Context-dependent foraging behavior in Chinese mantids (*Tenodera sinensis*)

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Abstract

Mantids are a group most often studied in lab environments. While labs lend themselves well to the ability to control the variables in an experiment, it is difficult to gauge the impact of the environment itself on the data. This experiment aimed to see if different environmental contexts would change the learned behavior of Chinese praying mantids (*Tenodera sinensis*) in a captive setting. Trials were conducted over the span of four months and in two environmental contexts. Mantids were introduced to one initial context where they learned to avoid toxic prey and were then switched to the other context. With data from 10 mantids and a total of 151 trials, the mantids overall did not change their behavior when introduced to the second environment. This suggests, contrary to previous experiments suggesting a low learning efficacy, mantids may have the capabilities of learning at a higher level than other insects. Furthermore, it lends more validity to previous trials that had been conducted in labs before, given that mantids will still perform learned behaviors regardless of context.

A somewhat interesting behavior was observed over the course of the trials that had only been recorded once before. The mantids, rather than just not attacking toxic prey, chose to attack and then reject the prey after learning they were toxic. This finding could suggest that the taste of a learned toxic prey stimulates the response to reject it. These findings help give more information about mantises as sit-and-wait predators, and how they might react in the wild when encountering a toxic prey item.

Introduction

The term praying mantis refers to a larger family of insects that utilize their forelegs to capture prey items, typically other small insects (Brannoch et al. 2017). A distinctive trait of the family is the foraging strategy that they utilize to optimize their rate of prey capture in their environment. Described as “sit-and-wait” or ambush predators, mantids will perch in one spot on a plant or other raised object and wait for prey to pass by around them. They will then strike and consume the prey (Yamawaki 2017). This strategy reduces the energy expenditure of the mantids and likely evolved alongside their particular body shape and coloration to benefit through mimicry of the plants they perch on (Ross and Winterhalder 2015). As expected, mantids will opportunistically attack most prey that passes by due to the uncertainty of getting a second chance later, though this varies with the satiety of the mantid (Pickard et al. 2021). Some of these prey types may be too large, which is passed on, or may be toxic to the mantis (Berenbaum and Miliczky 1984). A variety of strategies have been noted in mantids to facilitate their survival and give the best benefit to attacking prey.

Previous behavioral studies on mantids have shown the ability to recognize and learn the aposematic colorations of unpalatable prey and avoid them in subsequent tests (Berenbaum and Miliczky 1984). This study also noted the behavior of each mantid changing throughout the trials as they gained experience with the toxic prey. The mantids would partially eat the milkweed bug after attacking but would choose to reject the prey eventually. Overall, each trial saw a decrease in the number of mantids attacking the toxic prey as well as a reduced time it took for the mantid to release the prey if they did still attack (Berenbaum and Miliczky 1984). Other studies saw other mechanisms of learning to eat toxic prey such as in toxic butterflies (Mebs et al. 2017). Mantids would eat around the gut of the butterflies and discard the remaining midgut. This behavior removed compounds found in the butterflies' host plants that could not be absorbed by the mantids after consumption. This behavior allows the mantids to eat the prey while specifically removing the aspects that were toxic to them (Mebs et al. 2017). Later studies on avoidance learning in mantids as sit-and-wait predators varied between specific prey species (Carle et al. 2018). Mantids would attack novel prey with conspicuous colorations more than novel prey without the coloration when both were made unpalatable. Yet, the mantids would go on to reject every conspicuous colored prey while still consuming some of the less-attacked novel prey. The mantids, contrary to the earlier 1984 study, actively attacked the conspicuous colored prey while still rejecting them as they would be expected to. These results showed varied effects on contextual learning on the foraging behaviors of mantids, as well as possible mechanisms of the evolution of foraging behavior (Carle et al. 2018).

The majority of previous behavioral studies on mantids required controlled environments achieved most efficiently in a lab. These animals are raised to maturity in these environments and are then studied in the same (Bosse et al. 2022). However, recent studies investigating the attack and defense behavior of mantids have shown that the previous environment of the mantid had an impact on its decision to ignore or react to a stimulus. Mantids that were wild-caught were equally likely to be aggressive or ignorant of the stimuli, while lab-raised mantids showed equal amounts of increased attention and aggressiveness to the stimuli. Wild mantids likely had more experience with what the simulated stimulus could have been and could make a decision about how to behave based on that experience. The lab-reared mantids had none of the prior experience and thus chose to react aggressively as a defensive tactic to novel stimuli. The context in which the mantids were reared heavily impacted their decisions in an attack or defensive set of behaviors yet were not analyzed for their prey behavior (Bosse et al. 2022).

Studies with jumping spiders, while not sit-and-wait predators, have shown that context did affect their avoidance behavior of unpalatable prey (Skow and Jakob 2005). Spiders taught in one environment were moved to another and subsequently had differing actions from what they had displayed as learned behavior. As the spiders were not sit-and-wait predators, they would encounter different environments more frequently, while the mantids are more likely to stay in one environment for their lifespan (Skow and Jakob 2005). Additionally, studies with fruit flies have revealed information about how the flies process context in response to visual stimuli (Oram 2022). A looming or approaching object would result in differing behaviors depending on what the object doing the looming was. For flies, this allowed them to react appropriately via landing, perching, fleeing, or courting the object (Oram 2022). In mantids, this external visual element could result in similar findings, allowing them to appropriately respond to a change in their environments.

Mantids and other sit-and-wait predators have been previously suggested to have lower or limited learning capabilities compared to other predatory or prey insects. With the jumping spider experiment, the data was used to examine how the change in environment would entirely remove what the spiders knew about the toxic prey (Skow and Jakob 2005). Mantids in other experiments have been shown to continuously attack generated stimuli with no reward over the course of all trials (Baum et al. 2014). This low learning capability could lead to the behaviors described in previous studies, particularly concerning the varied attack patterns for novel or conspicuous prey as in Carle et al. 2018. Mantids that attack all prey items will have more opportunities to attack prey that is not toxic. If mantids took the time to recognize toxic prey before attacking, they would likely miss the chance to attack at all. As how jumping spiders changed their behaviors when in a new context, it is possible that mantids would do so as well so they could raise the chances of attacking new non-toxic prey items.

Given the mixed results of other studies on prey behavior of mantids and learning, this study sought to observe if the mantids had a similar low learning capacity to jumping spiders and other sit-and-wait predators by observing if their learned behavior would change depending on the context it was learned in or switched to. As mantids were shown in other studies to have behavior skewed towards attacking prey or stimuli, it was hypothesized that they would revert to attacking and consuming the toxic milkweed bugs when introduced into a different environment than the one they had learned in.

Methods

Animal Care and Acquisition

Ten Chinese mantids (*Tenodera sinensis*) were captured as nymphs at instar levels varying from 4th to 5th. The mantids were obtained from the Avon Nature Study Area in Rochester Hills. The mantids as nymphs were kept in approximately 1-gallon containers with ventilation provided as slits in the top and sides of the container. Mantids were provided with one to two sticks that had been sterilized before use. Enclosures were misted once a day in the morning with only enough water that they would be dry by the end of the day. If any water remained at the end of the day, the enclosure was manually dried, and the sticks replaced. Nymphs were provided with small size crickets (*Gryllus assimilis*) that were no larger than forelimb length at a rate of one cricket every two days. If nymphs did not eat a cricket that day, they would not be offered another cricket until the next feeding cycle. Mantids were fed crickets in their home enclosures and not in any trial areas. Any molts were removed from the enclosures when they were noticed and the mantid's instar level was updated. When a mantid reached a size greater than three inches, they were moved to an approximately 2-gallon container with the same ventilation and sticks they had previously. When all mantids reached adulthood, trials began.

Crickets were purchased from local pet stores and kept in 2-gallon containers with slits in the top and sides as ventilation. Crickets were provided with paper egg cartons to use as hides and a damp sponge as a water source. Milkweed bugs (*Oncopeltus fasciatus*) utilized in the trials were captured from roadside milkweed plants and the Avon Nature Study Area. Milkweed bugs were not present in the study area until approximately two months after mantids had been captured and thus would not have come into contact with the mantids before the trials began. Milkweed bugs were kept in a 2-gallon container with seed pods from the host plant they were taken from. They were provided with a damp sponge to use as a water source and proper ventilation as slits in the top and sides of the enclosure. Milkweed bugs were captured at both adult and nymph stages but only adults were used in the trials. A few box elder bugs (*Boisea trivittata*) were found with the milkweed bugs when they were being acquired, and as a result, each bug was initially put in a separate container until they could be properly identified as milkweed bugs. Box elder bugs were released back onto the host plant if possible. If a box elder had been brought away from the host plant by accident with the milkweed bugs and identified later, it was released onto a similar plant that was close to the testing location.

Trial Arena

The trial area consisted of two separate containers, one larger (58.7 x 41.6 x 46 cm high) and one smaller (31.5 x 20.3 x 9.8 cm). The smaller container was set inside the larger container and would remain unchanged throughout all trials and contexts. The larger container would be decorated as either a natural or unnatural environment according to a randomly assigned starting context for each mantid. In the natural context, the larger container was wrapped internally with blue construction paper that had been taped on trees and clouds made from green, brown, and white construction paper. The bottom of the larger container was covered with green construction paper and fake plants were wrapped around the outside of the smaller container. In the unnatural context, the walls and bottom were covered in plain white construction paper with no additional visual elements. In all cases, the smaller container had not been altered such that the context change was purely visual.

The 10 mantids were randomly assigned a starting context of either the natural or unnatural context, with sexes being kept balanced between the two. Mantids were not fed for one feeding cycle before the initial trial, with each subsequent trial having a period of two days between them. After each trial with a milkweed bug, mantids were offered a cricket to consume. All mantids attacked and at least partially ate the cricket after each trial but would've been excluded if they hadn't.

Trial Procedure

The mantids were placed in the smaller container at the beginning of each trial and given 5 minutes to settle. A milkweed bug adult was then added into the smaller container in front of the mantid such that it would be seen. Then a 5-minute timer was started, at which the mantids had the chance to attack the bug. If not attacked or consumed at the end of the 5 minutes, the bug would be removed and reintroduced to the rest of the bugs in their enclosure. The mantid was then reintroduced to their home enclosure and offered a cricket.

The initial trials took place in the randomized starting context for each mantid and lasted for 10 trials to allow for a sufficiently long learning period based on the study by Berenbaum and Miliczky (1984). After these trials were completed, the mantids would then be instead trialed in the opposite context. This would take place with the same procedure and setup, with only the context surrounding the smaller container changing. These trials in the second context would continue until there were no mantids still alive to do the trials. Adult mantids that died were in their final instar stage and presumed to have died of old age, as it was around late winter when the final mantid died.

Behavior towards the milkweed bugs was categorized as either attacked and consumed "C," attacked but not consumed "A," or neither attacked nor consumed "D." Each mantid's data was recorded after the trial and attached to their enclosure to not mix up data between them. The data was formulated in a table using Microsoft Excel, with columns for each trial and rows for each mantid. The table was split into two after the first 10 trials, separating the data into the preliminary learning trials and the secondary switched context trials. This data was translated into learning curves for each mantid as well as averaged into an average curve for the entire population.

Results

Raw Data

A total of 151 trials were performed over 10 mantids, with a maximum of 17 trials for one mantid. Data was filled in regarding the type of behavior that was exhibited for each trial. Table 1 has been split into two sections, with the first being the learning trials and the second being the switched context trials.

Table 1. Raw data of mantid behavior over 17 trials for the 10 individual mantids. “C” refers to prey being both attacked and consumed. “A” refers to prey being attacked and not consumed. “D” refers to prey being neither attacked nor consumed. Data after the 10th trial is in the switched context.

Mantis # - Sex (Starting Context)	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7	Trial 8	Trial 9	Trial 10
Mantis 1 - Female (Natural)	C	C	A	C	A	A	D	A	A	D
Mantis 2 - Female (Natural)	C	C	C	A	A	A	D	A	A	A
Mantis 3 - Female (Natural)	C	C	A	C	A	D	A	A	A	A
Mantis 4 - Male (Natural)	C	C	D	A	D	A	D	D	A	D
Mantis 5 - Female (Natural)	C	C	C	C	A	C	A	A	A	A
Mantis 6 - Female (Unnatural)	C	C	C	A	C	A	A	A	A	A
Mantis 7 - Male (Unnatural)	C	A	C	C	A	D	D	A	D	A
Mantis 8 - Female (Unnatural)	C	C	A	C	A	D	A	D	D	D
Mantis 9 - Female (Unnatural)	C	C	C	C	A	A	C	A	A	A
Mantis 10 - Female (Unnatural)	C	A	C	A	A	D	A	D	A	A

Table 1 (cont).

Mantis # - Sex (Switched Context)	Trial 11	Trial 12	Trial 13	Trial 14	Trial 15	Trial 16	Trial 17
Mantis 1 - Female (Unnatural)	A	A	D	A	-	-	-
Mantis 2 - Female (Unnatural)	A	A	A	A	D	-	-
Mantis 3 - Female (Unnatural)	A	A	D	A	D	A	A
Mantis 4 - Male (Unnatural)	D	A	D	D	D	-	-
Mantis 5 - Female (Unnatural)	C	A	A	D	-	-	-
Mantis 6 - Female (Natural)	A	D	A	A	A	A	-
Mantis 7 - Male (Natural)	D	D	A	D	D	-	-
Mantis 8 - Female (Natural)	D	A	D	D	-	-	-
Mantis 9 - Female (Natural)	A	D	A	A	A	A	D
Mantis 10 - Female (Natural)	A	A	D	D	-	-	-

Learning Curves

This data was translated into an appropriate format for a program like Microsoft Excel to work with and was then made into individual learning curves for each mantid. These lines were then averaged into a single curve of which a linear equation was fit to determine the overall trend of learning across the entire span of the experiment.

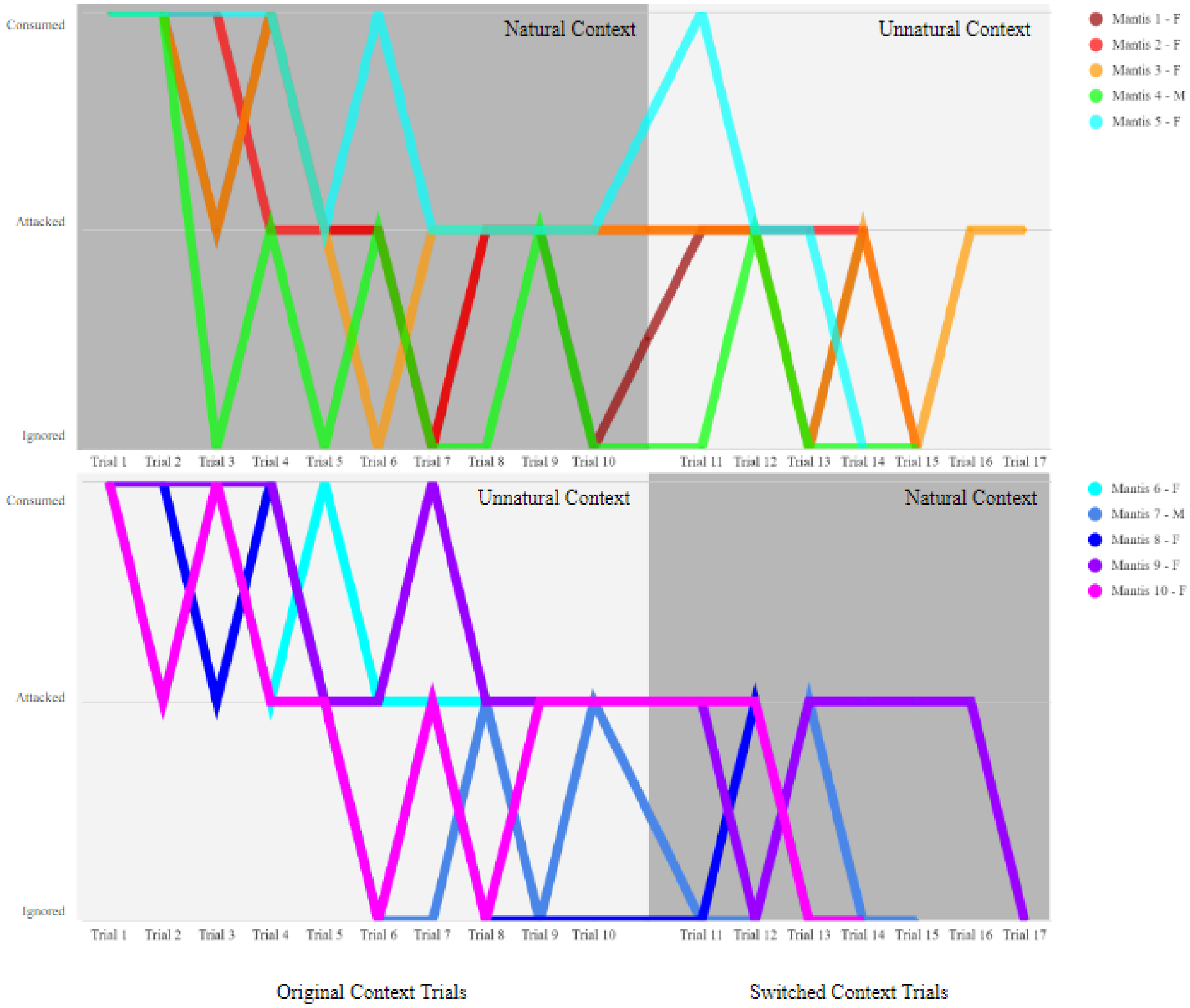

Fig. 1. Individual mantid learning curves spanning 17 trials. Each mantid received their own curve. The key on the right-hand side contains data about which mantid is represented on each line and what the sex of each mantid was. Background colors have been changed to represent which context was being tested at the time of the trial for each mantid.

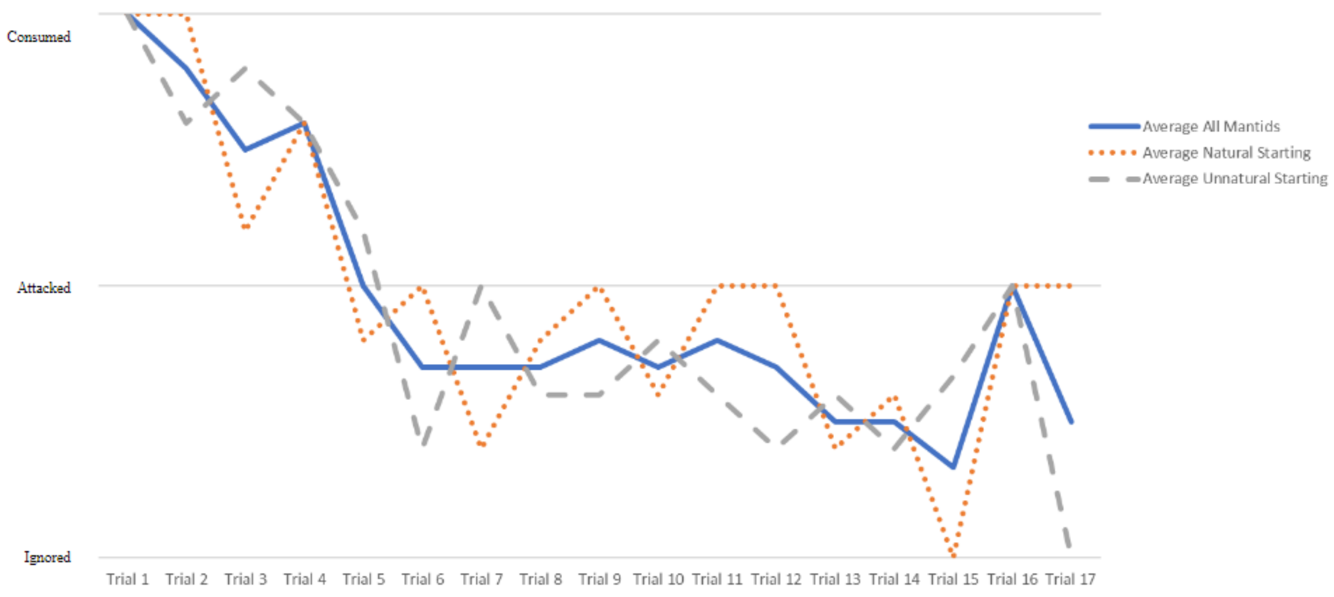

Fig. 2. Averaged learning curves for each mantid over all 17 trials. Distinctions have been made for each group of mantids: if they started in the natural context, the unnatural context, or if the data has been averaged across contexts.

The line fit to the data on the average learning curve showed an overall trend towards the mantids learning to stop consuming the toxic prey. From trials 1 to 5, there was a line fitting the data of y=-0.22x + 3.24 (R^2=0.8521). While from trials 5 to 17 the line that best fit was y=-0.0149x + 1.8327 (R^2=0.0919). An overall best fit line for the average of all learning curves was y=-0.0782x + 2.635 (R^2=0.6404).

In terms of the categorical data, 100% of mantids consumed the toxic prey in the first trial, but in the last trial with all ten mantids, 0% of mantids consumed the toxic prey. This trial was trial 14, which also had ratios of 50% of mantids attacking and 50% of mantids ignoring the prey. A chi-squared test was run between the last trial of the initial context and the first trial of the switched context to find there was no significant difference in the ratios of mantids attacking, consuming, or ignoring prey (p = 0.4949).

A third graph was created showing the differences in sex on the learning curves. This figure was brainstormed after it had been noted during the trials that the female mantids seemed to attack the toxic prey more readily than the males. The graph is composed similarly to the average learning curve graph Fig. 2 but is separated based on sex and not starting context. Error bars were added based on standard deviation to account for differences in the number of mantids in each group.

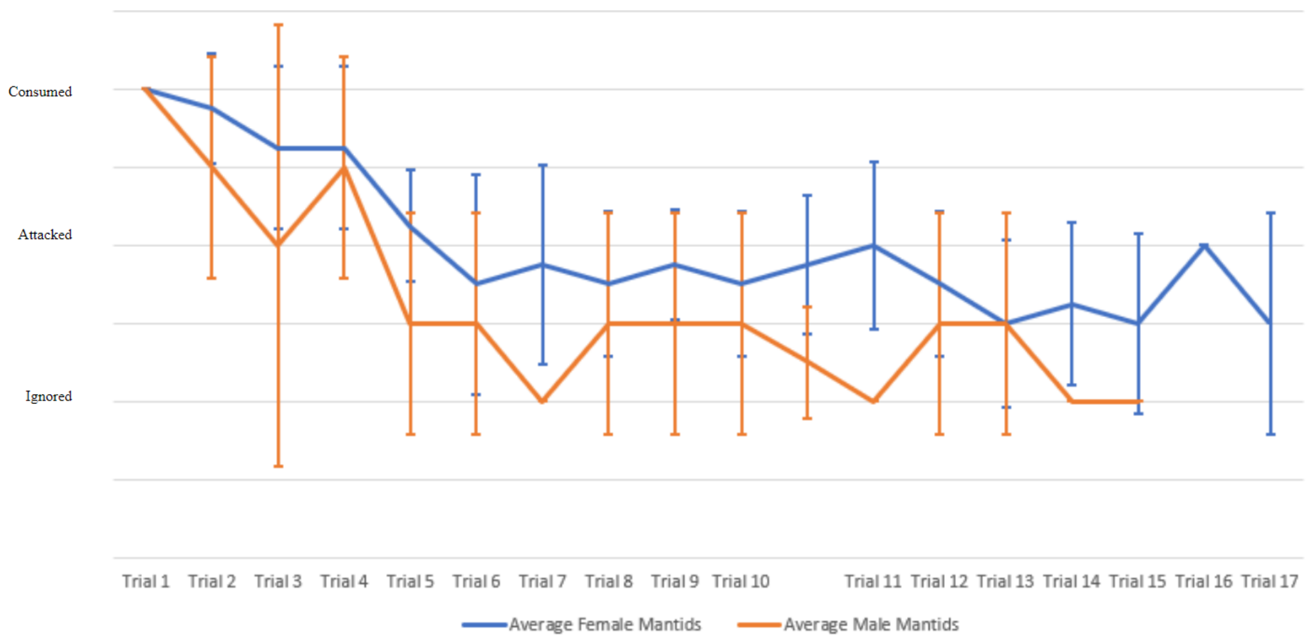

Fig. 3. Averaged learning curves for each sex over all 17 trials. Distinctions have been made for each group of mantids: if they were male or female. Note that only 2 male mantids were used for the trials while 8 female mantids were used. Error bars have been constructed based on standard deviation values.

Discussion

Learned Avoidance

In the initial 10 trials, there was a goal of teaching the mantids to recognize the milkweed bugs as toxic prey that should not be consumed. This goal was achieved within the four trials it took for the majority of the mantids to stop consuming the bugs after attacking. While one mantid in particular, Mantid 5, continued to occasionally eat the toxic bugs up to trial 11, the majority of mantids quit after the fourth trial. Given the data, it is likely that the mantids did not have an innate avoidance of the milkweed bugs and did need to learn that they were toxic. The percentage of mantids that consumed the milkweed bug was 100% for the first trial, which would be much too high to conclude they innately avoided the bugs.

This finding is in line with previous research that found an approximate 50% decrease in the consumption of toxic prey after each trial persisted (Berenbaum and Miliczky 1984). Learned avoidance is a better fit for the sit-and-wait style of predation that mantids utilize rather than innate avoidance. If mantids innately avoided certain prey items, it could result in the loss of prey that is not toxic but utilizes mimicry as a defense mechanism. As mantids tend to stay in one environment for their entire lives, it would be beneficial if they could learn the species in their environment as they encountered them rather than relying on an innate mechanism of avoidance (Kaltenpoth 2005). Any mantids that migrate before laying their oothecae would have a disadvantage of a new environment with new prey to learn to avoid. As mantids tend to be moved artificially through environments, it would not make sense for them to evolve an innate avoidance of any prey items (Hurd et al. 1983).

It is possible that as the mantids grew older and started to pass at the end of the trials, they tended to not attack their prey by being too weak. This still would grant trials 11 through 13 being early enough to potentially avoid these effects, as it would have a difference of about a week between the final trial of one mantis and its death. Studies in mantis before have found that mantids fed an exclusively milkweed bug diet experienced slower growth rates and were deterred from eating (Paradise and Stamp 1990). It was stated that it was likely the toxins in the milkweed bugs that were causing these effects, and that over a longer period of feeding would cause long-term effects on health. However, as the mantids only consumed a small number of milkweed bugs each, it is unlikely that the health detriments from the milkweed bugs would've caused an effect on feeding rates aside from mantids rejecting them outright. Milkweed bugs contain both a toxin and a bitter-tasting chemical that help to deter predators from consuming them (Duffey and Scudder 1972; Alrich et al. 1997). It is possible that upon the capture of the milkweed bug, the mantids were able to associate the taste with the previous toxins they consumed. This would facilitate the learning of avoidance and would allow the mantids to capture and reject the prey.

Attack and Rejection of Prey

As noted in the data of this experiment, the mantids continued to attack the milkweed bugs through all 17 of the trials. There didn't seem to be a preference between attacking and rejecting or just not attacking the milkweed bugs (R^2=0.0919). This is similar to data found by Carle et al., in which a mantis would attack conspicuous prey more often than inconspicuous prey that were both made bitter (2018). In contrast to that experiment, there was no comparison to an inconspicuous prey item, and thus it cannot be concluded that the conspicuous signals triggered the attack response of the mantid. The overall pattern of continuing to attack follows the data in that experiment, but it would need more research in this vein to determine if the lack of coloration on the mealworms in that experiment were the driving force reducing attacks.

Effect of Sex

It was noted that visually, it appeared the female mantids tended to attack the milkweed bugs and crickets more readily. As no data was taken for the timing of the attacks, a graph was created to compare the average learning curves between the male and female mantids. Figure 3 displays this data, alongside error bars to correct for the lack of male mantids used in the experiment. As mantids were collected as nymphs, they were unable to be sexed until later in their rearing. In the graph, there is overall only a small difference between the two groups, with this difference being largely insignificant. There were only a few trials where there was a significant difference, and for these trials, the female mantids were more likely to attack the prey than the males were. Female mantids tend towards being larger than males as well as having more morphological differences lending to catching larger prey (Kaltenpoth 2005). As males are readily consumed by female mantids, it is possible that they invest fewer resources into attacking and finding prey and instead tend towards moving through an environment to search for a mate (Birkhead et al. 1988). This would explain why the males in my experiment had slightly lower attack rates, but the difference was so low it would need to be repeated with a more equal distribution of males to females.

Effect of Context

Contrary to what had been seen with jumping spiders and to my hypothesis, the context that the mantids learned in seemed to have little to no effect on their learned behaviors (Skow and Jakob 2005). With jumping spiders, their behavior immediately changed after being switched to the other context, with about 75% of the spiders going back to attacking the toxic prey. As seen in this experiment, the mantids were largely unbothered by the switch, with a p-value of 0.4949 being found between the last trial of the first context and the first trial of the switched context. This suggests that the mantids retain their learned behaviors across environments and contexts, unlike what had been seen in some other insect species.

Previous research with learning and context has been used to suggest a lower intelligence level in jumping spiders as well as praying mantids (Baum et al. 2014; Skow and Jakob 2005). More research is needed to determine why these differences have appeared in mantids and not in other species of insects, as well as why different aspects of learning in mantids show differences in learning capabilities. It is possible that different spaces of the brain are devoted to different aspects of learning that differ in capacity. This would benefit the mantids by reducing energy expenditure for aspects of learning that would potentially reduce fitness, such as stopping attacks on prey over time.

As the mantids had a different outcome than other insects in terms of context-dependent learning, more research is needed in different classes of insects to see where the distinctions lie. If all sit-and-wait predators tend towards non-context-dependent learning, it could provide valuable information about how insects learn. It is also possible that the contexts in this experiment were not distinct enough to trigger a difference in the mantids, which could warrant more research into where the boundaries lie between a similar context and a completely different environment.

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I would like to thank Dr. Mark Sturtevant for his continued guidance and support on this project. Thank you for guiding me through the methods of obtaining the mantids, as well as the slight push in the right direction when my original topic idea fell through. I would also like to thank the caretakers of the Avon Nature Study area for keeping the park so well maintained as to foster the wide diversity of insects and plant species available in the park. Thank you to my peers at Oakland University for being so open to discussing my thesis, despite mantids being somewhat “gross” to some of the people I spoke to. Many of my ideas from my discussion come from conversations with graduate and undergraduate students alike, so thank you.

Biographical Note

I am a biology major at Oakland University. I've always had respect for people who work in conservation and wildlife preservation and wanted to work with an animal for my thesis. As the Chinese mantis is invasive in my area, it was easy enough to decide to work with them. While my thesis itself didn't go much into the mechanisms of invasive species, praying mantids as a whole are very interesting to me, and do still need research on their basic activities and behaviors.

In the future, I aim to work with animals in some form, be it conservation, ecology, or field research. This thesis and project began my work with a type of animal in a more professional setting, allowing research and study while still being a comfortable shift from personal work. At the moment, I am hoping to graduate with more experience under my belt and more confidence for future work with animal-related studies. I will be interning this summer after I graduate at a rehabilitation center for wildlife, which I couldn't be more grateful for. I hope that the internship will jumpstart my career in animal-related work that can help in the fields of conservation and protection of wildlife.

References

Aldrich JR, Leal WS, Nishida R, Khrimian AP, Lee C-J, Sakuratani Y. Semiochemistry of aposematic seed bugs. Entomol Exp Appl. 1997;84(2):127–135. doi:10.1046/j.1570-7458.1997.00207.x

Baum T, Katsman I, Rivlin E, Broza M, Moshkovich M, Katzir G. Response of the praying mantis, *Sphodromantis viridis*, to target change in size and to target visual occlusion. J Insect Behav. 2013;27(3):333–345. doi:10.1007/s10905-013-9422-4

Berenbaum MR, Miliczky E. Mantids and milkweed bugs: Efficacy of aposematic coloration against invertebrate predators. Am Midl Nat. 1984;111(1):64. doi:10.2307/2425543

Birkhead TR, Lee KE, Young P. Sexual cannibalism in the praying mantis *Hierodula membranacea*. Behaviour. 1988;106(1-2):112–118. doi:10.1163/156853988x00115

Bosse JW, Svenson GJ, Bowers TA, Bourges-Sevenier BM, Ritzmann RE. Context-dependent effects on attack and defense behaviors in the praying mantis *Tenodera sinensis*. J Exp Biol. 2022;225(11). doi:10.1242/jeb.243710

Brannoch SK, Wieland F, Rivera J, Klass K-D, Béthoux O, Svenson GJ. Manual of praying mantis morphology, nomenclature, and practices (Insecta, Mantodea). ZooKeys. 2017;696:1–100. doi:10.3897/zookeys.696.12542

Carle T, Horiwaki R, Hurlbert A, Yamawaki Y. Aversive learning in the praying mantis (*Tenodera aridifolia*), a sit and wait predator. J Insect Behav. 2018;31(2):158–175. doi:10.1007/s10905-018-9665-1

Duffey SS, Scudder GG. Cardiac glycosides in *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). I. The uptake and distribution of natural cardenolides in the body. Canadian Journal of Zoology. 1974;52(2):283–290. doi:10.1139/z74-035

Hurd LE, Eisenberg RM, Washburn JO. Effects of experimentally manipulated density on field populations of the Chinese mantis (*Tenodera Ardifolia sinensis* Saussure). American Midland Naturalist. 1978;99(1):58. doi:10.2307/2424933

Kaltenpoth M. Lebensweise und morphometrie der Chinesischen gottesanbeterin *Tenodera aridifolia sinensis* (Blattopteroidea: Mantodea) [Life history and morphometry of the Chinese praying mantis, *Tenodera aridifolia sinensis* (Blattopteroidea: Mantodea)]. Entomol Gen. 2005;28(1):1–16. doi:10.1127/entom.gen/28/2005/1.

Mebs D, Wunder C, Pogoda W, Toennes SW. Feeding on toxic prey. The praying mantis (Mantodea) as predator of poisonous butterfly and moth (Lepidoptera) caterpillars. Toxicon. 2017;131:16–19. doi:10.1016/j.toxicon.2017.03.010

Oram TB, Card GM. Context-dependent control of behavior in Drosophila. Curr Opin Neurobiol. 2022;73:102523. doi:10.1016/j.conb.2022.02.003

Paradise CJ, Stamp NE. Variable quantities of toxic diet cause different degrees of compensatory and inhibitory responses by juvenile praying mantids. Entomol Exp Appl. 1990;55(3):213–222. doi:10.1111/j.1570-7458.1990.tb01365.x

Pickard SC, Bertsch DJ, Le Garrec Z, Ritzmann RE, Quinn RD, Szczecinski NS. Internal state effects on behavioral shifts in freely behaving praying mantises (*Tenodera sinensis*). PLoS Comput Biol. 2021;17(12). doi:10.1371/journal.pcbi.1009618

Ross CT, Winterhalder B. Sit-and-wait versus active-search hunting: A behavioral ecological model of optimal search mode. J Theor Biol. 2015;387:76–87. doi:10.1016/j.jtbi.2015.09.022

Rossoni S, Niven JE. Prey speed influences the speed and structure of the raptorial strike of a 'sit-and-wait' predator. Biol Lett. 2020;16(5):20200098. doi:10.1098/rsbl.2020.0098

Skow CD, Jakob EM. Jumping spiders attend to context during learned avoidance of aposematic prey. Behav Ecol. 2005;17(1):34–40. doi:10.1093/beheco/ari094

Yamawaki Y. Decision-making and motor control in predatory insects: A review of the praying mantis. Ecol Entomol. 2017;42:39–50. doi:10.1111/een.12452

Zack S. Description of the behavior of praying mantis with particular reference to grooming. Behav Processes. 1978;3(2):97–105. doi:10.1016/0376-6357(78)90037-2