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Responses to Predator Recognition Odors in Marmorkrebs

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RESPONSES TO PREDATOR RECOGNITION ODORS IN MARMORKREBS

A Thesis

by

LOREN SAMANTHA BEARD

Submitted to the Graduate School of the
University of Texas-Pan American
In partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2012

Major Subject: Biology

RESPONSES TO PREDATOR RECOGNITION ORDORS IN MARMORKREBS

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August 2012

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ABSTRACT

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Marmorkrebs is a parthenogenetic crayfish with no indigenous populations. They have been introduced in several countries and could become an invasive species. Individuals introduced in Germany had longer, sharper spines, suggesting an adaptation to predators via developmental plasticity. This was tested by exposing juveniles to the odor of a fish during development and comparing them to controls. Subsequent spine length or sharpness did not differ.

Other crayfish detect predators via an alarm cue, hemolymph, and exhibit avoidant behavior in response. I hypothesized that Marmorkrebs would also treat hemolymph as an alarm cue. The behavior of adult crayfish exposed to food, fish odor, or hemolymph were recorded. Results showed no difference across conditions, indicating that Marmorkrebs do not use hemolymph or fish odor as cues.

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CHAPTER I

INTRODUCTION

Marmorkrebs are the only known obligate parthenogenetic crayfish, producing offspring genetically identical to each other and their mother via apomictic thelytoky (Scholtz, et al., 2003; Vogt et al., 2004; Martin, et al., 2007). This is their only means of reproduction; there are no males. They were discovered in the aquarium trade, and no wild, indigenous population of Marmorkrebs is known, leaving their origins shrouded in mystery (Vogt et al. 2004).

Since their discovery in the 1990s, researchers have been trying to discover the origins of the parthenogenetic crayfish Marmorkrebs. The morphological traits used to identify crayfish species are male reproductive organs (Hobbs, 1942a), which could not be used as all Marmorkrebs are female. Additionally, finding a starting point of comparison was difficult without a wild population. Earliest molecular analyses showed that Marmorkrebs are a member of the Cambaridae family, but used only a handful of species and a couple of genes, making conclusions that they are most closely related to *Procambarus fallax* somewhat speculative (Scholtz et al., 2003; Marzano et al., 2003). Other studies with equally small samples excluded *P. fallax* and so found it to be most closely related to *Procambarus alleni* (Jones et al., 2009; Vogt 2008). The most recent study by Martin et al. (2010) confirmed that Marmorkrebs are in fact most closely related to *P. fallax*, arguably so much so that they should be considered the parthenogenetic form of *P. fallax* rather than a separate species, *P. fallax* form *virginalis*.

Procambarus fallax is a North American crayfish native to the wetlands of Florida and southern Georgia (Hobbs, 1942b).

Marmorkrebs have been introduced in several countries, Germany, Italy, and Madagascar, among others, and pose a risk as an invasive species (Jones et al., 2009; Kawai et al., 2009; Marzano et al., 2009; Martin et al., 2010; Chucholl & Pfeiffer, 2010; Feria & Faulkes, 2011; Chucholl et al., 2012; Faulkes et al., 2012). Due to their parthenogenetic reproduction, they can establish a population from one individual which makes them especially susceptible to becoming an invasive species. Other North American species of crayfish have already been documented as invasive species in Europe and have devastated local populations due to their spread of crayfish plague (Holdich et al., 2009), making this a legitimate concern. Their pervasiveness in the pet trade also makes multiple and frequent introductions likely, stacking the odds in their favor (Chucholl et al., 2012).

Though the factors that predict highly successful invasive species remain unclear (Andersen et al., 2004), effective predation avoidance is likely to be one that aids in the success of invasive species. Unfortunately, without a wild population, the ecology of Marmorkrebs is unknown. Marmorkrebs can hold their own against *Procambarus clarkii* in a fight (Jimenez & Faulkes, 2011) when paired with equal sized opponents, but it is unknown how introduced Marmorkrebs might interact with any other species, including predators. Many aquatic species have predator-induced adaptations which can be morphological, behavioral, or chemical. I will be investigating possible morphological and behavioral predator-induced adaptations which would make Marmorkrebs a more successful invader if confirmed.

CHAPTER II

SPINES: A MORPHOLOGICAL DEFENSE?

Introduction

Despite being genetically identical and reared identically, Marmorkrebs show a wide range of variation in a number of visible characteristics, e.g. growth, lifespan, reproduction, coloration, number of olfactory and gustatory sense organs, fluctuating asymmetry (Vogt et al., 2008), as well as molecular characteristics, e.g. global DNA methylation (Schiewek et al., 2007; Vogt et al., 2008). These individual differences demonstrate the broad potential for phenotypic variation from environmental input.

Two individual Marmorkrebs found independently in German habitats both had pronounced spines on the carapace, larger and sharper than aquarium raised individuals. While the reason for this clear difference is unknown, it is hypothesized that these larger, sharper spines may be a predator-induced morph (Martin et al., 2010; Chucholl & Pfeiffer, 2010).

Another crayfish species, *Orconectes limosus*, shows a morphological adaptation to maximize efficiency and survival. This species alternates between a sexual and asexual form to maximize growth at the cost of an additional yearly moult. Smaller individuals of this species use the additional moult to enter an asexual form where all resources are devoted to growth because larger males are preferred as mates, and larger females have larger abdomens to protect their eggs. When maximum size is reached, the larger individuals forgo the additional moult and

remain in their sexual form throughout the year, as the additional risky moult is no longer advantageous (Buric et al., 2010).

Additionally, a wide range of animals have shown morphological adaptation, specifically to the presence of predators. Mayfly larvae develop longer caudal filaments per unit body size and relatively heavier exoskeletons in environments that expose them to fish (Dahl & Peckarsky, 2002). Threespined sticklebacks grow faster when exposed to trout, but are smaller as adults, most likely the trade-off for this initial advantage to avoiding predation (Bell et al., 2011). A species of marine snails grow thicker shells when exposed to crabs (Trussel & Smith, 2000).

Many species even grown spines, as proposed, in response to predator exposure. *Daphnia pulex*, a water flea, when exposed to *Chaoborus americanus* larvae, develops a spiny morph with a toothed crest and longer tailspine which decreases predation by *C. americanus* larvae. The marine bryozoan, *Membranipora membranacea*, is also able to grow spines in response to grazing by its nudibranch predator (Harvell, 1984; Harvell, 1986).

Consequently, it is predicted that Marmorikrebs exposed to predator fish odor will grow longer, sharper spines than those reared without predator fish odor. Oscars, *Astronotus ocellatus*, were selected as the predator. Oscars have been introduced and established populations in the Florida wetlands (Courtenay et al., 1974) native to Marmorikrebs' closest relative, *P. fallax*, making it a reasonable choice in the absence of a native population of Marmorikrebs from which to draw. Even if Marmorikrebs in fact have had no contact with *A. ocellatus* in their evolutionary history, novel predators are something it would encounter as an invasive species. Therefore, these results should shed some light on the question of Marmorikrebs invasive potential.

Methods

This experiment sought to determine if Marmorkrebs show a change in morphology in the form of spines as a result of exposure to predator cues. All experimentation was done in the laboratory at The University of Texas-Pan American. Adult Marmorkrebs living in individual aquaria, 22 cm long \times 9 cm wide \times 15 cm high, with a shared water circulation system were monitored, and three mother's reproducing at the same time, within the same week, were selected for the experiment . Once the offspring became physically independent of the mother, they were randomly assigned to either control condition, water, or experimental condition, oscar water and housed collectively by group in a closed water system aquarium [need size]. Marmorkrebs were exposed to 100 mL of water taken from a tank housing an oscar twice a week from their first independent stage to sexual maturity. Control group received dechlorinated tap water. Concurrently, photographs of the rostrum were taken monthly for both groups resulting in four sets of photographs.

To analyze the photographs, carapace spine length was measured and then standardized using the width of the rostrum between the eyes. The sharpness was quantified by measuring the angle of the spine at the tip of the rostrum. Photographs published by Martin et al. (2010) and Chucholl et al. (2010) were also analyzed by these measures for comparison.

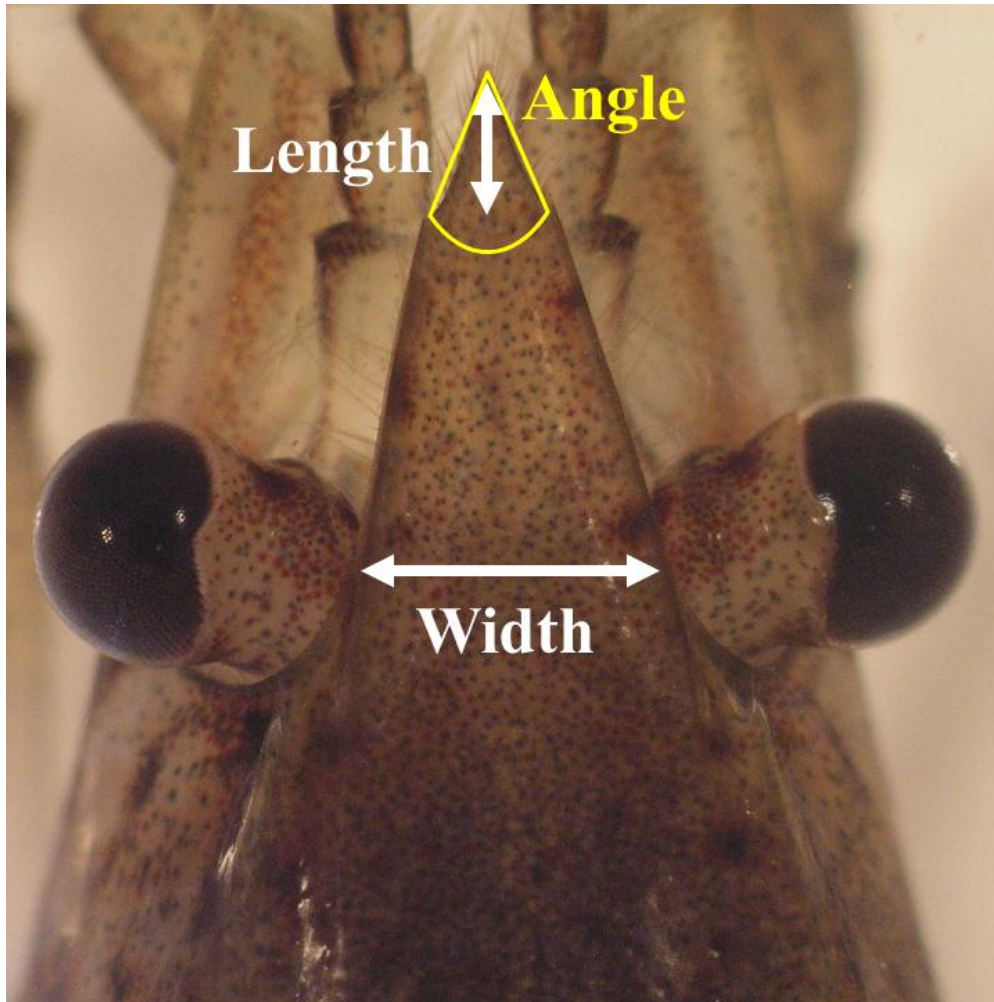


Fig. 2.1 Photo of Marmorkrebs Spine Measurement Methodology

Results

There was no difference in the angle of the spine between predator odor and control group ($t = -0.25$, $df = 38$, $p = 0.80$), nor in the rostrum spine length ($t = 1.198$, $df = 38$, $p = 0.238$) using a T-test.

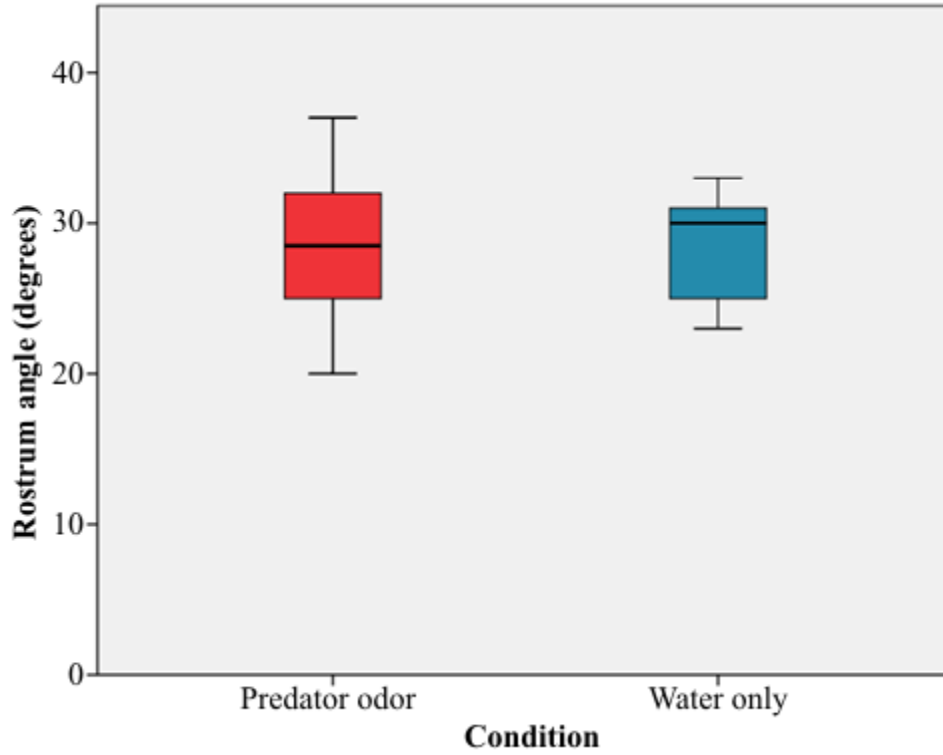


Fig. 2.2 Box Plot of Rostrum Angles

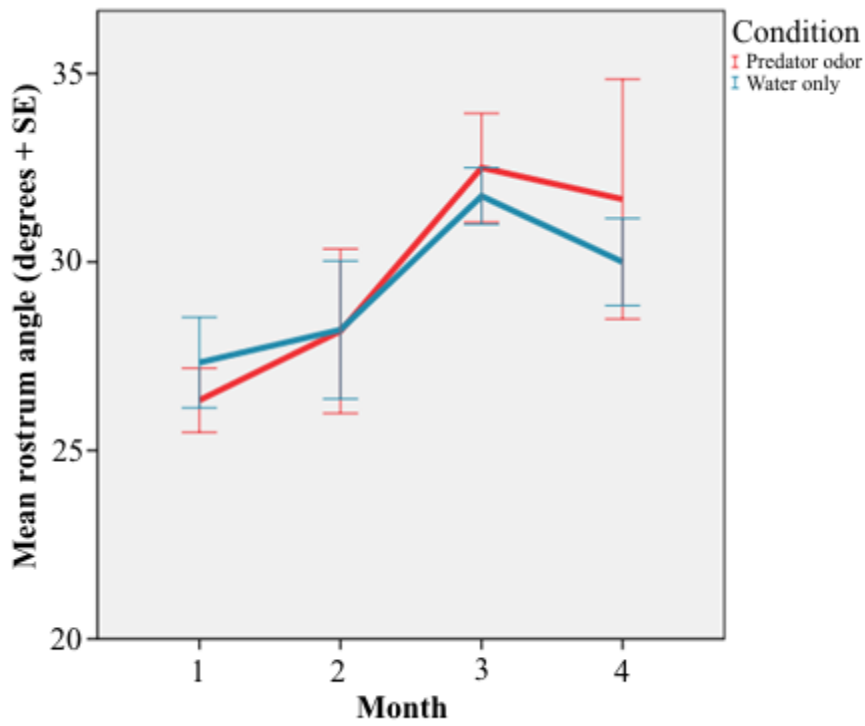


Fig. 2.3 Line Graph of Mean Rostrum Angles Over Time

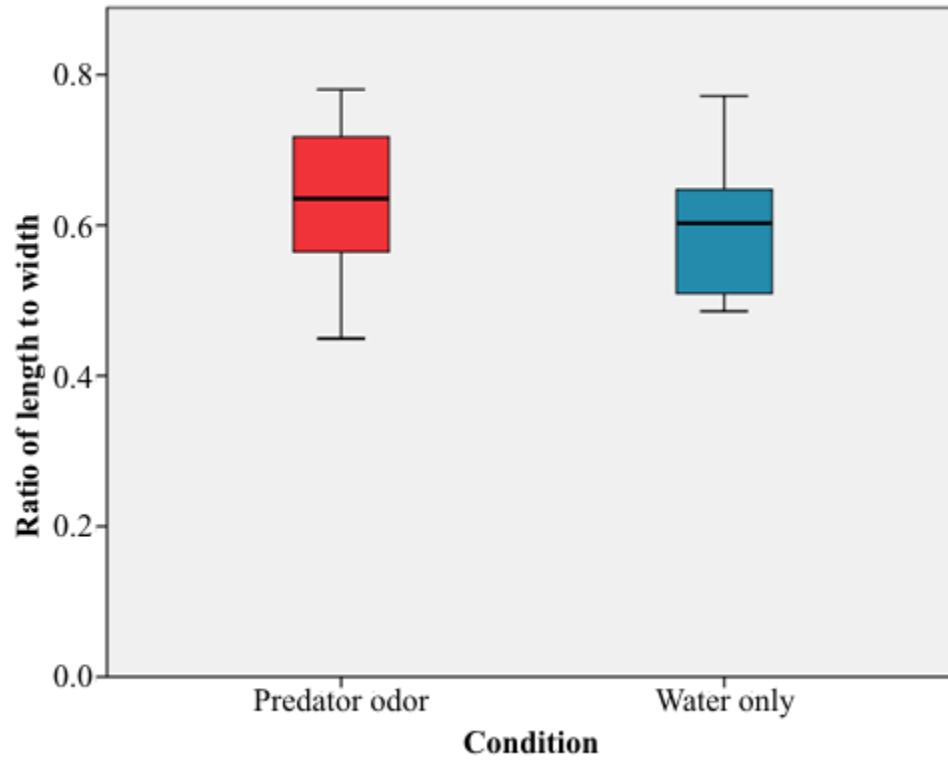


Fig. 2.4 Box Plot of Ratios of Spine Length to Rostrum Width

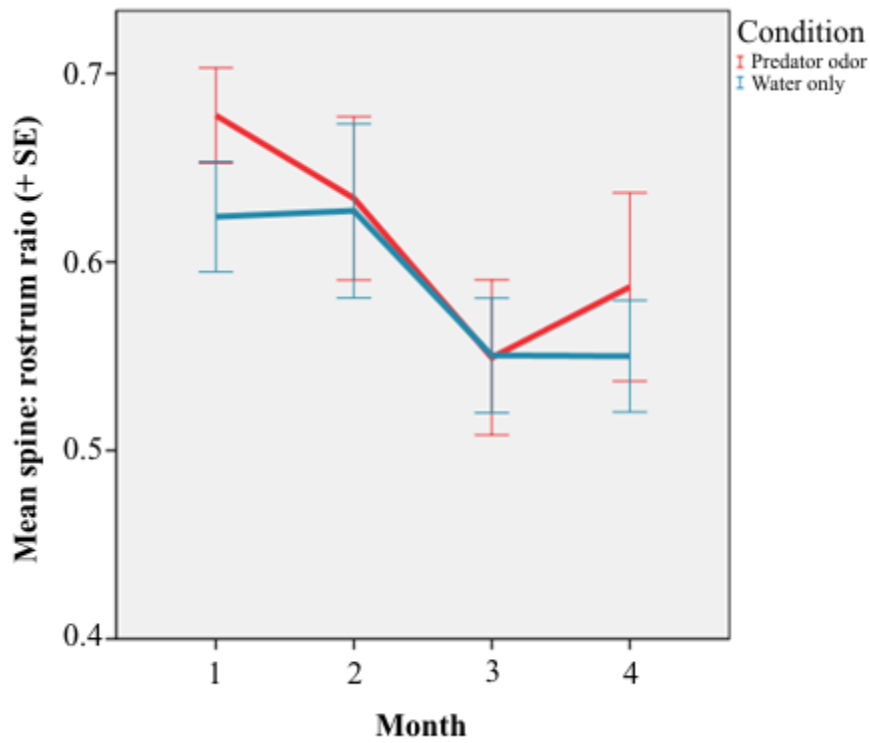


Fig. 2.5 Line Graph of Mean Ratios of Spine Length to Rostrum Width Over Time

Discussion

Marmorkrebs did not show a morphological reaction to oscar fish odor. It is possible that other cues are used preferentially as indicators of heightened predation. Further research will examine the use of the odor of hemolymph from crushed crayfish as a cue, which has been shown to result in behavioral inhibition in other crayfish species (Hazlett, 1994; Hazlett, 2000; Aquistapace et al., 2002; Aquistapace et al., 2003; Hazlett, 2003).

Analysis of the images provided in previous papers (Martin et al., 2010; Chucholl et al., 2010) indicate that both the experimental and control groups of Marmorkrebs match the wild specimens, rather than the lab-reared specimen. The lab reared specimen had a rostrum spine angle of 60 degrees, whereas both the wild specimens and this experiment's Marmorkrebs had rostrum angles in the approximately 20-40 degrees range. Spine length ratio was not possible to calculate on the lab-reared specimen because of its difference in morphology, but the wild specimens with ratios of 0.67 and 0.59, fell well within the range of ratios seen in this experiment's Marmorkrebs, 0.4 – 0.8. In light of this, it would seem that the pictured lab-reared specimen requires more explanation than the “spiny” crayfish found in German.

CHAPTER III

HEMOLYMPH: A PREDATOR AVOIDANCE CUE?

Introduction

The earliest studies on predator avoidance behavior by crayfish used the odor of the predator itself to elicit the avoidance behavior. Using juvenile *Pacifastacus leniusculus* and its predators, eels and perch, Blake and Hart (1993) found that the crayfish spent less time walking and climbing and more time in shelters when they came in contact with chemical cues from either of the two predators.

Additional studies by Willman et al. (1994) using *Orconectes rusticus*, *O. virilis*, and *O. propinquus* showed no effect or an opposite effect, i.e., greater activity rather than inhibition, when exposed to a fish predator odor, live largemouth bass. Behavior with exposure to fish predator was compared to behavior with exposure to carrion. *Orconectes rusticus* showed more behavioral activity with both exposures than the other two species, suggesting that the odors were perceived as cues to food rather than a threat and that *O. rusticus* used these cues most for effective foraging. Though it is not suggested in this paper, it is consistent with later support that the invasive *O. rusticus* reacts to a wider range of environmental cues than non-invasive species (Hazlett, 2000).

Hazlett and Schoolmaster (1998) also used the same three *Orconectes* species as well as *Cambarus robustus* with two predatory turtle species as predator odor. In contrast to the findings by Willman et al. (1994), *O. virilis* showed behavioral inhibition with exposure to one of the

turtle species. Conversely, *C. robustus* showed a similar behavior pattern to *O. rusticus* from the previous study. Because of the wide variety of responses by crayfish species to different predator odors, it is impossible to make any across-species generalizations.

Inspired by responses to odors of damaged conspecifics in other animal species, Hazlett (1994) tested this response in *O. virilis* and *O. propinquus*, using crushed crayfish. Results were mixed, with *O. virilis* showing inhibition but *O. propinquus* not. Nonetheless, this led the direction of research away from the odor of predators and towards conspecific alarm odor as a means of eliciting behavioral inhibition or avoidance behavior.

Further studies on *Orconectes* spp. showed that those crayfish, when exposed to odors of fish paired with an “alarm cue” of crayfish hemolymph, learn to associate the fish odor with danger and exhibit hiding behavior. This fish odor association can be made with a fish species that has no capacity to be a crayfish predator, goldfish.

Crayfish can also learn to ignore fish odors if they are repeatedly exposed to them without the alarm odor (Acquistapace et al., 2003; Hazlett, 2003). The ability to learn and unlearn associations with new predators and disregard harmless species would be an important behavior in an invasive species. Indeed, while both non-invasive species (*O. virilis* and *Austropatmobius pallipes*) and invasive species (*O. rusticus* and *Procambarus clarkii*) can learn predator associations in this way, the invasive species tend to remember this association longer (Acquistapace et al., 2002).

Additionally, invasive species recognize a wider range of other species’ hemolymph as a predator cue in previously used *Orconectes* spp. (Hazlett, 2000).

This study seeks to replicate the pervasive previous findings that crayfish use the odor of injured crayfish as an alarm odor with Marmorcrebs in an effort to further assess their invasive

potential by determining if they can inherently perceive predator threats through odor without an alarm pairing. It is predicted that there will be no significant behavioral differences between the control condition and predator fish odor (i.e., it is hypothesized that Marmorkrebs do not innately recognize predator odors) and that they will show significantly inhibited feeding behavior and locomotion when exposed to hemolymph compared to the control condition, consistent with previous findings.

Methods

Marmorkrebs were selected from same adult population in the same housing as referenced in Chapter II. Only adults not currently oviparous were selected. Two experimental conditions, oscar fish odor and Marmorkrebs hemolymph paired with food odor, were compared with the control, food odor alone, using the behaviors used by Acquistapace et al. (2003), feeding, raised posture, and locomotion, as measures. Feeding was defined as time spent physically ingesting food. Raised posture was defined as time spent with a raised posture and chelipeds raised relative to the position of the abdomen. Locomotion was defined as time spent walking or tail-flipping. Crayfish were normally fed every 48-72 hrs. For the experiment crayfish were instead not fed for roughly 144 hrs, or 5 days, to ensure that any lack of feeding behavior was not due to lack of hunger. Oscar fish odor was administered as 25 mL of water taken from an oscar aquarium tank. Hemolymph was obtained by crushing an average sized adult Marmorkrebs in 150 mL of water strained through cheese cloth and administered as a 5 mL dose. Odors/water were injected into the center of the Marmorkrebs' tanks which were filmed for 2 min to record behavior. These recordings were then analyzed by a blind rater to record time in seconds of each of the three behavior measures.

As an additional control, *P. clarkii* were also used to confirm the soundness of the methodology as their behavioral inhibition in the presence of hemolymph has already been confirmed in previous studies (Aquistapace et al., 2002). *Procambarus clarkii* were housed in 17 cm long \times 10 cm wide \times 10 cm high individual bare tanks. Crayfish were moved to larger individual tanks, 25 cm long \times 15 cm wide \times 17 cm high, in order to better see any locomotion. Only two conditions, food and food with hemolymph, were necessary to demonstrate the effect of hemolymph with all other methodology remaining consistent. Of the pre-existing lab population of *P. clarkii*, 15 adults had the appearance of good health and were selected for the experiment. After the initial control trial (food alone), the crayfish appeared to fall into two categories, responsive to food and unresponsive, ten and five respectively. To confirm this, a second control trial was conducted. The individual crayfishes' behavior was consistent, so only the responsive crayfish were used for the final experimental trial. Unresponsive crayfish were identified as a crayfish that showed zero feeding behavior in both control trials. One crayfish in the responsive group died, presumably of old age, before the experimental condition, bringing the sample size to nine.

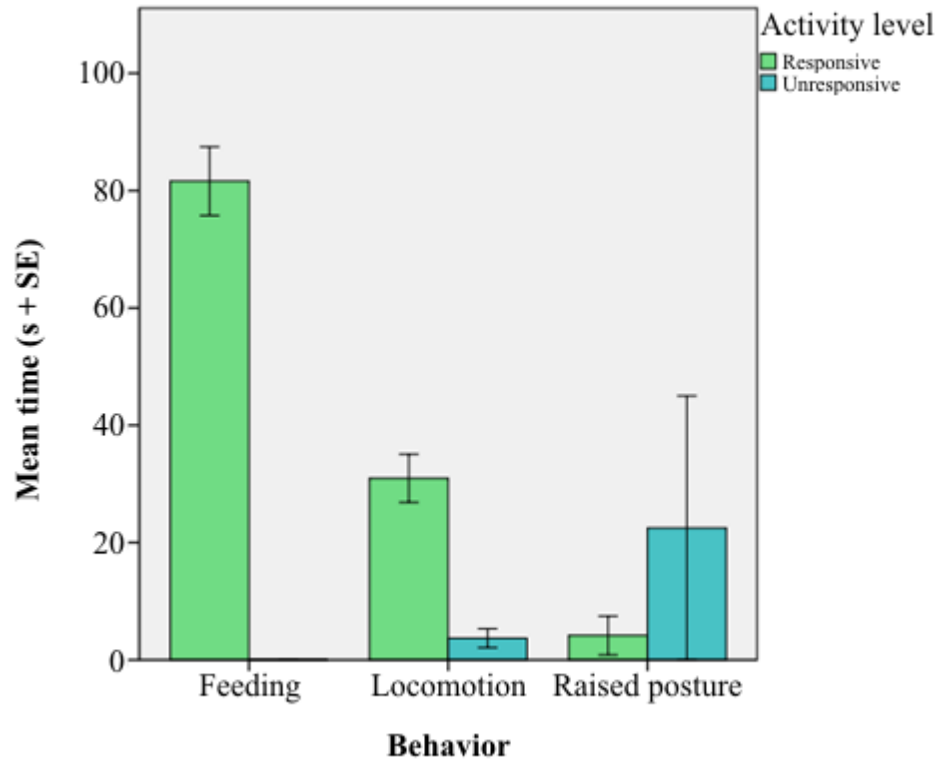


Fig 3.1 Mean times spent in each behavior over the first two control trials for *P. clarkii*.

Results

No significant difference was found across the three conditions for any of the three behavioral measures, feeding ($\chi^2_{2,83} = 0.526$, $P = 0.769$), locomotion ($\chi^2_{2,83} = 2.853$, $P = 0.240$), and raised posture ($\chi^2_{2,83} = 2.428$, $P = 0.297$) using the Kruskal-Wallis test.

Using the Wilcoxon Signed Ranks Test, *P. clarkii* showed a highly significant reduction in feeding behavior when exposed to hemolymph from a crushed crayfish ($Z = -2.666$, $df = 16$, $p = 0.008$). Locomotion ($Z = -1.836$, $df = 16$, $p = 0.066$) and raised posture ($Z = -1.841$, $df = 16$, $p = 0.066$) showed a near significant reduction in each behavior, not reaching significance likely due to small sample size.

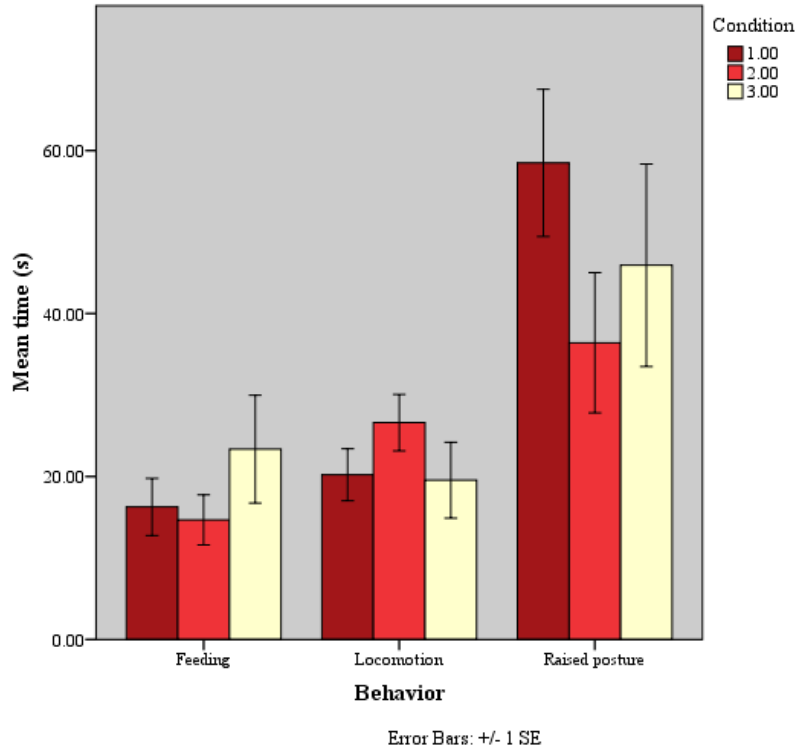


Fig. 3.2 Mean times spent in each behavior across the three conditions for Marmorkrebs.

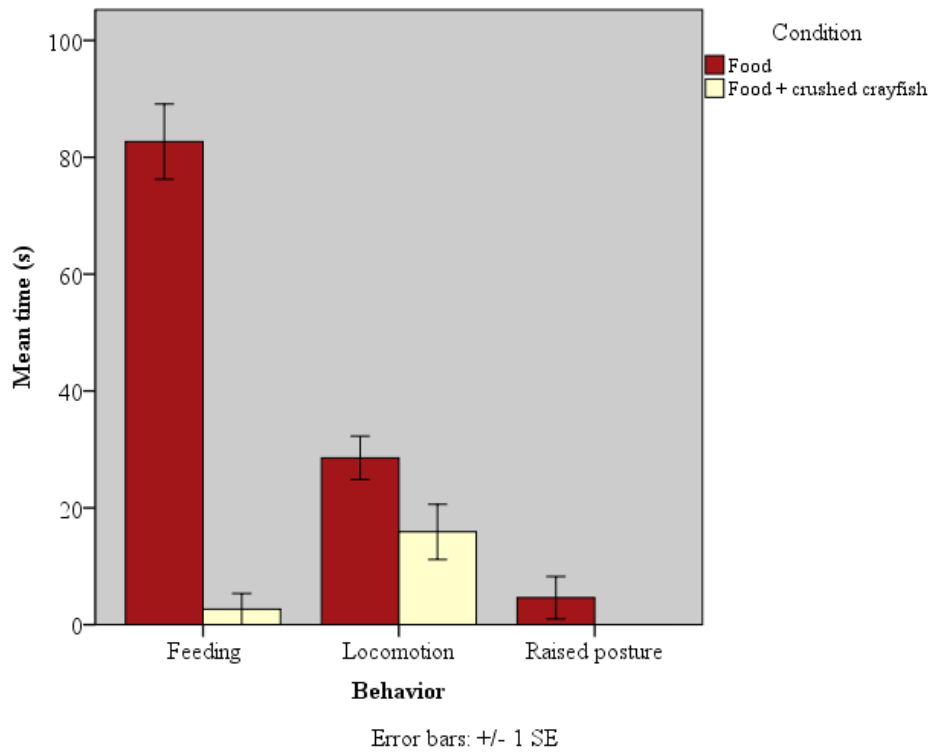


Fig. 3.3 Mean times for each behavior for the responsive group of *P. clarkii*.

Discussion

Contrary to expectation, Marmorkrebs did not alter their behavior in response to hemolymph, unlike other crayfish species. Rather than showing a pattern of active feeding across all conditions, their behavior indicates an inhibition across all conditions. In previous studies, feeding behavior ranged from 30-90 seconds in control conditions, whereas Marmorkrebs range from 15-20 seconds. The inhibited feeding range for previous studies was in a 5-20 second range, closer to the control conditions of Marmorkrebs.

The fact that *P. clarkii* fell into two groups, responsive to food and unresponsive, was surprising. This did not seem to be the case in previous studies. It is possible this is an artifact of long-term laboratory living. All crayfish used in the previous studies were taken directly from wild populations, whereas our crayfish have all been living in a laboratory setting for several months, if not the entirety of their lives. Studies using a range of animals have shown that an unenriched laboratory environment can cause behavioral abnormalities (Meehan et al., 2004; Balcombe, 2006). While the crayfish do not seem to exhibit the stereotypy found in other higher order animals, it is possible that our unresponsive crayfish essentially have some form of “cabin fever.” The pattern of some crayfish remaining responsive could be explained by different lengths of time living in laboratory conditions, or simply reflect differences in susceptibility. The age and time spent in the laboratory is not known, and therefore entirely speculative, however, the death of a crayfish in the responsive group would suggest that old age is not responsible for the lack of responsiveness in the other crayfish.

If this behavioral inhibition is due to the laboratory setting, it could explain the Marmorkrebs findings. As they seem to be an aquarium-based organism currently, it is possible this has led to them having an abnormal suite of behaviors, in the absence of the appropriate

environmental cues. If this pattern is irreversible, it is possible this could make them dysfunctional relative to other crayfish and less capable of establishing invasive populations in the wild than previously thought.

CHAPTER IV

CONCLUSION

Marmorkebs currently show neither a morphological nor behavioral adaptation in response to odor-based cues to avoiding predation. Because Marmorkebs do not respond in the typical manner to the presence of hemolymph, it is unlikely to be a cue responsible for the increased spine length and sharpness found in Germany (Martin et al., 2010; Chucholl & Pfeiffer, 2010). The similarity between the control group and wild caught Marmorkebs also suggest that this is not an effect of predation, but rather seems to be a more typical form than the lab-reared specimen. As populations of Marmorkebs expand in Germany (Chucholl et al., 2012), collection of more specimens may resolve whether this spiny morphology is the norm for wild Marmorkebs populations. Additionally, a closer examination of lab-reared Marmorkebs may be necessary for resolution.

With regard to Marmorkebs invasive potential, the results of these experiments may be good news. The current opinion is that Marmorkebs is a high risk as an invasive species, based on several pieces of evidence. Marmorkebs only need one individual to grow a population, are frequently introduced in the wild due to their pervasiveness in the aquarium trade, are equally as capable in a fight as other equal-sized crayfish species, are highly fecund, and have already shown their capability to wreak havoc in Madagascar (Jiminez & Faulkes, 2011; Chucholl et al., 2012; Faulkes et al., 2012). While these results do not invalidate any of these claims, they may provide some hope. Marmorkebs may not be as successful or competitive as some have warned,

and their introduced populations may be an especially good candidate for biocontrol through use of effective predators.

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