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Variation in the Fear Response of Atlantic Sand Fiddler Crabs (Leptuca pugilator) to Anthropogenic Disturbance

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VARIATION IN THE FEAR RESPONSE OF ATLANTIC SAND FIDDLER CRABS (*LEPTUCA PUGILATOR)* TO ANTHROPOGENIC DISTURBANCE

by

KATRINA BUTTRAM

(Under the Direction of Michele Guidone)

ABSTRACT

Leptuca pugilator is a common inhabitant of southeast Georgia salt marshes. This study examined the boldness of *Leptuca pugilator* across environmental conditions and human impacts. Here, boldness was defined as time taken to reemerge from a burrow after a fear stimulus. I hypothesized that crabs would vary in their boldness based on their surroundings, reproductive timing, and sex. Field and experimental trials were conducted to isolate which factors most influence boldness. Field trials were conducted at four sites varying in human influence throughout the breeding season. During each survey, vegetation height, substrate temperature, average burrow width, burrow count, and distance to/from vegetation was measured. The presence of a vegetative foreground was further investigated in the lab study. Crabs residing at Lazaretto Creek Boat ramp displayed less bold behaviors, possibly due to human activities. Male and female *L. pugilator* expressed similar boldness, but reacted differently to environmental conditions. Opposing my hypothesis, boldness of male crabs increased with substrate temperature. Female crabs took less time to reemerge when adjacent to wider burrows. Experimental trials found that male crabs reemerged faster when given a foreground of vegetation, although not observed in the field trials. This study provides further insight on fiddler crab behavior as varied by environmental conditions in Southeast Georgia. Results of this study should be expanded on to be inclusive of more populations that face high human influence. Measurements for boldness and peak reproductive periods should be explored further to best identify how they should be classified for future research.

INDEX WORDS: Fiddler crab, *Leptuca pugilator*, Salt marsh, Reproductive behavior, Human influence, Behavioral modification, Behavior plasticity

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KATRINA BUTTRAM

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DEDICATION

I would like to dedicate to a few people. First of all, I would like to thank my parents, without them I would still be twiddling my thumbs trying to figure out what to do with my life. You two have supported me in more ways than I can remember. I thank you so much for sticking by my side throughout my life and believing in me when I doubted myself. This work is dedicated to you most of all because without you, I would be lost.

Next, I would like to thank my adoring husband. We met while I was drowning in the depths of this program. Even though we barely knew each other in the beginning, you saw I could succeed, and you pushed me through the hardest days. Thank you for also believing in me when I felt exhausted and scared. You did not believe failure was an option and pushed me to never give up. I thank you for that.

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CHAPTER 1

INTRODUCTION

Study Habitat: Coastal Salt Marshes

Coastal freshwater and saltwater wetlands line approximately 40 million acres of the continuous territory of the United States (EPA, 2022) equaling about 5% of the terrestrial surface of the earth (Zedler et al. 2008). Coastal salt marshes are areas adjacent to saline water source(s) and are heavily influenced by tidal regimes (Barbier et al. 2011). Their substrates are predominately vegetated by grasses, brushes, and shrubs (Barbier et al. 2011). As one of Earth's most productive ecosystems, coastal salt marshes provide direct and indirect resources to humans (Gedan et al. 2011, Barbier et al. 2011). Globally, marshes serve as a carbon sink when the system's plant and microorganism inhabitants are of sufficient number and health and sediment disturbances are relatively low in frequency and intensity (Connor et al. 2001). The biogeochemistry of salt marsh sediment provides vital inorganic and organic substrates needed for environmental nutrient cycles such as the microbially influenced nitrogen cycle (Hopkinson and Schubauer 1984) and the carbon cycle (Kathilankal et al. 2008). Diverse detritivore populations can shift sediment biogeochemistry and microbial composition via their behaviors that mix sediment layers together, such as burrowing (Booth et al. 2019) or feeding (Cueller-Gempeler and Munguia 2013). Additionally, salt marshes provide animals with habitat for foraging, reproduction, and nursery sites (Seitz et al. 2014).

Coastal salt marshes support the economy by protecting items of value such as homes, sites of recreation, and businesses from storm events and the continuous erosion that occurs due to flowing water (Costanza et al. 2008, Barbier et al. 2011, Leonardi et al. 2018). The presence of salt marsh plants dampens the speed of coastal waters via friction; as the water interacts with salt marsh vegetation, a decrease in wave energy occurs (Barbier et al. 2011). Salt marsh sediments also absorb storm surge waters, further dissipating storm energy across the landscape (Barbier et al. 2011). Costanza et al. (2008) created a model analyzing the presence/absence of vegetation in relation to damages caused by 34 past hurricanes. They concluded that the loss of 1 hectare of salt marsh area could increase damages by 33 thousand US dollars (Costanza et al. 2008). They further reported that salt marshes provide an estimated 23.2 billion US dollars in storm surge protection (Costanza et al. 2008).

Approximately 2.4 million Americans live in coastline counties along the Atlantic coast (Wilson and Fischetti 2010); as this number has increased, so too has the need to protect items of economic and emotional value. Nevertheless, global total salt marsh area decreased by 87% in the past 300 years due to anthropogenic behaviors such as ditching, vegetation clearing for construction, transformation into aquaculture arenas, and nutrient runoff (IPBES 2018, Gedan et al. 2011). From 2000-2019, global salt marsh area decreased by 1,452.84 km^2 through land development and indirect processes such as pollution, overfishing, and accelerated climate change (Campbell et al. 2022). Tropical storms, hurricanes, and associated storm surges (henceforth collectively referred to as storm events) present a challenge to coastal living as homes and businesses could be destroyed beyond repair with strong winds or record flooding (Costanza et al. 2008). Some permanent structures that create hardened shorelines, such as groins, jetties, seawalls, and bulkheads, cut off water supply and, subsequently, sediment supply to their areas. These are short-term solutions that temporarily protect the area from storm event wave energy that could destroy structures of economic value but have been found to subsequently worsen erosion (Landry and Golden 2018). As the rate and intensity of storm events increases due to climate change (Wilberg et al. 2020), the need for healthy salt marshes with an adequate acreage and an intact marsh community to diffuse storm energy and protect coastlines increases. Human built structures are not the only cause of marsh decline. The seafood industry, while economically valuable, could be damaging if organisms are overharvested. For example, overharvesting of predators, such as blue crabs (*Callinectes sapidus*), initiates an increase in herbivore populations such as *Sesarma reticulatum* (Altieri et al. 2012). The increase of *S. reticulatum* individuals produced areas of die-off of *Spartina alterniflora* dominated salt marshes in New England (Altieri et al. 2012). This inadvertently changed the shape of the salt marsh, as once retained sediment became free to erode (Altieri et al. 2012).

Climate change, while normal on a geologic time scale, in recent years has been accelerated primarily by anthropogenic influence (IPCC 2007). Climate change effects include sea level rise, increased frequency of wildfires, increased intensity of hurricanes, increased flooding, and melting of polar caps (IPCC 2021). Due to a decreasing area from the landward side because of human activity, salt marshes are becoming more vulnerable to sea level rise with the possibility of being unable to retreat before complete submergence occurs (FitzGerald and Hughes 2019). Loosened substrate resulting from overgrazing by herbivorous species prompts more substrate to be carried away with the tides at a rate higher than it is being deposited; combined with sea level rise, a dramatic increase in area loss could occur faster than area accretion (Gedan et al. 2011, FitzGerald and Hughes 2019). Record breaking temperatures and nutrient runoff accumulating in the substrate of salt marshes dramatically impacts inhabiting organisms by either initiating stressful conditions or organismal death (Gedan et al. 2009). Coastal salt marshes are nursery sites and feeding grounds for many economically and ecologically important species; the loss of these organisms through the rise in temperature and inability to cope with environmental stressors is a cascading affect that could lead to marsh failure and loss (Gedan et al. 2009). Coastal salt marsh loss could result in total loss or reduction in defense against storm events, nutrient cycling systems, detoxification and clarification services, and recreation sites that could greatly devastate coastal economies and communities (Gedan et al. 2011).

Study Organism: Fiddler Crabs

Salt marshes are incredibly biodiverse vegetated ecosystems that support a distinct variety of animal species (Kennish 2001). Fiddler crabs are common inhabitants of salt marshes around the world (Crane 1975). They are burrowing detritivores that promote the turnover of typically anoxic sediment, which allows roots to obtain oxygen (Bertness 1985). As detritivores, they aid in the process of nutrient cycling by breaking down organic materials into smaller parts (Teal 1958). They serve as an important food source for various bird species as well as raccoons, feral cats, and aquatic predators such as the blue crab (Christy 1980). Fiddler crab species are well studied and a prime example of sexual dimorphism because the males develop an exaggerated cheliped that is anatomically useless in their foraging activities (Crane 1975). However, the enlarged cheliped serves during reproductive behaviors and in defensive battles against competing males, heterospecifics, and predators (Crane 1975, Christy 1980).

Fiddler crabs are visual animals that greatly depend on their sight to identify threats, mates, and conspecifics (Land and Layne 1995). When a fiddler fearfully responds to a visual stimulus, they fight by engaging their claws, freezing, or fleeing from the stimulus into a burrow, with fleeing being the most common response (Christy 1978, 1980). Fiddler crabs are startled easily, fleeing from even butterflies (Hemmi 2005, M. Guidone, personal observation) resulting in descent into nearby burrows. However, hiding greatly reduces the time a fiddler crab spends on the surface, as they are mostly active during low tides (Darnell et al. 2020, DiNuzzo et al. 2020). These relatively short periods of surface activity are vital because this is the only time fiddlers forage and engage in reproductive activities such as courting, which do not occur simultaneously for males of most fiddler species (Christy 1980). Bold behaviors, such as remaining surface active despite the presence of a potential predator, are beneficial in reducing fear reaction frequency or improving its latency and thus increase successful matings (Reaney and Backwell 2007). However, remaining surface active increases the risk of predation and desiccation (Allen and Levinton 2014).

Boldness – an individual's propensity to take risks (Cooper 1999) – in fiddler crabs is dependent on multiple factors. Within my study, I measured boldness as the time taken to reemerge from a burrow after a fear invoking event, adopted from Pratt et al. (2005). Boldness could aid in successful courtship, but the associated risk of predation and desiccation becomes a factor (Allen and Levinton 2014). For example, male *Leptuca pugilator* individuals were bolder during times of peak reproduction as well as when there were high numbers of female *L. pugilator* surface active (Pratt et al. 2005). Similarly, in the Australian species *Austruca mjoebergi*, the presence of a female in a quadrat containing males caused increased time spent out of the burrow (Reaney and Backwell 2007, Gruber et al. 2019, Darnell et al. 2020). Male *A. mjoebergi* also reemerged more quickly during peak mating periods compared to non-mating periods, and overall, regardless of mating period if a focal female was presented during the trial (Gruber et al. 2019). Additionally, while bold and shy males engaged in similar wave rates, bold males spent significantly more time exhibiting courtship waving and received more matings than their shy counterparts, despite no significant difference in female visits (Reaney and Backwell 2007). However, signaling effectiveness when waving for courtship is also influenced by the male major claw size; males with larger major claw sizes had increased effectiveness (McLain and Pratt 2007). In addition, while waving aids in the attraction of mates, males will also wave to ward off opponents in territorial battles (Christy 1980). Thus, the expression of bold tendencies by fiddler crabs may, in part, increase an individual's fitness.

A fiddler's range of vision across a vertical landscape is also limited (Smolka and Hemmi 2009); the inability to accurately see above a certain degree point could prompt an individual to hide for longer periods due to its uncertainty of the conditions. For example, the presence of vegetation in front of a crab's field of view may hinder its ability to see predators. Therefore, marsh conditions such as vegetation density and height are suspected to influence fiddler crab boldness.

Related to their limited vision, several factors influence the probability and strength of a fiddler crab fear response, including the angle of approach of the stimulus, initial proximity of the fear stimulus to a focal crab, and the repetition of the stimulus. Direct linear approaches caused a higher proportion of crabs to respond quickly by hiding, while an angled approach decreased the proportion of crabs responding and delayed their response timing (Koga et. al 2001, Hemmi 2005). Repeated, consistent movement of waving a hand over a group of focal crabs initiated little to no response after a duration as short as 30 minutes (Walker 1972). Subsequent studies found when a dummy predator remained in the focal crabs' line of sight, a delayed reaction to its' approach occurred (Hemmi and Merkle 2009). The researchers stated that while habituation is a possibility, the proximity of the stimulus to the focal population and its repetition dictated the likelihood of habituation (Walker 1972, Hemmi and Merkle 2009).

Further, environmental factors also alter behaviorally plastic invertebrates such as fiddler crabs (Kerr et al. 2014). An increase in substrate temperature significantly decreased the waving behavior of male *L. pugilator*, including the probability of male waving and rate of male waves (DiNuzzo et al. 2020). Researchers examining the role of substrate temperature and reproductive behavior of *Uca terpsichores* established that the period in which females incubate their eggs varied with substrate temperature changes (Kerr et al. 2012). As substrate temperature increased, the time in which a female spent incubating her clutch decreased; the converse occurred when substrate temperature decreased (Kerr et al. 2012). Males of this species courted more intensely during higher substrate temperatures and higher tidal amplitudes (Kerr et al. 2014). Further, the presence/absence of vegetation as well as the height of it may interact with substrate temperature (Shashua-Bar and Hoffman 2000) in addition to potentially obscuring a fiddler's perception of a predator's approach.

Finally, the imposing presence of humans onto the threatened marsh ecosystem could lead to behavioral shifts in between and within species of animals (Hammond et al. 2020). Humans negatively impact fiddler crab populations indirectly by depleting their already narrow ranged habitat of resources and by their direct presence in marsh zones by invoking frequent fear responses (DiNuzzo et al. 2020). *Leptuca pugilator* reaction to direct approaches from humans was indistinguishable to the reaction of a predation attempt, resulting in fleeing to a nearby burrow and descent into it (Pratt et al. 2005). DiNuzzo et al. (2020) found that per pedestrian, the likelihood of a male to wave within a 5 min observational period was reduced by 47.8%. Due to humans causing *L. pugilator* to respond fearfully, human presence on salt marshes initiates frequent fiddler hiding with reduced surface time to engage in mating rituals and foraging activities (Pratt et al. 2005). Both of these activities are necessities for the species to survive.

Study Species: Leptuca pugilator

Of the three most common species found in southeastern Georgia salt marshes, this study focused on *Leptuca pugilator* due to their abundance in the sandy portions of Georgia salt marshes (Teal 1958) and prevalence near public access points within Chatham County (Buttram, personal observation). *Leptuca pugilator* resides in the upper, sandy marsh vegetated by short and tall form *Spartina alterniflora.* Alongside *L. pugilator* in these areas is the red jointed fiddler crab, *Minuca minax.* In the lower marsh colonized by *S. alterniflora*, resides the mud fiddler crab, *Minuca pugnax.* I observed *L. pugilator* in large quantities prior to the final selection of sites and start of human observation protocols. Their specialized chela and mouthparts allow for the scooping of sand and pulling the desired materials out, then rejecting the sand itself (Crane 1975). The major cheliped constitutes up to 48% of a male's dry weight (Christy 1980) and significantly effects metabolism and endurance (Allen and Levinton 2007).

The mating process of sexually mature *L. pugilator* individuals is primarily composed of visual displays and engagements executed by the males of this species. Observable reproductive behaviors present in the forms of waving, dashing in and out of burrows, and although uncommon, physical contact of a male forcefully thrusting a focal female into the male's burrow (Crane 1975, Christy 1978, Christy 1980). Males are deemed sexually mature once they reach a carapace width of approximately 9.5-10.5 mm (Christy 1980). However, the size at which females are sexually mature is unknown (Christy 1980). Their reproductive behavior follows the moon and tidal cycles with peak courting activity approximately 3-5 days prior to the nocturnal spring tide (Christy 1978, 1980). These courting behaviors are inclusive of a male displaying waving behaviors to a focal female and the construction of a hooded burrow that contains multiple chambers including a separate chamber for mated female(s) to reside in during egg incubation (Christy 1980). Females typically incubate their clutches for about 10-days prior to their release at the nocturnal spring tide in the estuaries, but incubation periods have been found to vary depending on substrate temperature (Christy 1978, 1980, 2011). Their reproductive cycle follows with the tidal regime as larval offspring are released by the females during the nocturnal spring tide, discharging into the estuary, allowing larval megalopae to be further pushed out and discharged along the estuary's banks for successful settlement (Christy 1978, 1982).

Project Goals

I hypothesized that local populations of *L. pugilator* boldness is dependent on the extent of human influence experienced, timing within the reproductive cycle, and a range of environmental factors including substrate temperature, vegetation height, distance from the edge of the vegetation, maximum crab size as estimated with burrow width, and crab density estimated with burrow density. If *L. pugilator* behavior is context specific to environmental conditions and/or human influences, then a difference in boldness will be present between populations at different sites and possibly even within a population if conditions vary greatly within the site.

First, I predicted that increased human influence such as pedestrian volume, parked car density, or traffic counts near the site would result in decreased boldness. I did not anticipate habituation to occur in relation to these anthropogenic factors due to their irregularity; previous study indicates consistency and repetitiveness are needed for habituation to occur in a field setting (Walker 1972, Hemmi and Merkle 2009). Second, I predicted that populations would exhibit bolder behavior during times of peak versus lower reproduction. Third, I predicted that crab boldness would be modified by environmental conditions that influence substrate temperature and the visual range surrounding the focal crabs, such as height and extent of vegetation, with decreased boldness at higher temperatures and increased boldness with taller vegetation. Further, I predicted that boldness would differ between male and female crabs, due to either the male drive for reproductive competition or the differential effects of environmental factors impacting each sex. Finally, I predicted boldness would increase with average crab size proxied by burrow width and increase with crab density explained by the number of burrows present or the number of active *L. pugilator* in a quadrat.

This study addressed the lack of understanding of how human influences coinciding with environmental conditions and reproductive timing impact the behavior of male and female *L. pugilator* inhabiting coastal Georgia. Previous research on *L. pugilator* provided insight into how their behavior changes in the presence of humans, with the reproductive cycle, and altered environmental conditions. However, none of these factors had been examined in combination and studies had not occurred in the low-country area with high populations of humans present on marsh lands inhabited by fiddler crabs. This study adds to the current knowledge of how fiddlers behave in relation to their ecosystem that is ever changing due to the actions of humans.

CHAPTER 2

METHODS

Field Study

Field Sites

Field observations were conducted at 4 sites in the Northeast region of costal Georgia. Sites were selected to account for variation in the magnitude of human impact observed, with a preliminary assessment categorizing them as low and high impact (n = 2). The sites under investigation were the presumed high impact Rodney J. Hall Boat Ramp in Savannah and Lazaretto Creek Boat Ramp on McQueen's Island, and the low impact sites were Byer's Street North Beach Access Point on Tybee Island and Priests Landing on Skidaway Island (Fig. 1). *Leptuca pugilator* occurs in high densities with observed feeding swarms composed of hundreds of individuals at all sites (Buttram, personal observation). The low to mid marsh of all sites is dominated by *Spartina alterniflora*; the mid marsh to high marsh also includes a mix of other common species of salt marsh vegetation (mainly *Salicornia virginica* and *Distichlis spicata*) adjacent to bare patches without vegetation and varying levels of wrack (Buttram, personal observation). The range of plant heights, area, and number of bare patches vary by site.

In this study, I estimated human impact by assessing eight variables including proximity to a major road, paved parking spaces, boat ramp availability, beach access, picnic table availability, number of pedestrians in a given period of time, number of cars that drove by, and number of cars parked in the immediate area (Table 1). The highly impacted sites Lazaretto Creek and Rodney J. Hall Boat Ramp share proximity to a major multilane roadway where cars pass frequently (Table 1). Additionally, both sites support boat ramps where frequent deployments were witnessed during observation periods (Buttram, personal observation). For example, on one particular day as many as 12 cars were seen at Rodney J. Hall Boat Ramp equipped with tow kits for boats in comparison to 5 non-tow equipped cars. Parking availability also varies, Rodney J. Hall Boat Ramp has an extensively paved parking area contrasting Priests Landing, which has a paved road but graveled parking spaces with lower holding capacities (Table 1).

Human activity measurements were completed prior to observational protocol periods. Human activity was measured in 2022 from July 20th to August 15th then again in 2023 from May 22nd to May 25th. The metrics were measured twice within an approximately 19-minute period. This time period allowed an initial 2 minute recording observation period which was followed by a 15 minute general observation period then followed by an additional 2 minute recording observation period. Upon arrival to the sites, the number of cars parked and people present were recorded. Then I counted the number of cars that drove by for a two-minute period. A four-minute period was enacted to determine if longer periods were more inclusive of variability. I found that the four-minute period equaled the average of two, two-minute periods so the shorter duration was chosen for time saving measures. All metrics were remeasured after 15 minutes of observation during which I noted activities of interest including boat activity and building construction. To best account for the variations of human activity during the week, these measurements took place during morning periods and afternoon periods on various weekdays (Table 2).

Field Observation Protocol

Observational trials occurred during daily low tides as that is when *L. pugilator* are most active and visible (Teal 1958). Observations occurred throughout the monthly tidal cycle including the days prior to the monthly spring and neap tides when peak and reduced boldness were expected to occur (Christy 1978, Christy 1980, Pratt et al. 2005). Observations commenced 2 hours prior to low tide and continued up to 2 hours after low tide to conduct the maximum number of trials (DiNuzzo et al. 2020). Video footage was collected from at least 6 areas of either bare or vegetated substrate throughout the marsh; additional trials were conducted whenever possible. Each sampling area was a minimum of 10 m from the previous area (Pratt et al. 2005, DiNuzzo et al. 2020; this study, see results), but could be more depending on the presence of active burrows inhabited by the study species. In my pilot study, I found that the longest distance at which a fiddler responded fearfully to an approacher was 7 m (see below section and results); I elected to add an additional 3 m distance to ensure observation would not startle the focal crabs. The filming area was mainly contained within the mid to high zones of the intertidal where the edge of *Spartina alterniflora* monoculture stops and mixed species vegetation begins.

To document fiddler boldness, a tripod mounted camcorder (Sony HandyCam HDR-CX405) was positioned 45 cm above the substrate (DiNuzzo et al. 2020). Prior to enacting a fear invoking event, I scouted the marsh for areas of fiddler activity with binoculars from a distance of at least 10 m (Pratt et al. 2005, DiNuzzo et al. 2020, this study). Once an area was selected, I initiated a crab fear response by approaching the burrows (Jordão and Oliveira 2001) at a steady pace of 16 m/min with arms by my sides. A 36 cm by 36.5 cm bamboo quadrat was placed on the substrate around the burrows; thin (2 mm diameter) bamboo was used as the quadrat material to allow crabs to enter and exit the area unimpeded. The camera apparatus was set with the camcorder’s lens pointing down onto the substrate such that the entire quadrat was seen in the viewing screen but without the tripod’s feet (Fig. 2). The tripod mounted camcorder was positioned so that the shadow of the camcorder would not infiltrate the recording area. After the installation, I retreated to an observation point 10 m away while walking with the same consistent pace. A 3-minute timer was then started; this period is defined as the recovery period (Pratt et al. 2005, Decker and Griffen 2012). This recovery period allows the crabs to reemerge and resume their previous activities prior to the initial scare. During this time, a field assistant and I observed the subjects through binoculars for reemergence and the surrounding area to watch for human activities or predatory attempts. If all estimated subjects reemerged prior to the end of the recovery period, the trial was deemed complete. In contrast, if the subjects did not reemerge or if I was unable to view the subjects due to vegetation, an extension of 2 minutes was added to the original 3-minute recovery period, for a total of 5 minutes. The additional two minutes was granted to ensure all crabs had the opportunity to recover and reemerge from their burrows. Following recovery, the area was approached to obtain materials and the substrate temperature taken with a handheld infrared thermometer (ThermPro TP-30). I then scouted for a subsequent spot while the field assistant took measurements of the height of the tallest plant within the quadrat, the distance within or from the closest living vegetation, and the width of the 5 largest burrows within the quadrat. The size of a male’s major claw isometrically grows with its body width (Swanson et al. 2013), which positively correlates to burrow width (Christy 1982, Reaney and Backwell 2007, Chou et al. 2019). This allowed burrow width to serve as a proxy to estimate the maximum size of potential inhabitants, though I was unable to directly track which burrow belonged to which crab. If less than 5 burrows were present within the quadrat, all burrows were measured. During windy environmental conditions, three Ziploc^{TM} bags containing approximately 97.5 g of playground sand were wrapped around the tripod’s feet to stabilize the tripod mounted camcorder. Trials where human intrusion, companion animal intrusion, or predatory attempts affected the behavior of the subjects were promptly ended and not included within the dataset.

Recordings were uploaded to Adobe Premiere Pro v14.0.0 to apply contrast for improved visualization. I measured boldness as time taken for a crab to reemerge from a burrow within 3-5 minutes following the fear invoking stimulus (Pratt et al. 2005). Footage was watched to time male and female *L. pugilator* that fully reemerged from burrows within the quadrat. Fiddler crabs of a different species were not counted but noted if present. Gender was determined by the presence of a major cheliped. The start time of the trial was defined as the time stamp in the footage ten seconds after I waved my hand under the lens or showed a whiteboard with coinciding information about the trial. The time stamp in which an entire individual's carapace was in view out of the burrow was defined as the end point for that individual (Decker and Griffen 2012). The time stamps were subtracted from one another, resulting in a measurement in seconds of time taken to reemerge, i.e. boldness. Once individual boldness was measured, I counted the number of crabs that were active in the quadrat during the trial period; this was completed as burrows could be uninhabited at the time of observation and gives a species comparison if other species of crabs were present during trials.

Field Pilot Studies

In the summer of 2022, I conducted a pilot study measuring boldness at Rodney J. Hall Boat Ramp to test the methods for their viability. Also during summer 2022, another pilot study was conducted at Rodney J. Hall Boat Ramp and Priests Landing to determine the distance for observations. Previous studies listed varying observation distances; Pratt et al. (2005) observed from 2 m away, while DiNuzzo et al. (2020) observed from 10 m away. Due to these inconsistencies, I aimed to determine what distance from a focal group of crabs would invoke a fear response of hiding. To do this, I approached the crabs from approximately 15 meters away while an observer used binoculars to observe the focal group during my approach. As soon as a crab quickly retreated to descend into a burrow in response to my approach, the observer alerted me to stop. I marked this area in the substrate and measured its distance from the focal group to my stopping point. I conducted the pilot study at two sites in case one population might react sooner to my approach than the other.

Field Observation Statistical Analyses

Three predictor variables were explored as ways to best account for peak courtship: tidal cycles, sex ratio, and waving activity seen in video trials. Christy (1980) utilized moon phase as the correlating variable with reproductive behavior. In this study, I followed tidal cycles as a metric to define period of peak boldness with the peak periods falling 3-5 days prior to the nocturnal spring tide (Christy 1980). Moon phase is closely correlated to tidal cycles; I opted to use tidal cycle as the metric due to clearer cut offs than provided by moon illumination for defining peak and nonpeak periods. Sex ratios may also indicate reproductive timing; a low proportion of females that are surface active could indicate non-peak periods in which females are underground in burrows incubating their clutches, as they remain there until dispersal (Christy 1978, 1980). The typical sex ratio found for the average sized *Leptuca pugilator* measured as carapace width of 10.1-15.0 mm was approximately 50/50 at a given period using various traps (Johnson 2003). Thus, I used the sex ratio that was determined when I watched the film for timing and defined peak days as days with a sex ratio that was greater than or equal to 45% female of the quadrat’s active individuals. The lower value of 45% was more inclusive of days in case the timing of reproduction was not the same for every individual and accounts for individuals that may be foraging away from the burrows. The final metric used to determine peak versus non-peak periods was the waving activity of male crabs in video footage. I defined peak days as days when one or more focal males were visibly seen waving in the recorded video, which was obvious even when the camera was placed in vegetated areas. Waving is a known behavior used in courting, but is also conducted in offensive battles against other males (Crane 1975, Christy 1980). Due to the multiple facets of waving, using waving to define peak versus nonpeak period was more subjective than my other factors.

Prior to analysis of boldness in relation to peak versus non-peak time periods, reemergence times for males and females were averaged for all observations within a site on a sampling date, yielding two values (male and female reemergence) per site for each date. Analyses were conducted separately for males and females. Data were checked for normality and homogeneity of variance via Shapiro-Wilk and Levene tests, respectively. Non-parametric data were transformed when possible or appropriate non-parametric analyses were used. When peak reproduction was defined using tidal timing, the data for both sexes could not be transformed to achieve normality but did meet the assumption of homogeneity of variance. Therefore, data were analyzed using the Kruskal-Wallis nonparametric analysis. When defining peak versus non-peak reproduction by the observed sex ratio, male data were not normal and could not be transformed to obtain normality but had equal variance. The male data set was analyzed via Kruskal-Wallis test. The dataset for females was square-root transformed to obtain normality. Resulting female data had unequal variance, thus it was analyzed using Welch’s t-test. When defining peak versus non-peak reproduction by the presence of waving males, both data sets for the sexes were not normal and could not be transformed but had equal variance; data were analyzed via Kruskal-

Wallis tests. To account for multiple tests, a Bonferroni corrected alpha value of 0.0167 was used to assess differences in boldness due to peak and non-peak reproduction.

To identify which environmental factors covary with boldness, I conducted Pearson's product-moment correlation analysis between reemergence time and vegetation height, distance to vegetation edge, substrate temperature, burrow count, active *L. pugilator* count, total active crab count, and mean maximum burrow width diameter. Prior to analysis, outliers were examined using Mahalanobis distances; severe outliers were removed to improve the bivariate normal relationship. One outlier was removed from the female Rodney J. Hall Boat Ramp dataset; this did not alter which variables were significantly correlated. A second outlier was removed from the male data for Byer's Street North Beach Access Point; this resulted in the loss of a weak, though significant, correlation between reemergence time and vegetation distance and thus the more conservative interpretation of no relationship is reported in the results.

To identify the best explanatory model for boldness, I utilized the informatic theoretic approach to model selection. I constructed seven linear models (Appendix A) for each sex and examined both the BIC and AICc values for each model as well as the ΔAICc and relative likelihood values. Models having a ΔAICc of < 2 are well supported by the data while ΔAICc values > 2 and < 4 are moderately supported (Burnham and Anderson 2002). Male and female crabs were analyzed separately as I anticipated their behaviors would vary with environmental factors differently based on previous research. Prior to analysis, reemergence times for each sex were averaged within a quadrat. Correlations between reemergence times and measured environmental factors for each sex at each site were examined to determine factors that may influence boldness; those factors that were significantly correlated with reemergence time for either sex at two sites were used to build the linear models for comparisons (see results). These variables were vegetation height, substrate temperature, burrow count, and mean maximum burrow diameter. Active *L. pugilator* count was not included in the model due to its strong correlation with burrow count. Peak or non-peak reproduction, as defined by males waving during video recordings, was also included as a fixed factor. To account for additional spatial and temporal variation among samples, all models examined also included the random factors of site, week of observation, and quadrat nested within site. Data for both sexes were log transformed and two outlier male mean return times were removed to achieve normality and homogeneity of variance of the residuals; outlier status of these abnormally fast reemergence times was confirmed using Huber Outlier Distance. Variables that were significant within the best models (site and temperature for both sexes and burrow width for females, see results) were explored further using analysis of covariance (ANCOVA).

All statistical analyses for the pilot study were conducted using JMP Pro 16. All other analyses were conducted using JMP Pro 17.

Experimental Methods

Experimental trials were conducted to determine whether the visual depth of vegetated foreground in front of a group of focal crabs influenced fiddler behavior, as this showed a trend with female reemergence times in the Pilot Study (see results). A vegetated foreground was simulated using constructed plant mimics (Fig. 3) in front of an erected arena (Fig. 4). Leaves of the *Butia capitata* tree served as a proxy for *Spartina alterniflora* as *S. alterniflora* is a protected marsh plant that would require a permit to collect. Fresh stems would also die during trials while the proxy plant remained rigid and dry during trials. Leaflets were collected from a live individual outside of the Science Center at Georgia Southern’s Armstrong campus in Savannah, GA. This species serves as an adequate proxy due to leaflet length being comparable to the maximum *S. alterniflora* height in field observations. Additionally, half of the leaflet width was similar to average *S. alterniflora* stem diameter (~ 6 mm) (Joesting et al. 2020). Leaflet color and flexibility with the wind was also similar. To construct the *S. alterniflora* mimics, leaflets were removed from the rachis, halved lengthwise, cut to a length of 65-75 cm, then hot glued to a 15.24 cm bamboo skewer where 10.16 cm of the plant was adhered to the skewer and 5.08 cm of the bamboo skewer was free to implant to the ground. The mimics were allowed to dry for at least 48 hours before use. Leaves were spaced 15 cm apart in front of the arena for a density of 49 plants per m^2; this was the maximum density that allowed a person to walk through the mimics without damaging them. The two treatments were: control (no plants) and a treatment with 8 m of plants in front of the arena edge (Fig. 3).

A 60 cm x 30 cm x 30 cm arena with walls consisting of clear acrylic sides was erected between two greenhouses on Georgia Southern University's Armstrong campus (Fig. 4). This size arena was slightly smaller than another used in a field study by Natálio et al. (2017). This area is outdoors but fenced in, allowing for natural light and temperature while preventing unauthorized entry to prevent additional human contamination. Walls of the arena were taped together to prevent crab escape and arena collapse during trials. A semitransparent sheet of plastic was overlayed on three of the four walls of the arena to prevent unintended stimuli from startling the crabs. Only the front wall that I approached was fully transparent. Additional plastic material was attached approximately 3 cm from the bottom of the walls to serve as an overlay from the sides to the plant box to prevent crab escape along the bottom edges. Within the arena, all-purpose additive-free sand (American Countryside) served as the substrate. The sand was poured to an approximate depth of 6 cm within a 25.4 by 50.8 cm plant tray. New sand was used for each day of trials to prevent any scent signals from being detected by following subjects. Prior to crab addition, 6 artificial burrows were created in the sand using a 2.54 cm wide garden dibber (Garland Brand Seed & Plant Dibber) inserted at a 45° angle to approximately 5 cm depth (Darnell et al. 2019).

Subjects were collected from Rodney J. Hall Boat Ramp while congregating in a feeding swarm to best achieve equal and random chance selection of crabs with varying baseline behavior (Christy 1980, A. Collier personal communication). Collected individuals were sexed by the presence or absence of a major cheliped, and subsequently housed in a large cooler with moistened paper towels lining the bottom for transportation back to the campus. Collected fiddlers were then transferred to blue opaque plastic containers 37 cm length by 25 cm width by 30 cm height located within the Armstrong Campus greenhouse. Housed crabs were given artificial seawater with a salinity of ~ 25 ppt (Instant Ocean® Sea Salt) in two 9 cm by 9 cm dishes that were equally spaced at corners of the enclosure. The enclosure contained sand filled to a depth of approximately 8 cm to allow burrowing (Christy 1982). Enclosures were aerated by two buried air stones per container that were premoistened and located at opposing corners within the containers. As recommended by Wilson et al. (2021), collected crabs were allowed an acclimation period of at least 12 hours prior to arena trials; most were given 14-24 hours. Due to the stress of handling that could interfere with experimental trials, human interaction during the acclimation period were avoided. Handling time and the time taken to transport housed crabs into the arena for trials was also minimized as much as possible.

The experiment was conducted from September 8th – 15th, 2023. All trials were performed within 2.5 hours of low tide (Darnell et al. 2020). Due to time constraints of experimental trials, 10 trials were conducted each day during the 5-hour window of a low tide period. Each day, at least one control and one experimental treatment trial was conducted to account for date related differences in expressed behaviors.

Before each crab addition, the arena's sandy substrate was inspected for contaminating materials, which were removed. In between trials within the same day, the sand in the arena was mixed and new burrows made that were approximately equidistant from one another with the garden dibber. Once the arena was set for the experimental treatment, three living crabs (male = 2, female = 1) were randomly collected from a housing unit by hand and placed into the arena. Due to permitting restrictions, fewer crabs of one sex were collected. I opted to utilize one female and two males because male boldness is partially driven by competition for females (Christy 1980). There was uncertainty if the same phenomenon would occur with two females and one male. The three crabs were allowed to acclimate to the arena for 10 minutes prior to the presentation of the fear invoking stimulus. A research assistant and I stood 10 m away from the arena to observe the crabs through binoculars. This was to ensure crabs were not escaping the arena and in case any local fauna infiltrated the arena. After the 10-minute acclimation period, how many crabs were surface active and their approximate location within the arena were noted. As in the field study, I served as the fear stimulus and walked along a previously laid out 10 m tape at a steady pace either through the 8 m field of erected *S. alterniflora* mimics or the control of no plants. When I finished my approach, I turned on the tripod mounted camcorder to begin recording. I then retreated to the 10 m observation point and started a timer of 3 minutes to serve as the minimum recovery period. If the observer did not see at least 2 surface active crabs at the end of this time, the timer was gradually extended to a total of 15 min, at which time the trial would end regardless of number of surface-active crabs. The time extension was greater than that granted in the field because the laboratory setting was stressful for the crabs. This extension gave extra recovery time for crabs to reemerge. Subjects were then collected from the arena and rehoused in individualized critter cages. Crabs were only used once to prevent behavioral habituation (Walker 1972, Hemmi and Merkle 2009).

Video footage was analyzed as described for the field study to measure time taken for each crab to reemerge from a burrow. Weather information, beginning substrate temperature, and air temperature were also documented for each day. Crab carapace width was measured at the conclusion of all trials.

Experiment Statistical Analyses

To determine if reemergence time differed with the presence of the proxy vegetation, ANCOVAs were completed separately for each sex using carapace width as a covariate. Male times and carapace widths were averaged together for each trial. Prior to analysis, residuals were checked for normality and heteroscedasticity; data were box-cox transformed to remove heteroscedasticity. Analyses were conducted using JMP Pro 17.

CHAPTER 3

RESULTS

Field Study

Site Characterization

While Rodney J. Hall Boat Ramp was visited by many people on a daily basis (Table 1) and was expected to be most similar to Lazaretto Creek Boat Ramp, the distance the burrows were located from the beach and parking lot likely reduced how much human impact the fiddlers experience. For comparison, the distance from the edge of the parking lot at Rodney J. Hall Boat Ramp to the first burrows within that marsh was 16.02 m, while the distance from commonly used parking spaces at Lazaretto Creek Boat Ramp was 7.57 m away from burrows located within the marsh.

Pilot Study

For the distance trial data, crabs at Priests Landing could be approached significantly more closely than at Rodney J. Hall Boat Ramp ($H_1 = 6.64$, $p = 0.01$), with crabs reacting when the approacher was a mean of 4.73 ± 0.55 m and 6.64 ± 0.55 m from the burrows, respectively. At Rodney J. Hall Boat Ramp, the farthest approach distance at which the crabs reacted was 7.70 m; at Priests Landing, that distance was 6.93 m.

Of the variables examined in the 2022 pilot study, substrate temperature was the only one with a significant correlation with female *L. pugilator* reemergence time (Table 3). As substrate temperature increased, time taken to reemerge decreased (Fig. 5). Male reemergence time did not correlate to any measured variable (Table 3). Though not statistically significant, female boldness was also greatest in individuals inhabiting the edge of the vegetation compared to those farther into the bare substrate or farther into vegetated areas (Fig. 6).

Field Observation Results

There was no significant difference between peak and non-peak periods for reemergence times when defining peak and nonpeak periods by tidal cycle (Male $H_1 = 2.19$, $p = 0.14$; Female $H_1 = 0.76$, $p = 0. 38$; Fig. 7A). Additionally, there was no significant difference between peak and non-peak periods for male ($H_1 = 0.24$, $p = 0.62$; Fig. 7B) or female ($t_1 =1.41$, $p = 0.38$; Fig. 7B) reemergence times when defining by sex ratio. When defining peak versus nonpeak period by the presence of waving, males reemerged significantly faster on days defined as peak periods due to the presence of other waving males ($H_1 = 6.10$, $p = 0.014$; Fig. 7C). For females, there was no significant difference in reemergence time between peak periods and non-peak periods ($H_1 = 0.15$, $p = 0.70$; Fig. 7C).

Correlations between environmental factors by sex and site were examined as influencers of boldness. Burrow count, active *L. pugilator* count, height of vegetation, mean maximum burrow width, and substrate temperature were each significantly correlated to reemergence time in at least two instances across the sexes and sites (Table 4). No significant correlations were observed in the initial analysis at Rodney J Hall Boat Ramp. Therefore, the data were split into bare and vegetated patches due to the abundance of both at this site. There were no significant correlations detected during analysis when splitting the dataset this way indicating the bare and vegetated microhabitats that *L. pugilator* resides within do not strongly influence behavior at this site (data not shown).

For the linear models constructed using those variables with observed correlations to reemergence time, three models were retained for females and one for male crabs (Table 5). Models shown are those with the lowest BIC and AICc values and with a ΔAICc less than 2 (see Appendix A for all models). The variables that were included within the best fit model for the males were average substrate temperature, site, week, and trial by site; average substrate temperature and site were significant. For the females, variables retained within the best fit models were substrate temperature, mean maximum burrow width, site, week, and trial; site, mean maximum burrow width, and temperature were significant in at least one of the retained models.

ANCOVA analysis demonstrated females inhabiting Lazaretto Creek Boat Ramp took longer to reemerge compared to females at other sites ($p < 0.0001$; Figs. 8, 9, 10). Females inhabiting all sites took longer to reemerge as mean maximum burrow width increased ($p = 0.0003$; Fig. 10). Temperature, though significant in the linear models (Table 5), was not significant within the ANCOVA ($p = 0.11$; Fig. 9). Similarly, males inhabiting Lazaretto Creek Boat Ramp had, on average, longer reemergence times than males at other sites ($p = 0.0025$; Fig. 11). Male reemergence times decreased as temperature increased ($p < 0.0001$), with those inhabiting Lazaretto Creek Boat Ramp and Priests Landing showing the strongest negative relationship between these variables (site*temperature $p = 0.044$) (Fig. 11).

Experimental Results

For males, reemergence time was significantly greater in the 8 m plant treatment ($F_1 = 6.69$, $p = 0.017$; Fig. 12) and was unrelated to carapace width ($F_1 = 0.035$, $p = 0.85$). For females, reemergence time significantly decreased with increasing female carapace width ($F_1 = 11.25$, $p = 0.0043$) but was not different between the plant treatments ($F_1 = 0.044$, $p = 0.84$; Fig. 12).

CHAPTER 4

DISCUSSION

I hypothesized that fiddler crab boldness would decrease with human impacts as measured by time taken to reemerge from their burrow after a fear invoking event. In agreement with this prediction, I found that crabs residing at Lazaretto Creek Boat Ramp had, on average, longer reemergence times than crabs residing at other sites. Males and females took nearly twice as long to reemerge compared to their corresponding sex at the other sites. Lazaretto Creek Boat Ramp is arguably the most impacted site with its proximity to a major road, inconsistent road traffic that varied by time of day, burrows located directly next to sidewalks and the access road for the boat ramp, and varying pedestrian counts. For example, on one particular day a dump truck drove along the boat ramp's access road four times within a 30-minute period loading and unloading vegetative debris.

The variance in reemergence times at Lazaretto Creak Boat Ramp was also intriguing as crabs inhabiting marsh areas vegetated with *Spartina alterniflora* that were adjacent to the parking lot exhibited less variance in their reemergence times than crabs inhabiting high human traffic areas directly next to the sidewalk or in the sand bordering the road (standard deviation for both sexes combined of 39.18 and 89.18 sec, respectively). The maximum observed reemergence time at this site was a male fiddler that took nearly 4 minutes to reemerge, which was approximately 2 times the maximum found for an in-marsh crab. Another previous study found that *Carcinus maenas* crabs retreating from a dummy predator in a laboratory experiment took significantly longer to return home when boat noise played compared to ambient noise (Wale et al. 2013). In future studies examining this population of crabs, I would suggest utilizing substrate vibration or airborne acoustics as a possible metric to estimate the influence of traffic on fiddler behavior. A previous study found that vibrations from road traffic affect the reproductive behaviors of anurans (Caorsi et al. 2019). While it is not yet known if vehicular traffic impacts the behavior of fiddler crabs, substrate vibrations are sensed by fiddler crabs and utilized during courtship activity (Christy 1978). *Leptuca pugilator* senses substrate vibrations through vibration sensors found along the walking legs, with females detecting male made vibrations during courting from 45 to 100 cm away (Christy 1980).

DiNuzzo et al. (2020) found that each additional pedestrian that walked by a male fiddler crab would decrease the likelihood of it waving by 47.8%. I found that I could approach focal fiddler crabs more closely at Priests Landing than at Rodney J. Hall Boat Ramp, despite crabs at both sites having similar reemergence times within the 2023 field observations. Therefore, other measurements of crab behavior should be taken to better assess boldness from a multivariate perspective. Measurements should include time taken to reemerge, time taken to resume activity, waving patterns prior to and post fear stimulus, as well as overall courtship effort. Additional environmental variables could be measured to quantify human impact on a site such as soil chemistry, which has been found to vary in high versus low impacted sites (Numbere 2020).

I hypothesized that fiddler boldness is greater during times of peak reproduction. This was not supported in the linear models as peak reproduction as defined by waving males being present was not retained within the best linear model. Peak periods can be defined in various ways, such as moon phase (Christy 1980), tidal cycle, majority behaviors across the marsh, or observing sex ratios in feeding swarms. In this study, waving within the recorded videos was the best indicator of male boldness, however the video offered a restricted view of behavior in the marsh. Future work should look at behavior across a wider area of the marsh and consider temperature impacts on incubation rates (Christy 1978).

I also hypothesized that higher substrate temperature would negatively influence fiddler crab boldness. Waving behavior in male fiddlers decreased as substrate temperatures increased, and this was attributed to the increased risk of desiccation that comes with increasing temperature (DiNuzzo et al. 2020). Darnell et al. (2019) found that the fiddler crab species *Austruca mjoebergi* preferred microhabitats shaded by mangrove foliage, trading the cost of desiccation with increased competition to prevent death. In this study, an inverse relationship between reemergence times and temperature occurred for males, especially at Priests Landing and Lazaretto Creek Boat Ramp (Fig. 11). This trend of increased male boldness with increasing temperature not only contradicts my hypothesis but also disagrees with previous work that found males have a 92% increased likelihood of not waving per each degree increase in temperature (DiNuzzo et al. 2020). However, since the observations were during peak breeding season, and higher temperatures at 3 of the 4 sites were recorded later in the study, it is possible the reason for the decreased time taken to remerge with increased temperature is due to an increased inclination to engage in mating rituals and competitions as the breeding season progresses. In *Uca terpsichores*, incubation timing decreased and male courting efforts were greater with warmer substrate temperatures (Kerr et al. 2012, 2014). These shifts in behavior allow crabs to acclimate to changing conditions to be most fit to their environment (Kerr et al. 2012, 2014). A study examining reemergence behaviors at the same site across numerous days in a row of varying temperature would help to separate the influences of temperature and seasonality. The male fiddler crab ability to decrease their time taken to reemerge despite high temperatures may be due to their advantageous possession of an appendage that acts like a heat sink (Darnell and Munguia 2011). Males with the major cheliped removed exhibited a rapid and significant increase in overall body temperature after being exposed to radiating heat in comparison to males with an intact major cheliped (Darnell and Munguia 2011). The researchers state that the major cheliped works by moving heat away from the main body to allow heat to dissipate into the atmosphere (Darnell and Munguia 2011).

While temperature as a factor for females was retained within one of the best models based on ΔAIC_C value, it was not significant in the subsequent ANCOVA analysis examining differences across sites with temperature as a covariate. I hypothesize that the present trend of females showing no significant difference in reemergence times in relation to temperature is due to their decreased engagement in competition for mates. During nonpeak periods, females were commonly found within breeding burrows incubating their eggs rather than surface active (Christy 1980). In comparison, males must compete for mates; this could increase their boldness and willingness to risk desiccation (Reaney and Backwell 2007).

I hypothesized that residing in taller vegetation, or having a burrow located further into a vegetative stand, inhibits fiddlers from seeing predators and cause a false sense of safety for fiddlers. Fiddler crab vision is panoramic with a zone of identification including two predator zones at approximately 70º and 15º then a social zone below the horizon of their sight (Zeil and Hemmi 2006). These zones allow fiddlers to see conspecifics as well as avian predators. Field observations distance from the edge of the vegetation showed no correlation to boldness and I found that vegetation height was not significant in the linear models. I also found that for the greenhouse experiment, when given zero vegetation cover, males reemerged more quickly while females showed no difference in reemergence. However, subjects of this experiment behaved abnormally as they did not always hide when I approached the arena. When this occurred, I used a clipboard to coax the fiddler to descend into an open burrow and notated that this had occurred. This was to force the focal crabs into a burrow so that a reemergence time was possible. Given this, the distance in which I was able to approach a focal group of fiddlers in the field may be a better measurement of fear as it relates to vegetation presence, similar to Hemmi and Merkle (2009).

I also hypothesized that boldness would increase with increasing crab size, as estimated by mean maximum burrow diameter, which would correlate with the body width of the largest crabs (Swanson et al. 2013). This hypothesis was based on previous research that females will choose larger focal males when deciding on a mate (McLain and Pratt 2007). In my study, female crabs reemerged more slowly when they were in proximity of burrows with greater maximum burrow width. Also, it was found that there was no effect of mean maximum burrow width for males. As I measured the five largest burrows within a quadrat, this is not inclusive of all possible sizes that could inhabit the area observed, nor does it indicate the proportion of each size class. Further, while it served to indicate the possible maximum size crab that could inhabit the area, the presence of a large burrow does not confirm that a large crab is presently using that burrow. An explanation for the observed pattern with burrow width is that the specific location of the burrows within the marsh may have been a confounding factor; larger crabs reside in the high areas of the marsh (Christy 1982), which experience different environmental stresses than the low marsh. These observations could be clarified with a field experiment that examines boldness while also manipulating crab size within high and low areas of the marsh.

Finally, I postulated that fiddler crab boldness increases with crab density. In contrast, it was found that burrow density had no effect on active female or male crab boldness. In DiNuzzo et al. (2020), likelihood of male waving increased by 35% per each additional burrow. Thus, while burrow density increased competitive waving, I theorize boldness as measured by reemergence time does not appear to respond in a similar manner. Due to the infrequency of waving, I could not quantify wave rates in this study. Two response variables were measured to estimate crab density, number of burrows and active crab count per quadrat. Initial Pearson correlations indicated that both variables were occasionally significant correlates to reemergence time, suggesting that the relationship between boldness and crab density may be inconsistent and influenced by other unmeasured factors.

CHAPTER 5

CONCLUSION

Salt marshes have a history of recovering from sudden changes such as oil spills (Zengel et al. 2021), extreme storm events such as Hurricane Katrina (Campbell et al. 2022), and introduction of invasive species (Bertness and Coverdale 2013), but current changes are imposing threats faster than salt marshes can recover or adapt. Global total salt marsh area has decreased by 87% in the past 300 years due to anthropogenic behaviors such as ditching, vegetation clearing for buildings, transformation into aquaculture arenas, and nutrient run off (IPBES 2018, Gedan et al. 2011). The intrusion on salt marshes not only impacts the land area but the organisms residing within this vital habitat.

Fiddler crabs are fundamental aspects of the marsh ecosystem. The loss of fiddler crabs, either directly or indirectly through human impacts, would harm the marsh ecosystem. The ever-encroaching presence on salt marshes by humans could negatively affect fiddler foraging and reproductive efforts by causing frequent fear responses resulting in hiding (Christy 1980, DiNuzzo et al. 2020, this study). Hiding for extended periods of time decreases the time a crab has to find a mate and feed, likely reducing fitness (Pratt et al. 2005). Overall, I found the crabs residing at Lazaretto Creek Boat Ramp were the least bold and most impacted by human influence. Further studies examining fiddler crabs at sites with similar features would be needed to determine if crab overall fitness, as ability to survive and reproduce, is decreased as a result of such great human influence.

In this study, I aimed to understand how environmental conditions influence fiddler behavior. I found that the behavior of crabs varies depending on the site they reside within and that varying measured factors influence one or the other sex more strongly, such as temperature.

Subsequent studies can extend these results by being conducted over periods of time that are inclusive of varying substrate temperatures (DiNuzzo et al. 2020) and the non-reproductive season. More studies should be conducted on how male versus female boldness differs when isolated.

Table 1. Human impact metrics assessed for each site. RJH = Rodney J Hall Boat Ramp, PL = Priest's Landing, NB = North Beach, LZ= Lazaretto Creek. Sites are in order of most disturbed to least disturbed based on personal observation and metrics.

Variable	LZ	RJH	NB	PL
Major Road Proximity (m)	17 m	215 m	283 m	22 m
Number of Paved Parking Spaces	0	128	2	2
Beach Access	No	Yes	Yes	No
Number of Picnic Tables	0	4	0	0
Average Number of Pedestrians (± 1 SD)	1 ± 0.769	4 ± 0.177	25 ±4.950	1 ± 0.5
Average Number of Cars Passing the Site in 2 min (± 1 SD)	37 ± 5.235	41 ± 1.546	43 ± 14.142	< 1± 3
Average Number of Parked Cars (± 1 SD)	6 ± 1.598	14 ± 1.414	1 ± 0	2 ± 0
Distance to nearest human structure	2.67m	25.54 m	30.41m	15.92 m

Table 2. People observation diary. RJH = Rodney J Hall Boat Ramp, PL = Priest's Landing, NB = North Beach, LZ= Lazaretto Creek.

Date	Site	AM/PM
07/20/2022	RJH	PM
07/26/2022	RJH	PM
07/26/2022	PL	PM
07/27/2022	RJH	AM
07/27/2022	PL	AM
07/27/2022	LZ	PM
07/27/2022	NB	PM
07/28/2022	LZ	PM
07/28/2022	NB	PM
8/02/2022	LZ	AM
08/02/2022	NB	AM
08/03/2022	NB	AM
08/03/2022	LZ	AM
08/15/2022	LZ	PM
08/15/2022	NB	PM
05/22/2023	RJH	AM
05/22/2023	PL	AM
05/22/2023	RJH	PM
05/22/2023	PL	PM
05/23/2023	LZ	AM

05/23/2023	NB	AM
05/23/2023	LZ	PM
05/23/2023	NB	PM
05/24/2023	RJH	AM
05/24/2023	RJH	AM
05/24/2023	PL	AM
05/24/2023	RJH	PM
05/24/2023	PL	PM
05/25/2023	NB	AM
05/25/2023	LZ	AM
05/25/2023	NB	PM
05/25/2023	LZ	PM

Table 3. Correlation coefficients (r) for measured variables in the 2022 pilot study. Bolded values indicate a p-value < 0.05. (Females N = 11, Males N = 10)

Response variable	Re-emergence time	Substrate temp. (℃)	# of active burrows	Distance to vegetation (cm)	Height of vegetation (cm)
Female					
Re-emergence time	1.0000	-	-	-	-
Substrate temp. (℃)	**-0.7749**	1.0000	-	-	-
# of active burrows	-0.2527	0.1423	1.000	-	-
Distance to vegetation (cm)	0.5410	-0.2807	-0.4147	1.0000	-
Height of vegetation (cm)	-0.2534	-0.2983	0.4084	-0.5047	1.0000
Male					
Re-emergence time	1.0000	-	-	-	-
Substrate temp. (℃)	-0.1725	1.0000	-	-	-
# of active burrows	-0.2127	0.1374	1.0000	-	
Distance to vegetation (cm)	-0.0509	0.2303	0.5391	1.0000	-
Height of vegetation (cm)	0.0222	-0.4254	0.5618	0.2705	1.0000

Table 4. Correlation values (r) for biotic factors covarying with mean reemergence time for each sex at each site in the 2023 observational study. Bold values are significant ($p < 0.05$).

Variable	RJH Boat Ramp		Priests Landing		North Beach		Lazaretto Creek	
	M	F	M	F	M	F	M	F
Height of Vegetation (cm)	0.1118	0.0039	**0.4258**	**0.4900**	**-0.4489**	-0.0561	0.3249	0.0046
Distance to Veg Edge (cm)	0.0266	0.0604	0.0152	0.1290	-0.2115	-0.1417	-0.2537	-0.2174
Substrate Temp (°C)	-0.0794	0.0119	**-0.4580**	-0.2540	-0.0696	-0.0536	**-0.4609**	-0.0267
Burrow Count	0.0522	0.0669	**0.3600**	0.0405	0.1159	0.0449	**-0.5002**	**-0.5820**
Active *L. pugilator* present	-0.1595	-0.0954	-0.1414	**-0.3466**	-0.1093	0.0465	-0.3819	**-0.4577**
Total crab count	-0.0951	-0.1551	-0.1305	-02889	-0.1093	0.0465	-0.3395	**-0.4801**
Burrow Width Average	0.2657	0.1303	0.3005	**0.3499**	**0.4415**	**0.3725**	0.2005	0.2747

Table 5. Models for female and male observational data with the best model bolded respectively.

(Female N = 134, Male N = 130)

Candidate Models	AICc	BIC	ΔAIC_C	Relative likelihood
FEMALE				
AVERAGE BURROW WIDTH + SITE + WEEK + TRIAL[SITE]	**113.22**	**193.90**	**0**	**1**
TEMP + SITE + WEEK + TRIAL[SITE]	113.64	197.00	0.42	0.81
AVERAGE BURROW WIDTH + TEMP + SITE + WEEK + TRIAL[SITE]	114.06	194.84	0.83	0.66
MALE				
TEMP + SITE + WEEK + TRIAL[SITE]	**70.30**	**150.01**	**0**	**1**

Figure 1. A) Map of study locations, Green Plus: Rodney J. Hall Boat Ramp, Blue Star: Priests Landing, Yellow Square: Lazaretto Creek Boat Ramp, Purple Square: Byer's Street North Beach Access Point, B) An image of Rodney J. Hall Boat Ramp marsh entrance, C) A Google Earth image of Priests Landing, D) A Google Earth image of Lazaretto Creek Boat Ramp, E) An image

of North Beach, Tybee Island, GA. In B-E, the circled area indicates where *Leptuca pugilator* burrows were observed.

Figure 2. The tripod mounted camcorder positioned over the quadrat with stabilizing sandbags.

Figure 3. Experimental treatment with 8 m of proxy plants (*Butia capitata*) in front of the plexiglass arena.

Figure 4. The enclosed arena.

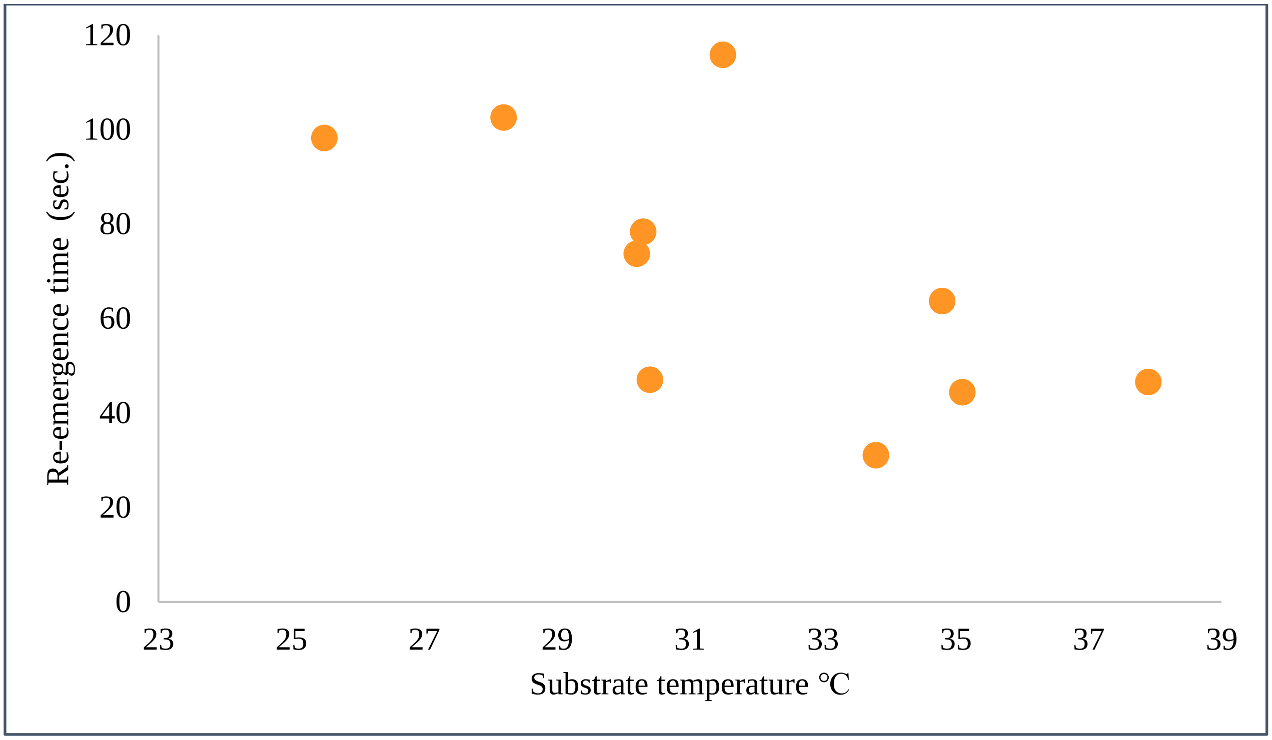

Figure 5. Female reemergence time by substrate temperature (r = -0.7749) (N = 11)

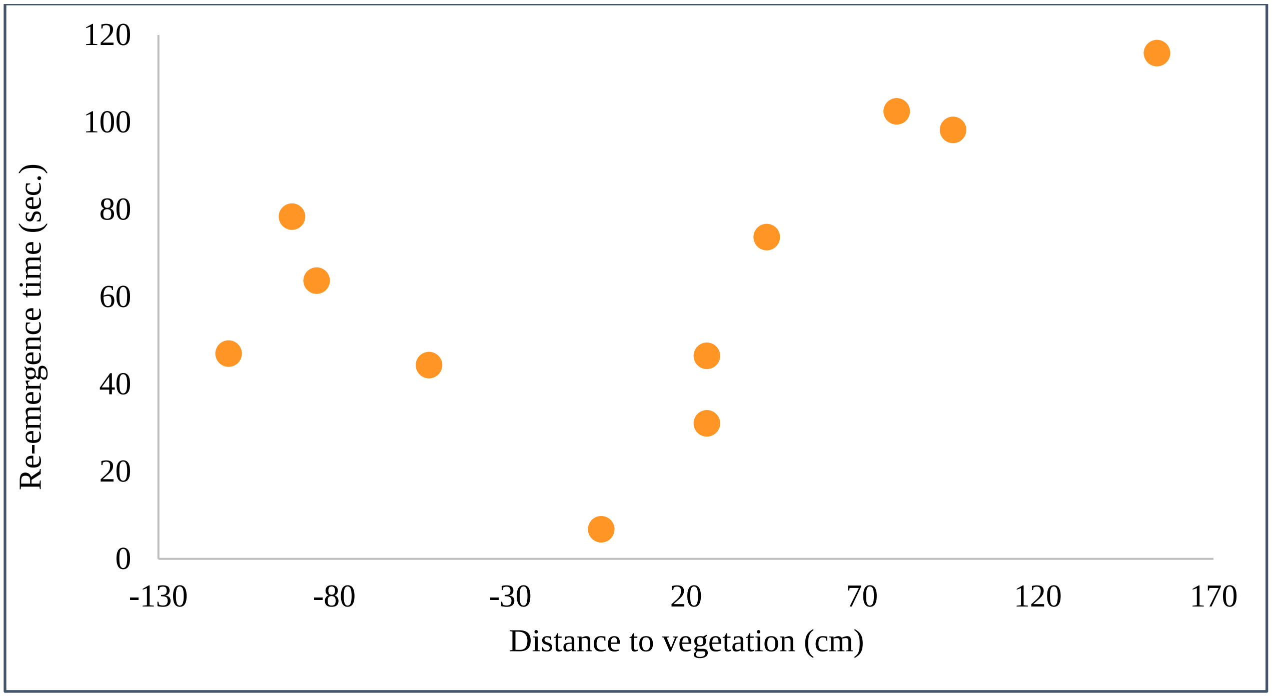

Figure 6. Female reemergence time in relation to distance into the vegetation (negative distance values) or a bare patch (positive distance values) from the edge of the marsh vegetation (0 m). (N = 11)

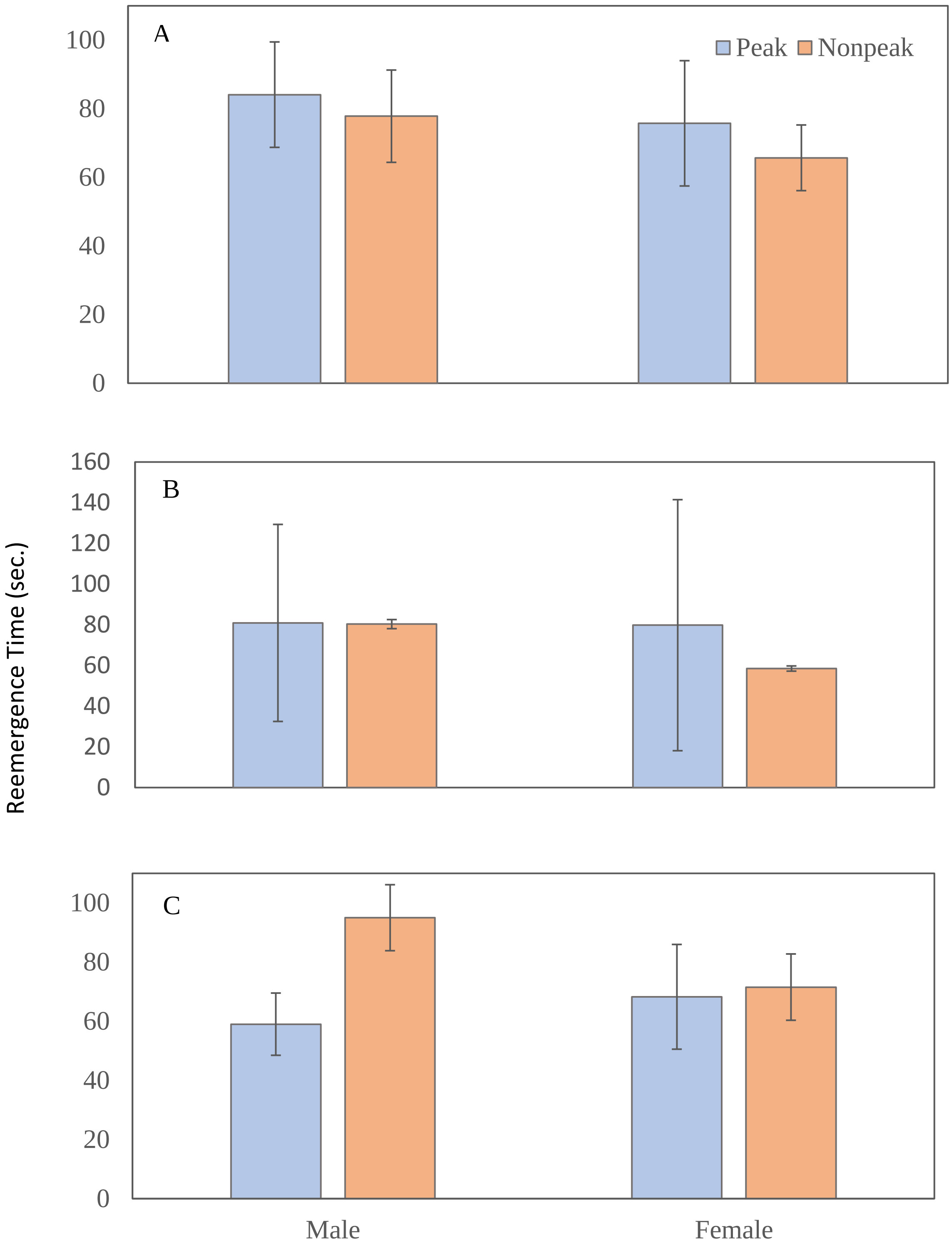
Reemergence Time (sec.)
A
Peak
Nonpeak
100
80
60
40
20
0
B
160
140
120
100
80
60
40
20
0
C
100
80
60
40
20
0
Male
Female

Figure 7. Mean reemergence times examined by peak and non-peak reproduction defined by A) tidal cycle B) sex ratio, and C) male waving. Error bars represent ± 1 standard error. (N = 20 for each comparison)

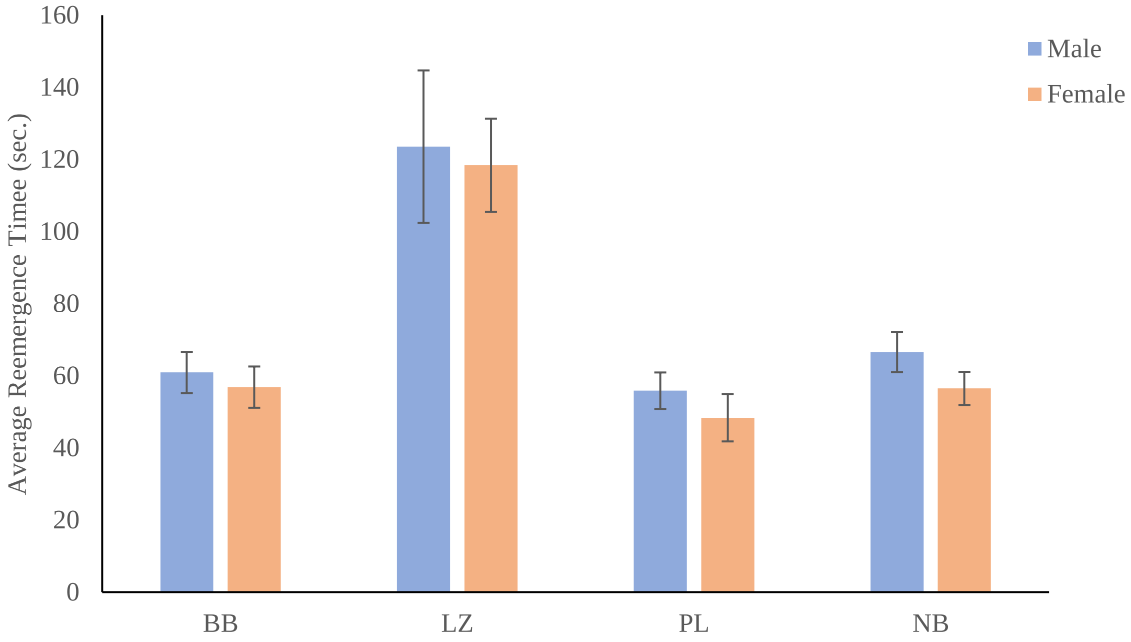

Figure 8. Mean reemergence time by sex and site. Error bars represent ± 1SE. (N = 267)

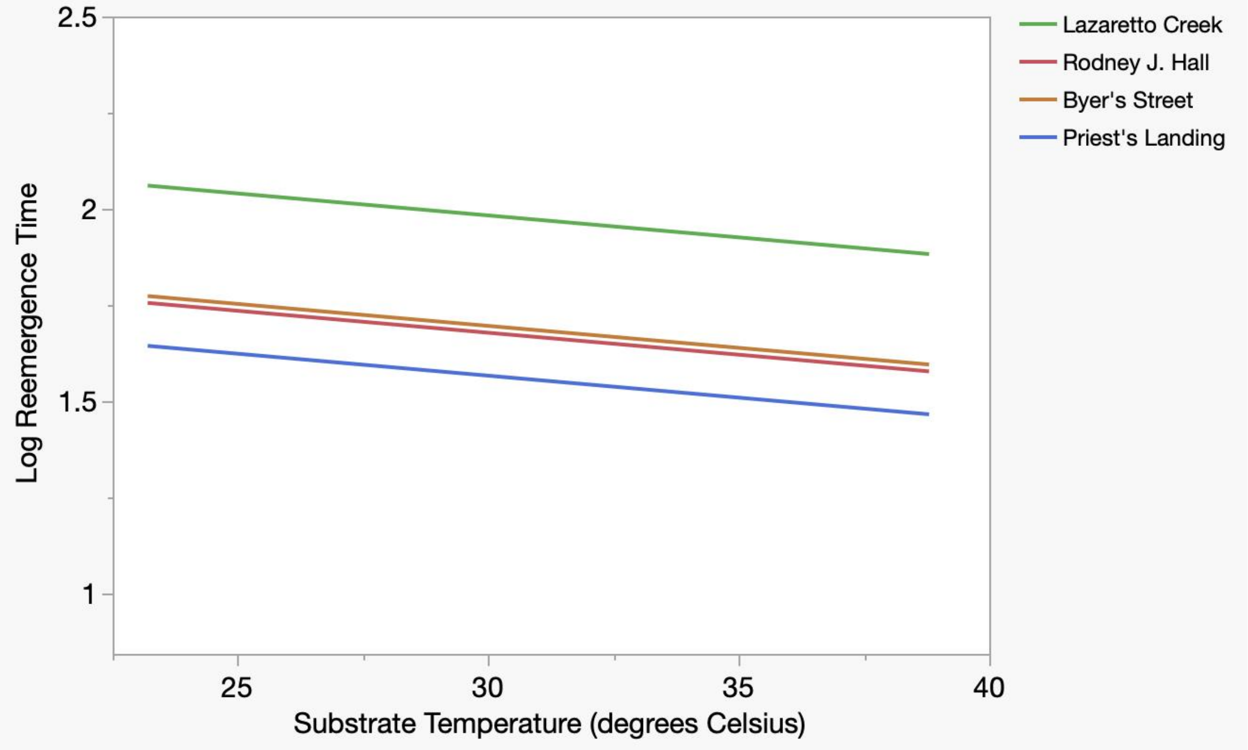

Figure 9. ANCOVA of female reemergence time as covarying with substrate temperature (N = 134)

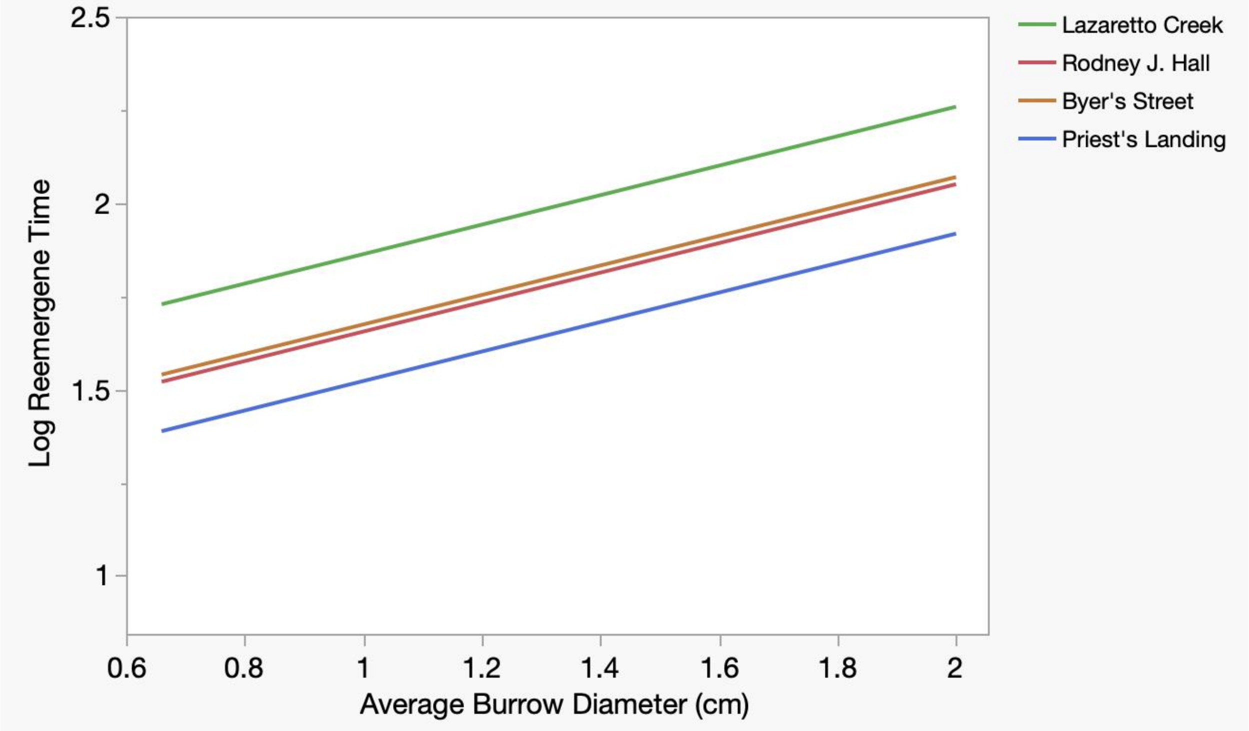

Figure 10. ANCOVA results for female reemergence times as covarying with mean maximum burrow diameter. (n = 134)

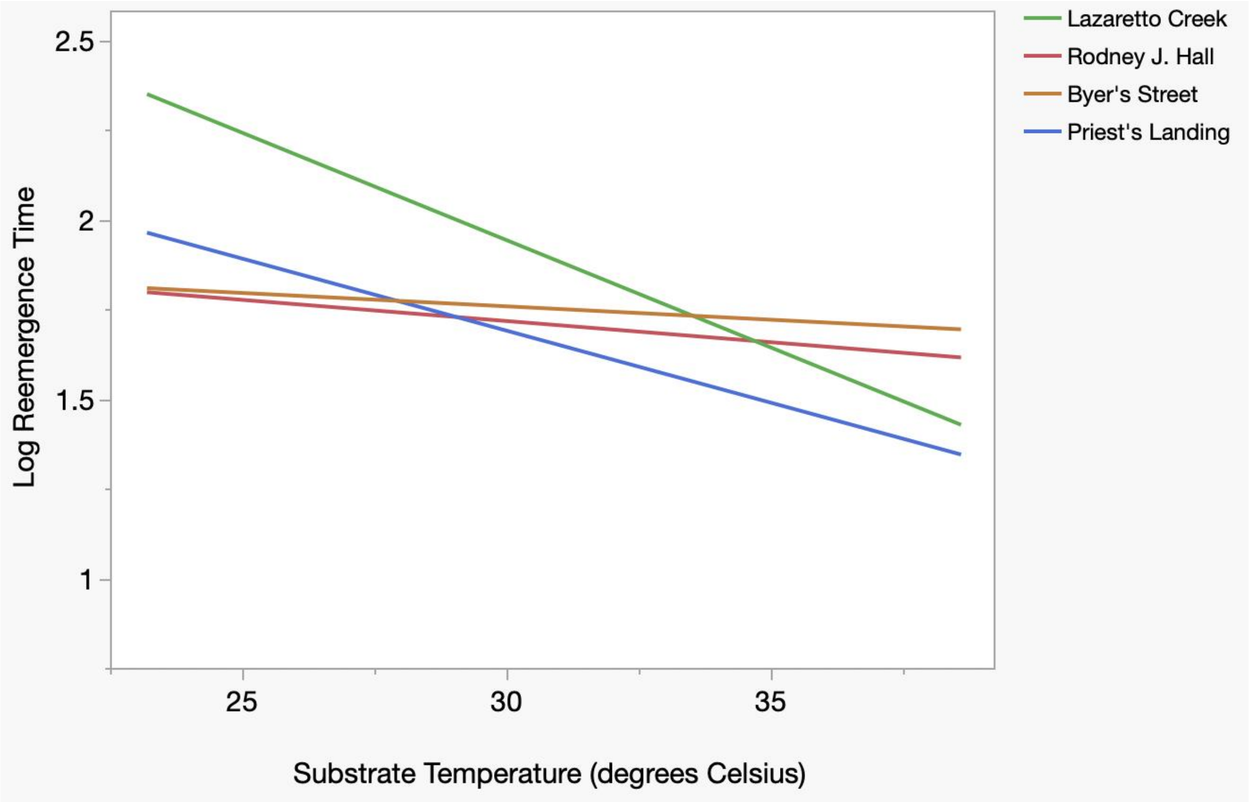

Figure 11. ANCOVA results for male reemergence time as covarying with substrate temperature. (n = 130)

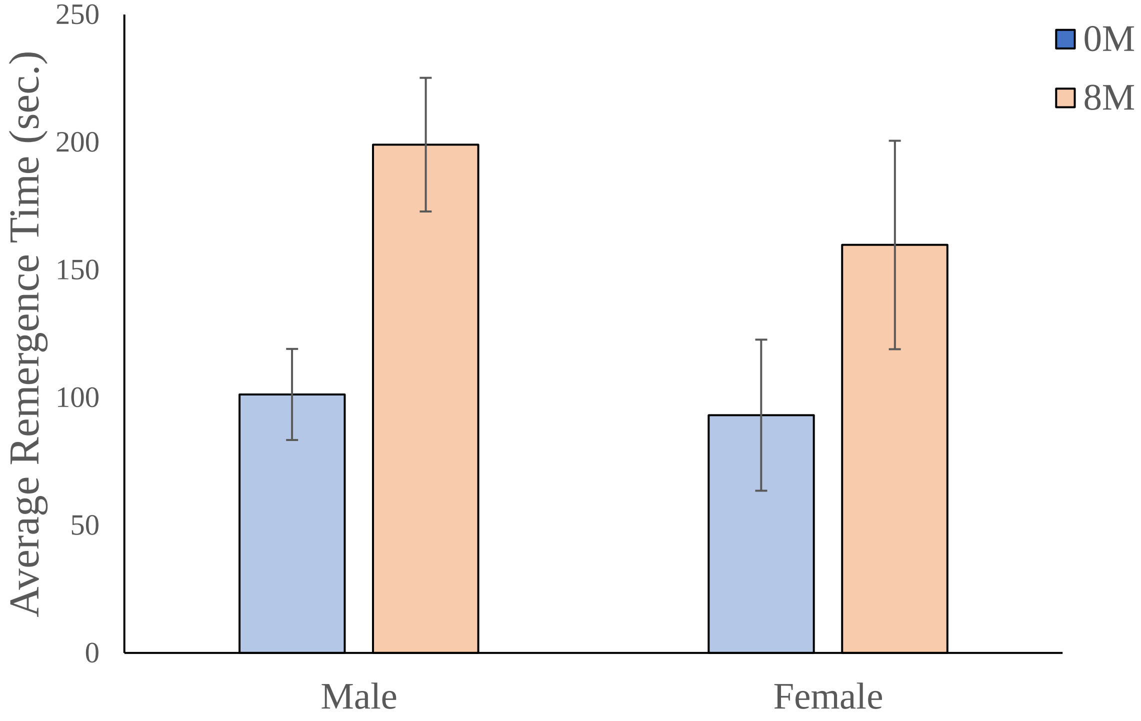

Figure 12. Mean reemergence times for experimental data divided by sex and treatment type. Error bars represent ± 1 standard error. (0M N = 15, 8M N = 19)

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APPENDIX A

Linear Models Examined for both Male and Female *Leptuca pugilator*

Model Variables

1. Average Burrow Width + Height of Vegetation + Burrow Count + Substrate Temperature + Site (Random) +Week (Random) + Peak/Nonpeak Period + Trial [Site] (Random)
2. Average Burrow Width + Height of Vegetation + Burrow Count + Substrate Temperature + Site (Random) +Week (Random) + Trial [Site] (Random)
3. Average Burrow Width + Burrow Count + Substrate Temperature + Site (Random) +Week (Random) + Trial [Site] (Random)
4. Average Burrow Width + Substrate Temperature + Site (Random) +Week (Random) + Trial [Site] (Random)
5. Substrate Temperature + Site (Random) +Week (Random) + Trial [Site] (Random)
6. Site (Random) + Week (Random) + Trial [Site] (Random)
7. Average Burrow Width + Site (Random) + Week (Random) + Trial [Site] (Random)