

THE INFLUENCE OF TASTE PERCEPTION IN FORAGING CHOICES IN RUSTY
CRAYFISH

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ABSTRACT

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Organisms use chemical cues in their environment to extract relevant information in order to perform a variety of tasks. To forage effectively, organisms must locate and assess the quality of food sources based on these chemical cues. When determining the quality of these food sources, crayfish use chemical cues in the form of amino acids to both locate food and to determine consumption. However, whether crayfish foraging in flowing systems is altered by differing amino acid concentration is currently unknown. Rusty crayfish collected from two different watershed locations were exposed to fish gelatin containing increasing concentrations of the amino acid β -Alanine (attractive amino acid) and L-Tyrosine (aversive amino acid). The gelatin was weighed before and after each 24-hour trial to determine consumption. The addition of an attractive amino acid (β -Alanine) caused a significant drop in consumption but only for crayfish collected from one of the locations ($p = 0.04$). The addition of an aversive amino acid (L-Tyrosine) had no effect on crayfish consumption from either location. This study demonstrates that the foraging and feeding behaviors of organisms are influenced by the presence of amino acids located in food sources.

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INTRODUCTION

Organisms use their senses to extract relevant information about their environment to perform a number of behavioral tasks, including important evolutionary behaviors such as foraging for food, locating shelter, and finding mates (Pohnert *et al.*, 2007; Hay 2009). In the aquatic environment, the chemical senses are a primary source of information for behavioral decisions (Blaxter & Hallers-Tjabbes, 1992). With predator-prey interactions, many species defend themselves against predators by using chemical defenses in their tissues or by releasing chemicals into the environment (Williams & Gong, 2007; Thoms & Schupp, 2008; Walling, 2009). For example, sea hares *Aplysia californica* (Cooper, 1863) use molecules in their ink secretion, skin, and mucus to chemically defend themselves against blue crabs *Callinectes sapidus* (Rathbun, 1896; Kamio *et al.*, 2010). Aquatic organisms can also use information found in chemical compounds from other organisms to find potential mates (Kamio & Derby, 2017). With female three-spot swimming crabs *Portunus sanguinolentus* (Herbst, 1782-1790), the females release a pheromone which signals the males to respond by performing searching behaviors (Ryan, 1966). To determine habitat settlement, chemicals are used by aquatic organisms like the juvenile spiny lobster *Panulirus interruptus* (Randall, 1840; de Lara *et al.*, 2005). With *P. interruptus*, odor signals are used to determine whether the selection of substrate is influenced by chemical signals (de Lara *et al.*, 2005). To forage for food, aquatic organisms use sensory information to perform ecologically relevant behaviors and to assess features in the environment (Von Der Emde & Bleckmann, 1998). For example, glass shrimp *Paratya australiensis* (Kemp, 1917) were exposed to untreated and treated stormwater Zn concentrations to determine how stormwater interfered with foraging behavior (Oulton *et al.*, 2014). After being exposed to both untreated and treated storm water, abnormal foraging behavior was observed in

the shrimp that were exposed to the Zn in the untreated stormwater concentrations (Oulton *et al.*, 2014). Changes in the composition and distribution of the chemical landscape of any aquatic realm has the ability to alter behavioral choices and the ecological impacts that result from those choices.

Keystone species are so defined because of the large influence that their behavioral choices and ecology niche play in structuring ecosystem function and services (Hale & Koprowski, 2018). Beavers *Castor canadensis* (Kuhl, 1820) are considered keystone species due to the fact that beavers dam streams which then leads to the creation of ponds (Pollock *et al.*, 1995). These ponds then serve as habitats for a diverse spread of species like plants, insects, and aquatic organisms (Pollock *et al.*, 1995). With the plateau pika *Ochotona curzoniae* (Hodgson, 1858), the pika serves as a keystone species in the Tibetan plateau ecosystem (Smith & Foggin, 1999). The majority of predators on the Tibetan plateau primarily consume pikas as the pika is the dominant small mammalian herbivore along with the fact that pikas do not hibernate (Schaller, 1998). When the pika population size decreases due to a lack of food, predators starve which then results in a loss of local biodiversity (Smith & Foggin, 1999). Sea otters *Enhydra lutris* (Linnaeus, 1758) are keystone species in the Aleutian Islands due to the otters' impact on kelp forest ecosystems (Estes & Duggins, 1995). Sea otters are predators of sea urchins *Strongylocentrotus polyacanthus* (Agassiz & Clark, 1907) and when sea urchins are at high densities, the urchins can completely deforest kelp beds (Harrold, 1987). When sea urchin populations are at low densities, sea otters lose their primary food source which then results in an overabundance of kelp forests (Riedman & Estes, 1988). If sea urchins were to be removed, the removal would result in community-level influences (Mills *et al.*, 1993). Thus, altering the foraging choices of keystone species has ripple effects throughout these ecosystems.

The ability of keystone species to extract information is important to the ecosystem as a whole (Power *et al.*, 1996). One key piece of information that organisms extract is the spatial and temporal location of objects in their environments which forms the basis of their ecological interactions (Moore & Crimaldi, 2004). This piece of information allows organisms to locate stimuli that indicate objects that confer benefits (food, shelter, and mates) relative to threats (e.g., predators). When exposed to the cues given off by a predator, prey will reduce their vulnerability to those predators by changing their behavior, morphology, or their life history strategy (Brönmark & Hansson, 2000). Under mechanical disturbance, various species of jellyfish will reverse their gravity-controlled direction when swimming upward (Horridge, 1971). Female fishes will release their metabolites or their sex hormones into the water after the fish have ovulated, which alters the behavior and physiological state of male fishes (Sorensen, 1992). The behavioral use of ecological information can be altered due to the presence of environmental stressors.

With chemical stressors, behaviors like foraging for food, finding mates, or evading predators are altered (Atema, 1988; Veselovský, 2005; Bierbower *et al.*, 2013). Both aquatic invertebrates and vertebrates when exposed to acidity, metals, or complex water containing interacting chemicals, exhibited behavioral changes (Gerhardt, 2001). The reproductive behavior and swimming behavior of zooplankton are altered by the presence of kairomones (Loose *et al.*, 1993). Farah *et al.* (2004) exposed freshwater fish *Heteropneustes fossilis* (Bloch, 1794), *Clarias batrachus* (Linnaeus, 1758), and *Channa punctatus* (Bloch, 1793) to PCP, Butachlor, and 2,4-D to determine how these chemicals influenced stress behavior in the fish. After exposure, the freshwater fish displayed behavioral changes in the form of loss of balance, anorexia, body jerks, restlessness, and abnormal swimming behavior (Farah *et al.*, 2004). With catfish *Ictalurus*

(Rafinesque, 1820) in particular, this organism has the ability to use their sense of taste to find distant chemical cues (Bardach *et al.*, 1967). Each of these examples demonstrate how alterations in the chemical composition of an organism's environment leads to changes in the resulting behavior. This is acutely evident with foraging behavior.

To forage effectively, organisms need to perform two different behavioral tasks. First, organisms need to find food sources within their environments. Second, the organisms then need to assess the quality of those food sources. Organisms use their senses to extract meaningful information about their environment to orient themselves towards attractive stimuli (Louis *et al.*, 2008). This information often contains temporal and/or spatial information that controls or influences movement patterns within environments (Wolf *et al.*, 2004). Crayfish, who are ecosystem engineers and keystone species, can facilitate or regulate macrophyte populations in aquatic habitats by their foraging choices (van der Wal *et al.*, 2013). The chemical composition of those macrophytes influence crayfish foraging choices.

When determining the quality of food items prior to consumption, crustaceans primarily use amino acids as chemical cues (Adron & Mackie, 1978). Several species of macrophytes, like the *Azolla* spp. have been found to have increased amino acid concentrations (Fiogbe *et al.*, 2004; Cruz *et al.*, 2011). For crayfish, various amino acids, like alanine, glycine, and tyrosine, alter behavior and increase the time spent feeding (McLeese, 1970; Kay, 1971; Hamner & Hamner, 1977; Hartman & Hartman, 1977). Tierney and Atema (1988) determined that two different species of crayfish *Faxonius virilis* (Hagen, 1870) and *Faxonius rusticus* (Girard, 1852) responded to different chemical feeding stimulants in the form of amino acids. With *F. virilis*, tyrosine altered feeding behavior, resulting in reduced time spent performing feeding movements. However, with β -Alanine, there was an increase in the time spent performing

feeding movements (Tierney & Atema, 1988). One reason why crayfish respond positively to β -Alanine but respond negatively to tyrosine is the dactyl chemoreceptors of crayfish. One of the dactyl chemoreceptors is sensitive to amino acids, specifically the compounds alanine, histidine, and serine, but not others, namely glutamate, lysine, and tyrosine (Hatt, 1984). The gap of knowledge being investigated is the alteration of crayfish behavior when two different amino acids are placed in the same environment. In this study, β -Alanine and L-Tyrosine will be mixed into gelatin. When placed inside the crayfish's environment, β -Alanine and L-Tyrosine in a gelatin could result in differential consumption of the gelatin due to the amino acids influence on time spent performing feeding movements.

We have several predictions regarding the addition of amino acids into gelatin. We believe the β -Alanine addition to the gelatin will result in an increase in crayfish feeding activity and consumption of the gelatin. When L-Tyrosine is added to the gelatin, the crayfish's feeding activity and consumption of the gelatin will decrease. Previous research has shown that β -Alanine increases feeding activities, while L-Tyrosine decreases feeding activities in crayfish (Tierney & Atema, 1988).

MATERIALS AND METHODS

Organisms (Collection and Housing)

Ninety-seven form II (non-reproductive) male rusty crayfish (*F. rusticus*) were captured using hand nets from Maple Bay of Burt Lake in Cheboygan County, Michigan, USA (45.4873° N, 84.7065° W). One hundred and ten form II male rusty crayfish were also collected from Carp Lake River in Emmet County, Michigan, USA (45.7497° N, 84.8292° W) using modified minnow traps baited with sardines. All *F. rusticus* were stored in a flow-through steel cattle tank (200 × 60 × 60 cm: *l* x *w* x *d*); cattle tanks were fed with unfiltered water from the East Branch of the Maple River (45.5280°N, 84.7738°W). Water entered the tank through a PVC delivery pipe and exited the tank via an overflow standpipe, which kept the water depth at approximately 60 cm. Crayfish fed on natural detritus which was contained within the unfiltered river water.

Shelters made from PVC pipes were provided in the housing tank to reduce resource-based aggression. Crayfish were housed separately, dependent on site of collection (Burt vs. Carp River). The post-rostrum carapace length, maximum carapace width, and left chelae length of each crayfish were measured to the nearest 0.5 mm before use in a trial. Burt Lake crayfish were 4.00 ± 0.065 cm (mean \pm SEM, carapace length) and Carp River crayfish were 3.16 ± 0.041 cm (mean \pm SEM, carapace length). Burt Lake crayfish were 3.47 ± 0.097 cm (mean \pm SEM, chelae length) and Carp River crayfish were 2.29 ± 0.056 cm (mean \pm SEM, chelae length). Housing conditions included a natural light/dark cycle (12:12 l:d) and 23 °C ambient water temperature were used to maintain the crayfish. Each crayfish was used only once in trials then frozen per collecting permit requirements.

Experimental Design

All trials occurred at the University of Michigan Biological Station (UMBS) Stream Research Facility in Pellston, MI (45.5641°N, 84.7508°W). To examine the impacts of diet-supplemented amino acids on crayfish foraging and consumption behavior, a two 2 x 4 factorial assay was implemented. The first factor was amino acid type (β -Alanine and L-Tyrosine). These amino acids were chosen because past research has shown that these amino acids influence crayfish behavior and food consumption (Tierney & Atema, 1988). The second factor was concentration. Each amino acid treatment had four different concentrations added to the gelatin food source. Control groups were provided gelatin as a food source with no added amino acids.

Treatment concentrations were modeled after environmentally relevant levels of amino acids reported in the literature (Carr *et al.*, 1984). β -Alanine treatments were one of four concentration levels: 0.214 mM, 2.14 mM, 21.4 mM, or 214 mM. L-Tyrosine treatments were one of four concentration levels: 0.0101 mM, 0.101 mM, 1.01 mM, or 10.1 mM. Around the same amount of crayfish (± 5 individuals) from Burt and Carp Lake sampling sites were assigned to each treatment. A total of 243 animals were used in this study for a total of 207 observations. Thirty-six crayfish were removed from data analysis due to escaping from the stream, molting, or death.

Table 1. Concentration and Sample Size of Amino Acids

Treatment Concentration	Burt Sample Size	Carp River Sample Size
Control – No β -Alanine and no L-Tyrosine	N = 10	N = 15
β -Alanine – 0.214 mM	N = 10	N = 10
β -Alanine – 2.14 mM	N = 13	N = 12
β -Alanine – 21.4 mM	N = 10	N = 15
β -Alanine – 214 mM	N = 10	N = 11
L-Tyrosine – 0.0101 mM	N = 10	N = 10
L-Tyrosine – 0.101 mM	N = 11	N = 11
L-Tyrosine – 1.01 mM	N = 13	N = 14
L-Tyrosine – 10.1 mM	N = 10	N = 12

Diet Production

Fish gelatin, which has been used to measure consumption in a number of studies (Edwards *et al.*, 2018; Jackson & Moore, 2019), was utilized as the food source. Plastic scintillation vial caps (20 ml) containing gelatin were placed at the upstream end of the arena, close to the head tank, for a consumption assay. Gelatin was made by homogenizing 7 g sardines with 175 ml of river water in a blender. The solution was then poured into a 1000 ml beaker and 7 g of Knox[®] unflavored gelatin was poured into the solution. After one minute, the beaker was then placed on a hot plate to boil. The solution was mixed periodically during the boiling process to prevent burning. After the solution boiled, the beaker was removed from the hot plate for 5 minutes to cool. A powdered form of the attractive amino acid (β -Alanine) or a powdered form of the adverse amino acid (L-Tyrosine) was added to the gelatin approximately 5 minutes after

the gelatin was made, before the gelatin solidified. The powdered β -Alanine and the powdered L-Tyrosine were obtained from Sigma-Aldrich. The solution was cooled 5 minutes prior to adding amino acids to prevent the amino acids from denaturing under the heat. The solution was then poured into scintillation vial caps (20 ml). The solution was placed in a refrigerator and allowed to set for 24 hours. All gelatin caps had a strip of Velcro[®] (1 cm x 1 cm; $l \times w$) attached to the bottom. A piece of plexiglass (11 cm x 16 cm; $l \times w$) with the opposing piece of Velcro[®] was used to affix the gelatins in place. The plexiglass with the gelatin cap attached was placed in the upstream center of each arena as a food source for the crayfish.

Experimental Stream Mesocosms

All trials occurred in flow-through experimental streams constructed from cinderblocks and plastic sheeting. These streams were used to imitate the natural aquatic habitat of crayfish (Wood *et al.*, 2018; Jackson & Moore, 2019). Concrete cinderblocks were stacked to make the stream mesocosm frame and lined with 6-mil polyethylene sheeting to hold water ($1.5 \times 0.5 \times 0.28$ m, $l \times w \times h$) (Moore & Grills, 1999; Wolf *et al.*, 2004). The bottom of each stream was lined with an approximately 2 cm thick layer of pea stone (approx. 0.97 ± 0.04 cm \times 0.75 ± 0.035 cm \times 0.75 ± 0.035 cm; $N = 50$). Egg crating was placed over each stream to prevent crayfish from escaping. Rocks were then placed on top of the screening to keep screening in place.

For each stream, a 208 L plastic drum served as a constant head tank that fed the stream with water from the Maple River. The plastic drum fed into the stream via two 1.0 cm diameter garden hoses. Water flowed through the streams at a flow rate of 0.1 ± 0.05 L/sec. To filter out macro invertebrate fauna and fine organic matter, nylon stockings were placed over the 7.6 cm PVC pipe that delivered the water. The water then exited the artificial stream through a

cinderblock fitted with mesh to prevent escape (0.1 cm mesh size). The mesh-fitted cinderblock was placed on the opposite side of the stream from the plastic drum. The water re-entered the Maple River approximately 200 m downstream of the intake for the stream research facility.

Experimental Protocol

One gelatin cap and one crayfish were used per trial. A single crayfish was placed in the middle of the stream at the downstream end and the gelatin was placed 0.5 m upstream from the crayfish (Figure 1). The gelatin was placed upstream to allow the crayfish to receive odors from the food source. The gelatin was weighed before and after each trial.

Each trial ran overnight for 24 hours. Trials were initiated around 9:00 AM every day; a single crayfish was selected from the housing tank and placed in the middle of the stream at the downstream end. Crayfish were marked with a one square centimeter white patch on their carapace before each trial using a non-toxic correction pen (BIC® Wite-Out® 2 in 1 Correction Fluid, Shelton, Connecticut, USA) to improve visibility. Crayfish behavior is not altered by the presence of Wite-Out application (Martin & Moore, 2007; Fero & Moore, 2008; Jurcak & Moore, 2018). One gelatin food source was weighed on an Ohaus® (OHAUS Corporations, Parsippany, New Jersey) scout scale (Model #H-5851) and then was placed exactly 0.5 m upstream from the crayfish. The crayfish was placed downstream, furthest away from the head tank while the gelatin was the closest to the head tank. Gelatin was removed from each mesocosm the following morning and was surface dried in a salad spinner (Farberware 176 Basics, Farberware Cookware Division, Fairfield, California) for 30 rotations to remove excess water before being weighed. The crayfish was removed from the stream and the water in the mesocosms was rinsed for 120 seconds to allow enough water to flow through and replace itself 24 times during the flush period.

Gelatin Consumption Analysis

Consumption of the gelatin was calculated as a percentage consumed. The absolute value of the final weight of the gelatin minus the initial weight which was then divided by the initial weight was used as a measure of consumption.

$$\text{Gelatin consumption} = \frac{(G_f - G_i)}{G_i} \times 100$$

Where, G_f = *Gelatin finished weight*, G_i = *Gelatin initial weight*

Consumption of each gelatin cap was assessed using a linear mixed effects model by running the lmer function from the lmerTest package in R (Kuznetsova *et al.*, 2017; R Core Team, 2019). Each gelatin consumption model was constructed with full interactions using two categorical factors (location crayfish were obtained and amino acid treatment), one continuous variable (weight of amino acid addition), and a random effects term (mesocosm). Following model construction, the outputs were extracted using the anova function from the car package in R (Fox & Weisburg, 2018).

All statistical models were performed using generalized linear mixed models (Zuur *et al.*, 2009). All models ran in R using the lmer function from the lmerTest package in R (Kuznetsova *et al.*, 2017; R Core Team, 2019). Following model construction, the outputs were extracted using the anova function from the car package in R (Fox & Weisburg, 2018). Amount consumed served as the dependent variable and location crayfish were obtained and amino acid treatment served as categorical factors while the amount of the amino acid added served as a continuous variable. Mesocosm was added as a fixed factor. Model selection was based on the Akaike's information criteria (Akaike, 1974). The selection of best model was based on the lowest AIC value while removing all models with a delta AIC greater than 2 from our selection process

(Burnham & Anderson, 2002). The statistical effect of each model was determined by extracting Cohen's D (Cohen, 2013) using the effectsize package in R (Ben-Shachar *et al.*, 2020).

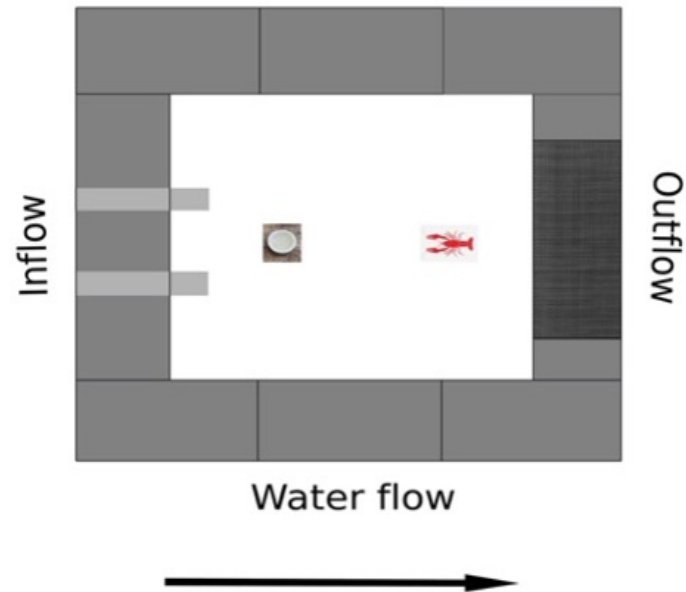


Figure 1. Experimental Mesocosm. A constant head tank fed filtered river water through the two inflow hoses on the left. Water then flowed out of the screened outflow on the right. The gelatin food source containing treatment was placed upstream, closest to the head tank; the crayfish was placed downstream, closest towards the screened outflow.

RESULTS

This study examined the impact that amino acid composition, β -Alanine and L-Tyrosine, had on *F. rusticus* consumption. The interaction effects of the addition of β -Alanine as well as location of capture had a significant impact on food consumption in crayfish (Table 2, $F_{1,87,0.05} = 6.8$, $p = 0.04$). Crayfish collected from Carp Creek had lower consumption of food, and this consumption decreased significantly with increasing concentrations of β -Alanine (Table 4, $p = 0.01$). While crayfish collected from Burt Lake had lower consumption with increasing β -Alanine, when compared to the lowered consumption with crayfish collected from Carp Creek, the decrease in consumption was not as drastic (Table 4).

The interaction effects of the addition of L-Tyrosine to a food source had no effect on crayfish, regardless of their location of collection (Table 3, $F_{1,87,0.05} = 1.2$, $p = 0.27$). Neither L-Tyrosine nor location of collection had significant one-way effects.

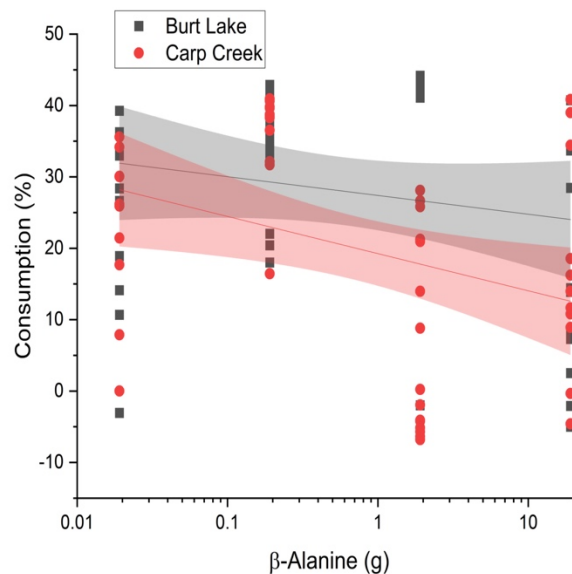


Figure 2. Scatter Plot of β -Alanine Mass and Percentage of Consumption from *F. rusticus*. Crayfish from Burt Lake (grey) and Carp Creek (red) are plotted in different colors, so the relationship between location, β -Alanine mass, and consumption can be determined.

Concentration of β -Alanine significantly affects consumption ($p < 0.001$) and location where crayfish were obtained significantly affects consumption ($p < 0.001$).

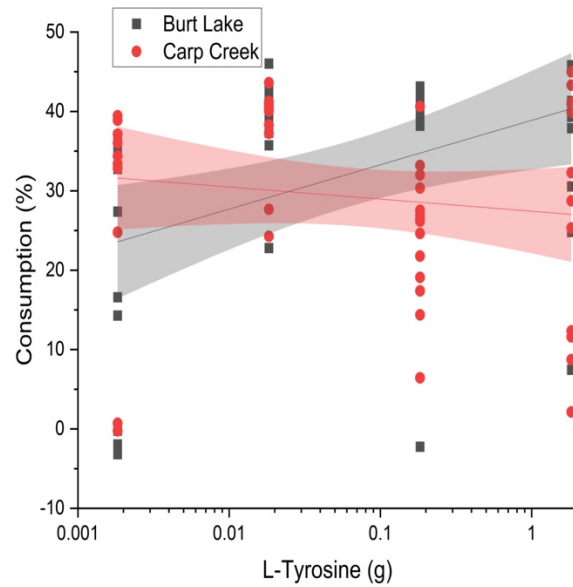


Figure 3. Scatter Plot of L-Tyrosine Mass and Percentage of Consumption from *F. rusticus*. Crayfish from Burt Lake (grey) and Carp Creek (red) are plotted in different colors, so the relationship between location, L-Tyrosine mass, and consumption can be determined. Concentration of L-Tyrosine insignificantly affects consumption ($p = 0.8$) and location where crayfish were obtained insignificantly affect consumption ($p = 0.8$).

Table 2. Statistical Output of Main and Interaction Effects on β -Alanine Consumption from *F. rusticus*

Model	F value	P value
Location	12.3	< 0.001
Concentration	27.0	< 0.001
Location:Concentration Interaction	6.8	0.04

Significant P values are highlighted in bold

Table 3. Statistical Output of Main and Interaction effects on L-Tyrosine consumption from *F. rusticus*

Model	F value	P value
Location	0.06	0.8
Concentration	0.07	0.8
Location:Concentration Interaction	1.2	0.27

Significant P values are highlighted in bold

Table 4. Statistical output of location effects on β -Alanine consumption from *F. rusticus*

Location	Slope of model	P value of slope	R ²
Burt Lake	-2.63	0.23	0.034
Carp Creek	-5.21	0.01	0.19

Significant P values are highlighted in bold

Table 5. Statistical output of location effects on L-Tyrosine consumption from *F. rusticus*

Location	Slope of model	P value of slope	R ²
Burt Lake	5.58	0.005	0.18
Carp Creek	-1.52	0.366	0.018

Significant P values are highlighted in bold

DISCUSSION

The addition of an attractive amino acid (β -Alanine) significantly decreased the foraging behavior of crayfish in artificial streams, but the degree of the effect was dependent upon the capture location of the crayfish (Table 2, $F_{1,87,0.05} = 6.8$, $p = 0.04$). Specifically, the addition of β -Alanine decreased foraging across all concentrations, but the magnitude of the decrease was greater for crayfish collected from the Carp Creek river system (Table 4, $p = 0.01$) than the Burt Lake system (Table 4, $p = 0.23$). Conversely, altering the concentration of an aversive amino acid (L-Tyrosine) did not alter foraging regardless of crayfish home location (Table 3, $F_{1,87,0.05} = 1.2$, $p = 0.27$). Thus, the alteration of the concentration of these two amino acids has differing effects based on both the location from which animals are captured and the amino acid.

Past research has examined the effect of amino acid molecular structure and concentration, along with foraging behavior on crustacean chemoreceptors under laboratory conditions (Hatt, 1984; Derby & Sorensen, 2008). At the physiological level, the dactyl chemoreceptors of crayfish experience an increase in neuronal firing to β -Alanine, as well as a number of other amino acids (Bauer *et al.*, 1981; Hatt, 1984). The chemoreceptors of spiny-creek crayfish *Faxonius limosus* (Rafinesque, 1817) exhibited an increase in neuronal impulse firing when stimulated by alanine and other amino acids presumably indicating an attractiveness to these amino acids (Bauer *et al.*, 1981). In comparison, chemoreceptor cells from stone crayfish *Austropotamobius torrentium* (Paula-Schrank, 1803) increased firing rates after being exposed to alanine, proline, and norvaline while other amino acids proved to be aversive at creating a cell response (Hatt, 1984). The work at the receptor level certainly shows variable responses to the presence of different amino acids, yet these peripheral reactions are the basis to foraging and

feeding responses. With my work in particular, β -Alanine decreased foraging and feeding responses while L-Tyrosine had no effect on behavior.

At the behavioral level, the supplemental addition of amino acids to food has shown similar variability to the receptor level findings. By injecting stimulus solutions containing different amino acids into stagnant tanks containing crayfish, Tierney and Atema (1988) demonstrated that the addition of several amino acids, including β -Alanine, increased the feeding behaviors of *F. virilis*. Previous research with Pacific white shrimp *Litopenaeus vannamei* (Boone, 1931) determined that gelatin pellets containing a combination of amino acids, including alanine and tyrosine, were selected more significantly (Nunes *et al.*, 2006). Past research has also found that after being exposed to increasing concentrations of glycine betaine, juvenile freshwater prawn *Macrobrachium rosenbergii* (de Man, 1879) displayed an increase in consumption (Felix & Sudharsan, 2004). In another study, juvenile carp *Cyprinus carpio* (Linnaeus, 1758) experienced significant effects on habitat exploration and attraction due to the presence of non-polar amino acids after being exposed to synthetic amino acids (Saglio *et al.*, 1990). However, basic amino acids and polar, uncharged amino acids did not attract *C. carpio*, while exploration did significantly increase (Saglio *et al.*, 1990). Similar to the results of this study, these past experiments indirectly support the hypothesis that amino acids do influence foraging and feeding behavior, either positively or negatively, of aquatic organisms. Although, the two distinct behaviors involved in the consumptive process, foraging and feeding, appear to be influenced differentially by the addition of amino acids during assays.

Any consumptive act requires at least two distinct behavioral steps. The first step is a foraging behavior. Foraging involves the identification and location of a potential food source within an environment (Galef & Giraldeau, 2001). Often, chemoreceptor systems, such as

olfaction, designed for the detection of distant odor sources are involved in this step (Giordano *et al.*, 2017). Once found, animals perform the second step which is feeding, typically involving a chemoreceptor system, such as taste, which has evolved for a more localized odor source (Giordano *et al.*, 2017). Certainly, there is overlap in the two systems across different animal species (Devine & Atema, 1982; Ache, 1987). In the aquatic environment, amino acids can serve as chemoattractants (during foraging), feeding stimulants (during feeding), or as both a chemoattractant and a feeding stimulant. The foraging behavior of decapod crustaceans towards amino acids along with betaine and taurine is species specific. Glycine, taurine, and betaine have been found to act as both feeding stimulants and chemoattractants to a wide variety of decapod crustaceans (Deshimaru & Yone, 1978; Tolomei *et al.*, 2003; Truong, 2008). With banana prawns *Penaeus merguensis* (de Man, 1887-1888), glycine was found to increase searching behavior (Hindley, 1975), but when glycine was exposed to kuruma shrimp *Penaeus japonicus* (Bate, 1888), the shrimp's searching behavior was not altered, even though the shrimp did experience an increase in feed consumption (Deshimaru & Yone, 1978). After exposure to betaine, mud crabs *Scylla serrata* (Forskål, 1775) experienced a longer duration of searching behavior along with a higher rate of feed consumption (Truong, 2008). However, the ornate spiny lobster *Panulirus ornatus* (Fabricius, 1798) only had a significantly higher rate of feed consumption after betaine exposure (Johnston, 2006). When viewed as two separate behavioral steps, the acts of foraging and feeding play a significant role in the aquaculture industry.

The use of artificially enhanced diets with amino acids can increase both the attractiveness and feeding rates of aquaculture diets. In general, decapod crustaceans are slow feeders and because of delays in food detection, nutrients will be lost from the food (Mendoza *et al.*, 1997; Smith *et al.*, 2005). To prevent this loss, crystalline amino acids have been used in the

past to act as both feeding stimulants and chemoattractants towards decapod crustaceans (Nakamura, 1987; Coman *et al.*, 1996; Felix & Sudharsan, 2004). Most free amino acids, including glutamic acid (Hindley, 1975), alanine (Archdale & Nakamura, 1992), arginine (Harpaz *et al.*, 1987), serine (Archdale & Nakamura, 1992), and cysteine (Lynn *et al.*, 1994), serve as chemoattractants in decapod crustaceans. With the results conducted during our experiment, β -Alanine was found to neither be a feeding stimulant or a chemoattractant under more realistic feeding conditions with both flow and natural light settings. In fact, with β -Alanine, foraging behavior of crayfish significantly decreased (Table 1, $F_{1,87,0.05} = 6.8$, $p = 0.04$). With L-Tyrosine, crayfish exhibited no significant change in foraging or feeding behavior (Table 1, $F_{1,87,0.05} = 1.2$, $p = 0.27$). It is possible that the results from this study were contrary to past studies due to the flow through nature of the experiment. In these trials, crayfish needed to both find and consume the food. These two separate behavioral acts could possibly integrate chemosensory information differently. Overall, the presence of amino acids in aquatic systems can influence foraging and feeding behaviors of aquatic organisms, though these influences are different in realistic flow through mesocosms compared to static tanks.

Amino acids are widely distributed and can be found freely in freshwater (Thurman, 2012), macrophyte tissues (Boyd, 1971), and in the tissues of many prey organisms (Carr *et al.*, 1996). In water, amino acids are released by a wide variety of organisms which include vertebrates (Olsén, 1986), phytoplankton (Daumas, 1976), and zooplankton (Nicol, 1967). In oligotrophic lakes, concentrations of total dissolved amino acids had an average of 100 ug/l while the average concentration of total dissolved amino acids in eutrophic lakes was 600 ug/l (Burnison & Morita, 1974; Tuschall & Brezonik, 1980). Thomas and Eaton (1996) found similar results in their experiment as the concentrations of individual free amino acids was much higher

in eutrophic lakes than in oligotrophic lakes. In lakes, the total amount of amino acids accounted for 14-35% of the dissolved organic nitrogen (Tuschall & Brezonik, 1980). Given the ubiquitous and fluctuating presence of amino acids in habitats, omnivorous foragers, like crayfish, may be faced with changing perceptions of foraging landscapes. The responsiveness to potential food items, like macrophytes or carrion, could be influenced by the differences in the natural background concentrations of amino acids (Johnson & Atema, 1986) and/or changes in the relative concentrations of amino acids in prey tissues (Derby & Zimmer, 2012). If foragers are altering prey selection based on changes in background amino acid levels, changes in food web dynamics can have ripple effects throughout the ecosystem (Stewart *et al.*, 2004).

With freshwater macrophytes in particular, the abundance and distribution of macrophytes are influenced by nutrient availability and the addition of amino acids (Chambers & Kalff, 1985). This results in freshwater grazers undergoing selective pressure over food sources (Dale, 1986). With grazers, the selective foraging of freshwater macrophytes influences the diversity, distribution, and abundance of these macrophytes (Jupp & Spence, 1977). Due to the fact that β -Alanine decreases food consumption, if macrophytes have an abundance of β -Alanine, organisms may not select that macrophyte to consume. If macrophytes contain amino acids that do increase food consumption, like isoleucine and glycine (Tierney & Atema, 1988), aquatic organisms will likely remove submerged macrophytes in ponds and lakes (Saiki & Tash, 1979; Feminella & Resh, 1986). When in abundance, amino acids can play an important role in the selection of food sources.

Some organisms' behaviors or foraging choices have larger or more profound effects for ecosystem dynamics (Naiman, 1988; Guariento *et al.*, 2014). Crayfish function as both keystone species and ecosystem engineers for both lentic and lotic habitats (Statzner *et al.*, 2000; Reynolds

et al., 2013; Albertson & Daniels, 2018). As such, a crayfish's foraging choices impact macrophyte community dynamics such as abundance, diversity, and species-richness (Chambers *et al.*, 1990). For instance, increased foraging led to the decimation of water vegetation in lakes (Lorman, 1980). When predator cues are present, crayfish can also consume large quantities of macrophyte tissue (Wood *et al.*, 2018). With elevated CO₂ levels due to human activities, crayfish diet may shift from leaf detritus to macrophytes (Adams *et al.*, 2003). We saw a decrease in foraging effort with increasing β -Alanine concentrations; this clearly indicates that foraging and consumption are highly dependent on the chemical landscape perceived by crayfish and possibly many other herbivores. Altering foraging and consumptive choices in keystone species, like crayfish, has community-wide effects that need to be understood as ecosystems and their abiotic compositions are altered by human activities (Giling *et al.*, 2009).

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