Differences in running velocity and boldness between male and female Atlantic sand fiddler crab (*Leptuca pugilator*)

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This manuscript has been submitted for publication in Journal of Crustacean Biology. Please note that, despite having undergone peer review, the manuscript has yet to be formally accepted for publication. Subsequent versions of this manuscript may have slightly different content. If accepted, the final version of this manuscript will be available via the 'Peer-reviewed Publication DOI' link on the right-hand side of this webpage. Please feel free to contact any of the authors; we welcome feedback.

ABSTRACT

Atlantic sand fiddler crabs (*Leptuca pugilator)* exhibit an extreme case of sexual dimorphism with the male crabs wielding an enlarged dominate claw that can account up to 40% of an individual's total body mass. The salt pans found in marine marshes are commonly colonized by fiddler crabs and have limited coverage from avian predators, making the ability to quickly run back their burrows, an important part of life. After threats have passed, making the decision of when to exit is important for securing resources and finding a mate, but if done too early could mean falling victim to a predator. This study pairs experiments and observations to determine if crab anatomy or personality is more important influence on running velocity and boldness. Crabs (21 males & 21 females) were ran and timed on a sand racetrack for 1m, behavior assays were conducted to determine each individuals boldness, and measurements of various anatomical measurements were taken. Female crabs were found to have faster run velocities than male crabs. However, male crabs displayed bolder behavior than female crabs. Overall, personality was found to be the most important factor on a crab's running velocity and boldness.

Key words: Behavior, Personality, Sapelo Island

INTRODUCTION

Sexual dimorphism is well studied in several ecosystem and organisms, prime examples include ungulates (e.g. elk and white-tailed deer) (Ruckstuhl and Neuhaus 2002), Peacocks (*Pavonini)* (Price and Birch 1996) and Brown Anoles (*A. sagre*) (Butler 2007). Differences between male and female for each of these species range from color differences and additional or enlarged body parts. While it has been well studied that sexual dimorphism is used for attracting mates and represent overall organism fitness (Keyser and Hill 2000), these extreme differences can come with costs (Ditchkoff et al. 2001). Bright colors inconsequently allow for predators to spot males, large body parts are at higher risk of breaking, reduced mobility, and increased nutritional requirements (Moen et al. 1999; Zuk and Kolluru 1998). Consequences of these displays of fitness are found in almost every case. For male Atlantic sand fiddler crabs (*Leptuca pugilator*) sexual dimorphism is expressed by an enlarged claw and larger body size, yet there seems to be minimal evidence of downsides in this display of fitness.

The enlarged claw of the Atlantic Sand Fiddler crab has been recorded to be large percentages of their body mass, up to 42% (Allen and Levinton 2007; Darnell and Munguia 2011). This enlarged claw is used to attract mating partners, fending off competing male crabs, and for defense against predators (Lane and Darnell 2020; Milner et al. 2010). Natural predators of the fiddler crab include several birds (egrets, ibis, herons, and other shore birds), blue crabs, red drum fish, and raccoons (Shanholtzer 1973). Having the enlarged claw has been shown to slightly reduce the foraging efficiencies of the males compared to females (Valiela et al. 1974; Weissburg 1992). Even with this reduction in foraging efficiencies, Atlantic sand fiddler crabs as a population still account for approximately 15% of energy flow through as secondary production within salt marshes (Teal 1962). Males carrying extra mass of the enlarged claw has been shown to slow down the running velocities of fiddler crabs (Martin 2019). There have been several Sand Fiddler Crab running velocity studies, but none have focused on the differences between males and females while taking into consideration personality traits (Frix et al. 1991; Full and Herreid 1984; Jordao and Oliveira 2001).

Personality is an important variable when it comes to successfully securing resources, growth rates, reproduction, and behavior that organisms exhibit (Godin and Dugatkin 1996;

Stamps 2007). Several working definitions of personality have been used to try to capture this intangible trait (Kaiser and Muller 2021) but for this study I settled on the commonly used definition introduced in Real et al 2010, "behavioral differences between individuals that are consistent over time and across situations". Evidence of personality exists for several different taxa (Dingemanse and Reale 2005; Koolhaas et al. 1999; Reale et al. 2007), including a growing number of studies focused on Decapods (e.g. freshwater prawns, sand bubbler crabs, new Zealand crab, fiddler crab, noble crayfish, and hermit crabs) (Gherardi et al. 2012). These studies explore different methods to quantify personality such as startle response, aggression, re-emergence, catatony, or dispersion. While none of these studies have specifically been conducted with the Atlantic sand fiddler crab, there is reason to believe that personality plays a role in this species' behavior and survival tactics.

fiddler crab's first line of defense is the ability to run quickly to the safety of a burrow, but immediately after there is a difficult decision to make regarding when to emerge. This calculation must balance the risk of encountering another predator or rival male and the opportunity to forage on premium resources and mating prospects. Can personality types determine a crabs' behavior to run fast or slow and the amount of time they spend in their burrow or is it determined by their autonomy? To address this overarching question, I measured running velocities of crabs and conducted a behavioral assay to determine boldness. I also took anatomical measurements that may be relevant to running velocity and a crabs' boldness. I hypothesized that female crabs will have faster run velocities than males, because of their lower mass from not having an enlarged claw and the dependance on solely running as their defense mechanism. I also hypothesize that crabs with longer legs will have faster run velocities because of the ability to take longer strides, regardless of sex. I also hypotheses male crabs will show bolder behavior than female crabs, because of their enlarged claw acting as secondary defense mechanism and boldness will be positively related to the length of the primary claw.

MATERIALS AND METHODS

Atlantic sand fiddler crabs (*N* = 42) were collected at Dean Creek Marsh (31°23′35.62″N, 81°16′17.14″W) on Sapelo Island, GA, USA from 16 to 22 October 2021. Collections were conducted manually by corralling crabs into the direction of a person holding a net and bucket as an attempt to bias our sampling pool for slower crabs (Biro and Dingemanse 2009). Crabs were then brought to the lab space within half an hour of being captured. The lab environment was kept at 22° C and approximately 75% humidity for the duration of the study.

Velocity Tests

Crabs were allowed to acclimate as a group in a single container with marsh soil and water for a minimum of four hours before timed running trials began. The running track consisted of a 2m long container with tall walls that was divided in half lengthwise (allowing two crabs to acclimate at once) and filled with about 2cm of marsh topsoil. The tub was filled with marsh soil for a total length of 1.5m, there was an extra 0.25m on each end, allowing the crabs to finish their run at full speed and to prevent any veering. The 1m distance was indicated with a brightly colored string at both ends of the track (Supplement Figure 1). Before each timed trial a crab was placed into one half of the track and allowed three minutes to acclimate, then repositioned to the closest end of the track to start a run. Crabs were then chased with one hand approximately one inch behind the crab while the other hand I held a stopwatch. After each timed run, crabs were placed in individual containers with marsh soil and water. All individual containers were covered with cardboard to minimize stress from noise and shadows coming from the lab environment (Wale et al. 2013). Crabs that were not cooperative with running, were placed back to their respective containers and were allowed to rest for at least an hour before being re-ran, only 3 of the 126 total run trials resulted in an uncooperative crab. Each crab (21 males & 21 females) were ran three times over two days and were allowed at least three hours of rest between each run. All crabs were observed to be feeding and creating burrows in their individual containers.

Behavior Assays

This behavior assay was designed to quantify boldness of each individual crab, there is no existing literature about how to quantify this trait specifically for Atlantic sand fiddler crabs so inspiration was drawn from other studies focusing on other organisms (Johnson and Sih 2007; Pollack et al. 2021; Reale et al. 2007, Reaney and Backwell 2007). Crabs were allowed to acclimate to their individual containers for at least 24 hours before the behavior assays. Buckets were used to house the behavior assays; they were filled with marsh soil leaving the last 10 cm of the container to act as a wall. The soil was smoothed over and a dole of 1.5cm in diameter was inserted in the middle of each container 4cm deep, to create a pseudo-crab burrow. Cameras were placed above the containers to record the time it took for crabs to exit each burrow after being scared into it (Supplement Figure 2). One at a time, crabs were placed into the behavior assay buckets and allowed 30 seconds to acclimate to the new environment before being scared into the pseudo-burrow. After the crab entered the pseudo-burrow, I exited the room for 15mins as to not influence any behavior with sounds or shadows (Wale et al. 2013). I considered a crab to have exited the burrow when the carapace was parallel with the top of the soil. Videos of the crab behavioral trials were than saved and watched at later time. The time it took the crab to exit the burrow was recorded, along with other behavior such as finding the hole before being scared into it, building its own burrow, or constructing a door to the burrow. Each crab (the same 21 males & 21 females from the velocity trials) underwent this behavioral assay four times over three days and were allowed at least four hours between each trial. There were two behavior data points that were not recorded due videos becoming corrupted before they could be watched (1 male and 1 female). This study design aligns with the guidelines for a reproducible experiment in which sex, body condition, and age do not hinder the organism to complete a trial (Dingemanse et al. 2002).

Crab Anatomical Measurements

Measurements of each crab occurred after both velocity trials and behavioral assays. Mass of each crab was recorded, carapace length measured, the length of one set of legs measured, the length of the enlarged claw (propodus), and mass of the enlarged claw (Figure 1). Measurements of the walking legs and the enlarged claw were done after the crabs were placed in freezer for two hours. Length measurements were taken with calipers (± 0.02mm) and mass on a digital scale (± 0.01g).

Statistical Analysis

Checking for normality was conducted using qqplots and Shapiro-Wilk test. Boldness measurements did not meet any normality, even after transformations, while running velocities were normally disturbed without the need of any transformation (See supplemental Figures 1 & 2). The effect of trial number on run velocity and boldness data were estimated using a Pairwise

T test with a Bonferroni correction. Comparisons between male and female crabs for running velocities and boldness were tested for significance using a T-test. One-way ANOVA analysis was also used to identify important variables influencing running velocity and boldness. Linear regressions were used to further explore relationships between crab anatomy and running velocity or boldness. Boldness values were categorized as “shy” if it was above the mean (531 sec) of the dataset and as “bold” if it was below the mean. Linear regressions were also run on boldness data after “bold” or “shy” categorization was assigned. All statistical analysis and plotting was done in R (R Core Team 2020). Data collected and used in this study are available through (Ortiz 2022).

RESULTS

The range of running velocities ranged from 0.002 - 0.212 m s^{-1} for all crabs, with female crabs having a higher running velocity ($p < 0.05$) (Table 1 and Supplemental Figure 5A). The mean running velocity of females was 0.109 m s^{-1}, being 0.009 m s^{-1} faster than the male crabs. Running velocities were not significantly correlated to any anatomy measurements recorded (mass, cumulative leg length, carapace, claw mass, or claw length) (Figure 2). However, there were significant ($p < 0.05$) linear relationships between female crab’s running velocities and cumulative leg length (Figure 2F).

The behavior assay times ranged from 13 – 900 seconds (the maximum allowed trial time) for all crabs (Table 1 and Supplemental Figure 5B). Male crabs spent less time in the pseudo-burrow before exiting and exploring their new environment than female crabs ($p < 0.05$). Male crabs on average spent 123 seconds less inside the pseudo-burrow than their female counterparts. Linear regressions and crab anatomy variables suggest that there is significant relationship between all variables ($p < 0.05$), except for run velocity. As crabs became larger, had longer leg lengths, and had larger claws they spent less time in the pseudo-burrow and more time exploring their surroundings. Behavior trends continued in the same direction with all crab anatomy variables when data were parsed by sex, with the strengths of the relationships increasing for female crabs relative to when regressions were done on the combined dataset (Figure 3 B, D, F). The directionality changed from positive to negative in the relationship between boldness and running velocities when the analysis focused only on male crabs, while the positive tendency increased for females (Figure 3H).

A boldness trait was assigned to a behavior assay time if the value was above or below the mean of the dataset ("bold" if $x <$ mean, "shy" if $x >$ mean). Linear regressions after assigning a boldness categorization for all crabs and parsed by sex lead to non-significant relationships between boldness and the metrics of crab anatomy and running velocity. (Supplemental Figures 6-9).

One-way ANOVA was performed to estimate the influence of trial number on running trials and behavior assay results, analysis suggests that there was no difference between the trials for both variables (Figure 3). One-way ANOVAs were performed to compare the effect of crab sex, trial number, individual crabs, running velocities, and/or boldness on running velocities and boldness. The two variables that had a statistical importance to boldness was the sex ($p < 0.05$) of the crab and the individual crabs ($p < 0.001$) (Table 2). While running velocities only had one variable that was significant ($p < 0.001$), individual crabs (Table 3).

DISCUSSION

Running Velocity

Running velocities recorded in this study are within the range of previous studies of fiddler crabs (Full and Herreid 1984; Gerald and Thiesen 2014; Martin 2019; Weinstein 1998). There were some discrepancies between minimum and maximum ranges, for example Martin 2019 reported a minimum velocity value near the mean of this study and a maximum velocity that is 1.8 times faster than the maximum of this study. Weinstein 1998 reported the slowest and smallest range of running velocities, 0.03-0.09 m s^{-1}, which is in the bottom half of the range of this study. Jordao and Oliveria 2001 reported fastest maximum velocities for a different, and one of the largest fiddler crab species, but used drastically different methods, including a running distance twice the distance and only allowing crabs to rest only five minutes before the next trial. Previous studies, focused on Atlantic sand fiddler crabs, did not allow for an acclimation period to the track, like that in this study this could explain the differences in velocities.

Female crabs in this study ran faster their male counterparts by nearly 10 cm s^{-1}, which is a similar difference found in *Afruca tangeri*, (Jordao and Oliveira 2001). This confirms predictions made about males running slower, but the explanation for this difference is not clear as large claws and more mass did not have a slowing effect on males. Having less total body mass and not having a secondary defense mechanism (enlarged claw) were part of my predictions for female crabs having faster run velocities. Only female leg lengths were shown to be significantly related to running velocities, which was my prediction for crabs overall. Male crabs had was similar in slope and directionality, in the relationship between leg length and running velocity but without the statistical significance. Interestingly, leg length is strongly correlated to the total mass of a crab, carapace length, claw mass, and claw length, but none of these other crab anatomical variables have significant linear relationship with running velocity.

The binary distinction of having an enlarged claw or not seemed to influence a crab’s running velocity, with no evidence for enlarged claw length or mass having an influence. The sex of a crab seemed to be an important influence on a crabs’ running velocity (Figure 2B, D, F, H), while the ANOVA analysis suggests that the individual crab is the most important variable. The sex of the crab was not a significant ($p = 0.86$) factor on a crab’s running velocity in the same ANOVA analysis (Table 2).

Boldness

Male crabs on average spent about two minutes less in the pseudo-burrow after entering than female crabs. Linear regressions were used on the entire dataset to assess relationships between crab anatomical variables and the time it took crabs to exit the pseudo-burrow, all showed significant relationships (Figure 3). To further explore crab behavior, trials were classified as “bold” (<531 sec) or “shy” (>531 sec) and all significant relationships were lost (Supplement Figures 6-9), but maintained district directional trends. For example, “bold” female crabs were bolder when they had more mass. In contrast, “bold” males with less mass behaved bolder than larger crabs (Supplemental Figure 6B). This pattern of “bold” crabs having opposite directionality (either being positive or negative) when parsed by sex also held true for cumulative leg length and running velocity, but not for carapace length (Supplemental Figure 6C). When looking at sex differences for “shy” crabs the relationships are more difficult to interpret as they mostly have the same maximum boldness value (Supplemental Figure 9). The classification method of “bold” or “shy’ I used is dramatically different from the single previous fiddler crab behavior study where a similar burrow exit experiment was conducted. Reaney and Backwell 2007 report that their threshold for being a “shy” fiddler crabs was not leaving within 25 seconds. In this study there was only one instance where a male exited burrow prior to 25 seconds of the 166 trials. In this study 58% of the time spent inside the pseudo-burrow were longer than the entire observation period than that in Reaney and Blackwell 2007, which was only 300 seconds. This shortened window of observation may have allowed for increased number of observations, but I believe it greatly biased their analysis and conclusion of what a "bold" and "shy" fiddler crab is. While the species are not the same, (*Uca mjoebergi*) in Reaney and Blackwell 2007 and this study, there should be a standardization of how behavioral studies are conducted for ease of comparison and synthesis especially within the same order.

In this study there were not any significant correlations between crab anatomy and boldness, the one-way ANOVA analysis suggests that each individual crab ($p<0.001$) and sex ($p < 0.05$) are the two important factors influencing the time to leave the pseudo-burrow. This suggests that the most important variable of Atlantic sand fiddler crab behavior is their individual personality. Trial number and running velocity were not identified to have a major effect on a crab's boldness (Table 3).

Personality

Both running velocity and boldness were best explained by the individual crab (Tables 2 & 3). This unexpected result suggests that each crab has a personality and is the driving factor when it comes to running velocities and boldness, regardless of the crab's sex, size, mass, or enlarged claw characteristics. Atlantic sand fiddler crabs are social organisms, in such that they depend on each other to spot potential risks. The separation of crabs from their colony for study could have influenced the behavior and strategies implemented by each crab, as it is generally safer to leave refuge in pairs or in groups to forage (Crane 1975; Rands et al. 2003). Crabs are constantly taking ques from each other regarding when it is best to leave their burrows and what direction to run in.

Conclusions

Laboratory studies on other decapods report similar results related to having personality (Gherardi et al. 2012). In addition to identifying personality in the Atlantic sand fiddler crab in this study, I also identified the role that sex and body size plays in predicting boldness. Future studies should conduct similar behavior and running experiments with more than one crab at a time. This would be an interesting study that could distinguish the importance of group dynamics on crab behavior and personality. In the meantime, this study brings up questions about the ecological implications of having identified differences between male and female running velocities and how personality influences survival strategies (Crane 1975; Rands et al. 2003). Investigating the distribution of personality types of fiddler crabs (and other decapods) and how sexual dimorphism plays a role in an individual's behavior will be an important and interesting avenue of future work. Especially as work expands to determining whether generic drivers, hormones, or past experience drive behavior (Beekman and Jordan 2017). Bettering our understanding of Atlantic sand fiddler crab and their boldness behavior can help ensure the survival of the species throughout the Anthropocene with changing climate, habitat, and the inevitable expansion of invasive non-native species (Sih et al. 2004). This is an exciting and timely finding as a large scope report (Birch et al. 2021) provides strong evidence for a group of cephalopods and decapods to be sentient, of which Atlantic sand fiddler crabs are a part of. I hope that this study is a call to action for continued work revolving personality, behavior, and performance of fiddler crabs.

ACKNOWLEDGEMENTS

This research was made possible because of the collaborative efforts with the Long Term Ecological Research Center of the University of Georgia on Sapelo Island. Many thanks go out to the course instructors for feedback and advice Emily Stanley, Claudio Gratton, and especially Olaf Jenson for his profound insight on behavior assays. I also want to thank my peers that attended Sapelo with me in the fall of 2021, especially Adam Rexroade, Adrianna Gorksy and those peers that helped me reach my committee quota. I hope that you all remember our time on the island for a while and your ✨SIA✨. Recognition goes to Ben Martin for his previous work with Fiddler crabs and conversations at the terrace that helped guide my study. I also want to thank the Birge Limnology Graduate Support Fund for supporting this project.

Data Availability Statement

The data that were collected and support the findings of this study are available from Environmental Data Initiative repository: https://portal.edirepository.org/nis/mapbrowse?packageid=edi.1084.1

Conflict of Interest Statement

There are no conflicts of interest to declare.

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Figures & Tables

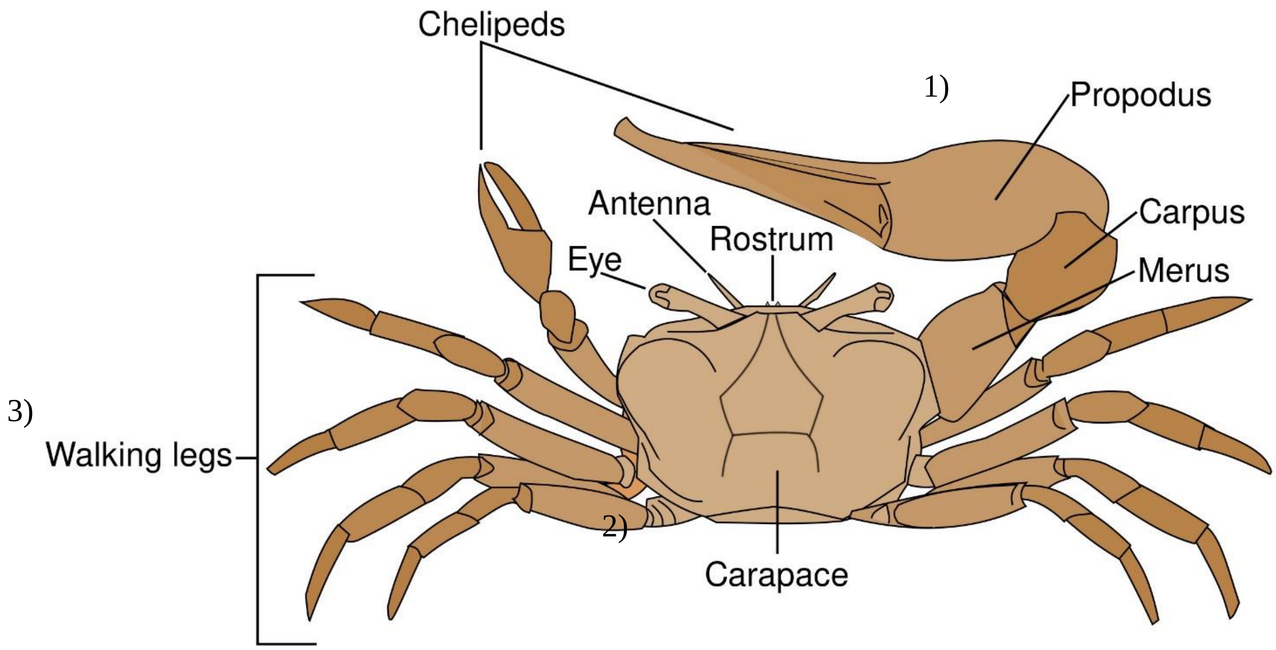

Figure 1. Measurements taken for fiddler crabs 1) propodus length, 2) carapace width, and 3) walking legs length. Image by Christopher Thomas, distrusted under a CC BY-SA 3.0 license.

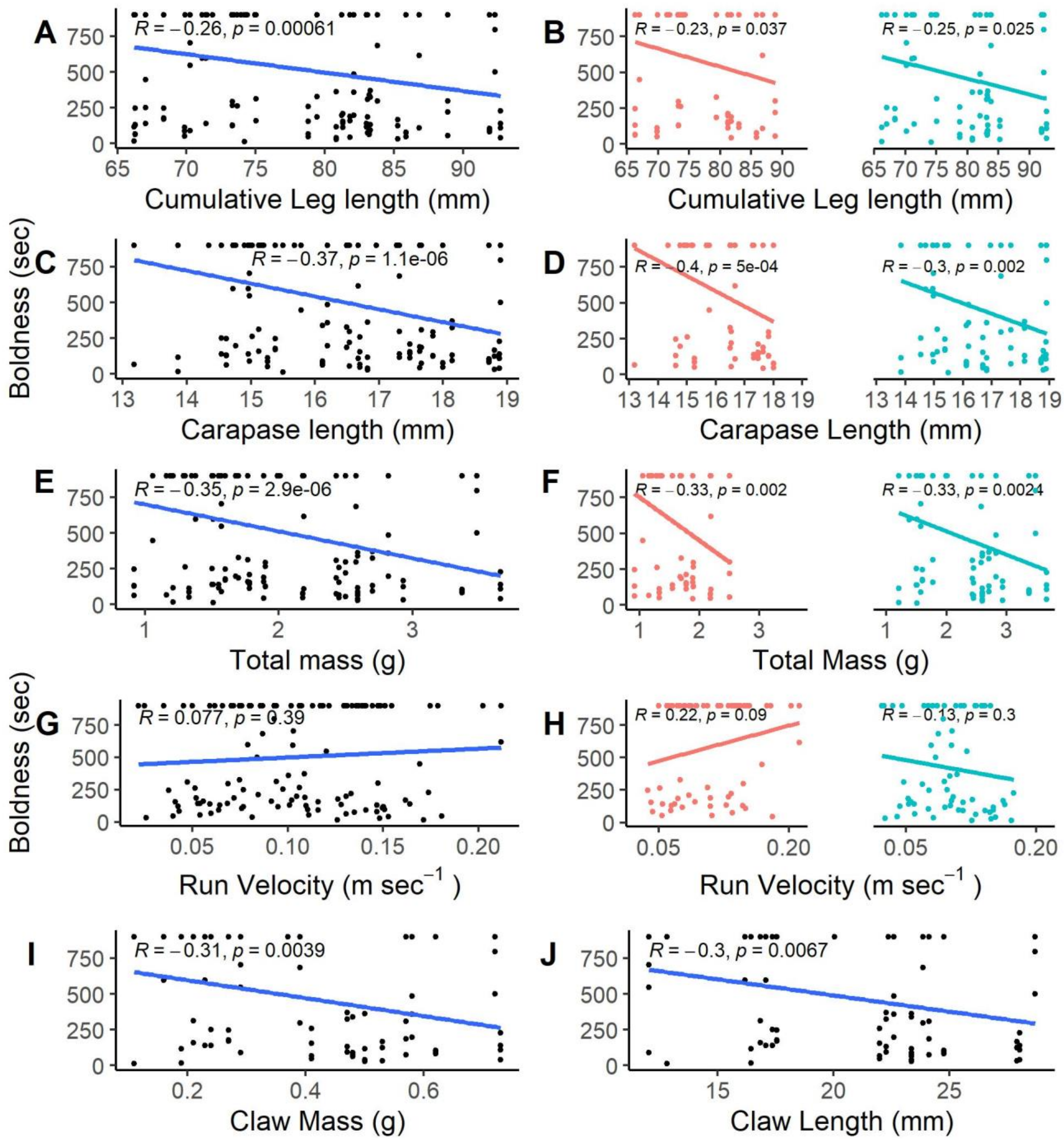

Figure 2. Running velocities of all running trials plotted against crab anatomy and behavior. (A,C,E,G,I, & J) All crabs running velocities are included in the plots, (B,D,F, &H) show the same variables being plotted against running velocities broken down by sex, female crabs are red and males are blue. Note that the Claw mass and claw length plots (I & J) are only of enlarged claws found only on males. Linear regression are the blue lines in plots A,C,E,G,I, and J.

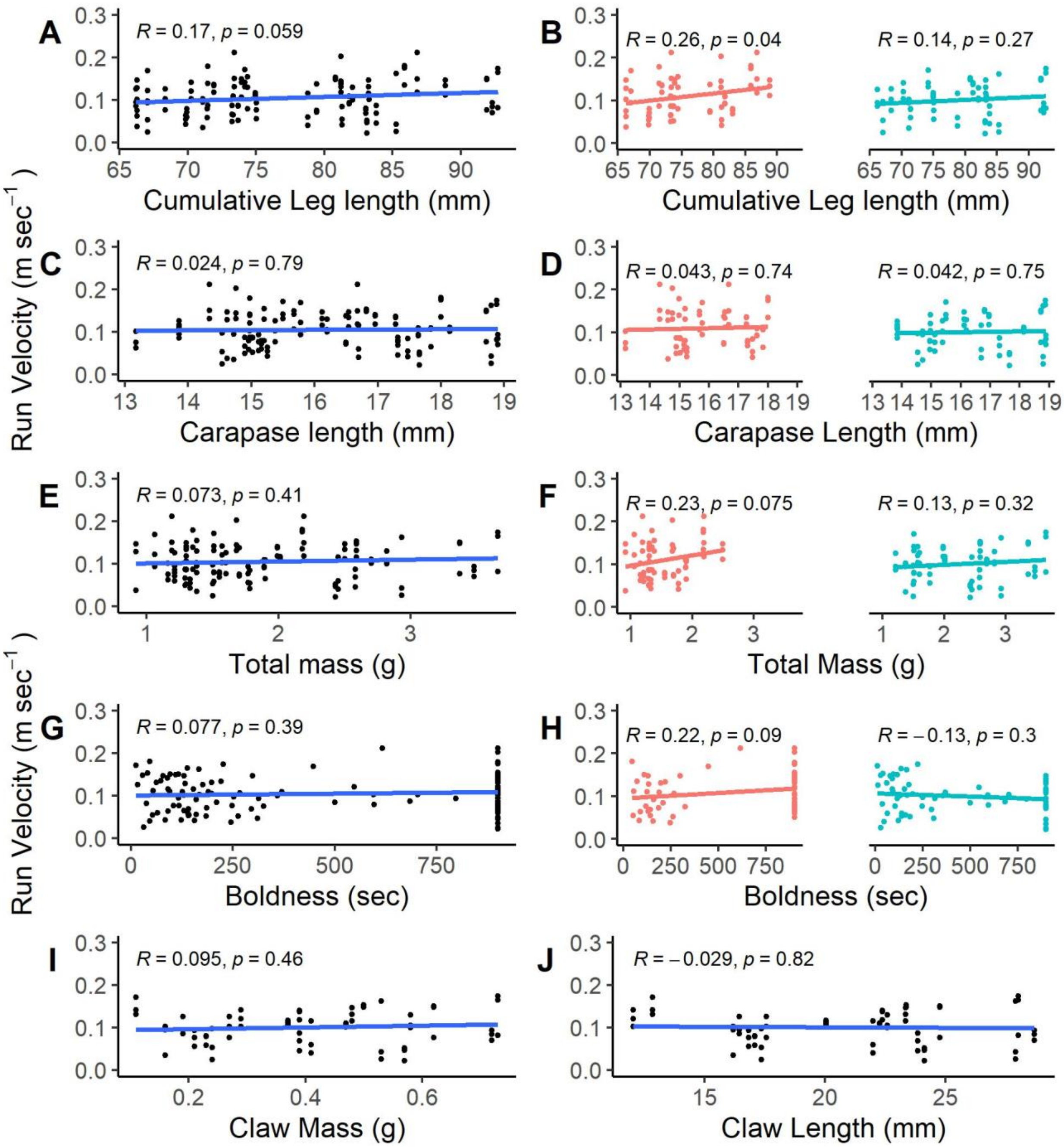

Figure 3. Bold time of behavior assays plotted against crab anatomy and running velocities. (A,C,E,G,I, & J) All crabs behavior assay data are included in the plots, (B,D,F, &H) show the same variables being plotted against behavior assay data broken down by sex, female crabs are red and males are blue. Note that the Claw mass and claw length plots (I & J) are only of enlarged claws found only on males. Linear regression are the blue lines in plots A,C,E,G,I, and J.

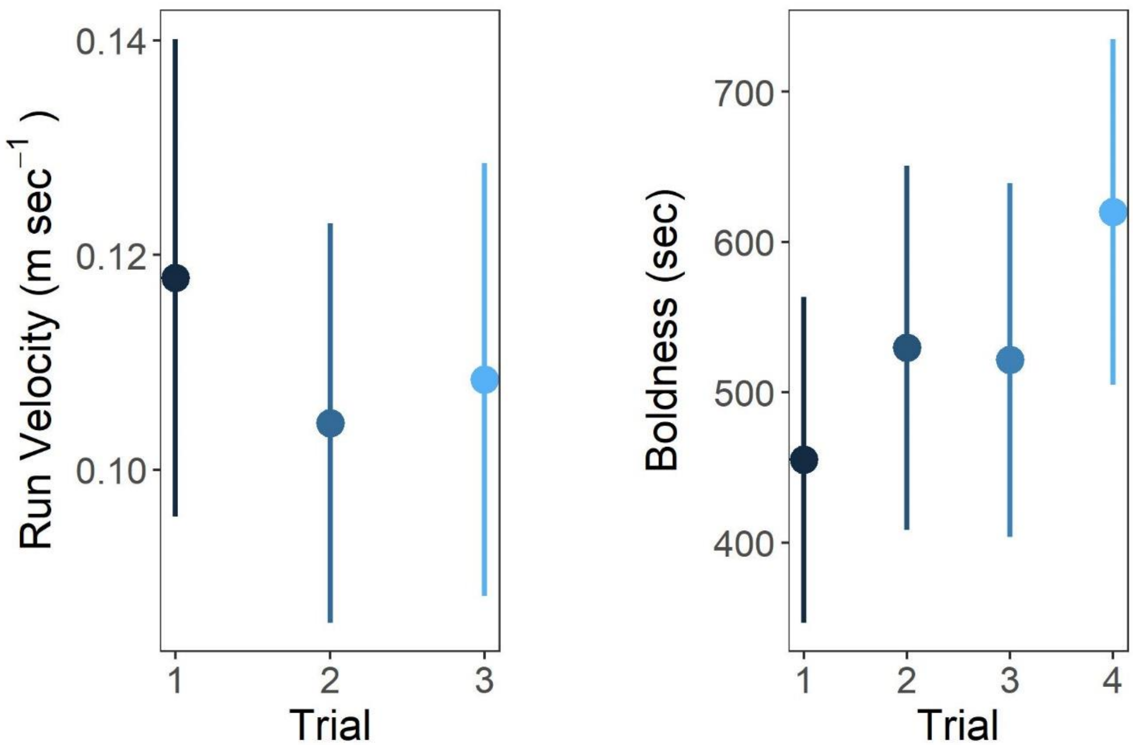

Figure 4. Effect of trial on run velocity and boldness data. Points represent the mean of each trial with lines representing the range of each variable for each trial. Pairwise T-test with Bonferroni correction, does not indicate that any trial combination comparison was significantly different.

Running Velocities ($m\ s^{-1}$)	*Min*	*Mean*	*Max*	*Standard Deviation*
All	0.022	0.105	0.212	0.042
Female	0.037	0.109	0.212	0.044
Male	0.022	0.100	0.174	0.039
Boldness (sec)	Min	Mean	Max	Standard Deviation
All	13	531	900	369
Female	42	592	900	371
Male	13	469	900	361

Table 1. Summary of running velocities and boldness assay data.

	Df	*Mean Square*	*F Value*	*Significance*
Boldness	1	0.00023	0.26	0.61
Trial	2	0.0016	1.74	0.18
Sex	1	0.0027	3.07	0.086
ID	40	0.0034	3.25	< 0.001

Table 2. Summary of one-way ANOVA analysis of different effects on running velocities.

	Df	*Mean Square*	*F Value*	*Significance*
Running Velocity	1	16075	0.22	0.64
Trial	2	82091	1.10	0.34
Sex	1	833052	11.15	0.0013
ID	40	245730	3.29	< 0.001

421 **Table 3.** Summary of one-way ANOVA analysis of different effects on boldness.

Supplemental Material

Title: Differences in running velocity and boldness between male and female Atlantic sand fiddler crab (Leptuca pugilator)

Author: David Ortiz

Figures

Figure 1. Track set up for velocity trials. Trough was divided in half to allow for two crabs to acclimate at the same time and ran consecutively.

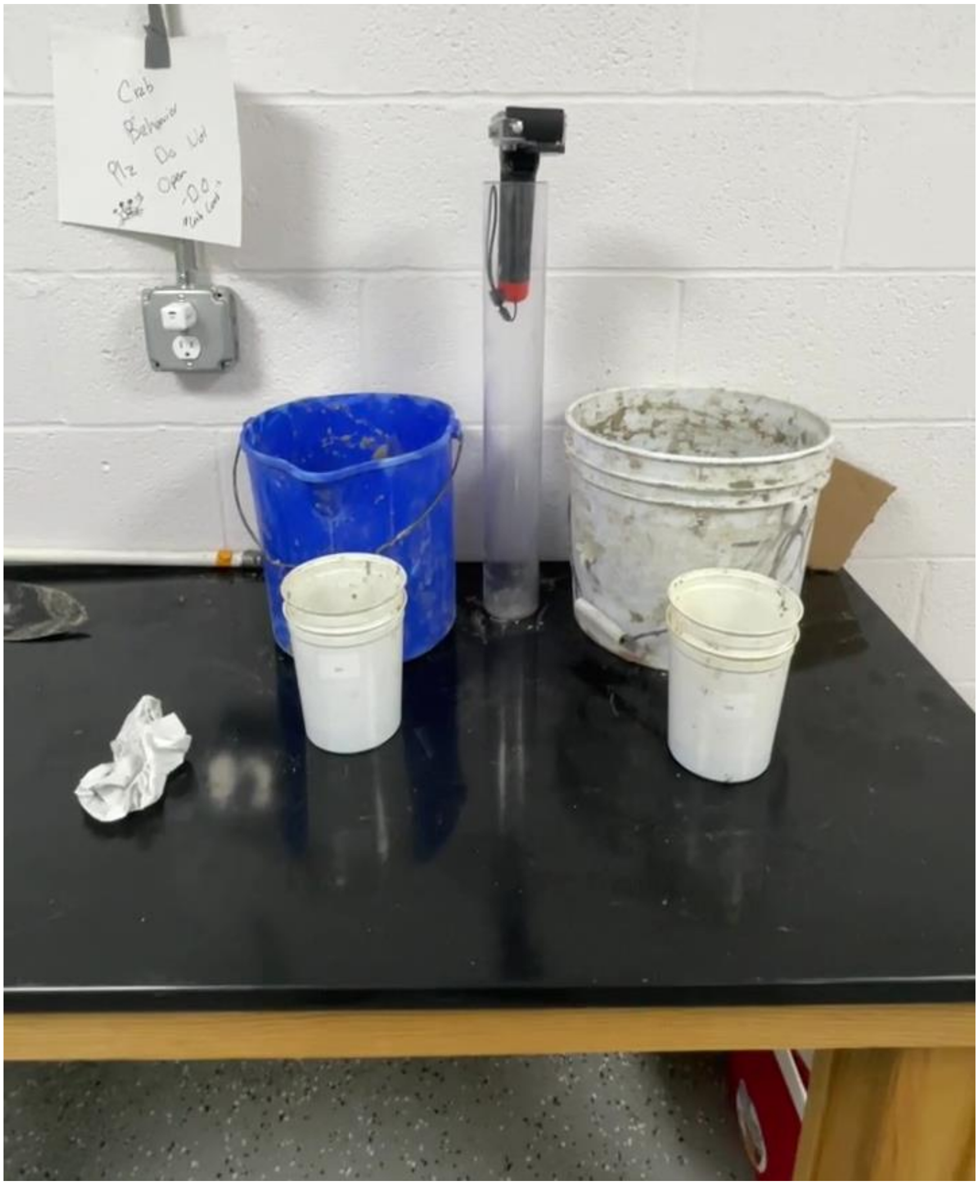

Figure 2. Behavioral assay setup. Crabs were moved from their individual containers into the large bucket. Then the camera was turned on for 15 minutes to capture crab behavior after I scared the crab into the pseudo-burrow while I left the room.

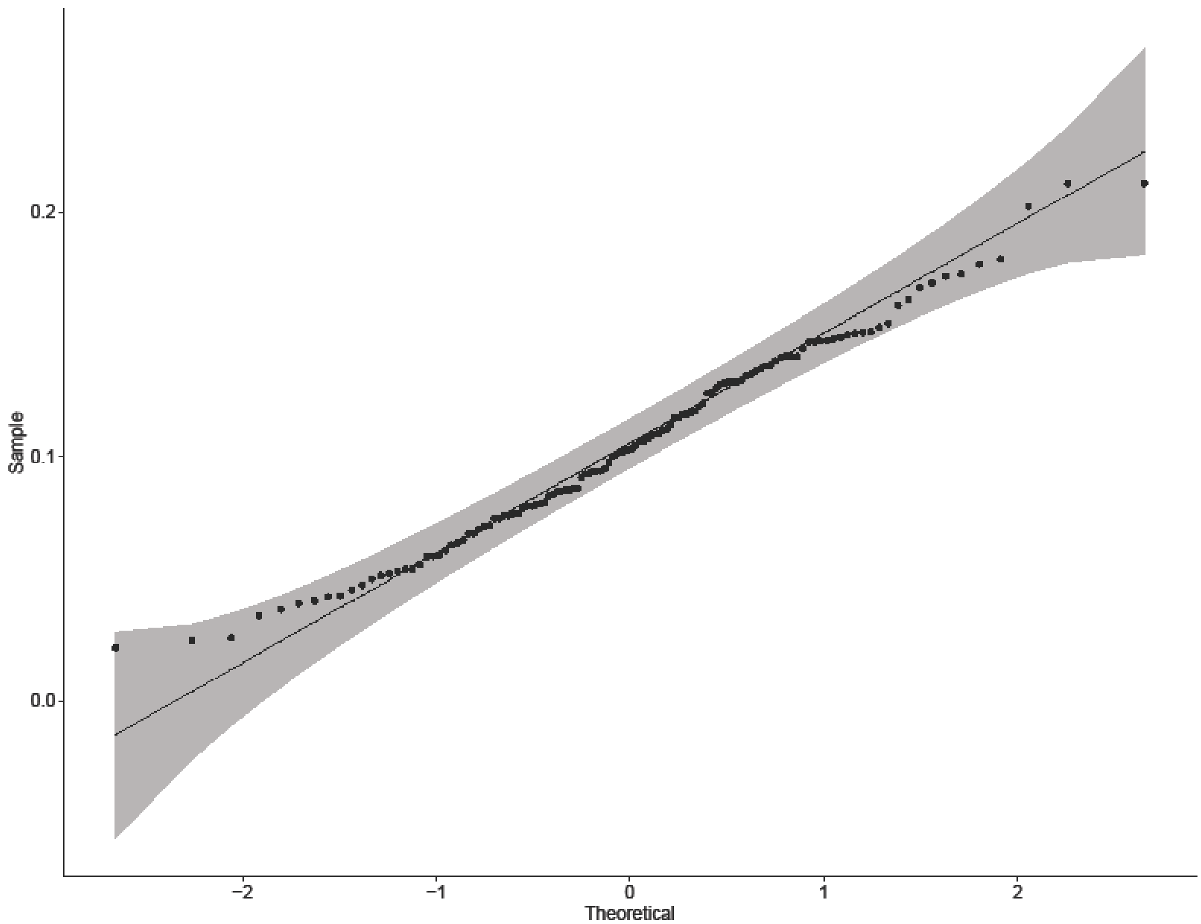

Figure 3. Normality check of running velocity data.

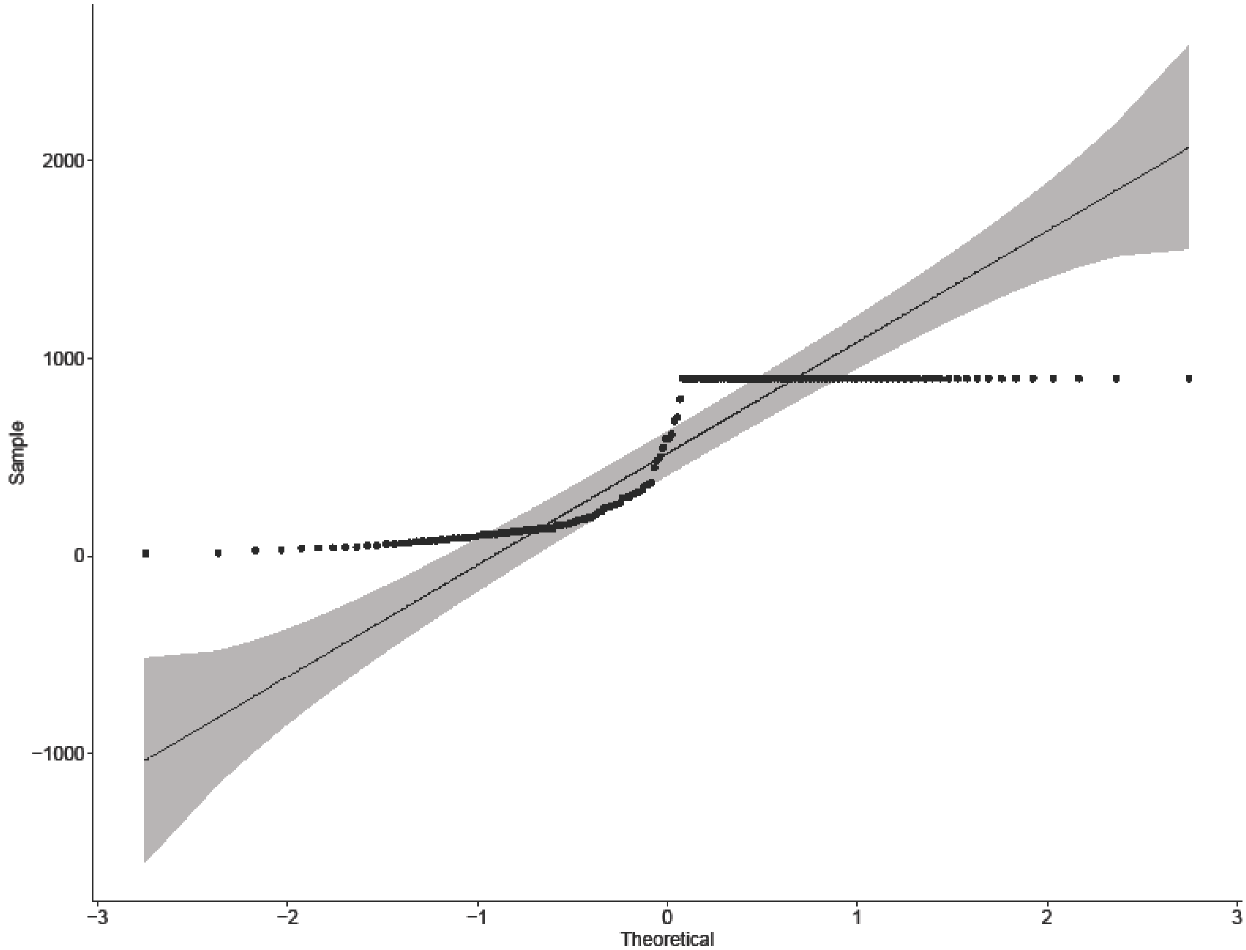

Figure 4. Normality check of boldness data.

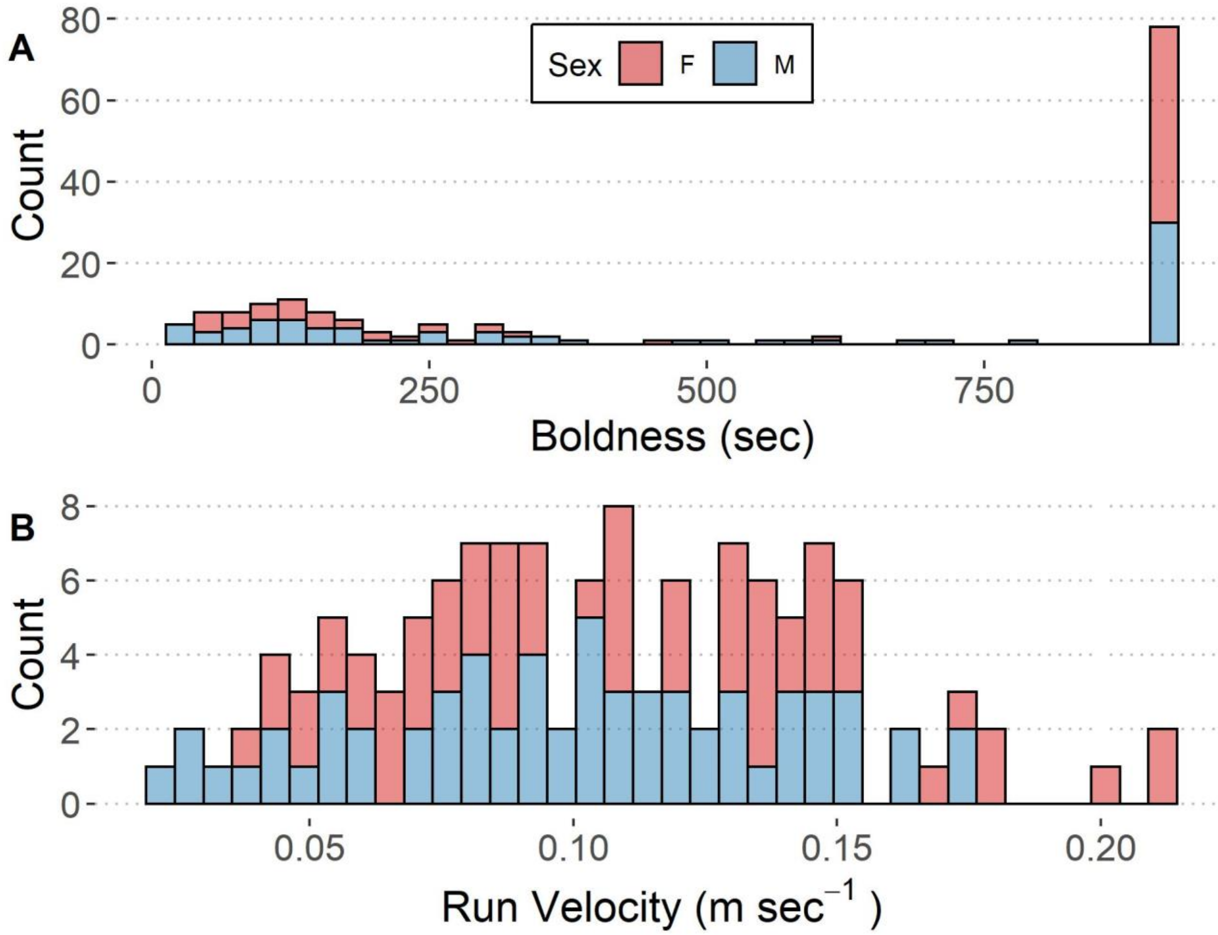

Figure 5. Distribution of A) boldness and B) running velocities for all crabs. Female crabs are represented in plots with red bars and males are blue.

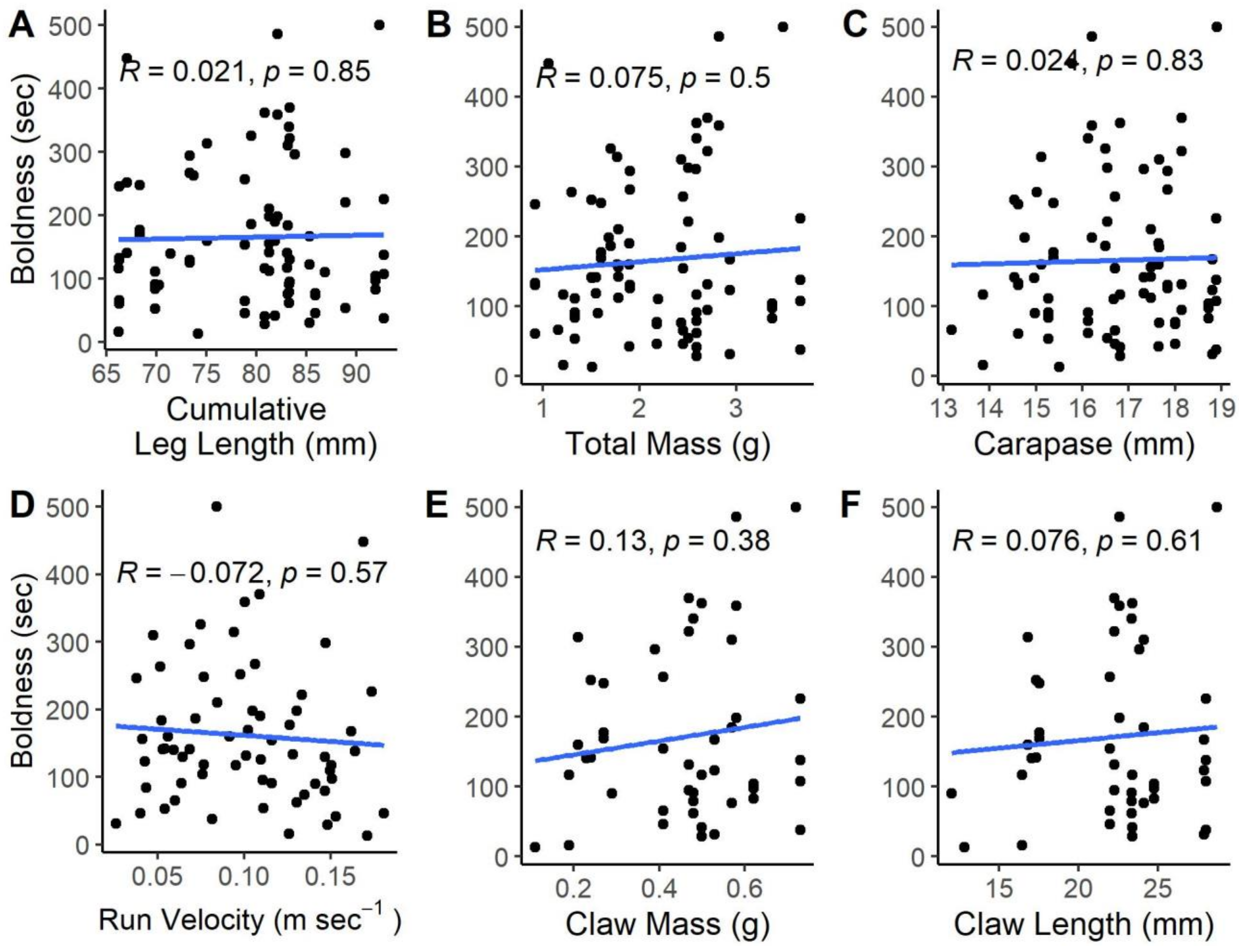

Figure 6. Boldness parsed by "bold" crab behavior data plotted against crab anatomy and running velocity. Blue lines represent linear regressions.

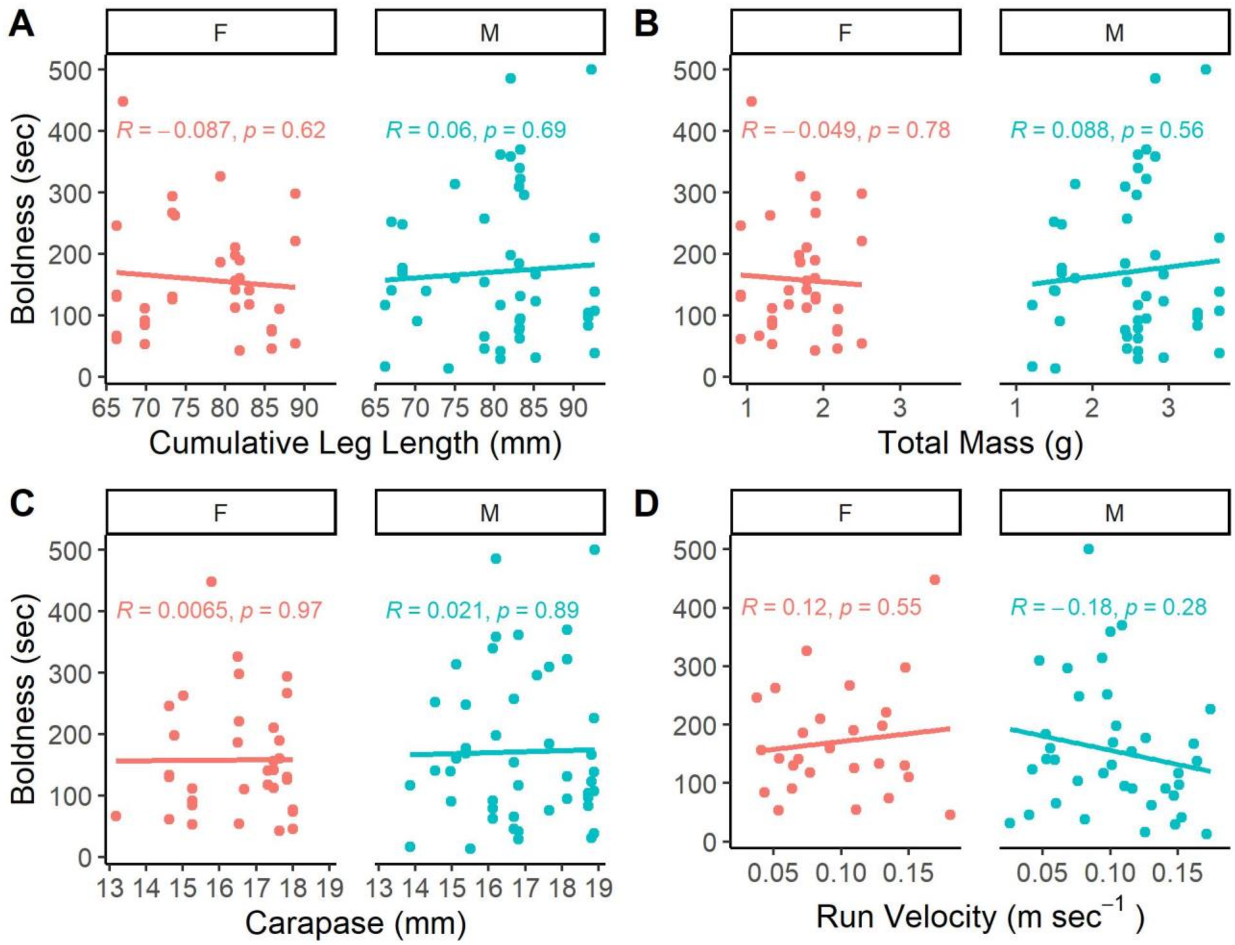

Figure 7. Boldness parsed by "bold" crab behavior data and sex plotted against crab anatomy and running velocity. Blue lines represent linear regressions. Female crabs are represented in plots with red points and males are blue.

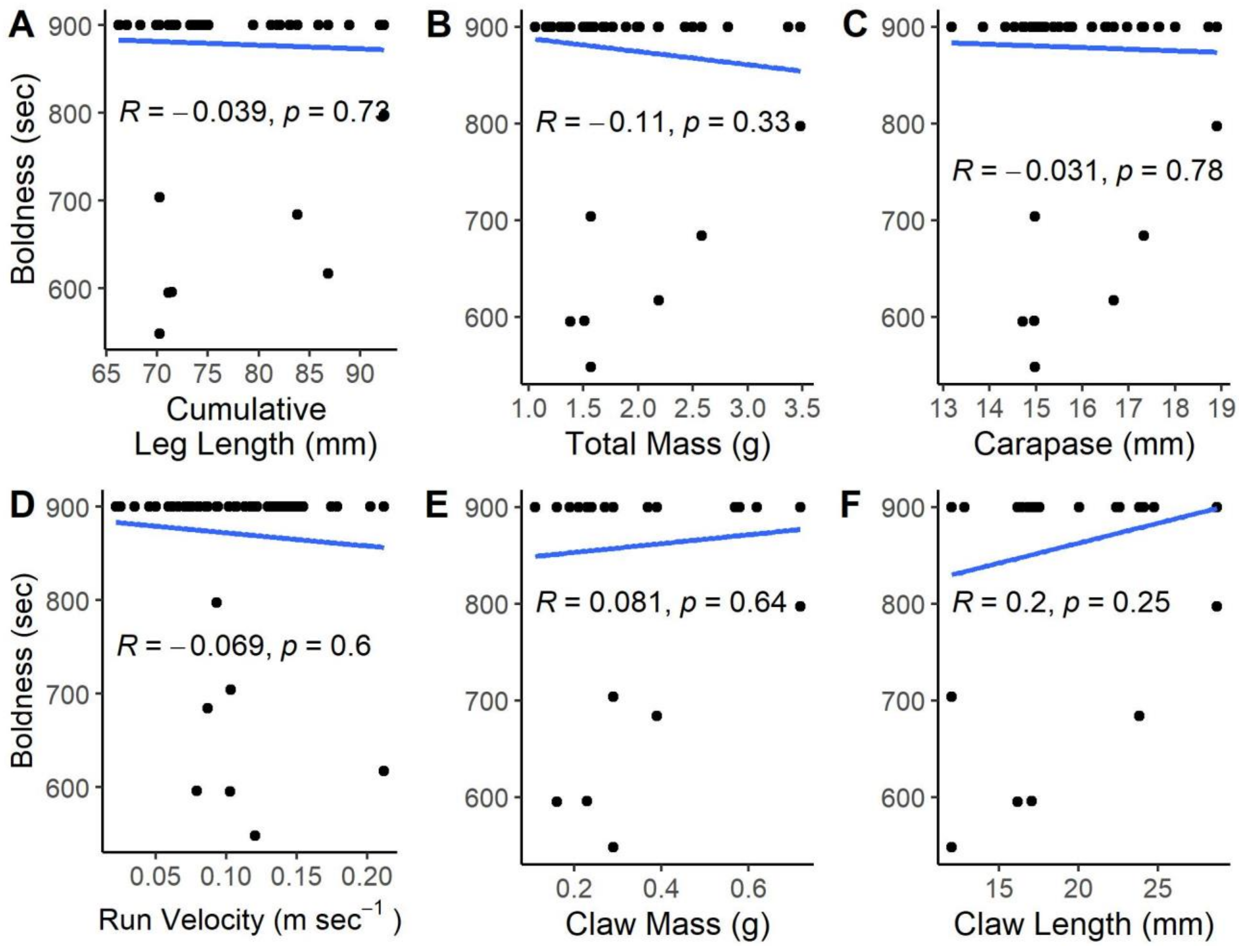

Figure 8. Boldness parsed by "shy" crab behavior data plotted against crab anatomy and running velocity. Blue lines represent linear regressions.

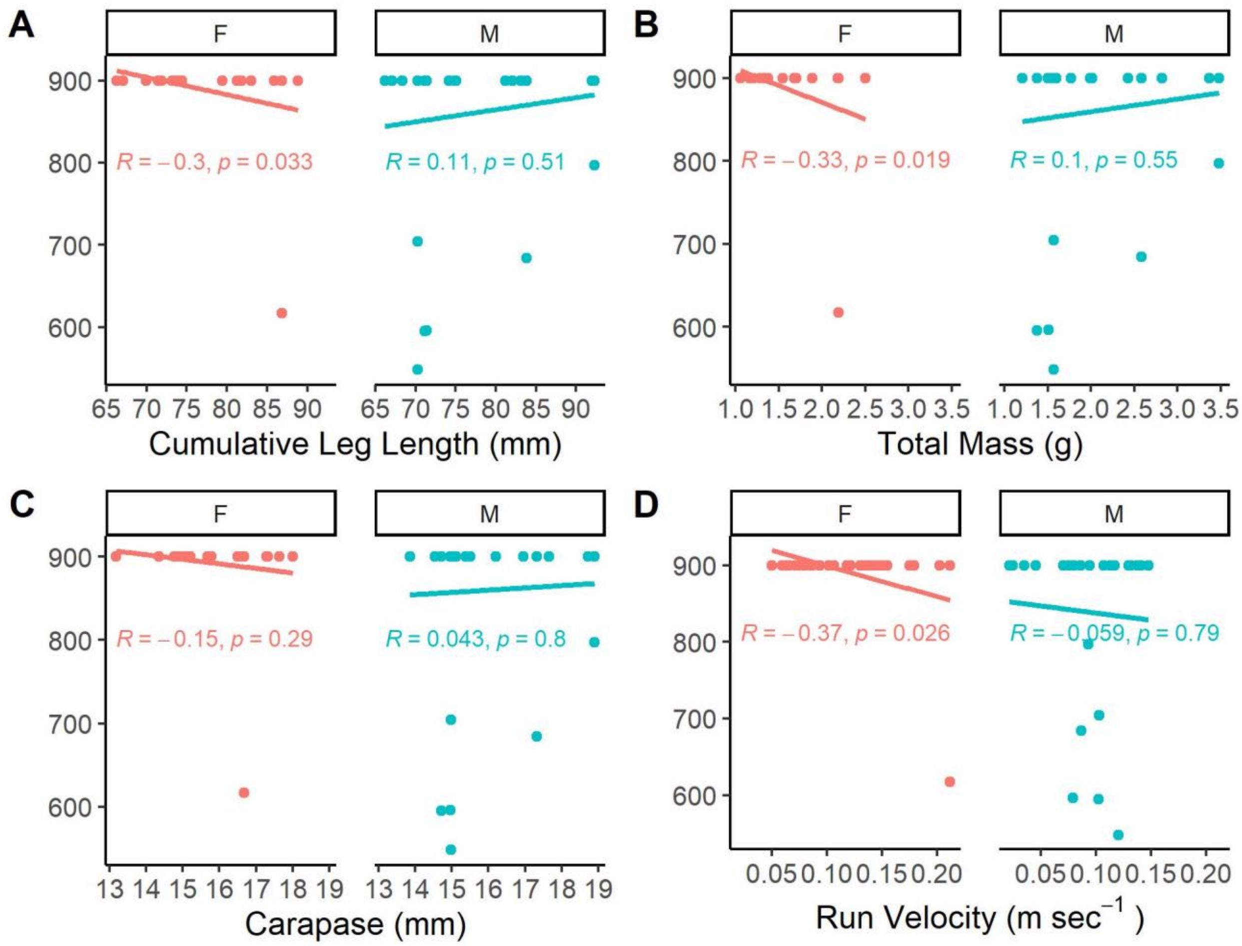

Figure 9. Boldness parsed by "shy" crab behavior data and sex plotted against crab anatomy and running velocity. Blue lines represent linear regressions. Female crabs are represented in plots with red points and males are blue.