Experiment F – Decorating Behavior with Visual Cues Removed

Light was removed from the experimental setup to quantify *C. retusa's* decorating behavior in the absence of visual cues. The individuals significantly differed in their decorating behavior (ANOVA F=2.5389, p=0.0371). Similar to Experiment E, the significant difference was once again driven by the behavior of individual crabs (Fisher's LSD p=0.0280) rather than the color of the selected pompoms (Fisher's LSD p=0.1559), or the color of the aquarium in which the crab was held (Fisher's LSD p=0.6816; Figure 8). In this experiment, a single individual decorated with six pompoms, approximately five pompoms above the mean number (1.3 ±1.6 SD). On average, individuals decorated with 0.6 ±0.7 SD black pompoms while in a black aquarium and 1 ±1.1 SD white pompoms while in a white aquarium, 0.6 ±1.1 SD black pompoms while in a white aquarium, and 0.4 ±0.5 SD white pompoms while in a black aquarium.

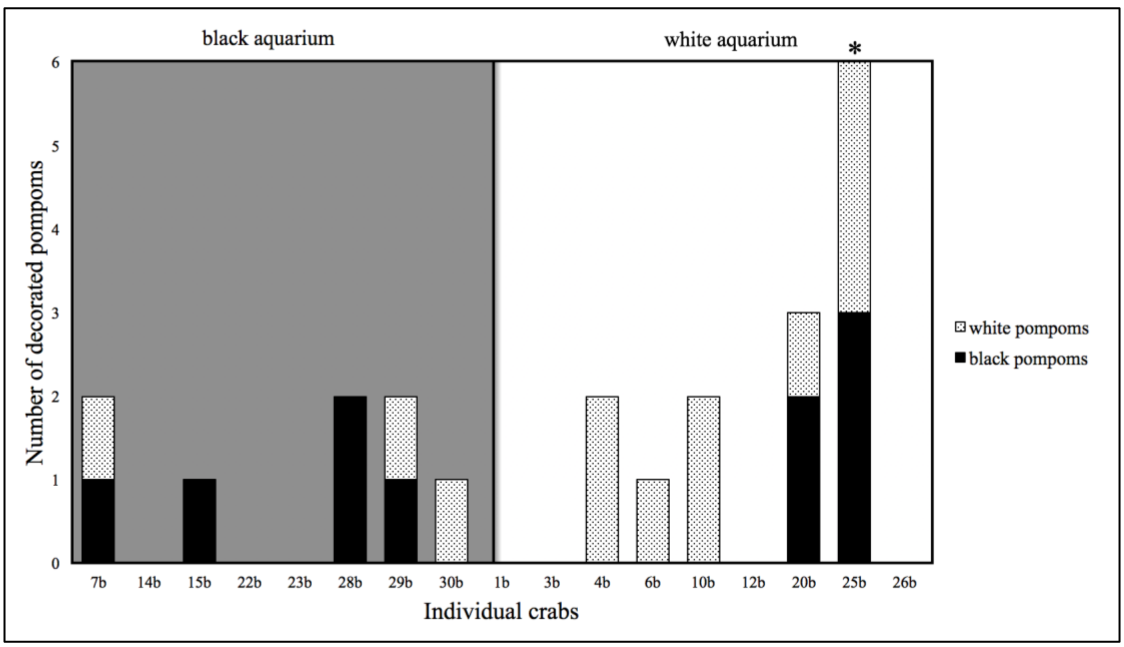

Figure 8. Decorating Behavior with Visual Cues Removed. Number of each color pompom individual crabs used to decorate in different color aquaria after 10 hours without visual cues; * indicates significantly different decorating behavior (α=0.05).

When comparing the number of pompoms crabs used to decorate after 10 hours from both Experiment E (light) and Experiment F (dark), the crabs significantly differed in the number of pompoms they used to decorate (ANOVA $F=4.1012$, $p=0.0086$). Neither the color of the aquarium ($p=0.5725$) nor the color of the pompoms ($p=0.7364$) impacted the number of pompoms they used to decorate. But condition (dark or light) was statistically significant ($p=0.0008$). In the dark, *C. retusa* decorated with less pompoms however, the color of pompoms was not statistically different from when it was in the light.

Chapter 4

DISCUSSION

Camposcia retusa does not decorate to achieve background color matching. Crabs displayed no preference for selecting decorations that matched a background when held in a single-color aquarium, and also displayed no preference for a background that matched the color of their pre-decorated pompoms. The more compelling evidence that background color matching is not being utilized is the comparisons of Experiments E and F, which analyzed the decoration selection in the presence and absence of light. Although crabs placed more decorations on their bodies when light was available, no significant difference was found between the color selection of the pompoms when crabs were in a light versus a dark aquarium.

While the use of background color matching was not identified for *C. retusa*, a number of other camouflage strategies could still explain the decoration behavior in this species. While the specific predator that targets *C. retusa* has not been identified, a variety of Indo-Pacific reef predators that are known to consume other crab species are likely candidates, including eels, cephalopods, and fishes. The most common predator to *C. retusa* is unknown, but once a common predator has been identified, follow up research on the predator's visual field is necessary to better understand the decoration selection by *C. retusa* in the wild.

Visually inconsistent backgrounds make it difficult to optimize cryptic coloration (Merilaita & Lind 2005; Michalis et al. 2017). For *C. retus*a, cryptic camouflage strategies not involving color may work better as this species lives on the benthos of coral reefs with visually-inconsistent backgrounds. Background pattern matching occurs when an organism appears as a random sample of its natural background (Cuthill et al. 2005). Crabs pick up various materials from the reef, and as a result they are never one color. Instead, they are mottled like their background. The bottom of a coral reef is littered with various organisms, debris, sand, and a suite of other material with various colors and forms. It was found that a single 20-m coral reef transect contained three types of algae, eight coral species, three echinoderm species, various sponges, worms, and ascidians, and several reef substrate types (Ramos et al. 2010). With such a diverse benthic community in a relatively small area of reef, the benthic environment is constantly shifting. The background is eclectic and ever-changing, potentially the reason why this species evolved decorating behavior as a camouflage strategy rather than an inherent carapace color or pattern. Decorating would allow crabs to change *with* their background.

Behaviors such as background choice can enhance an organism's background matching camouflage (Stevens & Ruxton 2019). Three non-mutually exclusive mechanisms have been proposed for how organisms make the correct background choice: (1) have a genetic preference for certain habitats, (2) learn to associate with certain habitats, or (3) use senses to determine how close their visual appearance matches their habitat (Stevens & Ruxton 2019). Research conducted here only experimentally evaluated the third mechanism, and conclusively demonstrated that *C. retusa* is not able to determine its visual appearance to match the habitat. However, the first and second mechanisms require further research. *Camposcia retusa's* habitat preference could have evolved before its camouflage strategy, or it could have learned to associate with its habitat for other reasons such as food, age, reproductive status, etc. (Stevens & Ruxton 2019). Living in coral reef benthos, scavenging for food, and moving through backgrounds that change every few inches, *C. retusa* would be unable to have an optimized visual camouflage strategy (Ramos et al. 2010). Additionally, the crabs that were sourced for this experiment were adult individuals, collected from a reef. If decoration behavior is a learned process, the behavior displayed in this experiment was developed on a coral reef rather than in a laboratory. This could be site specific or age specific, therefore additional experiments focused on naïve individuals collected from different locations would provide additional evidence if mechanisms 1 or 2 were being used.

Background matching and disruptive coloration are the two main strategies for avoiding predator detection, but they are not mutually exclusive (Merilaita & Lind 2005). *Camposcia retusa* could be trying to accomplish both. More research has been conducted on background matching than disruptive coloration, but disruptive coloration appears to be a more effective camouflage strategy (Merilaita & Lind 2005, Cuthill et al. 2005). Disruptive coloration is a set of markings that creates the appearance of false edges and boundaries, and hinders the detection or recognition of an organism's, or part of an organism's, true outline and shape (Table 1; Stevens & Merilaita 2009a). *Camposcia retusa's* decorating behavior might be facilitating a modified version of the cryptic camouflage strategy of disruptive coloration (Table 6). Rather than relying on two-dimensional markings as most other organism, *C. retusa* utilizes three-dimensional decorations to disrupt its form in order to prevent visual predators from recognizing the crab as a crab. The three-dimensional decorations utilized in this modified strategy may be able to more effectively break up an outline than the two-dimensional markings involved in disruptive coloration. Further research into the visual ability of *C. retusa's* predators to detect two-dimensional markings versus three-dimensional form is required to validate this hypothesis.

Table 6. Proposed Modified Camouflage Strategies.

term	defintion
disruptive decoration	a cryptic camouflage strategy in which three-dimensional objects attached to an organism's exterior surface create the appearance of false edges and boundaries, and hinders the detection or recognition of an organism's true outline and shape (modified from Stevens & Merilaita 2009a)
distractive decoration	a cryptic camouflage strategy in which three-dimensional objects attached to an organism's exterior surface direct the attention or gaze of the target from traits that would give away the organism (modified from Stevens & Merilaita 2009a)
chemical disruption	a cryptic camouflage strategy in which the odor of an organism's decorations hinders the detection or recognition of the organism's true odor (modified from Stevens & Merilaita 2009a)
background chemical matching	a cryptic camouflage strategy where the odor of the organism generally matches the odor of one or several background types (modified from Stevens & Merilaita 2009a)
chemical aposematism	an anti-predator strategy where an organism uses an odor signal to warn predators that it is unpalatable or poisonous (modified from "aposematism" 2020)
tactile disruption	a cryptic camouflage strategy in which three-dimensional objects attached to an organism's exterior surface create the feeling of a false texture and hinders the detection or recognition of an organism's true texture (modified from Stevens & Merilaita 2009a)

It is thought that some visual predators identify organisms as prey by recognizing their physical form. Insects have evolved to decorate to make their physical form unrecognizable (Jackson &Pollard 2007). Visual predators could detect the decorated insects as items separate from the background but not recognize them as items of prey (Jackson &Pollard 2007). Through this disruptive decoration strategy, *C. retusa's* decorating behavior could aim to disrupt the edges of its outline in order to simply not look like a crab, making themselves unrecognizable as a viable prey item to a predator. Wild-caught *C. retusa* were most commonly decorated with sponge (Brooker et al. 2018). The sponges' variable shapes aid in disrupting the outline of the crab and therefore potentially make it visually unrecognizable by predators. Additionally, many Majoid species show little discretion in their choice of decorations and have been seen decorating with a variety of unnatural materials in aquariums, including strips of paper, chips of cement, and pieces of hamburger (Wicksten 1993, Wicksten 1980). This could be further evidence that the crabs are simply aiming to not look like a crab, instead of attempting to match their background.

As with disruptive coloration, *C. retusa's* decorating behavior could be classified as a modified distractive decoration strategy (Table 6). Distractive markings direct the attention or gaze of the target from traits that would give away the organism (Table 1; Stevens & Merilaita 2009a). Again, markings are typically two-dimensional features on an organism's exterior, however *C. retusa* utilizes three-dimensional decorations to distract predators from its most recognizable features. In a laboratory experiment, *C. retusa* actively chose to decorate different parts of itself with varying amounts of pompoms (Brooker et al. 2018). This indicates there is a strategy involved in *C. retusa's* placement of decorations, potentially prioritizing distraction from the most visible or recognizable parts of itself. *Camposcia retusa* concentrated its decorations on its rear walking legs, potentially as the best way to evade recognition by predators by breaking up its shape, since the large legs make up the majority of the crab's outline (Brooker et al. 2018). It is also common for Majoid crabs to cover their mouth parts with decorations since they are constantly moving and twitching and could easily reveal a crab's location and identity in an otherwise static environment (Hultgren & Stachowicz 2009).

Both disruptive decoration and distractive decoration camouflage strategies make sense for *C. retusa* from an evolutionary point of view. Disruptive coloration and distractive markings would have had to evolve into inherent features on the crabs' carapace, which might not have been effective in *C. retusa's* mottled and ever-changing environment (Ramos et al. 2010). The crabs' use of three-dimensional objects might better serve as an antipredator function in their unique habitat.

Camposcia retusa's decorating behavior might be facilitating the camouflage strategy of masquerade. Masquerade occurs when recognition is prevented by resembling an uninteresting object (Table 1; Stevens & Merilaita 2009a). The crabs decorate with material from their benthic, coral reef habitat. Coral reefs are littered with broken shells, bits of coral skeletons, live sponges, and many other types of debris. By attaching any number of these items, the crabs could be aiming to look like them. Appearing to be anything other than a crab will help them avoid their visual predators.

Lastly, there is the possibility that *C. retusa's* decorating behavior might not be facilitating any camouflage strategy. Rather, it might be doing the opposite. Instead of attempting to conceal itself and avoid detection, *C. retusa's* decorating behavior could be an aposematic strategy. Aposematism is an anti-predator strategy where an organism uses a signal, especially a visual signal of conspicuous markings or bright colors, to warn predators that it is unpalatable or poisonous (Table 1; "aposematism" 2020). The most common material found on wild-caught *C. retusa* was sponge (Brooker et al. 2018). Certain sponges contain secondary metabolites that are noxious.

Whether or not they are conspicuously colored, sponges are recognized by many marine organisms as unpalatable and therefore use of sponge decorations could serve as a warning. However, sponge decorations could also facilitate non-visual camouflage strategies. Enhancing visual camouflage via behavior may be mediated by olfaction or other sensory systems (Stevens & Ruxton 2019). Backgrounds vary in most habitats so organisms in those habitats need to be able to choose the background that will best conceal them from predators, whether that be through vision, olfaction, or a selection of other sensory modalities (Stevens & Ruxton 2019).

An understanding of the sensory systems of *C. retusa*, and its predators might provide insight into the mechanism behind its decorating behavior. Their predators likely use a variety of sensory systems for hunting, including vision, olfaction, and touch. The variety of senses used by predators indicates a need for a variety of camouflage strategies. It has been suggested that the obvious decorating behavior of some organisms can function in ways other than vision (Brandt & Mahsberg 2002). Evidence for effective crypsis in senses other than vision, including hearing, olfaction, electroreception, mechanoreception, and temperature sensors has been identified (Ruxton 2009). *Camposcia retusa* could be using decorating to disrupt many of these sensory modalities of its predators. Majoids' setae, instead of their eyes, might provide information to the crab on where their decorations are located. If this is the case, vision might not be an important sensory system for the decorating process or even the crabs' decoration selection. Crabs might choose decorations based on the material's scent, texture, or some other combination of properties in order to disrupt predator senses other than vision.

Background *chemical* matching by *C. retusa* could facilitate a modified version of cryptic camouflage (Table 6). While *C. retusa* is not background *color* matching, there are many other ways this organism could be avoiding detection or recognition by its predators. It might be that *C. retusa* is trying to blend into its chemical background by integrating chemical cues from its variable habitat through its decorations, allowing the crabs to mask their odor cues with environmental chemicals rather than producing only the odor cues of a crab.

In addition to chemical cues masking the chemical signature of the crabs, the chemical cues of the crabs' decorations could be beneficial in another way. Using a modified aposematic strategy, crabs could be enlisting chemical aposematism to conspicuously decorate, displaying unpalatability through chemically defended sponges and seaweeds (Table 6). Sponges are well-known for their noxious properties. Similarly, juvenile *Libinia dubia*, a western Atlantic decorator crab species, preferentially cover themselves with *Dictyota menstrualis*, a brown alga with secondary metabolites unpalatable to herbivores (Stachowicz & Hay 1999). Decorating with this chemically noxious alga deters *L. dubia's* omnivorous fish predators that actively avoid consuming *D. mentrualis* (Stachowicz & Hay 1999).

Further, by adorning their legs and carapace with abiotic and biotic elements, *C. retusa* could also be employing *tactile disruption* (Table 6). The three-dimensional decorations can break up the crabs' natural texture so that they do not feel like a crab to their tactile predators. Experiments with two West African assassin bug species found that a dust coat prevents chemical and tactile recognition by their prey and backpacks of ant carcasses confused visual predators by making the bugs unrecognizable as valid prey (Brandt & Mahsberg 2002). The decorations of *C. retusa* could function in the same manner. The dust coat and ant carcass backpack made the bug unrecognizable to blind, tactile, and chemical predators (Brandt & Mahsberg 2002). Not all species of spider crab decorate, especially if their carapace texture already matches that of their habitat (Wicksten 1980). *Camposcia retusa* might be trying to make the texture of its carapace unrecognizable to a tactile predator that might crawl right over it.

In summary, *C. retusa's* decorating behavior does not facilitate the cryptic camouflage strategy of background color matching. Decorating might prevent predation by facilitating a number of other camouflage and non-camouflage strategies aimed at impacting the visual or non-visual sensory systems of its predators. Further research into the mechanism behind decorating and the sensory systems of *C. retusa* and its predators is required to test the strategies proposed here.

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