

SIMPLE SHAPE LEARNING OF THE TWO STOMATOPOD SPECIES: HAPTOSQUILLA TRISPINOSA AND PSEUDOSQUILLA CILIATA

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Current climate conditions and anthropogenic activities have resulted in coral cover homogenization, reef structural complexity simplifications, prey item decline. Recognizing changes in shape, especially in a visually-dominant organism, can assist in dealing with these reef structure changes and prey availability loss. I examined the ability of two stomatopod species: *Haptosquilla trispinosa* and *Pseudosquilla ciliata* to learn to distinguish between a circle and a square, using simple food conditioning techniques for 30 days and 15 days, respectively, including a priming period of 10 days per group. Both *H. trispinosa* and *P. ciliata* groups were conditioned to the circle. Each group had four individuals. *H. trispinosa*'s total number of responses decreased over time, with an increase in correct responses and decrease in incorrect responses. This trend indicates the presence of shape discrimination learning as well as test learning. *P. ciliata* had a higher percentage of correct responses across all time blocks in comparison to *H. trispinosa* due to their differing predator tactics. *P. ciliata* are spearers, ambush predators that rely on quick information intake to surprise prey, while *H. trispinosa* are smashers, foraging predators that depend on repetitive impacting motions to stun/ kill prey. More behavioral studies need to be conducted to assess the stomatopod's ability to cope with current environmental conditions, but there is clear visual discriminatory learning capability in this organism that can assist in flexible adaptations.

Introduction

Coral reefs are some of the most diverse and delicate habitats in the world, supporting a multitude of species (Sale 1977). These ecosystems are very fragile and are sensitive to disturbances and anthropogenic activities (Wilson et al. 2006). Current climate conditions and anthropogenic activities have altered the coral reef habitat, by reducing settlement rate and increasing physical stress and algal growth (Riegl et al. 2012). Recurrent heavy mortality of corals through these events could cause a homogenization of coral cover, meaning lower coral cover and alteration of coral community structure by disadvantaging branching, encrusting and arborescent corals (Riegl et al. 2012), which has significant implications for coral reef organisms. Trawling, an anthropogenic fishing event in which a large net is dragged along the sea floor, not only leads

to a decrease in the reef's overall structural complexity, but also a decrease in the diversity of local marine crustaceans (Maynou and Cartes 2012). These changing conditions lower the diversity of habitats that organism may choose from and can also alter the availability and size of potential prey. Habitat degradation will compound effects of fishing on coral reefs as increased fishing reduces large-bodied target species, while habitat loss results in fewer small-bodied juveniles and prey that replenish stocks and provide dietary resources for predatory target species (Wilson et al. 2010). With decreasing numbers and size of prey, it is important that an animal be able to recognize the prey available, especially if it is an exceedingly visually-reliant predator.

Stomatopods, marine crustacean with highly developed visual systems (Cheroske et al. 2006), are one of the most sensitive coral reef species to ecological disturbances (Schiff 1989, Erdmann 1987). Their complex visual system may have facilitated the evolution of visually-dominant intraspecific behaviors (Chiao et al. 2000). Stomatopods are known to signal to conspecifics using brightly-colored body parts (Caldwell and Dingle 1979) to communicate a willingness to mate or aggression (Cheroske and Cronin 2005). These highly optically-reliant behaviors indicate the importance in stomatopods being able to visually assess their conspecifics and surroundings (Schiff 1989, 1996). Therefore, to further our understanding of these unique creatures, it is important to recognize the extent of their visually reliant shape-learning abilities.

Although stomatopods are excellent models for learning research due to their behavioral complexity (Cronin 2006), little is known about their shape-identifying abilities. There have been multiple studies conducted that have shown their capability in learning tasks through training due to their flexible behavior (Reaka 1980, Caldwell and Lamp 1981, Caldwell 1982, Caldwell 1985, Caldwell 1992, Marshall et al. 1996, Marshall et al. 1999). Shape-learning studies in crustaceans have a variety of behavioral implications, from predatory tactics (Wells 1962) to diet choices (Kaiser et al. 1993). Studying their ability to learn shapes can lead to more knowledge about the associations between their behaviors and their environment (Langdon 1971). To further understand the effects of climate change, trawling, and loss of prey on these marine crustaceans, it will be important to look at the extent of their ability to recognize novel shapes and make the relative cost/benefit associations, especially with an animal

who relies heavily on visual discrimination and lives in a structurally and ecologically changing habitat.

The primary objective of this study is to explore the learning ability of the stomatopods, *Haptosquilla trispinosa* and *Pseudosquilla ciliata*, to distinguish between two different simple shapes, the square and the circle. I hypothesize the stomatopod will be able to differentiate the shapes, because stomatopods have such functionally complex eyes: apposition compound eyes that contain more photoreceptor types than any other animal (Marshall et al. 2007).

Methods

Experimental setup I placed the eight *H. trispinosa* and 4 *P. ciliata* individually into their own custom-constructed habitat. The constructed habitat is a plastic tank (22 x 15 x 13.5 cm) filled halfway with a mix of sand, gravel, and coral rubble (Figure 1). I washed the mixture 10-15 times in deionized water then soaked in salt water, pH 7.8 and 34 ppm salinity, for 2 days. A glass vial (radius 2 cm and 5.08 cm long) wrapped in black electric tape, served as the “burrow” and was buried in the sand with the opening emerging. I poured in water to one inch below the top. The water pH was maintained at a constant 7.9, which is the current standard oceanic pH (Bindoff et al. 2007) and at a salinity of 34 ppm. Temperature was maintained at 25°C, and tanks were kept in a lab lit from 8-5 PM. Water was changed daily.



Figure 1. The constructed habitat. Gravel mixture was maintained in a hill-like structure to support the glass vial “burrow” that housed the animals. The mixture was purchased from a local aquarium enthusiast store.

Priming Technique I introduced the eight stomatopods into the system in the late afternoon at 3 pm and gave them 24 hours to acclimate to their new surroundings. During these 24 hours I did not feed them. After 24 hours passed, I primed the stomatopods for 2 weeks with 2 trials per day, once in the morning between the hours of 9-11, and once in the afternoon between 2-4, in order to familiarize the stomatopods to the ziptie. To prime the stomatopods, I attached food, bits of grass shrimp, to the circle, the positive stimulus in this experiment, on the priming device so that the stomatopods

would associate the shape with food. The priming devices were a singular zipties with a black plastic circle (radius of 3.4 mm) glued on the front of bottom area (2A and 2B).

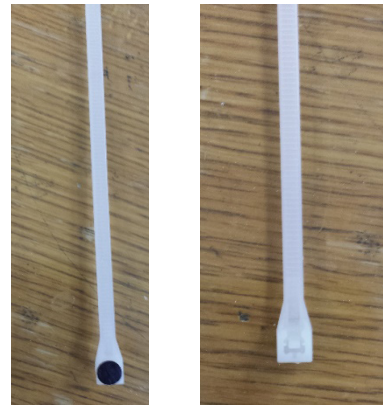


Figure 2. Priming devices and procedure. (A) Front of priming ziptie. Animals were only primed using zipties with their respective positive stimulus. This was a priming device used for groups conditioned to circles. (B) Back of priming ziptie. Bits of grass shrimp stored in square crevice for easy access if animals made contact with ziptie.

Each species was represented by 4 stomatopods per group. Both species, *Haptosquilla trispinosa* and *Pseudosquilla ciliata*, were primed and conditioned to the circle. The stomatopods were only presented with the “positive” shape, the circle, during this priming period to encourage responsiveness through acquisition of food. The square, the negative stimulus, was not used in order to maintain consistency with respective positive or negative shape associations. I held the ziptie an inch in front of the burrow until the stomatopod swam out and touched it. I gave the stomatopod 3 minutes to touch the ziptie. Once the stomatopod made contact with the ziptie, I turned around the ziptie so that the stomatopod could access the bits of grass shrimp. If the stomatopods did not respond and failed to make contact with the shapes after 2 weeks of priming, I altered my priming technique: holding the “positive” shape’s ziptie, the circle, in front of the burrow for a minute and then presenting them the feeding rod directly after for a feeding opportunity.

Conditioning Technique To begin testing, I conditioned the *H. trispinosa* for one month and *P. ciliata* for 15 days due to time constraints, after the stomatopods actively responded to the shapes repeatedly during the priming period. I used standard conditioning procedure (Barker et al. 1977): if the animal selected the right shape, the circle, it was given positive reinforcement in the form of food, if not (selected the square), it was deprived of that chance to eat. The constructed testing device was held one inch in front of their “burrow” (Figure 3A), so that the animal could see the shape, but would not be given the opportunity to feed unless it swam out and made contact with the “positive” stimulus, the circle (Figure 3D). If the animal touched the circle, it was rewarded with a food stick (Figure 4A and 4B) immediately after. If the animal swam toward the square, negative stimulus the device was abruptly yanked up, and a feeding opportunity was denied. I ran 2 trials on each stomatopod per day for a month; Once in the AM,

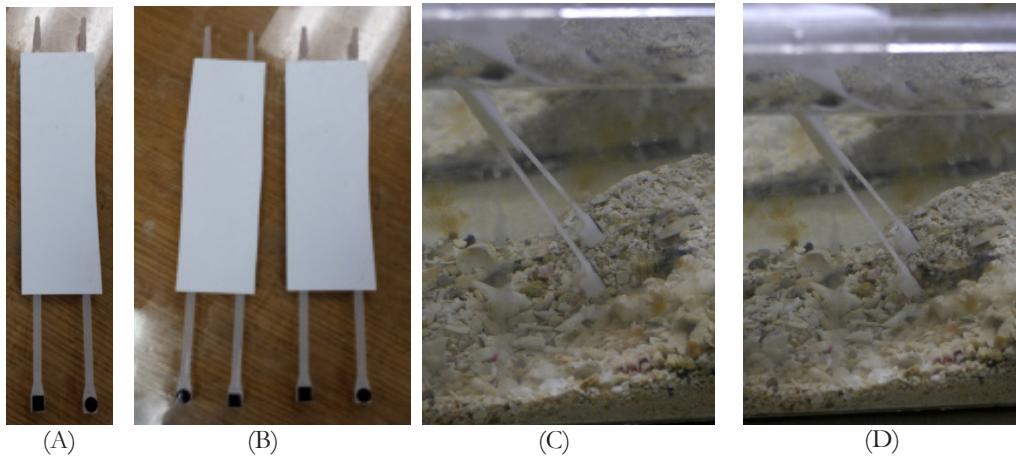


Figure 3. Stomatopod testing. (A) Constructed device. Shapes were cut out of black plastic. The two zipties were stabilized with a rectangular piece of white plastic. Animals had to actively select one of the shapes, either the square or circle. (B) Mirror zipties. To reduce bias, I randomly picked one of the two testing devices that were mirror images of each other for that day's testing. (C) Testing Method. Testing device is held one inch in front of "burrow" for up to 3 minutes. (D) Stomatopod Making Contact with Testing Device. The *H. trispinosa* had chosen its respective positive stimulus, the square.

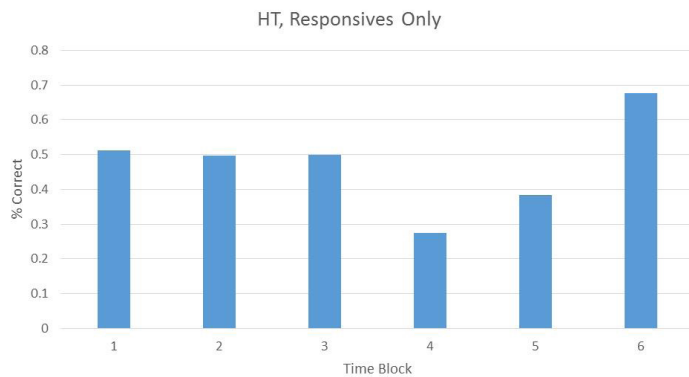


Figure 4. HT's responses in testing period. Histogram displays the responses of 4 animals over the 30-day conditioning period.

between the hours of 9-11 and once in the PM, between the hours of 2-4.

Testing To test the learning ability of the stomatopod to identify different shapes in conjunction with the conditioning period, I constructed a testing device consisting of 2 white zipties, one inch apart. These zipties were held together with a thin strip of white plastic and a black plastic shape was glued on the back crevice, flat side, of the ziptie (Figure 3A). These devices were used previously in the conditioning period as well. To minimize bias, I made 2 constructed testing devices, that were mirror images of each other, with opposite shape orientations glued on the zipties (Figure 3B); For example, in the first device, I put the circle on the right ziptie and the square on the left ziptie of the constructed testing device and in the second device, I put the circle on the left ziptie and the square on the right ziptie of the constructed testing device. I then closed my eyes and arbitrarily chose a constructed testing device for the day.

Data Collection and Analysis I collected data for 4 *H. trispinosa*, with 2 trials per day, once in the AM and once in the PM, over a month, and for 4 *P. ciliata* similarly. The data that I collected were the stomatopod's reactions, length of time each took to make a decision, the ziptie shape orientation, date, and operator. I then categorized the stomatopod's reactions into selected the "right shape" (if it chose the correct positive stimulus), the circle, "wrong shape", the

square, or "unresponsive". If the stomatopod failed to make contact with the ziptie after 3 minutes, it was counted as unresponsive.

To answer my research question, I determined if the number of times the stomatopods selected the right shape, the circle, increased over time. I took proportions of the right shape chosen over the total number of times and proportions of right shape chosen over total number of responses. I split the experimental time period into 5-day increments and then examined how the average per Time Block changed over the month-long period or 15-day period. In effect I calculated whether the number of times they selected the positive stimulus, the circle, increased over time and number of times they selected the negative stimulus, the square, decreased over time. I calculated these proportions and reported the data in percentages, following research papers that tested for the same outcomes (Kawamura 2001, Wells 1962).

Results HT, *Haptosquilla trispinosa*: The percentage of correct responses, in which the individuals selected the circle, increased from 51% in Time Block 1 to 68% in Time Block 6 (Figure 4). With unresponsives not included, the percentage correct was 50 for Time Block 2 and 3. Time Block 4 was 28% while Time Block 5 was 38%. There was a significant drop in percent correct responses in Time Block 4 and then a gradual increase over the next 2 Time Blocks.

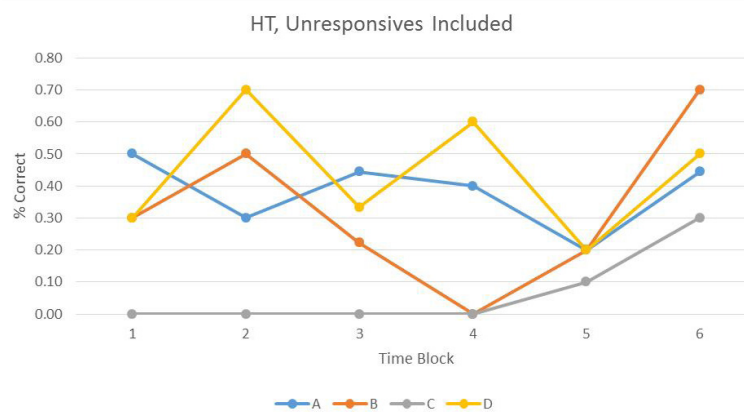


Figure 5. HT individual responses in testing period. Line graph displaying the percent corrects of each animal in each Time Block over the 30-day conditioning period, including counts of "unresponsive".

For individual responses, when unresponsives were scored as incorrect, Stomatopod A started at 50% incorrect while B started off at 30, C did not respond until Time Block 5, and D's initial percentage was 30 (Figure 5). All animals, except Stomatopod A, had a higher final percentage correct than initial. Everytime Stomatopod A responded, it selected the positive stimulus correctly. The highest percentage of correct responses occurred in either the 2nd or 3rd Time Block for each animal. Stomatopod A's peak was 44% in 3rd Time Block. Stomatopod B's peak of 50% in the 2nd Time Block and Stomatopod D's peak, 70%, in 2nd Time Block. Stomatopod C went from 10% to 30% respectively for Time Block 5 and 6. After the peak, the time period with the highest percentage of correct responses, there was a drop in percentages leading to the lowest percentages for the entire conditioning period per animal. Stomatopod's A lowest percentage was 20, in Time Block 5, following a decline from the peak in Time Block 3. Stomatopod B chose the positive stimulus 0 times in Time Block 4, after the peak in 2 Time Blocks previous. Stomatopod D's lowest percentage was the same as Stomatopod A, 20%, in Time Block 5.

When "Unresponsives" were not included in the totals, percentages increased overall. In the post-peak periods, "Unresponsives" increased while there was a decrease in counts of wrongs. (Figure 6).

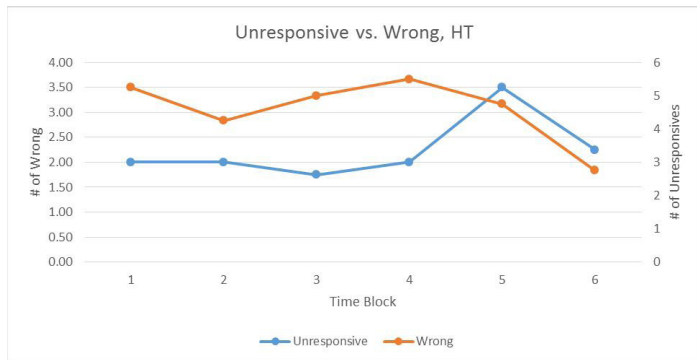


Figure 6. HT's number of unresponsives and wrong. Line graph displaying the count of unresponsives and wrong for further investigation into the post-peak drop.

PC, *Pseudosquilla ciliata* PC overall percentage decreased from 80% to 74% to 59% in Time Blocks 1, 2, and 3 respectively (Figure 7). Individual responses are shown for "Responsives Only" as there was no difference between counting "Unresponsives" and "Responsives Only". Stomatopod I's percentage increased from 67 to 80 to 100. Stomatopod J's percentage went from 100% to 67% to 57%. Stomatopod K's, 100%, 50%, 80%, and Stomatopod L 50%, 100%, 0% (Figure 8). Two stomatopod's molted during this testing period. Stomatopod K molted during the second Time Block, and Stomatopod L molted during the last Time Block.

Discussion

The ability of stomatopods to recognize shapes may provide assistance in analyzing a risk and the importance of that resource (Caldwell 1987), as well as help in recognizing

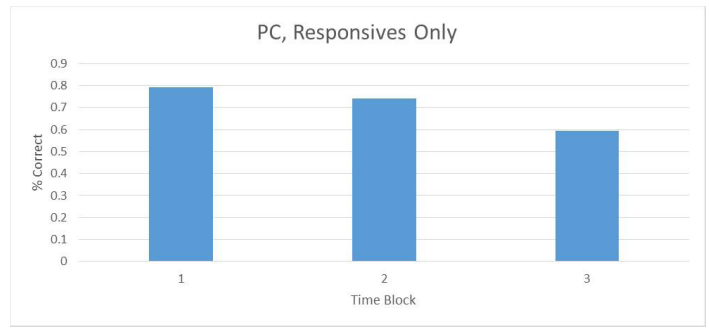


Figure 7. PC individual responses in testing period. Histogram displays the responses of 4 animals over the 15-day conditioning period.

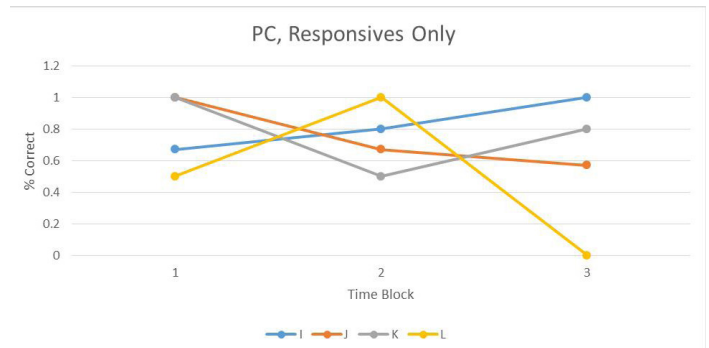


Figure 8. PC individual responses in testing period. Line graph displaying the percent corrects of each animal in each Time Block over the 15-day conditioning period, not including counts of "unresponsive".

another individual, prey, predator, or environment (Cronin 2006). HT responses varied across time blocks, with peaks mainly in the 2nd and 3rd blocks, indicating successful acquisition of shape discrimination learning. There were a greater number of unresponsives after peaks, which decreased the overall percentages, but the stomatopods still correctly selected the positive stimulus in a similar proportion as the peak period's percentage correct. This implies that they did learn that their respective positive stimulus was associated with food and instead of hazarding an uneducated 'guess' as to the positive stimulus, they had ascertained that a particular shape corresponded with the food reward, and therefore only responded when the value of the resource was important enough to them. PC individuals, who were conditioned for 15 days, had higher percentages than HT across all the Time Blocks, which may be attributed to differing food acquisition styles; PC's are spearsers and HT's are smashers.

HT, *Haptosquilla trispinosa* HT overall percentage increased from 51% to 68% (Figure 4). The percentage correct was around 50 until later in the experimental period and then rebounded to 68% by the end of the experiment. There was a decrease in percent corrects after the peak time blocks, the time block with the highest percentage correct, due to the saturation of data with unresponsives; There was an increase in the number of unresponsives after the peak time block. This increase in unresponsives explains the decrease in percentage correct. However, the number of correct responses post-

peak period, is equivalent and even higher, in some cases, than the peak number correct. The number of incorrect selections also decreased after the peak period as compared to the rest of the periods, when not including unresponsives (Figure 6).

Analysis of Post-Peak Drop Although the average percent correct dropped significantly after the peak period, to below the initial percentage, the animals still correctly selected the positive stimulus at equal or greater percentages as during the peak period, because the data was saturated with unresponsives. This increase in correct responses as well as decrease in incorrect responses, while disregarding unresponsives, indicates that the stomatopods were learning. For example, Stomatopod B's peak percentage was 50%, and post-peak was 22%, then a drop to 0% subsequently. Stomatopod B scored 20% after the 0%, which is the post-drop period. When looking at the result that counts responsives only, the post-drop period's percentage is 50 which is equivalent to the percentage of Stomatopod B's peak period. Therefore the stomatopod had selected the positive stimulus the same proportion of times during peak and post-peak, implying that the stomatopods were learning, despite low percentages in the post-peak period. However, the final percentage was always higher than the initial in every animal, except for Stomatopod A which started out with 100%.

There were variations in learning rates among the 4 animals. Although the animals were all the same species, *H. trispinosa*, they were not all collected from the same habitat and were different sexes. They also exhibited different behaviors; Stomatopod D responded rapidly every time, while Stomatopod C did not start responding until later in the experiment. Stomatopod A started out with 100% correct immediately, selecting the positive stimulus for each response every time, and therefore had begun learning during the priming period. The animal had not only acclimated but also made the association between the shape and food in the priming period, therefore selecting the positive stimulus 100% of the time as soon as the testing period began.

PC, Pseudosquilla ciliata PC-Circle stomatopods averaged around 75% correct responses across all time blocks; The response pattern may have been disrupted by the molting of two individuals, Stomatopod K and Stomatopod L, during the middle of the experiment. Activity is known to drop steeply at ecdysis (Lipcius and Herrnkind 1982) and one study found that lobsters showed low food intake for about one month prior to molting (Koike et al. 2003). Both stomatopods had an increase in unresponsives directly before and after their ecdysis. As molting can disrupt behavioral patterns and alter sensory abilities (Lipcius and Herrnkind 1982), Stomatopod K's normal responses may have been changed with this physiological metamorphosis, leading to a decrease in correct responses. Because the conditioning was stopped after 15 days, it is difficult to ascertain the extended effects of molting on shape discrimination for Stomatopod L. Stomatopod I had an increase in percent correct responses per time block, along with a decrease in number of incorrect responses. This

pattern indicates learning was occurring as percent correct responses increased over time and percent wrong responses decreased over time. Stomatopod J was unusual in that the percent correct responses decreased over time. Observing the trends in HT suggests that although the first three Time Block percentages may be subsequently decreasing, it does not signal that the animal is not learning.

HT vs. PC Although HT and PC were both conditioned to circles, they showed different results, probably due to species-specific learning behaviors respective to their prey-capturing methods. *Haptosquilla trispinosa* belong to the stomatopod group of foragers. These are known as smashers because they use a calcified dactyl appendage to crack open shells and stun prey (Weaver et al. 2012, Caldwell and Dingle 1975, Caldwell and Dingle 1976, Dingle and Caldwell 1978). *Pseudosquilla ciliata* are ambush predators or "speakers" which hide in their sandy burrows and capture evasive prey (Caldwell and Dingle 1975, deVries et al. 2012). Ambush predators have to be able to quickly and accurately assess their prey and surroundings as their success relies on speed and knowledge (deVries et al. 2012). They typically only have one chance to obtain their prey, as they rely on the element of surprise. "Smashers" on the other hand rely on repeated striking to break open shells, using their biological "hammer". Ambush predators rely heavily on that first strike to obtain the targeted prey. Smashers depend on the pursuit, search, and repetitive hits to stun or kill prey. This feeding behavior means that speakers only have a limited time frame to react and therefore must counteract that loss of mobility through speed and accuracy. This fits with what I observed as PC's average was higher than those of HT's for each Time Block. This implies the use of a more discriminatory visual system or perhaps slightly more complex eyes. Since the first Time Block, PC had higher percent corrects and therefore was able to distinguish the positive stimulus earlier than HT. Results show that speakers are more likely to recognize shapes and make the relative cost-benefit associations quicker than smashers.

Environmentally-adapted behaviorisms and learning It has been found that stomatopods inhabiting shallow waters have the largest diversity of filter pigments to take advantage of the broad spectrum of light in the environment (Porter et al. 2010; Cronin et al. 2002; Cronin and Caldwell 2002; Cheroske et al. 2003; Cheroske et al. 2009). In another study, the same species of stomatopod, *Gonadactylus smithii*, had different conspicuous color spots and therefore spectral differences as well as invariant eye spot (meral spot) detection as their conspecifics from different depths (Cheroske and Cronin 2005). These all indicate the possibility of variability in behavior and morphology as a result of differing environmental needs. This phenomenon is known as natural selection, in which animals over time respond to changes in their environment through evolving different adaptive morphologies (Darwin 1914). It may be possible that the smashers have a different set of eyes compared to speakers to suit their predator tactic, and this would be an interesting topic to pursue further.

Identifying shapes assists in selecting prey or choice habitats is an important skill for any animal. Learning which shapes are associated with preferred and dangerous prey respectively can prevent fitness-costing circumstances and actions (Caldwell and Childress 1990). Research with cuttlefish suggested that in the natural environment sign-tracking could be adaptive by allowing cuttlefish to associate certain stimuli (e.g., specific rock crevices) with the presence of prey (Cole and Addamo 2005). It is not difficult to imagine such capacities of learning being used in the natural environment by the predator to select prey. This selectivity implies capacities for discrimination and visual control that is important in the behavior of stomatopod (Cronin et al. 2006). The ability to learn the implications of a stimulus can assist the individuals in making any decision, and overall fitness is increased when individual's ability to accurately weigh the cost and benefit of obtaining a resource improves (Caldwell and Childress 1990).

My findings also support the claim that spearers learn more quickly than smashers. The speed at which an animal learns the implications of a stimulus depends on a variety of factors, one of which is the method in which it obtains prey. Spearers, who are ambush predators, rely on rapid assessment of the environmental elements and their relative costs and benefits as opposed to smashers.

Conclusion

My study shows that there is evidence of presence of a visually discriminatory system that is used to distinguish relatively important and unimportant items. If an individual is able to learn quickly and make connections between novel environmental objects and its respective value, then it can make informed decisions and react appropriately with this knowledge and perhaps survive catastrophic events such as climate change and trawling (Caldwell 1987; Caldwell and Childress 1990). Predator tactics play a significant role in learning speed and may influence the abilities of different species in adapting to these visually obvious changes, such as alterations in coral cover and decrease in prey size and availability. However, more studies need to be conducted to further investigate the stomatopod's capabilities in behavioral learning, as well as the spearer's shape-learning dominance over the smashers. Further studies should address the number of unresponsives through increasing the n, number of stomatopods. This study has implications for stomatopods to be able to learn to identify and recognize the associated environmental rewards and costs of their changing landscape.

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