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## Personality in Stomatopod Crustaceans

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# PERSONALITY IN STOMATOPOD CRUSTACEANS

By

JILLIAN BLENDERMAN, Bachelor of Science in Biology

Presented to the Faculty of the Graduate School of

Stephen F. Austin State University

In Partial Fulfillment

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May 2020

Personality in Stomatopod Crustaceans

By

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ABSTRACT

Stomatopods, or mantis shrimp, are small, predatory crustaceans of tropical and subtropical waters. Mantis shrimp research has focused largely on their agonistic interactions and complex visual systems. Despite their broad behavioral repertoire, stomatopods have not yet been investigated for consistent behavioral differences at the individual level, referred to as animal personality. Fifteen individual *Neogonodactylus oerstedii* were tested in three scenarios designed to measure potential differences in behaviors: 1) exploration of a novel environment, 2) response to and recovery from a startling event, and 3) response to a novel object. Each individual went through the series of tests twice, with a 14-day interval, to test for consistency over time. Sixteen measured behavioral variables were found to be statistically significantly repeatable. Six of these variables were run through factor analysis and found to align with three factors: one representing exploration, and two representing boldness (foraging prior to startling event, and startle recovery). Overall, the findings suggest that these stomatopods do exhibit personality. Combining a study of exploration and boldness with possible differences in agonistic behaviors could give greater insight to the ecological significance of personality in mantis shrimp.

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TABLE OF CONTENTS


I. Abstract ..... i
II. Acknowledgments ..... ii
III. Table of Contents ..... iii
IV. List of Figures ..... iv
V. List of Tables ..... v
VI. Introduction ..... 1
  a. Animal Personality ..... 1
    i. Causes of Personality ..... 5
    ii. Consequences of Personality ..... 7
    iii. Behavioral Syndromes ..... 9
    iv. Personality in Invertebrates ..... 11
  b. Stomatopods ..... 12
    i. Agonistic Interactions in Stomatopods ..... 14
  c. Study System ..... 16
  d. Objectives ..... 17
  e. Significance ..... 18
VII. Methods ..... 21
  a. Experimental Design ..... 21
    i. Test 1: Exploration of Novel Environment ..... 24
    ii. Test 2: Startle Response and Recovery ..... 24
    iii. Test 3: Response to a Novel Object ..... 25
  b. Data Collection ..... 26
  c. Statistical Analyses ..... 27
VIII. Results ..... 31
  a. Initial Test Results ..... 31
    i. Test 1: Exploration of Novel Environment ..... 31
    ii. Test 2: Startle Response and Recovery ..... 32
    iii. Test 3: Response to a Novel Object ..... 33
    iv. General Results and Additional Variables ..... 34
  b. Factor Analysis ..... 35
IX. Discussion ..... 37
X. Bibliography ..... 44
XI. Figures and Tables ..... 52
XII. Vita ..... 82

## LIST OF FIGURES

Figure 1. Flow chart of data collection and statistical methods..... 52

Figure 2. Outline of the experimental process for one individual stomatopod. .. 53

Figure 3. Basic setup of the three tests. ..... 54

Figure 4. Diagrams showing an individual “part exposed” and “half exposed”. .. 55

Figure 5. Examples of “jump” responses given during startle tests ..... 56

Figure 6. Different responses during the novel object (straw) test..... 57

Figure 7. Loading plots of the factor analysis for Round 1..... 58

Figure 8. Loading plots of the factor analysis for Round 2..... 59

Figure 9. Plot showing individual boldness (startle recovery) scores compared across rounds. ..... 60

Figure 10. Plot showing individual boldness (pre-startle) scores compared across rounds. ..... 61

Figure 11. Plot showing individual exploration scores compared across rounds. ..... 62

Figure 12. Plot showing the relationship between individual factor scores for exploration and boldness (pre-startle) in both rounds..... 63

Figure 13. Plot showing the relationship between individual factor scores for boldness (startle recovery) and exploration in both rounds ..... 64

Figure 14. Plot showing the relationship between individual factor scores for boldness (pre-startle) and boldness (startle recovery) in both rounds ..... 65

## LIST OF TABLES

Table 1. Data from Test 1 (exploration test). ..... 66-68

Table 2. Data from Test 2 (startle test). ..... 69-73

Table 3. Data from Test 3 (novel object test). ..... 74

Table 4. Variables used in or based off of other personality studies. ..... 75

Table 5. Results from paired two-sample t-tests comparing results between rounds for the exploration test. ..... 76

Table 6. Results from paired two-sample t-tests comparing results between rounds for the startle test. ..... 77

Table 7. Repeatability statistics (*r*) of significantly repeatable variables. ..... 78

Table 8. Factor loadings from factor analyses. ..... 79

Table 9. Variance explained by each factor. ..... 80

Table 10. Factor scores of each individual. ..... 81

# INTRODUCTION

## Animal Personality

Animal personality is a relatively new area of study, having gained increased attention in the last few decades (Gosling 2008). In a general sense, animal personality, sometimes called temperament (Réale et al. 2007), can be described as behavioral differences between individuals that are consistent over time (Dall et al. 2004; Dingemanse et al. 2009a; Kralj-Fišer & Schneider 2012; Biro et al. 2013; Jeanson & Weidenmüller 2014). Based on early frameworks created for human personality study (Gosling & John 1999), Réale et al. (2007) define five categories encompassing the most commonly studied animal personality traits (i.e., behavioral traits involved in personality differences): shyness-boldness, exploration-avoidance, aggressiveness, activity, and sociability. Each can be thought of as a spectrum of expression levels for a trait, with individuals falling anywhere between the two extremes. As outlined by Réale et al. (2007), boldness is defined as the willingness to take risks or engage in behaviors in risky situations. Exploration is distinguished from boldness by the stimulus or environment being novel, although novelty is frequently included under the definition of boldness (Sinn et al. 2008; Kralj-Fišer & Schneider 2012; Carter et al. 2012b). Aggressiveness describes the frequency and intensity of an

individual's "agonistic or attacking behaviors" (Sinn & Moltschaniwskyj 2005). Activity describes an animal's overall level of activity or movement through its environment. Sociability is defined by non-aggressive interactions with conspecifics (Réale et al. 2007).

Personality has two main requirements: 1) that individuals are consistent in their own behavior through time, and 2) that there are differences in behavior between individuals (Kralj-Fišer & Schuett 2014; Réale et al. 2007). Personality is a characteristic of the individual, but it only exists in the context of a population, as it requires individuals to differ from one another. There are a number of ways to determine if these requirements are met in a particular species, all of which involve quantifying personality trait expression in a number of individuals. The first component of personality is individual consistency, or whether an individual behaves consistently when measured multiple times under the same circumstances (Bell et al. 2009). In most studies, individuals are measured twice for a given trait (Bell et al. 2009), and the results are compared. Consistency may vary between individuals of the same population, with some being more consistent than others (Dingemanse et al. 2009a). Individuals may then be compared to each other by their average scores to see if they differ significantly, addressing the second component of personality.

Repeatability is a statistical measure used in quantitative genetics to describe the proportion of variance in a variable due to differences between individuals versus within individuals, and it has become a standard statistic used

in personality studies (Lessels & Boag 1987; Bell et al. 2009). Consistency describes behavior at an individual level, whereas a behavior is repeatable at the population level when consistent individuals differ from each other. In addition, only a single repeatability estimate is calculated per behavior for the entire test population in a study. Increasing the number of measurements per individual does not affect the repeatability estimate, hence why most studies choose to instead measure more individuals on fewer occasions (Bell et al. 2009). Additionally, there is the possibility of animals becoming habituated to the test scenarios with repeated exposures, which could influence the results.

One major challenge to the field is inconsistent use of definitions between studies. Different authors will often use the same terms in different ways, or use several different terms to refer to the same concept. However, a relatively consistent definition for ‘personality’ has been reached, but other terms still see considerable variation. One of the goals of Réale et al. (2007) was to provide a framework for future studies (such as Smith & Blumstein 2008, a meta-analysis) to use in defining personality traits, in hopes of lessening problems regarding definitions. In addition, there is also variation in which behaviors are used to quantify personality traits, depending on the species and questions being addressed. It is important to note that the reason for placing personality traits into categories is convenience. It does not imply that what is considered “boldness” in one species or behavioral context is the result of the same underlying mechanisms as “boldness” in another. In a study of wild chacma baboons (*Papio*

*ursinus*), individuals were tested for boldness in threat response to a predator and response to a novel food item. The responses of individuals were not correlated between the two contexts, suggesting that threat response behaviors are a property of a different personality trait than novel food investigation in this species (Carter et al. 2012b).

Another challenge to studying personality is behavioral plasticity, which is the ability to adjust behavioral responses based on the situation, or the current environmental conditions under which behaviors are taking place (Sih et al. 2004a; Sih et al. 2004b). Many studies will compare behavioral responses between situations of high and low predation risk (Briffa et al. 2008; Pintor et al. 2008; Vainikka et al. 2011; Mowles et al. 2012). With phenotypic plasticity, morphological changes are either irreversible or come with a time lag — changes are not instantaneous, and neither is reversing them. If the environment varies unpredictably, individuals may be left with a phenotype that is no longer advantageous for the current conditions (Sih et al. 2004b). A similar issue occurs with behavioral plasticity in that it creates the potential for individuals to select the "wrong" response. Individuals might not have the means to easily or accurately determine the environmental conditions they're currently experiencing. In these cases, it may be advantageous to stick to a particular strategy. For example, if a prey species has poor information available about predators in the area, it would be best to stay close to shelter, regardless of the actual predation risk (Sih et al. 2004b). Species with limited plasticity or without adequate variation in behavioral

responses in a population may be less able to adapt to sudden changes in their environment. Species that readily adapt to new habitats, such as urban areas, tend to have a mixture of bold, aggressive individuals and shy, sociable individuals (Pintor et al. 2008; Kralj-Fišer & Schneider 2012).

Behavioral plasticity and personality are not mutually exclusive. An individual can have relatively consistent behavior patterns while retaining the ability to adjust them somewhat. For example, individuals may all decrease a foraging behavior in the presence of predators. If behavioral plasticity and personality are both present, the boldest individuals would still engage in more foraging behavior when predators are present than the shyest individuals, even if levels of the behavior are reduced overall (Briffa et al. 2008).

Causes of Personality

Genetic variation is often an underlying cause of behavioral variation. Genes determine the neurological structures and physiology of an organism, which in turn shape behavior. Since these features are heritable, a certain degree of heritability can also be expected for personality. The upper limit of a trait's heritability is given by repeatability measurements (Lessels & Boag 1987; Bell et al. 2009). The degree to which variation is influenced by genetics varies by species. Neurological development is also affected by environmental factors. In some species, personality seems to have a strong genetic component, such as for exploratory behavior in great tits (Dingemanse et al. 2004). However, in the cichlid *Neolamprologus pulcher*, boldness has relatively low heritability

(Chervet et al. 2011). Heritability can also vary among traits within a species. In the bridge spider (*Larinioides sclopetarius*), aggressiveness toward same-sex conspecifics is significantly heritable, whereas activity in new environments and aggressiveness toward mates are not (Kralj-Fišer & Schneider 2012). Among vertebrates, heritability of personality traits tends to be higher among endotherms than ectotherms; this same pattern is seen with repeatability in these groups (Bell et al. 2009). In ectothermic animals, metabolic rate increases with the external temperature (reviewed in Biro et al. 2013), which may influence personality. Individual rock crabs (*Ozius truncatus*) not only consistently differ in their behavioral responses, but also in the degree to which their behavioral responses change with temperature (Biro et al. 2013). In pumpkinseed sunfish (*Lepomis gibbosus*), individual differences are significant in the field but disappear after the fish are maintained individually in a laboratory setting for a period of time (Wilson et al. 1993). In cases where genetics and environment are not particularly significant factors, personality may still be innate. The pea aphid, *Acyrthosiphon pisum*, reproduces asexually, producing numerous genetically identical individuals. Despite this, different behavioral phenotypes exist even among genetic clones raised under identical conditions (Schuett et al. 2011). This suggests that there are additional factors at play beyond genetics and environment.

Experience and age are other major contributors to behavioral differences (Sinn et al. 2008). Older individuals have more life experience than younger

individuals, and in species with indeterminate growth age can relate to body size and physical strength. Experiences can shape the ways an individual responds to similar scenarios in the future, and can influence their behavior long-term (Dingemanse et al. 2009b).

Consequences of Personality

Natural selection requires that there are different phenotypes in a population, that these phenotypes are heritable, and that different phenotypes result in differing fitness. When fitness differences occur, selective pressures act upon those differences. Natural selection can act on behavioral phenotypes. However, natural populations do not normally converge onto a single, 'optimized' behavioral phenotype. Instead, multiple behavioral phenotypes will be stable in a population (Taylor & Jonker 1978). Individuals do well in certain contexts and poorly in others, resulting in life history trade-offs. For example, in a foraging context, when predation risk is low, bolder individuals will have an advantage over shyer individuals. However, when predation risk is high, shy individuals will face lower mortality than bold individuals (Dingemanse et al. 2004). Maintaining the amount of behavioral plasticity required to respond optimally in every situation is costly (Mowles et al. 2012). Giving an optimal behavioral response requires accurately evaluating numerous factors about the environment at a given moment. Animals with low plasticity, while avoiding the high costs associated with maintaining plasticity, can only give an approximately appropriate behavioral response (Briffa et al. 2008). An individual on the shy end of the bold-

shy spectrum may forage less than bold individuals in high-predation environments, but risk of injury or mortality is lowered. Aggressive individuals more likely to fight for resources are also more likely to retain those resources, but at the same time face greater risk of injury or energy costs associated with losing (Caldwell 1987). Less aggressive individuals may lose out on some resources, but can avoid the costs of fighting with conspecifics.

The existence of personality variation within a population allows a species to more readily adapt to changes in the environment that may favor one phenotype over another. Differences in personality have been shown to affect dispersal, niche expansion, and social organization (Réale et al. 2007). Personality can also be considered at the population level, as separate populations of a species can differ in their frequencies of certain behavioral phenotypes. In Pintor et al. (2008), intraspecific aggression, foraging activity, and boldness to forage under predation risk were compared between populations of native and invasive signal crayfish (*Pacifastacus leniusculus*). Invasive signal crayfish in streams with no native crayfish scored higher in these three traits when compared to those sympatric with native crayfish as well as native range signal crayfish. Previous studies show that the signal crayfish is more aggressive in interspecific interactions with native species. These factors are thought to contribute to its outcompeting of the endangered Shasta crayfish (*P. fortis*) (reviewed in Pintor et al. 2008).

A life history pattern seen more frequently in invertebrates than vertebrates is drastic morphological changes from juvenile to adult. These species often face different selective pressures as juveniles than they do as adults. They also have different priorities (i.e., juveniles must survive and grow, while adults engage in behaviors related to reproducing). These factors mean that behavioral traits which are advantageous to one stage may be less so in another stage, and so personality may change with development (Gyuris et al. 2012). However, excluding adult-specific behaviors such as mating, there is little difference overall in repeatability between juveniles and adults (Bell et al. 2009). Selection for personality traits can also vary between the sexes, as males and females often differ in reproductive investment and may have different phenotypic frequencies as a result (Dingemanse et al. 2004; Smith & Blumstein 2008; Chapman et al. 2013).

Behavioral Syndromes

Though this study focuses on personality and repeatability, it is appropriate to briefly consider the related concept of behavioral syndromes. Personality focuses on behavioral consistency and differences between individuals. In contrast, Sih et al. (2004a) defined a new concept, behavioral syndromes, which look at interactions between personality traits. Behavioral syndromes are defined as “suites of correlated behaviors” (Sih et al. 2004a), where the expressed level of one personality trait is related to that of another personality trait. Correlations can occur in different behavioral contexts (e.g.,

feeding vs. mating) within the same situation (i.e., set of ecological conditions), or across different contexts and situations (e.g., correlations between boldness as a juvenile and mating success as an adult). Studies will often test for the presence of both personality and behavioral syndromes, but personality does not necessarily indicate that a species also exhibits a behavioral syndrome.

One early example of a behavioral syndrome was discovered in the three-spined stickleback, *Gasterosteus aculeatus* (Huntingford 1976), years before the concept was formally outlined. Huntingford investigated the relationship between boldness in a novel environment and reproductive aggression. Individuals which scored high in boldness in the new environment were more likely to be aggressive during the breeding season, forming an aggressiveness-boldness syndrome in this species. A behavioral syndrome of activity, anti-predator behavior, and exploratory behavior exists in bluegill sunfish (*Lepomis macrochirus*), with inspection of a predator and exploration of novelty being correlated (Wilson & Godin 2009). Bolder individuals were more willing to engage in risky behaviors (predator inspection), explore the novel test environment, and were more active overall. Noble crayfish (*Astacus astacus*) also show an aggressiveness-boldness syndrome, where individuals that are bolder under predation risk are also more aggressive toward conspecifics (Vainikka et al. 2011). In the rock pool prawn, *Palaemon elegans*, active individuals are also more exploratory, bolder (i.e., recover faster from a startle response), and are less likely to form groups (Chapman et al. 2013). Group formation is a common

anti-predator tactic in animals, so a lower tendency to form groups may indicate risk-taking (i.e., be indicative of boldness).

Behavioral syndromes provide another potential explanation for why some species exhibit seemingly non-optimal behavioral responses. If traits are correlated, then selection for particular levels of one trait can indirectly result in corresponding levels of the other (Sih et al. 2004b). While a correlation between traits may be optimal in some contexts, it may be detrimental in others, which is where non-optimal behaviors can occur (Sih et al. 2004b). It is possible to evaluate the evolution of correlations between traits when the heritability of a given personality trait is known (Dingemanse & Réale 2005). As with morphological traits, behavioral traits can be genetically linked, or certain combinations of traits can have higher fitness than others.

Personality in Invertebrates

Consistent individual differences have been observed in a variety of species. There has been a disproportionate focus on vertebrates (Bell et al. 2009), although in more recent years an increasing number of invertebrates have been studied (Sinn & Moltschaniwskyj 2005; Kortet & Hedrick 2007; Briffa & Greenaway 2011; Schuett et al. 2011; Kralj-Fišer & Schneider 2012; Watanabe et al. 2012; Krams et al. 2013). Among invertebrates, arthropods have received the most attention.

Personality has been particularly well studied in the European hermit crab, *Pagurus bernhardus*. Startle response is tested in this species by inverting a

crab, causing it to withdraw into its shell, and measuring latency to fully emerge. Briffa & Bibost (2009) tested startle response duration when crabs were provided with an appropriately-sized shell as well as with a shell smaller than the crab's optimum. Shell selection is important in these animals as their shell provides a mobile shelter and defense from predators. Overall, crabs took longer to emerge after a startle response when shells were too small. At the same time, rank order differences between individuals were maintained across situations, which is another way of showing individual consistency (Dingemanse & Wolf 2010). This supports the idea that the ability to modulate responses based on situation does not necessarily mean personality is nonexistent. There is also evidence of consistent individual differences in a behavioral syndrome in this species (Mowles et al. 2012).

## Stomatopods

Stomatopods (Subphylum Crustacea, Order Stomatopoda) are represented by around 500 species of small, marine predators found in tropical and subtropical waters worldwide (Van Der Wal et al. 2017). They are commonly referred to as mantis shrimp due to their enlarged second pair of legs (maxillipeds), which resemble the raptorial appendages of a mantid (Caldwell & Dingle 1976). These unique appendages are used for prey capture and combat. Stomatopods fall into two major functional groups based on the morphology of their raptorial appendages (Caldwell & Dingle 1975). Those known as 'spearers'

have elongate, slender raptorial appendages often lined with teeth or spines for grabbing soft prey items. The raptorial appendages of ‘smashers’ are heavier-built and generally lack teeth; the end of the appendage remains folded during a strike, hitting the receiving object with a blunt “heel” (Caldwell & Dingle 1976; Van Der Wal et al. 2017). The appendage can also be unfolded to use the smooth, pointed dactyl for stabbing.

The majority of smashers live in pre-formed cavities in hard substrates such as rock and coral which they modify for habitation (Caldwell & Dingle 1975). Cavities provide stomatopods with shelter from predators and other stomatopods. Those left without a cavity are vulnerable to injury and mortality (Caldwell 1987). In a natural environment, cavities are a valuable limiting resource for cavity-dwelling stomatopods, leading to fierce competition between individuals (Dingle et al. 1973). Stomatopods will inhabit virtually all cavities available, meaning many individuals may be found within a relatively small area (Steger 1987). Because of the high density of competitors for this limiting resource, many smashers are fiercely defensive of their cavities and show aggression toward potential opponents.

Spearers most often occur in habitats with softer substrates such as mud or sand (Caldwell & Dingle 1975). Their shelters take the form of self-dug burrows. In general, burrows are relatively easy to construct and thus don’t seem to have the same resource value as cavities do to smashers. Spearers also tend to defend their shelters less aggressively than smashers (Caldwell 1987).

Supporting the idea that shelter investment and aggressiveness are related is the fact that larger smasher species that construct burrows (*Hemisquilla ensigera* and *Odontodactylus scyllarus*) are also less aggressive than smaller smashers (Caldwell, unpublished, from Caldwell 1987; Reaka & Manning 1981). Within spearers, the cost of burrow construction is similarly related to aggressiveness, with species investing more time in digging also being more aggressive in defending their burrows (reviewed in Caldwell 1987).

Stomatopods also possess a highly complex visual system which is not yet entirely understood. Their compound eyes are divided into upper and lower regions by a third, the midband, responsible for detecting color and polarized light (Daly et al. 2017; Van Der Wal et al. 2017). Despite this, stomatopods' wavelength discrimination abilities appear to be quite limited (reviewed in Daly et al. 2017).

Agonistic Interactions in Stomatopods

Smashers tend to spend more time in the open and exhibit more complex agonistic behavior than spearers (Caldwell & Dingle 1975; Dingle & Caldwell 1975). Their morphology has been shaped along with behavior to produce creatures well suited for battle. Compared with spearers, the telson (tail) of smashing species is heavily armored and is used to shield against an opponent's strikes (Taylor & Patek 2010). The majority of strikes are directed at each other's telsons in a ritualized manner termed "telson sparring" (Caldwell & Dingle 1975; 1976; Green & Patek 2015). This allows contestants to gauge an opponent's

fighting ability in a non-lethal way and decide whether a resource is worth the investment of continuing the fight (Caldwell 1986). Strike force appears to be less important for success in contests than endurance or performance (Green & Patek 2015).

Because of their complex behaviors, much of the existing behavioral research on stomatopods has focused on smashing species and their interactions. Stomatopods adjust their behavior based on the information available about a resource and their opponent's ability (reviewed in Caldwell 1987). Contestants judge their size relative to opponents, and as little as a 5-10% difference in body size can influence the results of the interaction in some species (Caldwell & Dingle 1979; Caldwell 1987). A notable agonistic act known as a "meral spread" involves spreading the raptorial appendages to reveal a colorful meral spot on its medial surface (Dingle & Caldwell 1969; Franklin et al. 2017). Several properties of the meral spot, including hue, ultraviolet reflectance, and total light reflectance, play a role in visual signaling (Cheroske & Cronin 2005; Franklin et al. 2016; Franklin et al. 2017). In gonodactylids, the meral spread serves to prevent an opponent's entry into the cavity (Caldwell & Dingle 1975). Smaller individuals also use meral displays more frequently than larger ones, indicating an awareness of their own size in relation to others (Caldwell & Dingle 1979). Stomatopods will also employ different cavity defense methods when injured (Caldwell 1987) or during molting (Berzins & Caldwell 1983), times during which their fighting abilities are significantly reduced. In addition, they can

remember past interactions with specific individuals, altering their strategy based on the results of a previous fight or whether an opponent is a former mate (Caldwell 1979; 1985; 1992). *Neogonodactylus bredini* (Manning, 1969) can learn to recognize the odor of *Octopus joubini*, with which they may compete for cavities (Caldwell & Lamp 1981). The stomatopods learned to avoid, based on chemical cue, any cavities an octopus had recently inhabited. *Gonodactylus smithii* exhibit behavioral plasticity in visual signaling under different lighting conditions (Cheroske et al. 2009).

Mantis shrimp show a high amount of behavioral plasticity in agonistic interactions, but little is known about whether such flexibility occurs in other contexts such as foraging and predator avoidance.

## Study System

Stomatopods are a good system for studying invertebrate personality because much is already known about their social behavior. Of particular note is the monophyletic family Gonodactylidae. Species within this family exhibit behavior patterns typical of smashers. The taxonomic relationships between the groups of stomatopods have undergone several revisions in the last few decades, and new species continue to be described (Manning 1968; Manning 1969; Manning & Heard 1997; Ahyong & Harling 2000; Van Der Wal et al. 2017). Many species of gonodactylids were formerly placed in the genus *Gonodactylus*, with a handful of genera being separated from it since. The species to be used in

the present study, *Neogonodactylus oerstedii* (Hansen, 1895), is common in the western Atlantic and the Gulf of Mexico. It can be found in a variety of habitats, but prefers littoral zones usually at a depth of 5 m or less (Manning 1969). Studies of *N. oerstedii* have looked at use of the meral spot as a visual stimulus (Hazlett 1979), territorial aggression (Hazlett 1978), ocular tracking (Cronin et al. 1988), and grooming behavior (Bauer 1987).

No studies have yet focused on behavioral differences between individual stomatopods, but some studies have suggested the presence of behavioral differences. Individual *Gonodactylaceus falcatus* may have expressed differences in learning speed (Reaka 1980). The frequency of agonistic behaviors was shown to differ between two populations of the smasher *Haptosquilla glyptocercus* (Caldwell & Dingle 1977).

## Objectives

This study aimed to investigate behavioral variation in *N. oerstedii* at the individual and population level. If individual consistency in behavior is observed, and individuals are shown to differ from one another, the existence of personality can be demonstrated for this species. In this study, I investigated: 1) whether there are behavioral differences between individuals (i.e., between-individual consistency [Sih et al. 2004a]); 2) whether individual stomatopods show consistency in their behaviors (i.e., within-individual consistency [Sih et al. 2004a]); and 3) how repeatable behaviors relate to one another.

First, behaviors that were potential sources of variation (Tables 1, 2, 3) were quantified in three scenarios: 1) exploration of a new environment containing an empty shelter, 2) response to and recovery from a startle stimulus, and 3) response to a novel object. Second, each stomatopod was tested in these three scenarios again after a period of 14 days to test for individual consistency. Finally, statistical tests were performed to discover relationships among behaviors measured in the three tests and to see if behaviors could be categorized into personality traits.

## Significance

Because animal personality is a relatively new field of study, many questions have yet to be addressed. A better understanding of the evolution, development, and maintenance of personality requires a variety of taxa to be studied. As mentioned, until recently the bulk of personality research has concentrated on vertebrates, despite the fact that invertebrates comprise more than 90% of our planet's animal diversity (reviewed in Kralj-Fišer & Schuett 2014). Among invertebrates there are many diverse, unique life history features and strategies not seen in vertebrates, which may offer new ways of studying behavioral differences and their ecological impacts. The relative simplicity of some invertebrate nervous systems makes them ideal for studying neurological mechanisms of personality differences. Some work has been done on the neurobiology of invertebrate behavior, particularly among insects, but how this

might differ between individuals of different personality types has yet to be investigated (reviewed in Kralj-Fišer & Schuett 2014). Temporal patterns of behavior are a necessary component of personality studies, but multi-generational studies on the genetics of personality are lacking due to being impractical in long-lived vertebrates (Dingemanse et al. 2004 provides an example in great tits). Short-lived invertebrates that are quick to reach maturity could provide an alternative way to study patterns of personality between generations in a more reasonable time span (Kralj-Fišer & Schuett 2014). Invertebrates could also simplify studies on the relationship between personality types and sexual selection. Whether mate choice is random or non-random with regards to personality, and whether individuals expressing certain combinations of personality types are selected against, would help address questions of the evolutionary basis of personalities and their maintenance in a population. While this subject has seen some research (Dingemanse et al. 2004), it could benefit from more.

More studies are beginning to point toward the relevance of individual behavioral differences to non-personality, and even non-behavioral, studies. Capture method can lead to sampling bias by causing certain behavioral types to be over-represented, with some methods being more likely to capture individuals of a certain behavioral type. A study of the relationship between trapping and boldness in the Namibian rock agama (*Agama planiceps*) found that bold individuals were quicker to enter the traps, and as a result were captured more

often than shy individuals (Carter et al. 2012a). If the natural population's range of behavioral types is not well represented in a study, then the results may be missing important pieces of the overall picture.

Another practical application for animal personality research is captive breeding (McDougall et al. 2006). Usually, when animals are being raised for release, they do not experience predation risks during development, which could artificially boost reproductive success of bolder individuals in a captive, predator-free environment. When released, these bolder individuals may be more greatly affected by predation if they lack the appropriate behavioral responses necessary for survival. Additionally, because of the reduced challenges faced by captive animals compared to their wild counterparts, behavioral types selected against in the wild may persist in captive populations. In domestic and captive animals, bolder individuals have higher reproductive success than shyer ones, a trend not seen in wild animals (Smith & Blumstein 2008). If the released population is skewed toward a particular behavioral phenotype rather than representing the species' natural variation, this could reduce the population's ability to respond to environmental change and limit the success of the program (reviewed in Horvath et al. 2013).

# METHODS

## Experimental Design

Twelve *N. oerstedii* subjects used in this study were obtained in early 2017 from KP Aquatics in the Florida Keys. In September of 2017, Hurricane Irma struck the Florida Keys, which made obtaining additional mantis shrimp difficult due to disruptions in their habitat. Three more individuals were obtained in August 2018 from the same source, bringing the sample size up to fifteen. Due to the way in which cavity-dwelling mantis shrimp are captured, there is unlikely to have been any capture bias toward individuals of a certain personality type. Live rock is collected from reefs and broken into pieces, revealing any cavities occupied by a mantis shrimp.

The housing tank setup consisted of two tanks (approximately 500 liters total) with a shared pump system on a 12:12 light-dark cycle. The lighting consisted of two Coralife Aqualight High Output 36 inch T5 Fixtures, each with one 39 watt 10,000K Daylight Lamp and one 39 watt Actinic Blue Lamp. Water flowed between tanks at all times. Room temperature was maintained at 26°C and salinity was maintained at 34 ppt. Each stomatopod was housed in its own floating breeder box to allow water circulation and prevent physical interactions with other stomatopods. Breeder boxes were numbered to track individuals. To

act as a shelter, each stomatopod was given a piece of straight PVC tube with an attached elbow, open at both ends. Dates of molts for each individual were recorded. Stomatopods were fed frozen mysis shrimp three times weekly.

For all experiments, 15 individual *N. oerstedii* (3 males, 12 females) were tested in three experimental contexts. Each individual was tested in all three contexts once per round of testing, with two rounds for each individual. To test behavioral consistency over time, there was a 14-day period between Round 1 and Round 2 (Figure 2). The 14-day period was based on Reaka (1980). That study on learning and memory in a different gonodactylid, *Gonodactylaceus falcatus*, found that previous exposure to a novel shelter (an Erlenmeyer flask painted black) reduced time to enter the shelter for up to 14 days after the initial exposure. In other words, once familiarized with the novel shelter, stomatopods were quicker to enter it in repeated trials. The effect of previous exposure was strongest 3–7 days without exposure to the shelter. The 14-day period was established to minimize the effects of learning on successive rounds of testing. Stomatopods' behavior is significantly altered during the time around molting, as the lack of a hardened exoskeleton leaves them vulnerable and defenseless. They are unable to strike for the first two days after molting and gradually regain their fighting ability over the next several days (Caldwell 1986). To ensure that each individual's typical range of behaviors was tested, stomatopods were not tested for at least 10 days following a molt.

Shelters used for housing and during experiments were all 1/2” PVC pipe, with the exception of the two largest individuals (#20 and #22), for whom 3/4” PVC pipe was used. This was to reduce additional variables that could be introduced by changing the shelter’s size between individuals. Stomatopods show preference for certain cavity sizes based on their own body size (Steger 1987; reviewed in Caldwell 1987), and having a non-optimal shelter influences how the animal behaves.

All experimental trials were run in 38-liter aquaria with the same lighting and water conditions as the housing tank. Water depth during experiments was kept at 10 cm. A shallow layer of gravel substrate covered the bottom, reflecting the rocky habitats this species inhabits. Cardboard covered the back and side walls of the tank. The exploration test was performed first, followed by the startle test and then the novel object test. Test order remained the same for each individual in order to maintain a consistent feeding schedule, and because the exploration test needed to be performed while the environment was still unfamiliar. Individuals were then returned to their holding containers until the next round. The entire procedure for one individual is outlined in Figure 2.

During the design of this study, “boldness” was considered to include behaviors that involve risk-taking, regardless of whether there are elements of novelty involved (Briffa et al. 2008; Wilson & Godin 2009). Thus, the three experiments were designed to measure behaviors anticipated to relate to boldness in mantis shrimp.

Test 1: Exploration of Novel Environment

The first experiment measured behaviors in an exploratory context. The testing aquarium was separated into two even halves via an opaque, white plastic divider (Mowles et al. 2012) that could be raised or lowered via a string (Wilson & Godin 2009). Both halves contained an identical PVC pipe closed on the back end with a cap, positioned with open ends facing the middle of the tank (Figure 3). With the divider lowered, an individual was introduced to the left half of the experimental tank and allowed to acclimate for 24 hours prior to testing. This starting half of the tank was referred to as the "refuge area." At the start of the test the divider was raised, allowing access to the right half of the tank. Each individual's shelter usage (Figure 4) and movements throughout the tank were video recorded. Trials were run for 30 minutes after the divider was lifted or until the stomatopod entered the second shelter. If the shelter was never exited, the latency to exit was recorded as 1800 seconds (Sinn & Moltschaniwskyj 2005). After the test ended, the shelter in the exploration area was removed and the divider fully removed and set aside.

Test 2: Startle Response and Recovery

This test measured response to and recovery from a startling stimulus. The experiment took place in the same 38-liter testing tank with a layer of gravel substrate. An air tube ran down the right wall of the tank with the open end secured beneath the gravel, hidden from view. The open end was secured several centimeters from the tank wall. On the opposite end of the tank was the

same home shelter from the previous experiment. To prompt stomatopods to approach the startle area, food (frozen mysis shrimp) was added at the far end past the hidden end of the air tube. When the stomatopod approached within one body length of the air tube, air was blown into the tube to produce a sudden stream of bubbles (Figure 3). Degree of jump response (Figure 5) was graded on a scale from 0 (no response) to 4 (most extreme response) based on Heitler, et al. (2000). If the individual hid in its shelter, latency to re-emerge was recorded (Mowles et al 2012). Bolder individuals were expected to react less intensely and have shorter recovery times. Trials were run until the stomatopod successfully obtained a piece of food after the startle event.

Test 3: Response to a Novel Object

The third test measured boldness using the response to a novel object (Coleman & Wilson 1998; Pintor et al. 2008), this time in a cavity defense context. The test aquarium was the same used in the two previous experiments. A study on *N. oerstedii* response distance to a conspecific found that they were not strongly territorial until having been in the environment for at least three days (Hazlett 1979). In the present study, by the time of the novel object test, the stomatopod had been in the experimental tank for three days. Due to the number of influential variables involved and limited available resources, measuring cavity defense behaviors via staged interactions with conspecifics was unfeasible. Instead, for this test, a novel object was used (pink plastic straw) which had not been seen by the study animals prior to this test. This species' colors are

variable, with many being bright green or tan, but they can also be shades of blue, purple, red, and orange. Neon pink was chosen for the novel object's color because it seemed the least likely to have been previously encountered in the wild. Visibility of the selected color was not a concern due to their extensive color vision. While standing out of view of the individual, the end of the straw was placed into the water at the far end of the tank. The straw was then moved at a constant rate toward the opening of the shelter and held for approximately four seconds or until a grab or strike occurred. The straw would then "retreat" to the far end of the tank at the same rate, where it was removed from the water (Hazlett 1972; 1979) (Figure 3). Tests were video recorded and responses to the straw were scored during playback (Figure 6). Bolder individuals were expected to approach, strike, or grab the straw as opposed to withdrawing into the shelter. At the end of a round, body length of each stomatopod (from the tip of the rostral scale to the end of the telson) was measured to the nearest millimeter. All measured variables can be found in Tables 1, 2, and 3. Variables used in other personality studies are in Table 4.

## Data Collection

Trial observation and recording was performed from behind black, plastic shower curtains (Wilson & Godin 2009). Holes were cut in the curtains for viewing by the observer and as openings for the camera lenses. Observer movement was kept to a minimum to avoid distracting the test participants. Tests

were recorded using three Sony Handycam (Model HDR-CX200) cameras on tripods. Windows Movie Maker (Version 2012) was used for video playback during scoring. Long videos were split into multiple MTS files during recording, which Movie Maker is capable of playing as one continuous video. Movie Maker also allows moving frame by frame both forward and in reverse, as well as providing time down to hundredths of a second, both of which allowed for precise timing of quick actions.

JWatcher (Version 1.0) was used to collect data from video playback. Behaviors and the times when they occurred were entered manually rather than during live playback to allow greater accuracy. Data output by JWatcher was compiled into data tables in Microsoft Excel 2007 and later imported into JMP Pro 10 for further analyses.

## Statistical Analyses

Figure 1 provides a flowchart of data collection and analyses conducted. To test the hypothesis that individual *N. oerstedii* exhibit personalities, statistics were performed to test for the two requirements of animal personality: 1) individuals are consistent with themselves across time, and 2) observable behavioral responses differ between individuals. Many personality studies use repeatability statistics to test for consistent differences between individuals (Jones & Godin 2010; Niemelä et al. 2012; Pruitt et al. 2013; Toscano et al. 2014). Repeatability measures the amount of a population's overall variation due

to differences between individuals versus within a single individual (Lessells & Boag 1987; Bell et al. 2009). The process for calculating repeatability is outlined in Lessells & Boag (1987). The repeatability statistic, *r*, is calculated with:

$$r = \frac{{s^2}_A}{(s^2 + {s^2}_A)},$$

where $s^2_A$ is the variance among individuals and $s^2$ is the variance within individuals in a single situation and context. Variance within individuals, $s^2$, is calculated with:

$$s^2 = MS_W,$$

where $MS_W$ is the mean squares of the within-individual variance. Variance among individuals, $s^2_A$, is calculated with:

$${s^2}_A = \frac{(MS_A - MS_W)}{n},$$

where $MS_A$ is the mean squares of the among-individual variance and *n* is the sample size. The values for calculating repeatability are most commonly found by using one-way ANOVAs for continuous variables. When the repeatability of a behavior is high, that means that within the population there is more variation caused by individuals behaving differently from each other, rather than individuals varying their own behavior (Sinn & Moltschaniwskyj 2005). For example, a repeatability statistic of 0.37 would mean that 37% of the variation is due to differences between individuals. Measuring repeatability for each behavior allows comparisons to be made between them. Due to how repeatability is calculated, the statistic takes into account both individual consistency (quantified

from within-groups variation from the ANOVA) and differences between individuals (quantified with between-groups variation from the ANOVA), addressing both parts of the personality hypothesis (Bell et al. 2009). A repeatability value is significantly different from zero when the p-value from the ANOVA is less than α (in this case, α = 0.05) (Nakagawa & Schielzeth 2010). In this study, one-way ANOVAs were performed on each continuous variable. Groups tested for differences by the ANOVAs corresponded to the 15 individual stomatopods, each measured twice (Round 1, Round 2) (sample size *n* in the repeatability formula above). The term 'repeatable' herein is used for variables with significant p-values from the ANOVAs.

To investigate which personality traits (e.g., boldness) the repeatable behaviors best reflect, factor analysis was performed using JMP Pro 10. Factor analysis reduces multiple variables into underlying dimensions based on correlations between variables. It is used to determine which variables in a study group together in factors, and the possible significance of those underlying factors. Since personality trait levels cannot be measured directly, factors provide an approximation of the axis of variation of a personality trait. In some cases, the results of the factor analysis are compared to those found in similar studies; for example, it can be used to see if the same pattern exists in the study group as exists in a different population. In the present study, the variables that contribute to each factor were compared to those in other personality studies, particularly those of crustaceans. Only variables found to be repeatable were included in

factor analyses. Repeatable variables which were not strongly associated with a single factor, were excluded and factor analyses re-run. A modified weighted sum of the variables, called factor scores, are automatically calculated by JMP for each individual and show where that individual lies on that factor (i.e., more bold vs. less bold). Oblique factor rotation (Quartimin), a process which makes factor analysis results easier to interpret, was used as it assumes factors may be correlated. Factor analyses were run on measured variables separately for Round 1 and Round 2 (as in Jones & Godin 2010), and results were compared between them using Pearson's correlation tests. Factors were named based on the behavioral variables related to them, using the personality traits defined in Réale et al. (2007).

All variables from Test 3, the novel object test, were binary (i.e., the individual did or did not perform a behavior) with the exception of grab duration. As such, descriptive statistics were not calculated for these variables and ANOVA could not be used to calculate repeatability. Additionally, these variables were excluded from factor analysis; Pearson's correlations were used instead to see how they related to other measured variables (Figure 1).

To investigate whether responses differed significantly based on round, paired t-tests were performed on measured variables (Mowles et al. 2012) (Tables 5, 6). This was done to look for evidence of habituation to the test scenarios, which would be seen as a change in the average behavioral responses between rounds.

# RESULTS

## Initial Test Results

Test 1: Exploration of a Novel Environment

Seven measured variables from Test 1 were found to be repeatable: latency to first exit shelter, duration withdrawn, proportion of in-shelter time withdrawn, proportion of in-shelter time part exposed, times withdrawn (count), withdraw frequency, and latency to enter the unoccupied shelter (Table 7).

During the exploration test, only two individuals, #10 and #19, entered the unoccupied shelter within the test duration. A few more individuals entered the shelter within an hour after the test ended. Six individuals did not exit the starting shelter at all during either round. In both rounds, individual #19 exited the starting shelter before the divider was fully lifted. She was also the only individual to enter the unoccupied shelter in both rounds. During Round 1 she approached the second shelter quickly, but loitered and interacted with substrate in the vicinity before entering. In Round 2, she returned to the starting shelter briefly after the divider was raised, but still spent the least amount of time in the starting shelter out of all individuals. After exiting, she went straight to the unoccupied shelter. Individual #10 only entered the unoccupied shelter during Round 2, and in fact never left the starting shelter during Round 1. Apart from #19, #12 was the

fastest to exit the starting shelter in both rounds, but never crossed the midline, and also returned to the starting shelter numerous times. He also spent the second most time withdrawn in the shelter and the greatest number of times withdrawn in both rounds.

Latency to first exit the shelter was repeatable ($r = 0.5097$, $p < 0.05$). Latency to enter the unoccupied shelter was also repeatable ($r = 0.9011$, $p < 0.001$) (Table 7); for individuals who never entered the unoccupied shelter, latency to enter was recorded as the maximum of 1800 seconds, which may explain why the repeatability is so high. Individuals also differed in how they spent their time in the refuge shelter. The proportion of in-shelter time withdrawn ($r = 0.5508$, $p < 0.05$) and proportion of in-shelter time part exposed ($r = 0.5624$, $p < 0.01$) were repeatable, but the proportion of in-shelter time half exposed was not.

Test 2: Startle Response and Recovery

Eight measured variables from Test 2 were found to be repeatable: duration in shelter pre-startle, latency to first enter the exploration area, proportion of time in shelter, frequency of climb/swim events pre-startle, proportion of time swimming, duration in refuge area post-startle, duration in shelter post-startle, and latency to obtain food post-startle (Table 7).

In the startle test, individuals were generally quicker to initially exit the shelter and cross the midline than in the exploration test (Tables 1, 2). Total duration in the shelter pre-startle and latency to first cross the midline were

repeatable ($r = 0.553$, $p < 0.05$; $r = 0.532$, $p < 0.05$); however, unlike in the exploration test, latency to first exit the shelter was not. In most cases an individual would exit and re-enter the shelter multiple times before the startle occurred.

A number of different behaviors were seen as immediate reactions to the startle stimulus, including jumping, freezing, and fleeing (Table 2). The majority of individuals exhibited some degree of "jump" response, which were defined and graded by extremity using a scale based on Heitler et al. (2000) (see Figure 5). Some individuals were hardly disturbed and proceeded to forage, while others fled dramatically to the refuge area or shelter. Most would "freeze", remaining temporarily motionless (as described in crickets in Niemelä et al. 2012), either immediately before or following a jump or flight response. Latency to obtain food after startle was repeatable and ranged from less than 5 seconds to more than 2000 seconds ($r = 0.6400$, $p < 0.01$). While certain individuals showed subjective similarity in their fleeing actions or type of responses, across rounds, graded jump response and freeze duration were not significantly repeatable. The two were, however, significantly correlated with each other in both rounds (Pearson's $r$, Round 1: $r = 0.6440$, $p < 0.01$; Round 2: $r = 0.6885$, $p < 0.01$).

Test 3: Response to a Novel Object

Responses to the novel object were varied (Table 3). In addition to the anticipated responses of "strike", "grab", and "withdraw", a few individuals gave an "investigative" response. This was defined as moving closer to the straw, but

making no attempt at contact or pursuit. Eyes were directed at the straw and the striking appendages remained in a relaxed posture. Those that pursued the straw only did so following a grab, and none pursued it past the midline. No individual performed a strike during a grab as sometimes occurs when attacking an intruder. The only individual who left the shelter opening to initiate contact was #12, who struck the straw in both rounds.

Overall, behaviors from the novel object test were not significantly correlated with behaviors from the other two tests. “Exit shelter” in response to the straw was correlated with total duration in the shelter during the startle test (Pearson’s $r$, Round 1: $r = 0.7311$, $p < 0.01$; Round 2: $r = 0.5413$, $p < 0.05$). This is the only measured behavior from Test 3 that was significantly correlated with a behavior from the other two tests, and where that correlation was significant in both Round 1 and Round 2.

General Results and Additional Variables

Paired t-tests revealed that none of the variables measured were significantly different between rounds, indicating that habituation to the test scenarios did not occur across the sample group (Tables 5, 6).

Several variables related to general shelter use and activity levels were not exclusive to a single test, and therefore were measured separately in both the exploration and startle tests. Most of these were not repeatable. Those that were repeatable included times withdrawn in shelter and withdraw frequency in the exploration test and climbing/swimming frequency and proportion of time

swimming in the startle test. Activity-related behaviors are generally some of the least repeatable (Bell et al. 2009). The number of rocks in the shelter at the end of each round was repeatable ($r$ = 0.7127) and inversely correlated with body length (Pearson's $r$, Round 1: $r$ = -0.6252, $p < 0.05$; Round 2: $r$ = -0.6401, $p < 0.05$).

## Factor Analysis

Six repeatable variables were found to align with three factors through factor analysis (Table 8, Figures 7, 8). The first factor included duration in shelter post-startle and latency to obtain food post-startle. Both describe startle recovery and are often used in some variation as a measure of boldness (Briffa et al. 2008; Watanabe et al. 2012; Yuen et al. 2017). This factor explained the most variation of the three (Round 1: 33.6%; Round 2: 41.3%; Table 9). The second factor included duration in the shelter pre-startle and latency to first cross the midline, both from the startle test but before the startling event had occurred. The third factor included two variables from the exploration test, latency to first exit the shelter and latency to enter the unoccupied shelter. Latency to emerge from shelter or enter an empty shelter have been used as measures of exploration (Wilson & Godin 2009; Mowles et al. 2012; Niemelä et al. 2012).

The factor scores generated for each individual (Table 10) were highly correlated across rounds (Pearson's $r$, Factor 1: $r$ = 0.8978, $p < 0.00001$; Factor 2: $r$ = 0.5999, $p < 0.05$; Factor 3: $r$ = 0.8596, $p < 0.0001$) (Figures 8, 9, 10). The

pre-startle boldness and startle recovery boldness factors were slightly correlated in Round 2, but not significantly so ($r = 0.3774$, $p > 0.1$).

## DISCUSSION

This study found support for the hypothesis that mantis shrimp exhibit personality. Sixteen measured behaviors across three different scenarios were found to be repeatable (exploration test: latency to enter unoccupied shelter, latency to first exit starting shelter; startle test: duration in shelter pre-startle, latency to first enter exploration area, latency to obtain food post-startle, duration in shelter post-startle), and six of these were categorized into three areas of variation (i.e., personality traits) based on factor analysis: exploration, boldness (measured by startle recovery), and a third measured by foraging behaviors in a low-risk environment. The results of ANOVAs run on measured variables showed that individuals differ from one another in these sixteen variables, and the repeatability statistics derived from the ANOVAs support the consistency of differences between individuals. Factor scores were strongly correlated between Round 1 and Round 2, further suggesting that individuals were consistent over time.

The factor analyses support viewing environmental exploration as a separate personality trait from foraging boldness in this species (Figures 12, 13). For smasher mantis shrimps, exploration may come into play when locating a new shelter. *Neogonodactylus* population densities are directly limited by the

number of inhabitable cavities in rubble. Steger (1987) found an average density of 97 *Neogonodactylus* individuals per 10 $m^2$ in the study area, varying with cavity distribution. Stomatopods can be recruited to an area by adding artificial shelters to a habitat patch which was previously devoid of stomatopods despite an availability of prey (Caldwell & Childress 1989). A mantis shrimp may be evicted from its home by a competitor, or need to find a larger cavity as they grow. If all suitable cavities in the area are occupied, then that mantis shrimp has two options: 1) evict another resident or 2) move further away to look for an unoccupied cavity. The risks involved in seeking a new shelter elsewhere may be less costly than the risks of challenging a resident, and in fact eviction attempts are usually unsuccessful (Dingle & Caldwell 1969). Mantis shrimp can assess their own fighting ability (Caldwell 1987), which likely influences their choice in this scenario. Individuals with poor fighting ability may be better suited toward exploring new areas and avoiding costly conflicts with others.

The results of the factor analysis also suggest that foraging boldness before a startling event and recovery from startle represent separate personality traits. This is quite different from the expectation that both would contribute to a single boldness measure. By the beginning of the startle test, individuals had been in the testing environment for about 48 hours, of which 24 hours included access to the exploration area. No chemical cues from predators or other mantis shrimp were in the water, and no visible threats were present, so it can be assumed the mantis shrimp perceived this as a low-risk environment. Reef-

dwelling stomatopods are preyed upon by fish as well as herons (Steger 1987; Caldwell 1987). Threats can come from any direction, and their presence may not be detectable by chemical cues alone, as in the case of birds. Thus, for a mantis shrimp, no situation is ever truly “no-risk”. The sudden shift from low- to high-risk after the startling event may have caused the mantis shrimp to switch to a set of behaviors more suited for foraging in a high-risk environment. Refuge use by mud crabs (*Panopeus herbstii*) was found to be repeatable when chemical cues of predatory toadfish were present, but not when the cue was absent (Toscano et al. 2014). Individual mud crabs showed a shift in their behavior based on the threat of predation. In that study, the significant repeatability value of shelter use in the presence of predator cues was $r = 0.173$. Similarly, in the present study, the duration in shelter was more repeatable post-startle ($r = 0.7059$) than pre-startle ($r = 0.5527$).

It was expected that responses to the novel object would be correlated with behaviors seen in the other two tests, but this was not the case. For example, a correlation was expected between exploratory behavior and a tendency to investigate the novel object. The most exploratory individual, #19, did investigate in both rounds, but there was not a significant correlation overall. On the other hand, the shyest (least bold) individual, #21, grabbed the straw on both occasions and even followed it out of the shelter. It seems likely that individuals interpreted the straw in different ways; while some may have seen it as a threat and responded by striking or withdrawing, those that grabbed may

have been checking whether the straw was a food source. Both means of physical contact, as well as investigating, yield information about the object's nature. Mantis shrimp use tactile cues to assess and process prey items (Caldwell & Childress 1989) while striking may be used to judge an opponent's fighting ability during agonistic interactions (Caldwell 1987). This highlights the issue that even if a test was intended to measure a specific trait, it may in reality be measuring something different based on the animal's perception and the ecological relevance of the test scenario (Watanabe et al.2012).

If risk-taking tendency (boldness) was based solely on fitness and reproductive potential, we would expect older, larger individuals to be more risk-prone and smaller, younger individuals to be more risk-averse (Wolf et al. 2007). Young individuals have more future reproductive potential, and thus we would expect they have more costs associated with risk-taking. Body size was found to have an effect on shelter use in mud crabs. Their main predator is gape-limited and avoids eating larger crabs, while smaller crabs are at risk and seek shelter more frequently (Toscano et al. 2014). But in Briffa et al. (2008), boldness in hermit crabs was not related to size. Since the repeatable behaviors in the present study were not correlated with body size (in turn related to age in mantis shrimp), age was likely not a main contributor to personality here. In smasher mantis shrimp species that grow much larger than *Neogonodactylus*, such as *Odontodactylus scyllarus*, size may have a greater influence on personality.

Not much can be said about sex-based differences in behavior based on this sample group. Sex appeared to be correlated with some non-repeatable activity variables, but the same variables tended to correlate with body length as well. Sex and body length were also strongly correlated. This is likely because the smallest individual, #12, was one of only three males in the sample group. He was 34 mm in length, while all other individuals were at least 40 mm. Studies on other smasher species have noted a lack of behavioral differences between males and females outside of breeding contexts (Caldwell & Dingle 1979; Daly et al. 2017).

The distinction between “exploration” and “boldness” is not always clear, and whether a behavior best represents one or the other varies by species. In Cote et al. (2010), latency to emerge in a novel environment was used to measure boldness, rather than exploration, in mosquitofish (*Gambusia affinis*). This decision was based on previous studies suggesting that in small shoaling fish, latency to emerge from refuge best represents boldness, while exploration is better reflected by space use after emerging in the novel environment. In a study on hermit crabs, two variables presumed to measure boldness were loaded onto different factors during factor analysis: the latency to emerge from shells before a simulated predator attack was related to boldness, while the latency to emerge after attack was related to exploration (Watanabe et al. 2012). In López et al. (2005), two independent axes of shy-bold behavior were discovered in antipredator behavior of male Iberian rock lizards (*Lacerta monticola*): propensity

to hide from predators and time in refuge after predator approach. In that study, both are still referred to as representing “boldness”. Similarly, in the present study on stomatopods, behaviors expected to represent “boldness” loaded on two different factors, both separate from exploration. These two separate “boldness” axes reveal a problem with trying to categorize behaviors into generalized personality traits. Names such as “boldness” or “exploration” are mainly for human convenience, and do not necessarily describe a behavior’s actual function.

A tendency to collect gravel at the shelter opening could be a way of reducing the shelter opening’s diameter. If the opening is too large, a stomatopod will have a harder time blocking potential intruders from entering. Wild stomatopods will fill gaps in their cavities using bits of gravel, mud, or algae, and many cover the shelter entrance each night (Dingle & Caldwell 1969; Reaka & Manning 1981). The same size shelter was used for all subjects (with exception of the two largest individuals), and body length was negatively correlated with rocks stored (Pearson’s *r*, Round 1: $r = -0.6252$, Round 2: $r = -0.6401$). After both rounds of testing were complete, individuals were provided with some aquarium gravel in their home containers. The three who stored the most rocks during testing would regularly do so in their home containers, while the others generally did not.

Prior to crossing the midline in the startle experiment, the majority of individuals would suddenly exit the shelter and become active in the refuge half

of the tank. In addition to walking around, they would climb up the corners of the tank and swim along the walls numerous times. This behavior is similar to patterns seen in their normal housing during feedings. It may be that this behavior pattern became part of the routine of feeding time for these mantis shrimp or was positively reinforced by obtaining food.

The presence of personality in stomatopods creates new potential ways to explore their behavior. Individual differences in learning (Reaka 1980) and social dominance (Dingle & Caldwell 1969) have been noted in past studies where such was not the focus. Hazlett (1978) looked at individual differences in the distance at which *N. oerstedii* initiated agonistic acts toward an intruder and which acts were executed. No difference was found between the within-individual variance and among-individual variance. Rather, the distance between the intruder and the territory edge was more important. Because so much of mantis shrimps' ecology is shaped by agonistic encounters, a study combining exploration and boldness with individual differences in agonistic behaviors could reveal more about the ecological significance of personality in stomatopods.

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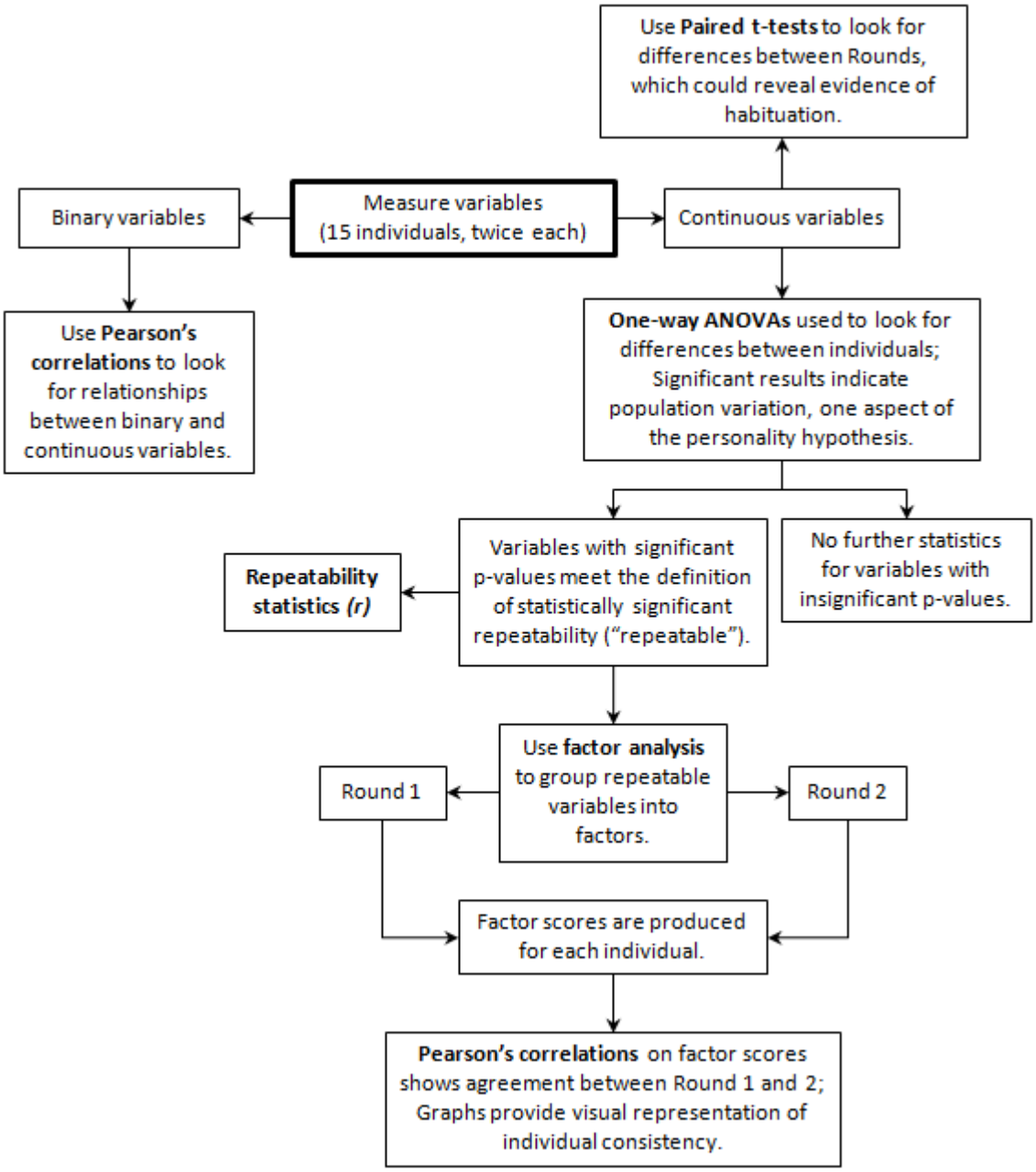


**Figure 1.** Flowchart of data collection and statistical analyses.

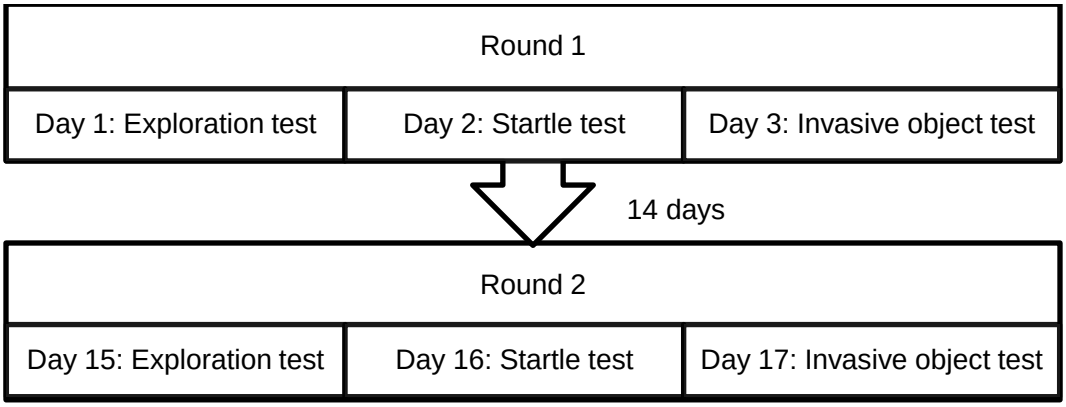


**Figure 2.** Outline of the experimental process for one individual stomatopod. During the 14-day period between rounds, the stomatopod was returned to its home container and the experimental tank cleaned and reset.

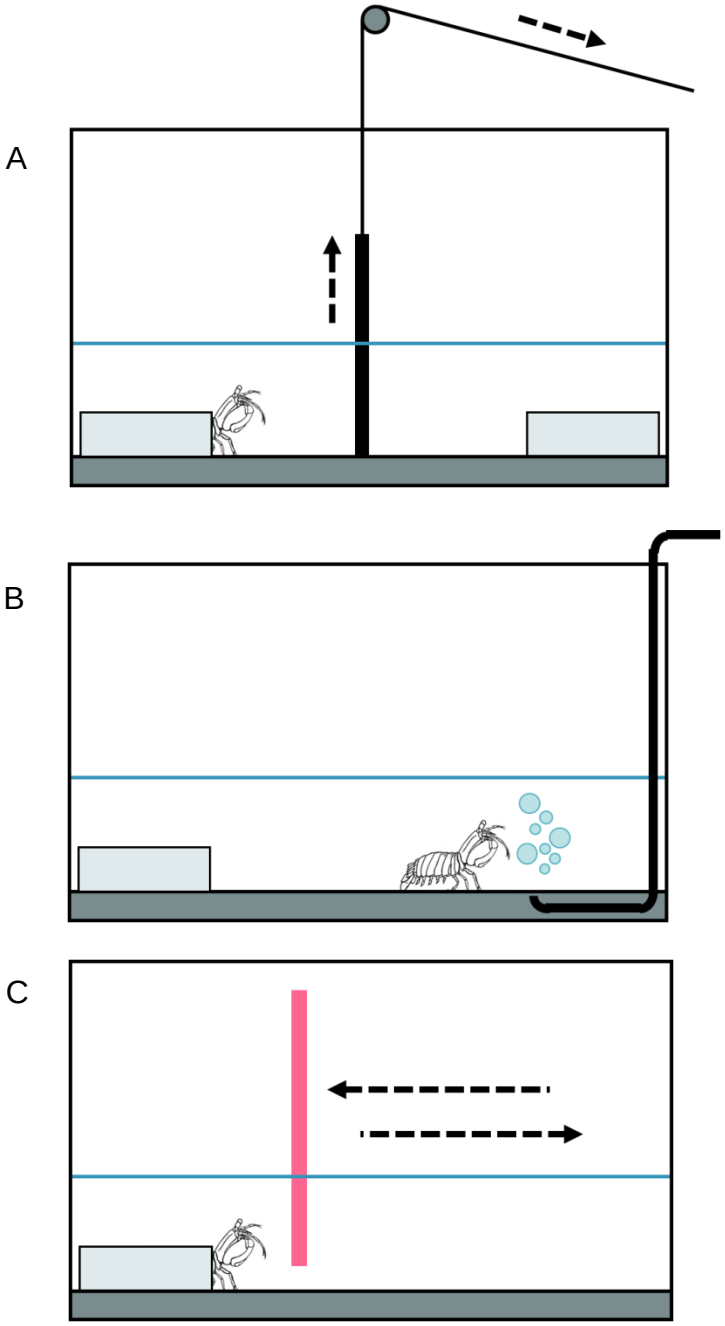


**Figure 3.** Basic setup of each test. A) Exploration test. B) Startle test. C) Novel object test.

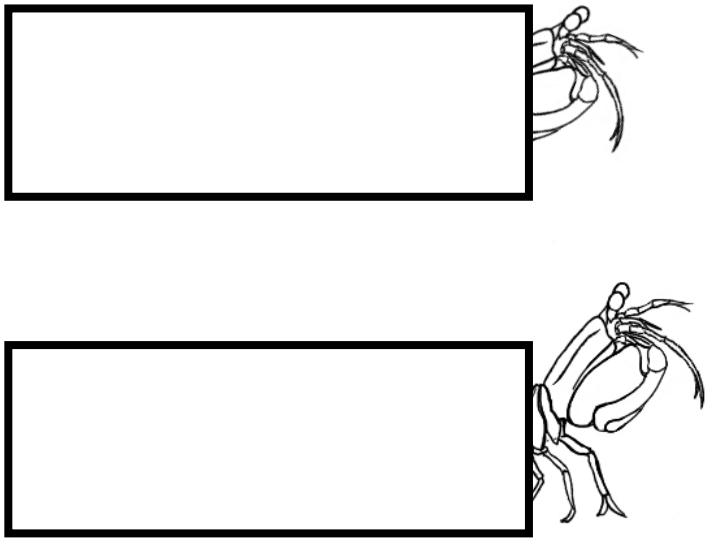

**Figure 4.** Diagrams showing an individual “part exposed” (upper) and “half exposed” (lower). Animals were considered “part exposed” if extended past the shelter entrance, but with less than the full merus (smashing appendage) visible. If the entire merus was visible, the animal was considered “half exposed”. The stomatopod was only considered to have exited the shelter once the entire body was out of the entrance. Being further extended from the shelter allows more information about the environment to be gathered, but increases the time required to fully withdraw to safety.

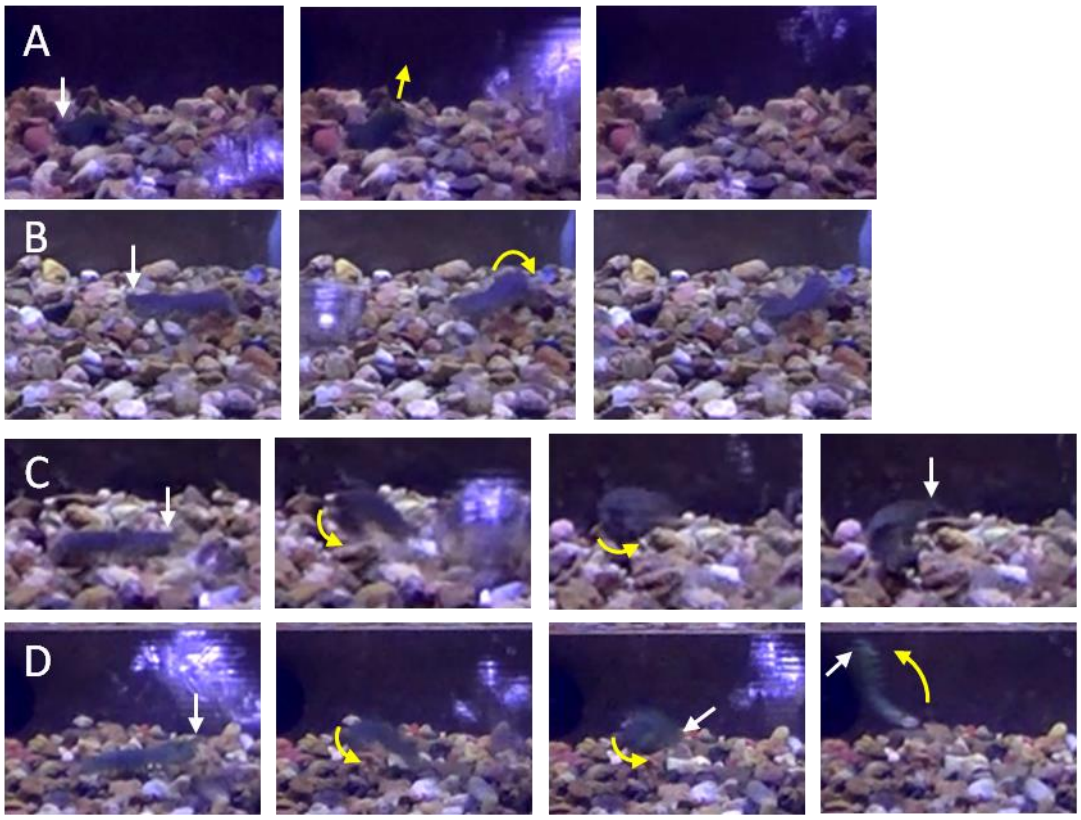


**Figure 5.** Examples of “jump” responses given during startle tests, scored 1–4 (based on Heitler, Fraser, & Ferrero 2000). A complete lack of response was given a score of 0. White arrows indicate position of the animal’s head. Yellow arrows indicate direction of movement. **A.** Limb-flick response (score 1). The walking legs are flexed, moving the body backward by a small amount. The tail and associated abdominal segments may be depressed and the body may “hop” off the substrate. **B.** Intermediate tail-flip response (score 2). The last several segments of the abdomen flex (yellow arrow), pulling the animal backward. The tail is depressed, but does not fold beneath the animal. **C.** A score 3 jump response. As in maximal tail-flip, the animal curls the tail beneath its body. The curl does not proceed to full inversion and fleeing, but rather the curled position may be temporarily held (as in fifth image). **D.** Maximal tail-flip response (score 4). The abdomen flexes strongly and the tail is pulled forward under the animal, inverting it to face away from the disturbance (fourth image).

**Figure 6.** Novel object (straw) test. First image shows an investigative response with no contact. Second image shows body posture immediately before a strike. Third image shows an individual grabbing and holding on as the straw retreats, leaving the shelter temporarily.

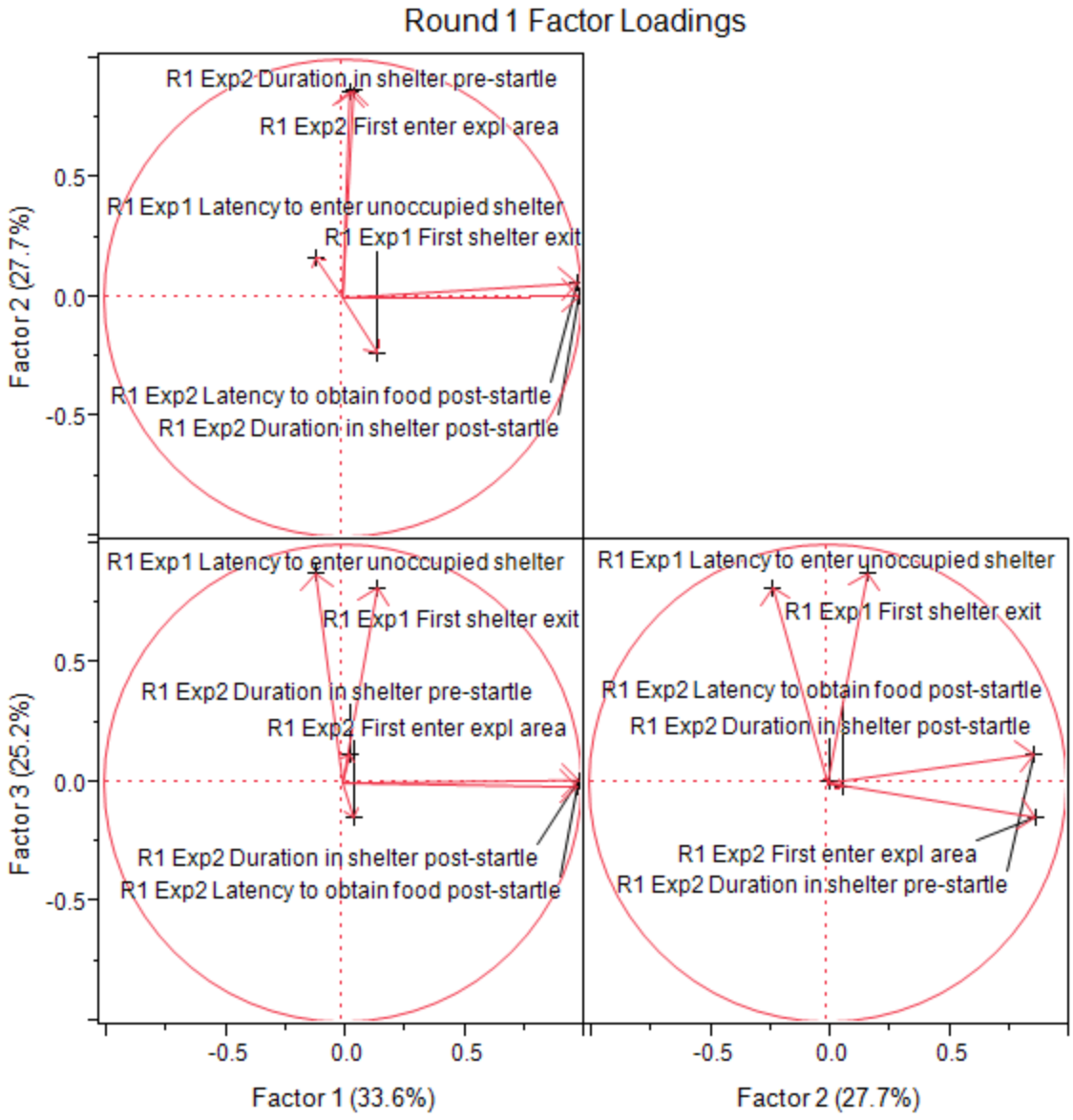


**Figure 7.** Loading plot of the factor analysis for Round 1. Loadings (red arrows) indicate strength and direction of influence of each variable. Variable groupings are more important than factor numbers when comparing between rounds.

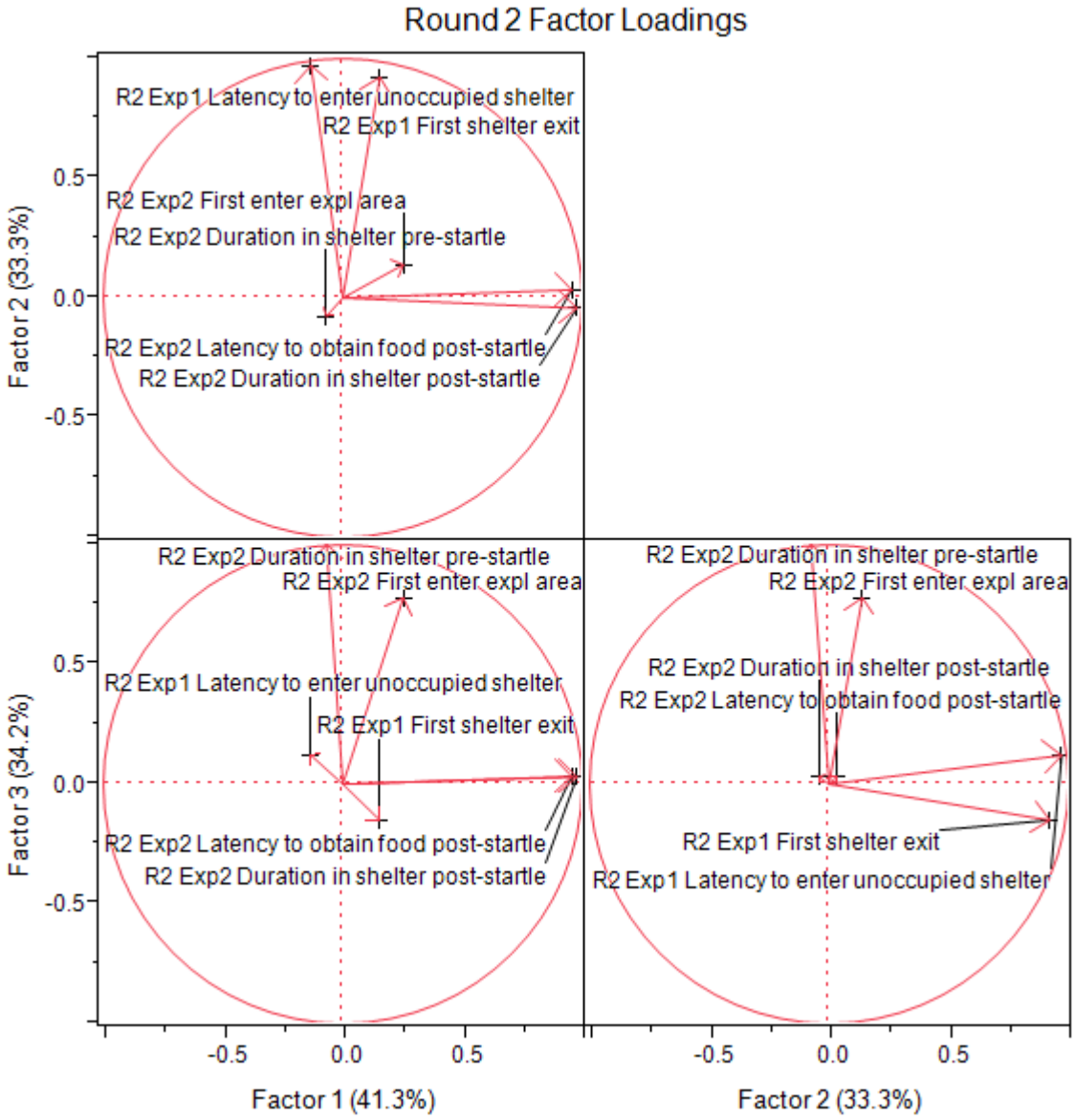


**Figure 8.** Loading plot of the factor analysis for Round 2.

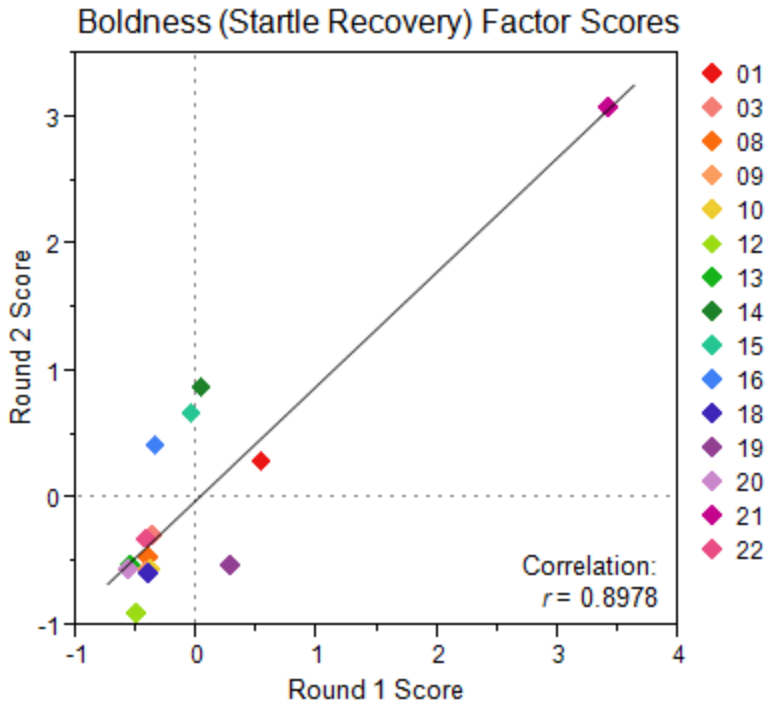


**Figure 9.** Plot showing individual boldness (startle recovery) factor scores compared across rounds. Lower scores are bolder.

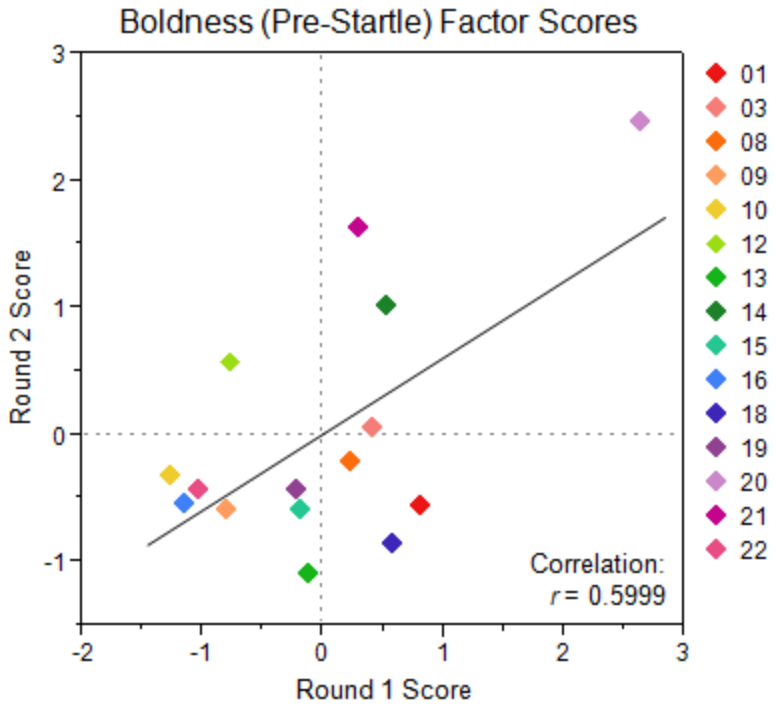


**Figure 10.** Plot showing individual boldness (pre-startle) factor scores compared across rounds. Lower scores are bolder.

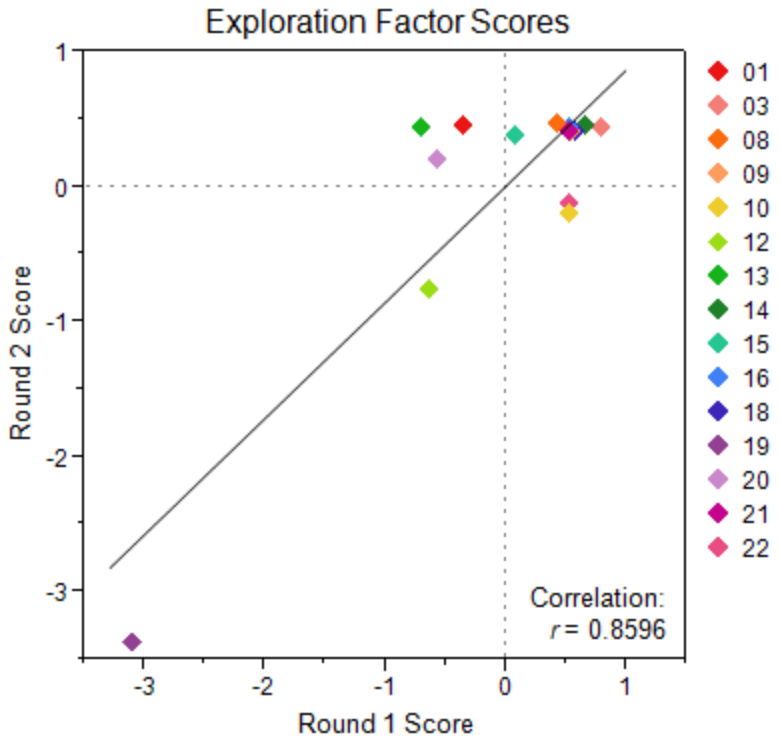


**Figure 11.** Plot showing individual exploration factor scores compared across rounds. Lower scores are more exploratory.

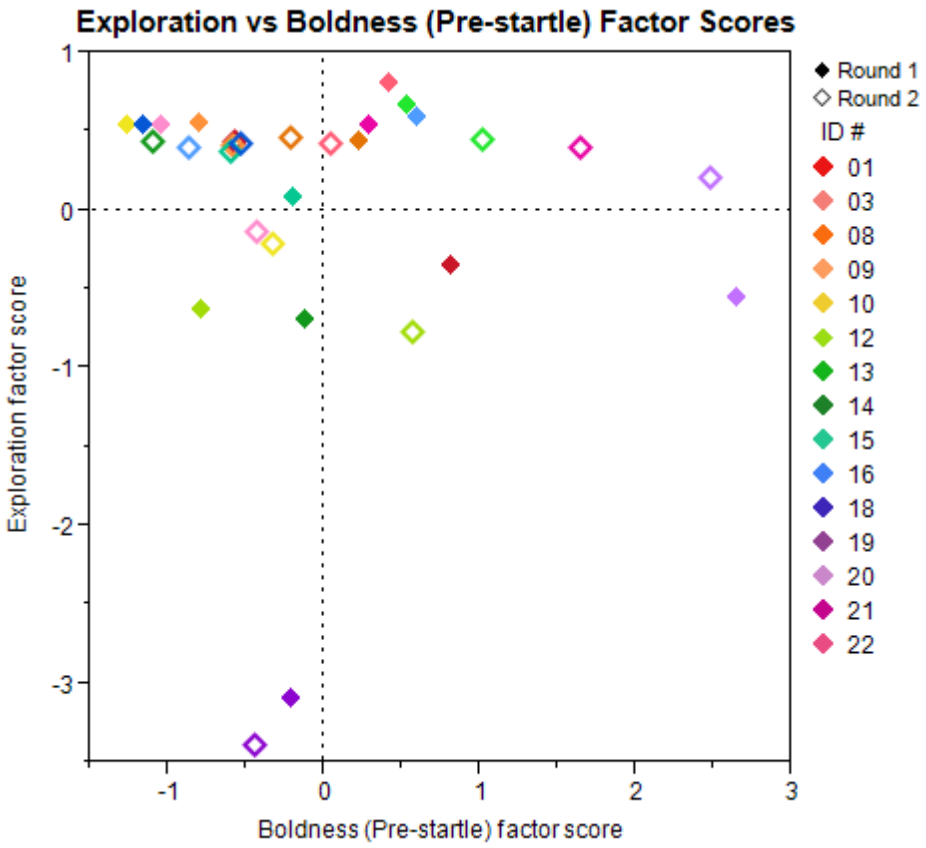


**Figure 12.** Plot showing the relationship between individual factor scores for exploration and boldness (pre-startle) in both rounds.

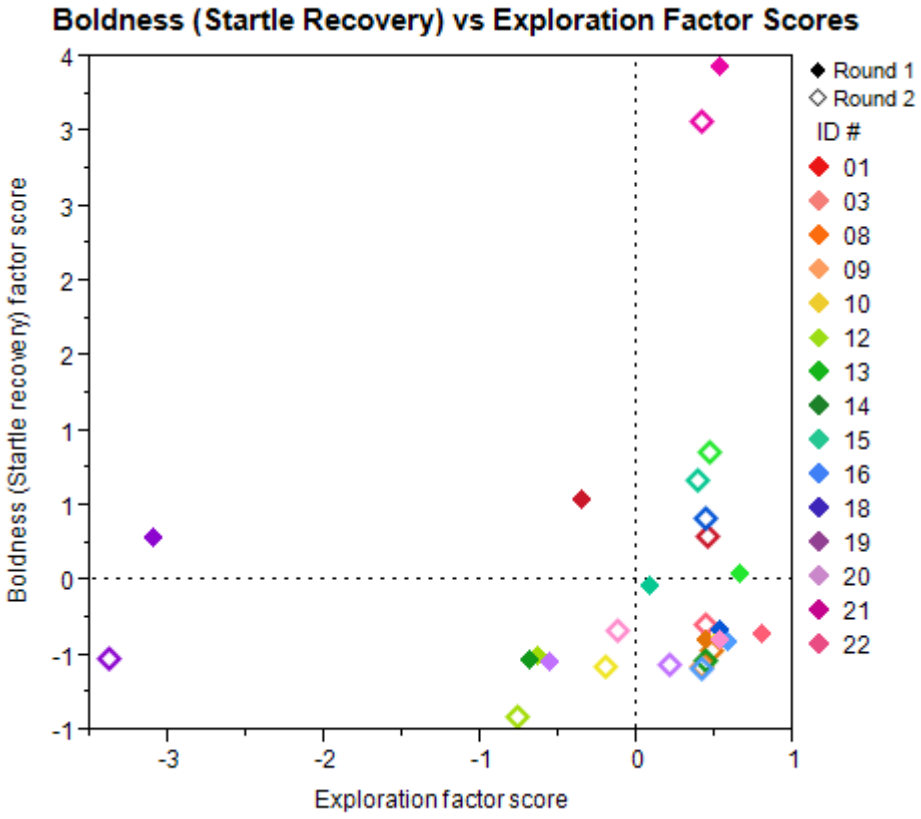


**Figure 13.** Plot showing the relationship between individual factor scores for boldness (startle recovery) and exploration in both rounds.

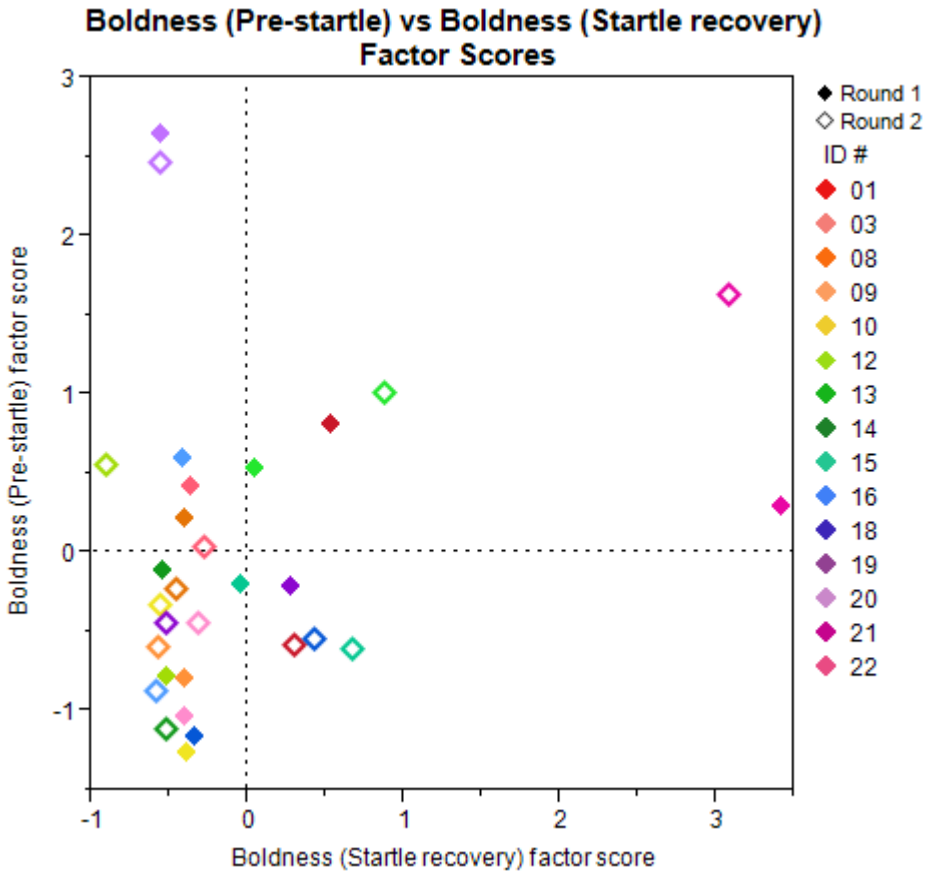


**Figure 14.** Plot showing the relationship between individual factor scores for boldness (pre-startle) and boldness (startle recovery) in both rounds.

**Table 1**. Data from Test 1 (exploration test).

| ID # | Sex | Body length (mm) | | First shelter exit (seconds) | | Exit shelter (count) | | Exit shelter frequency | | Duration in shelter (seconds) | | Proportion total time in shelter | | Duration withdrawn (seconds) | | Proportion in-shelter time withdrawn | | Times withdrawn (count) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | F | 41 | 43 | 679.97 | 1800 | 3 | 0 | 0.00167 | 0 | 1759.06 | 1800 | 0.9773 | 1 | 406.41 | 451.26 | 0.2310 | 0.2507 | 16 | 13 |
| 03 | M | 40 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 561.89 | 533.39 | 0.3122 | 0.3074 | 8 | 18 |
| 08 | F | 42 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 507.52 | 153.37 | 0.2820 | 0.0852 | 13 | 8 |
| 09 | F | 48 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 809.84 | 676.62 | 0.4499 | 0.3759 | 4 | 7 |
| 10 | F | 49 | --- | 1800 | 1466.07 | 0 | 3 | 0 | 0.00187 | 1800 | 1439.26 | 1 | 0.8993 | 582.12 | 419.41 | 0.3234 | 0.2914 | 15 | 12 |
| 12 | M | 34 | --- | 179.47 | 670.23 | 3 | 3 | 0.00167 | 0.00167 | 1669.51 | 1726.44 | 0.9275 | 0.9591 | 1000.96 | 1018.80 | 0.5996 | 0.5901 | 28 | 31 |
| 13 | F | 45 | --- | 250.30 | 1800 | 1 | 0 | 0.00056 | 0 | 1797.67 | 1800 | 0.9987 | 1 | 313.22 | 83.80 | 0.1742 | 0.0466 | 6 | 5 |
| 14 | F | 40 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 553.71 | 166.50 | 0.3076 | 0.0925 | 24 | 2 |
| 15 | F | 47 | --- | 1187.20 | 1800 | 2 | 0 | 0.00111 | 0 | 1562.43 | 1800 | 0.8680 | 1 | 573.03 | 424.43 | 0.3668 | 0.2358 | 13 | 12 |
| 16 | M | 44 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 766.06 | 22.93 | 0.4256 | 0.0127 | 11 | 1 |
| 18 | F | 49 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 949.12 | 1464.17 | 0.5273 | 0.8134 | 4 | 4 |
| 19 | F | 47 | --- | 0 | 0 | 1 | 2 | 0.00109 | 0.00447 | 0 | 311.47 | 0 | 0.6960 | 0 | 37.64 | 0.0000 | 0.1208 | 0 | 2 |
| 20 | F | 52 | --- | 215.43 | 1500.33 | 2 | 2 | 0.00111 | 0.00111 | 1732.83 | 1755.66 | 0.9627 | 0.9754 | 141.88 | 216.07 | 0.0819 | 0.1231 | 11 | 11 |
| 21 | F | 46 | --- | 1800 | 1800 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 | 87.55 | 342.28 | 0.0486 | 0.1902 | 9 | 16 |
| 22 | F | 57 | --- | 1800 | 1235.47 | 0 | 1 | 0 | 0.00056 | 1800 | 1779.37 | 1 | 0.9885 | 1064.70 | 397.77 | 0.5915 | 0.2235 | 2 | 12 |
| Avg | | 45.4 | 45.5 | 1247.49 | 1524.81 | 0.8 | 0.7 | 0.00048 | 0.00065 | 1648.10 | 1667.48 | 0.9156 | 0.9679 | 554.53 | 427.23 | 0.3148 | 0.2506 | 10.9 | 10.3 |
| SD | | 5.6 | 5.4 | 747.83 | 527.83 | 1.1 | 1.2 | 0.00066 | 0.00124 | 460.87 | 386.40 | 0.2560 | 0.0800 | 327.83 | 389.89 | 0.1867 | 0.2140 | 7.8 | 7.8 |

Table 1, continued.

| ID # | Withdraw frequency | | Duration part exposed (seconds) | | Proportion in-shelter time part exposed | | Duration half exposed (seconds) | | Proportion in-shelter time half exposed | | Duration out of shelter (seconds) | | Trial duration (seconds) | | Proportion time in refuge area | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 0.0089 | 0.0072 | 900.73 | 1201.61 | 0.5121 | 0.6676 | 451.92 | 147.13 | 0.2569 | 0.0817 | 40.94 | 0 | 1800 | 1800 | 1 | 1 |
| 03 | 0.0044 | 0.0100 | 983.18 | 941.43 | 0.5462 | 0.5230 | 254.93 | 305.18 | 0.1416 | 0.1695 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 08 | 0.0072 | 0.0044 | 1239.61 | 834.99 | 0.6887 | 0.4639 | 52.87 | 811.64 | 0.0294 | 0.4509 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 09 | 0.0022 | 0.0039 | 990.16 | 1123.38 | 0.5501 | 0.6241 | 0 | 0 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 10 | 0.0083 | 0.0075 | 1037.03 | 842.16 | 0.5761 | 0.5851 | 180.85 | 160.96 | 0.1005 | 0.0894 | 0 | 161.11 | 1800 | 1600.37 | 1 | 0.9558 |
| 12 | 0.0156 | 0.0172 | 505.11 | 381.58 | 0.3025 | 0.2210 | 163.44 | 326.06 | 0.0979 | 0.1889 | 130.49 | 73.56 | 1800 | 1800 | 1 | 1 |
| 13 | 0.0033 | 0.0028 | 1443.12 | 1699.80 | 0.8028 | 0.9443 | 41.33 | 16.40 | 0.0230 | 0.0091 | 2.33 | 0 | 1800 | 1800 | 1 | 1 |
| 14 | 0.0133 | 0.0011 | 981.26 | 1633.50 | 0.5451 | 0.9075 | 265.03 | 0 | 0.1472 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 15 | 0.0072 | 0.0067 | 872.47 | 1375.57 | 0.5584 | 0.7642 | 116.93 | 0 | 0.0748 | 0 | 237.57 | 0 | 1800 | 1800 | 0.9388 | 1 |
| 16 | 0.0061 | 0.0006 | 1033.94 | 1777.07 | 0.5744 | 0.9873 | 0 | 0 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 18 | 0.0022 | 0.0022 | 850.88 | 335.83 | 0.4727 | 0.1866 | 0 | 0 | 0 | 0 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 19 | 0 | 0.0045 | 0 | 75.57 | 0 | 0.2426 | 0 | 196.30 | 0 | 0.6302 | 915.57 | 136.03 | 915.57 | 447.50 | 0.1287 | 0.9964 |
| 20 | 0.0061 | 0.0061 | 1324.59 | 1383.87 | 0.7644 | 0.7882 | 266.36 | 155.72 | 0.1537 | 0.0887 | 67.17 | 44.34 | 1800 | 1800 | 1 | 1 |
| 21 | 0.0050 | 0.0089 | 1492.95 | 1260.19 | 0.8294 | 0.7001 | 220.00 | 197.53 | 0.1219 | 0.1097 | 0 | 0 | 1800 | 1800 | 1 | 1 |
| 22 | 0.0011 | 0.0067 | 699.77 | 1296.76 | 0.3888 | 0.7288 | 35.53 | 84.84 | 0.0197 | 0.0477 | 0 | 20.63 | 1800 | 1800 | 1 | 1 |
| Avg | 0.0061 | 0.0060 | 956.99 | 1077.55 | 0.5408 | 0.6223 | 136.58 | 160.12 | 0.0778 | 0.1244 | 92.94 | 29.04 | 1741.04 | 1696.52 | 0.9378 | 0.9968 |
| SD | 0.0043 | 0.0042 | 374.26 | 509.79 | 0.2078 | 0.2559 | 135.66 | 212.21 | 0.0768 | 0.1832 | 237.30 | 53.19 | 228.36 | 349.34 | 0.2244 | 0.0114 |

Table 1, continued.

| ID # | First enter exploration area (seconds) | | Enter exploration area (count) | | Enter exploration area frequency | | Climb/ swim events (count) | | Climb/swim frequency | | Duration swimming (seconds) | | Proportion total time swimming | | Duration digging (seconds) | | Proportion time digging | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 135.96 | 0 | 0.0755 | 0 |
| 03 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 08 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 09 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 1800 | 1529.67 | 0 | 1 | 0 | 0.00062 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 18.63 | 0 | 0.0116 |
| 12 | 1800 | 1800 | 0 | 0 | 0 | 0 | 2 | 0 | 0.0011 | 0 | 3.13 | 0 | 0.0017 | 0 | 38.51 | 37.26 | 0.0214 | 0.0207 |
| 13 | 1800 | 1800 | 0 | 0 | 0 | 0 | 1 | 0 | 0.0006 | 0 | 1.23 | 0 | 0.0007 | 0 | 0 | 0 | 0 | 0 |
| 14 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19.90 | 0 | 0.0111 | 0 |
| 15 | 1665.00 | 1800 | 1 | 0 | 0.00056 | 0 | 3 | 0 | 0.0017 | 0 | 0.53 | 0 | 0.0003 | 0 | 5.17 | 0 | 0.0029 | 0 |
| 16 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 18 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 14.50 | 445.87 | 2 | 1 | 0.00218 | 0.00223 | 0 | 3 | 0 | 0.0067 | 0 | 1.77 | 0 | 0.0040 | 266.80 | 9.13 | 0.2914 | 0.0204 |
| 20 | 1800 | 1800 | 0 | 0 | 0 | 0 | 2 | 1 | 0.0011 | 0.0006 | 1.77 | 1.44 | 0.0010 | 0.0008 | 0 | 0 | 0 | 0 |
| 21 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 22 | 1800 | 1800 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Avg | 1671.97 | 1691.70 | 0.20 | 0.13 | 0.00018 | 0.00019 | 0.5 | 0.3 | 0.0003 | 0.0005 | 0.44 | 0.21 | 0.0002 | 0.0003 | 31.09 | 4.33 | 0.0268 | 0.0035 |
| SD | 459.84 | 351.61 | 0.56 | 0.35 | 0.00057 | 0.00059 | 1.0 | 0.8 | 0.0006 | 0.0017 | 0.92 | 0.57 | 0.0005 | 0.0010 | 74.20 | 10.48 | 0.0758 | 0.0075 |

**Table 2**. Data from Test 2 (startle test).

| ID # | First shelter exit (seconds) | | Exit shelter pre-startle (count) | | Exit shelter frequency pre-startle | | Duration in shelter pre-startle (seconds) | | Proportion total time in shelter | | Duration withdrawn (seconds) | | Proportion in-shelter time withdrawn | | Times withdrawn pre-startle (count) | | Withdraw frequency pre-startle | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 353.90 | 145.70 | 4 | 2 | 0.0049 | 0.0045 | 385.46 | 155.93 | 0.4662 | 0.4506 | 40.68 | 97.01 | 0.0559 | 0.3196 | 3 | 3 | 0.0037 | 0.0068 |
| 03 | 156.50 | 328.10 | 13 | 2 | 0.0089 | 0.0032 | 728.42 | 329.74 | 0.4774 | 0.4187 | 65.25 | 32.60 | 0.0896 | 0.0981 | 16 | 4 | 0.0110 | 0.0064 |
| 08 | 253.50 | 174.87 | 3 | 10 | 0.0052 | 0.0178 | 266.37 | 216.02 | 0.4515 | 0.3661 | 2.50 | 8.74 | 0.0094 | 0.0405 | 2 | 9 | 0.0034 | 0.0160 |
| 09 | 224.70 | 217.50 | 2 | 4 | 0.0069 | 0.0106 | 228.77 | 223.40 | 0.7601 | 0.5732 | 0.37 | 101.91 | 0.0016 | 0.4562 | 1 | 3 | 0.0035 | 0.0079 |
| 10 | 70.67 | 254.13 | 2 | 2 | 0.0072 | 0.0049 | 139.17 | 255.13 | 0.4694 | 0.6144 | 8.40 | 1.40 | 0.0604 | 0.0055 | 2 | 1 | 0.0072 | 0.0025 |
| 12 | 198.27 | 163.37 | 1 | 6 | 0.0039 | 0.0086 | 198.27 | 538.95 | 0.6179 | 0.7704 | 2.03 | 187.14 | 0.0102 | 0.3472 | 1 | 7 | 0.0039 | 0.0101 |
| 13 | 132.67 | 78.23 | 6 | 2 | 0.0126 | 0.0061 | 180.40 | 81.93 | 0.3620 | 0.2432 | 7.40 | 1.17 | 0.0410 | 0.0143 | 5 | 1 | 0.0105 | 0.0030 |
| 14 | 326.67 | 478.47 | 4 | 1 | 0.0036 | 0.0012 | 598.76 | 478.47 | 0.3622 | 0.4769 | 21.94 | 172.53 | 0.0366 | 0.2676 | 7 | 5 | 0.0062 | 0.0061 |
| 15 | 281.70 | 215.20 | 2 | 6 | 0.0033 | 0.0138 | 298.20 | 230.63 | 0.4844 | 0.5597 | 55.45 | 61.70 | 0.1265 | 0.1359 | 5 | 6 | 0.0082 | 0.0138 |
| 16 | 126.13 | 170.30 | 5 | 5 | 0.0172 | 0.0058 | 158.96 | 193.91 | 0.5334 | 0.2700 | 35.17 | 20.82 | 0.1945 | 0.0639 | 5 | 4 | 0.0172 | 0.0046 |
| 18 | 497.97 | 168.43 | 2 | 1 | 0.0033 | 0.0049 | 501.07 | 168.43 | 0.8213 | 0.8041 | 56.97 | 0 | 0.1137 | 0 | 2 | 0 | 0.0033 | 0 |
| 19 | 372.57 | 120.70 | 1 | 2 | 0.0023 | 0.0034 | 372.57 | 251.73 | 0.6469 | 0.4250 | 62.00 | 36.00 | 0.1097 | 0.1430 | 0 | 2 | 0 | 0.0034 |
| 20 | 807.10 | 61.40 | 1 | 12 | 0.0012 | 0.0112 | 807.10 | 719.86 | 0.9185 | 0.6606 | 102.09 | 58.23 | 0.1265 | 0.0809 | 6 | 13 | 0.0071 | 0.0122 |
| 21 | 443.90 | 221.73 | 1 | 8 | 0.0021 | 0.0080 | 443.90 | 570.34 | 0.7841 | 0.6700 | 586.30 | 104.56 | 0.2839 | 0.0809 | 1 | 9 | 0.0021 | 0.0090 |
| 22 | 178.33 | 232.90 | 1 | 2 | 0.0040 | 0.0066 | 178.33 | 235.10 | 0.6842 | 0.4836 | 19.03 | 1.30 | 0.1067 | 0.0055 | 1 | 1 | 0.0040 | 0.0033 |
| Avg | 294.97 | 202.07 | 3.2 | 4.3 | 0.0058 | 0.0074 | 365.72 | 309.97 | 0.5893 | 0.5191 | 71.04 | 59.01 | 0.0911 | 0.1373 | 3.8 | 4.5 | 0.0061 | 0.0070 |
| SD | 187.14 | 102.13 | 3.1 | 3.4 | 0.0043 | 0.0044 | 212.18 | 181.44 | 0.1734 | 0.1667 | 145.59 | 61.74 | 0.0758 | 0.1433 | 4.0 | 3.7 | 0.0043 | 0.0045 |

Table 2, continued.

| ID # | Duration part exposed (seconds) | | Proportion in-shelter time part exposed | | Duration half exposed (seconds) | | Proportion in-shelter time half exposed | | Trial duration (seconds) | | Duration out of shelter pre-startle (seconds) | | Proportion time in refuge area | | Duration in refuge area pre-startle (seconds) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 495.84 | 139.77 | 0.6811 | 0.4576 | 191.46 | 67.05 | 0.2630 | 0.2228 | 1561.43 | 673.67 | 430.44 | 285.40 | 0.9117 | 0.9131 | 787.66 | 424.89 |
| 03 | 214.82 | 100.81 | 0.2949 | 0.3057 | 448.35 | 196.57 | 0.6155 | 0.5961 | 1525.80 | 787.53 | 724.81 | 292.16 | 0.9447 | 0.8565 | 1441.42 | 581.25 |
| 08 | 161.85 | 180.16 | 0.6076 | 0.8340 | 102.02 | 27.12 | 0.3830 | 0.1255 | 590.00 | 590.03 | 316.13 | 346.11 | 0.9776 | 0.9529 | 576.78 | 554.24 |
| 09 | 223.80 | 115.25 | 0.9783 | 0.5159 | 4.60 | 3.57 | 0.0201 | 0.0160 | 300.97 | 389.77 | 60.13 | 155.73 | 0.9308 | 0.7770 | 280.14 | 302.85 |
| 10 | 100.30 | 251.67 | 0.7207 | 0.9864 | 30.17 | 1.06 | 0.2168 | 0.0042 | 296.47 | 415.23 | 138.06 | 151.60 | 0.8905 | 0.8704 | 259.42 | 361.42 |
| 12 | 111.14 | 336.04 | 0.5605 | 0.6235 | 85.10 | 13.80 | 0.4292 | 0.0256 | 320.87 | 699.53 | 55.06 | 155.28 | 0.7215 | 0.9513 | 224.14 | 665.46 |
| 13 | 137.03 | 74.30 | 0.7596 | 0.9069 | 35.97 | 6.46 | 0.1994 | 0.0788 | 498.37 | 336.90 | 294.17 | 247.04 | 0.9119 | 0.9488 | 454.46 | 319.65 |
| 14 | 212.90 | 414.90 | 0.3556 | 0.6434 | 363.92 | 57.40 | 0.6078 | 0.0890 | 1653.27 | 1352.23 | 522.47 | 335.33 | 0.7549 | 0.9708 | 890.78 | 803.14 |
| 15 | 277.32 | 183.60 | 0.6324 | 0.4044 | 105.73 | 208.73 | 0.2411 | 0.4597 | 905.17 | 811.23 | 308.97 | 204.87 | 0.8665 | 0.8522 | 534.09 | 424.00 |
| 16 | 107.91 | 204.43 | 0.5967 | 0.6272 | 37.75 | 100.69 | 0.2088 | 0.3089 | 339.00 | 1207.00 | 132.44 | 671.92 | 0.9273 | 0.8041 | 274.48 | 748.72 |
| 18 | 302.10 | 167.37 | 0.6029 | 0.9937 | 142.00 | 1.06 | 0.2834 | 0.0063 | 610.13 | 209.47 | 101.73 | 37.47 | 0.9016 | 0.9585 | 549.69 | 200.78 |
| 19 | 127.89 | 153.64 | 0.2263 | 0.6103 | 371.24 | 59.86 | 0.6569 | 0.2378 | 873.50 | 592.27 | 64.83 | 334.64 | 0.9064 | 0.8817 | 415.94 | 522.20 |
| 20 | 616.18 | 219.01 | 0.7634 | 0.3042 | 88.83 | 442.12 | 0.1101 | 0.6142 | 878.73 | 1089.63 | 33.17 | 350.01 | 0.9420 | 0.9677 | 826.46 | 1054.43 |
| 21 | 463.77 | 525.23 | 0.2246 | 0.4063 | 1006.97 | 647.98 | 0.4876 | 0.5013 | 2633.73 | 1929.37 | 25.03 | 429.93 | 0.9775 | 0.9253 | 458.97 | 988.92 |
| 22 | 152.40 | 233.19 | 0.8546 | 0.9798 | 6.90 | 3.51 | 0.0387 | 0.0147 | 260.63 | 492.13 | 73.27 | 67.43 | 0.9311 | 0.9210 | 242.67 | 283.71 |
| Avg | 247.02 | 219.96 | 0.5906 | 0.6400 | 201.40 | 122.47 | 0.3174 | 0.2201 | 883.20 | 771.73 | 218.71 | 270.99 | 0.8997 | 0.9034 | 547.81 | 549.04 |
| SD | 158.95 | 122.17 | 0.2262 | 0.2470 | 263.77 | 188.05 | 0.2051 | 0.2238 | 682.58 | 455.59 | 209.23 | 157.79 | 0.0722 | 0.0607 | 328.83 | 259.10 |

Table 2, continued.

| ID # | First enter exploration area (seconds) | | Enter exploration area pre-startle | | Enter exploration area frequency pre-startle | | Climb/ swim events pre-startle (count) | | Climb/ swim frequency pre-startle | | Duration swimming (seconds) | | Proportion total time swimming | | Time of startle stimulus (seconds) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 606.83 | 424.87 | 1 | 1 | 0.00123 | 0.00453 | 4 | 4 | 0.00490 | 0.00906 | 4.21 | 3.13 | 0.0027 | 0.0046 | 815.90 | 441.33 |
| 03 | 253.33 | 428.03 | 2 | 1 | 0.00138 | 0.00643 | 35 | 11 | 0.02408 | 0.01769 | 57.35 | 14.18 | 0.0376 | 0.0180 | 1453.23 | 621.90 |
| 08 | 576.77 | 490.83 | 1 | 3 | 0.00172 | 0.00712 | 12 | 15 | 0.02060 | 0.02668 | 21.35 | 24.75 | 0.0362 | 0.0419 | 582.50 | 562.13 |
| 09 | 277.43 | 261.17 | 2 | 14 | 0.00692 | 0.03693 | 4 | 7 | 0.01385 | 0.01846 | 9.70 | 23.83 | 0.0322 | 0.0611 | 288.90 | 379.13 |
| 10 | 202.23 | 337.37 | 3 | 3 | 0.01082 | 0.00738 | 15 | 11 | 0.05411 | 0.02704 | 37.96 | 37.77 | 0.1280 | 0.0910 | 277.23 | 406.73 |
| 12 | 220.27 | 180.70 | 4 | 3 | 0.01579 | 0.00432 | 3 | 1 | 0.01184 | 0.00144 | 0 | 0 | 0 | 0 | 253.33 | 694.23 |
| 13 | 454.47 | 235.37 | 1 | 2 | 0.00211 | 0.00608 | 11 | 3 | 0.02318 | 0.00912 | 48.31 | 11.93 | 0.0969 | 0.0354 | 474.57 | 328.97 |
| 14 | 394.50 | 738.63 | 8 | 2 | 0.00714 | 0.00614 | 11 | 11 | 0.00981 | 0.01352 | 19.54 | 8.82 | 0.0118 | 0.0065 | 1121.23 | 813.80 |
| 15 | 380.83 | 272.47 | 7 | 3 | 0.01153 | 0.00918 | 40 | 16 | 0.06588 | 0.03674 | 45.18 | 46.95 | 0.0499 | 0.0579 | 607.17 | 435.50 |
| 16 | 220.03 | 377.70 | 3 | 5 | 0.01030 | 0.00693 | 5 | 31 | 0.01716 | 0.03580 | 3.53 | 20.77 | 0.0104 | 0.0172 | 291.40 | 865.83 |
| 18 | 500.63 | 200.77 | 4 | 1 | 0.00664 | 0.00486 | 0 | 0 | 0 | 0 | 2.00 | 0.30 | 0.0033 | 0.0014 | 602.80 | 205.90 |
| 19 | 415.90 | 262.17 | 1 | 6 | 0.00229 | 0.01023 | 0 | 11 | 0 | 0.01876 | 0 | 20.21 | 0 | 0.0341 | 437.40 | 586.37 |
| 20 | 821.40 | 1038.40 | 4 | 2 | 0.00476 | 0.00187 | 1 | 28 | 0.00119 | 0.02617 | 0.60 | 74.21 | 0.0007 | 0.0681 | 840.27 | 1069.87 |
| 21 | 458.93 | 989.00 | 1 | 1 | 0.00213 | 0.00300 | 0 | 6 | 0 | 0.00600 | 8.63 | 7.09 | 0.0033 | 0.0037 | 468.93 | 1000.27 |
| 22 | 242.67 | 268.63 | 1 | 2 | 0.00397 | 0.00992 | 0 | 0 | 0 | 0 | 0 | 8.87 | 0 | 0.0180 | 251.60 | 302.53 |
| Avg | 401.75 | 433.74 | 2.9 | 3.3 | 0.00591 | 0.00833 | 9.4 | 10.3 | 0.0164 | 0.0164 | 17.22 | 20.19 | 0.0275 | 0.0306 | 584.43 | 580.97 |
| SD | 176.04 | 274.23 | 2.2 | 3.3 | 0.00449 | 0.00826 | 12.5 | 9.3 | 0.0198 | 0.0123 | 20.17 | 20.01 | 0.0387 | 0.0282 | 348.25 | 261.66 |

Table 2, continued.

| ID # | Jump (graded 0-4) | | Freeze duration (seconds) | | Flee | | Lunge | | Duration in refuge area post-startle (seconds) | | Duration in shelter post-startle (seconds) | | Exit shelter post-startle (count) | | Exit shelter frequency post-startle | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 3 | 4 | 8.53 | 16.8 | 1 | 1 | 0 | 0 | 635.90 | 190.24 | 342.52 | 147.63 | 6 | 1 | 0.0080 | 0.0043 |
| 03 | 1 | 1 | 3.87 | 4.16 | 0 | 0 | 0 | 0 | 0 | 93.27 | 0 | 0 | 0 | 0 | 0 | 0 |
| 08 | 2 | 2 | 3.73 | 4.64 | 0 | 0 | 1 | 1 | 0 | 8.00 | 0 | 0 | 0 | 0 | 0 | 0 |
| 09 | 3 | 2 | 7.77 | 3.97 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 3 | 0 | 2.13 | 0 | 0 | 0 | 0 | 0 | 4.59 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 2 | 2 | 12.07 | 2.40 | 0 | 0 | 0 | 0 | 7.37 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 1 | 1 | 4.27 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 2 | 4 | 0.57 | 32.30 | 1 | 1 | 0 | 0 | 357.27 | 509.60 | 0 | 166.36 | 0 | 2 | 0 | 0.0037 |
| 15 | 4 | 4 | 29.00 | 14.70 | 1 | 1 | 0 | 0 | 250.24 | 267.33 | 140.30 | 223.40 | 1 | 1 | 0.0034 | 0.0027 |
| 16 | 1 | 3 | 0 | 13.57 | 1 | 1 | 1 | 0 | 39.87 | 221.83 | 21.87 | 132.03 | 1 | 1 | 0.0210 | 0.0029 |
| 18 | 1 | 2 | 0 | 1.20 | 0 | 0 | 1 | 1 | 0.40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 2 | 1 | 0.93 | 3.57 | 0 | 0 | 0 | 0 | 375.80 | 0 | 192.53 | 0 | 3 | 0 | 0.0069 | 0 |
| 20 | 1 | 3 | 8.96 | 0 | 0 | 0 | 0 | 1 | 1.30 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 1 | 2 | 0.60 | 0.70 | 0 | 1 | 0 | 0 | 2115.50 | 796.33 | 1621.18 | 722.30 | 16 | 2 | 0.0074 | 0.0022 |
| 22 | 1 | 3 | 3.96 | 0 | 0 | 1 | 0 | 0 | 0 | 169.54 | 0 | 2.90 | 0 | 1 | 0 | 0.0053 |
| Avg | 1.9 | 2.3 | 5.76 | 6.53 | | | | | 252.55 | 150.41 | 154.56 | 92.97 | 1.8 | 0.5 | 0.0031 | 0.0014 |
| SD | 1.0 | 1.2 | 7.42 | 9.10 | | | | | 551.37 | 231.28 | 417.86 | 190.65 | 4.3 | 0.7 | 0.0058 | 0.0019 |

Table 2, continued.

| ID # | Times withdrawn post-startle (count) | | Withdraw frequency post-startle | | Enter exploration area post-startle (count) | | Enter exploration area frequency post-startle | | Climb/swim events post-startle (count) | | Climb/swim frequency post-startle | | Latency to obtain food post-startle (seconds) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 8 | 5 | 0.0107 | 0.0215 | 4 | 1 | 0.0054 | 0.0043 | 1 | 1 | 0.0013 | 0.0043 | 745.53 | 232.34 |
| 03 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0.0181 | 0 | 4 | 0 | 0.0242 | 72.57 | 165.63 |
| 08 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.0358 | 1 | 1 | 0.1333 | 0.0358 | 7.50 | 27.90 |
| 09 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12.07 | 10.64 |
| 10 | 0 | 0 | 0 | 0 | 2 | 0 | 0.1040 | 0 | 0 | 0 | 0 | 0 | 19.24 | 8.50 |
| 12 | 0 | 0 | 0 | 0 | 1 | 0 | 0.0148 | 0 | 0 | 0 | 0 | 0 | 67.54 | 5.30 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0.1261 | 23.80 | 7.93 |
| 14 | 0 | 3 | 0 | 0.0056 | 4 | 3 | 0.0075 | 0.0056 | 8 | 3 | 0.0150 | 0.0056 | 532.04 | 538.43 |
| 15 | 2 | 2 | 0.0067 | 0.0053 | 3 | 1 | 0.0101 | 0.0027 | 5 | 2 | 0.0168 | 0.0053 | 298.00 | 375.73 |
| 16 | 1 | 2 | 0.0210 | 0.0059 | 1 | 1 | 0.0210 | 0.0029 | 4 | 3 | 0.0840 | 0.0088 | 47.60 | 341.17 |
| 18 | 0 | 0 | 0 | 0 | 1 | 0 | 0.1364 | 0 | 1 | 1 | 0.1364 | 0.2801 | 7.33 | 3.57 |
| 19 | 4 | 0 | 0.0092 | 0 | 3 | 0 | 0.0069 | 0 | 0 | 1 | 0 | 0.1695 | 436.10 | 5.90 |
| 20 | 0 | 0 | 0 | 0 | 1 | 0 | 0.0260 | 0 | 0 | 2 | 0 | 0.1010 | 38.46 | 19.80 |
| 21 | 17 | 3 | 0.0079 | 0.0032 | 2 | 2 | 0.0009 | 0.0022 | 6 | 0 | 0.0028 | 0 | 2164.80 | 929.10 |
| 22 | 0 | 1 | 0 | 0.0053 | 0 | 1 | 0 | 0.0053 | 0 | 9 | 0 | 0.0475 | 9.33 | 189.60 |
| Avg | 2.1 | 1.1 | 0.0037 | 0.0031 | 1.5 | 0.9 | 0.0222 | 0.0051 | 1.7 | 1.9 | 0.0260 | 0.0539 | 298.79 | 190.77 |
| SD | 4.7 | 1.6 | 0.0062 | 0.0057 | 1.5 | 1.1 | 0.0411 | 0.0097 | 2.7 | 2.3 | 0.0492 | 0.0820 | 565.68 | 265.07 |

**Table 3.** Data from Test 3 (novel object test).

| ID # | Investigate | | Strike | | Withdraw | | Grab | | Grab duration (sec) | | Exit shelter | | Rocks in shelter (count) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 | R1 | R2 |
| 01 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 34 | 7 |
| 03 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 3.87 | 0.87 | 1 | 1 | 0 | 0 |
| 08 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 09 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1.20 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 30 | 57 |
| 13 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 9 |
| 15 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 16 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0.60 | 0.10 | 0 | 0 | 0 | 0 |
| 18 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 19 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| 20 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0.53 | 2.13 | 1 | 1 | 1 | 0 |
| 22 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Avg | | | | | | | | | 0.41 | 0.21 | | | 5.1 | 4.9 |
| SD | | | | | | | | | 1.02 | 0.58 | | | 11.4 | 14.7 |

**Table 4.** Variables used in other personality studies.

| Variable | Reference |
|---|---|
| Latency to first exit shelter (sec) | Watanabe et al. 2012; Wilson & Godin 2009; Wilson et al. 2011 |
| Proportion of in-shelter time part exposed | Similar to Niemela, DiRienzo, & Hedrick 2012 |
| Latency to enter unoccupied shelter (sec) | Mowles et al. 2012 |
| Proportion of time in exploration area | Wilson & Godin 2009; Wilson et al. 2011 |
| Jump (graded 0-4) | Heitler, Fraser, & Ferrero 2000 |
| Freeze duration (sec) | Niemela, DiRienzo, & Hedrick 2012 |
| Latency to obtain food post-startle (sec) | Yuen et al. 2017 |

**Table 5.** Results from paired two-sample t-tests comparing averages of Test 1 variables between Round 1 and Round 2 (α = 0.05).

| Variable | t Statistic | P(T<=t) two-tail |
|---|---|---|
| Exploration test | | |
| Latency to first exit shelter (sec) | -1.76 | 0.0998 |
| Duration in shelter (sec) | -0.53 | 0.6063 |
| Prop time in shelter | -1.10 | 0.2892 |
| Duration fully withdrawn (sec) | 1.51 | 0.1527 |
| Prop time (in shelter) withdrawn | 1.33 | 0.2045 |
| Times withdrawn (count) | 0.32 | 0.7513 |
| Duration part exposed (sec) | -1.21 | 0.2469 |
| Proportion of in-shelter time part exposed | -1.49 | 0.1575 |
| Duration half exposed (sec) | -0.37 | 0.7134 |
| Proportion of in-shelter time half exposed | -0.86 | 0.4035 |
| Test duration (sec) | 1.35 | 0.1993 |
| Prop time in refuge area | -1.02 | 0.3264 |
| Duration out of shelter (sec) | 1.16 | 0.2646 |
| Duration digging (sec) | 1.42 | 0.1785 |

**Table 6.** Results from paired two-sample t-tests comparing averages of Test 2 variables between Round 1 and Round 2 (α = 0.05).

| Variable | t Statistic | P(T<=t) two-tail |
|---|---|---|
| Startle test | | |
| Duration in shelter (sec) | 1.61 | 0.1296 |
| Proportion of test in shelter | 1.90 | 0.0788 |
| Latency to first exit shelter (sec) | 1.51 | 0.1538 |
| Number of shelter exits (count) | 0.09 | 0.9295 |
| Test duration (sec) | 0.93 | 0.3687 |
| Prop time in refuge area | -0.14 | 0.8942 |
| Latency to first enter exploration area (sec) | -0.55 | 0.5937 |
| Enter exploration area (count) | 0.17 | 0.8687 |
| Duration fully withdrawn (sec) | 0.31 | 0.7580 |
| Prop time (in shelter) fully withdrawn | 1.33 | 0.2045 |
| Times fully withdrawn (count) | 0.26 | 0.8009 |
| Duration partially exposed (sec) | 0.58 | 0.5740 |
| Prop time (in shelter) part exposed | -0.69 | 0.5008 |
| Duration half exposed (sec) | 1.66 | 0.1199 |
| Prop time (in shelter) half exposed | 1.42 | 0.1767 |
| Latency to startle stimulus (sec) | 0.04 | 0.9725 |
| Jump response (graded 0-4) | -1.10 | 0.2885 |
| Latency to obtain food post-startle (sec) | 1.12 | 0.2798 |
| Climbing events (count) | -0.10 | 0.9217 |
| Duration swimming (sec) | -0.44 | 0.6678 |
| Prop total time swimming | -0.40 | 0.6969 |
| Swimming events (count) | -0.61 | 0.5492 |
| Freeze duration (sec) | -0.27 | 0.7888 |

**Table 7.** Repeatability statistics (*r*) of significantly repeatable variables. Asterisks (*) indicate variables used in factor analyses. (α = 0.05, between-groups df = 14, within-groups df = 15)

| | Behavior | *r* | *F* | *p* |
|---|---|---|---|---|
| Exploration Test | | | | |
| * | Latency to first exit shelter | 0.5097 | 3.08 | 0.0192 |
| | Duration withdrawn | 0.5628 | 3.57 | 0.0099 |
| | Proportion in-shelter time withdrawn | 0.5508 | 3.45 | 0.0116 |
| | Proportion in-shelter time part exposed | 0.5624 | 3.57 | 0.0099 |
| | Times withdrawn (count) | 0.4949 | 2.96 | 0.0227 |
| | Withdraw frequency | 0.4499 | 2.59 | 0.0389 |
| * | Latency to enter unoccupied shelter | 0.9011 | 19.23 | $4E^{-07}$ |
| Startle Test | | *r* | *F* | *p* |
| * | Duration in shelter pre-startle | 0.5527 | 3.47 | 0.0113 |
| * | First enter exploration area | 0.5324 | 3.28 | 0.0146 |
| | Proportion time in shelter | 0.5955 | 3.94 | 0.0062 |
| | Climbing/swimming freq pre-startle | 0.5793 | 3.75 | 0.0078 |
| | Proportion time swimming | 0.6301 | 4.41 | 0.0036 |
| | Duration in refuge area post-startle | 0.5950 | 3.94 | 0.0062 |
| * | Duration in shelter post-startle | 0.7059 | 5.80 | 0.0008 |
| * | Latency to obtain food post-startle | 0.6400 | 4.56 | 0.0030 |
| | Rocks in shelter | 0.7127 | 5.96 | 0.0007 |

**Table 8**: Factor loadings from factor analyses. Loadings indicate the degree to which each variable is related to a factor. Variables with a loading of at least ±0.32 were considered to contribute to a factor's meaning (Sinn & Moltschaniwskyj 2005).

Round 1:

| Test | Variable | Startle recovery | Pre-startle | Exploration |
|---|---|---|---|---|
| Exploration test | Latency to first exit shelter | 0.1456 | -0.2295 | 0.8187 |
| | Latency to enter unoccupied shelter | -0.1134 | 0.1675 | 0.8770 |
| Startle test | Duration in shelter pre-startle | 0.0293 | 0.8645 | 0.1195 |
| | Latency to first cross midline | 0.0453 | 0.8682 | -0.1431 |
| | Duration in shelter post-startle | 0.9825 | 0.0620 | -0.0160 |
| | Latency to obtain food post-startle | 0.9881 | 0.0053 | 0.0119 |

Round 2:

| Test | Variable | Startle recovery | Pre-startle | Exploration |
|---|---|---|---|---|
| Exploration test | Latency to first exit shelter | 0.1546 | -0.1504 | 0.9224 |
| | Latency to enter unoccupied shelter | -0.1327 | 0.1204 | 0.9718 |
| Startle test | Duration in shelter pre-startle | -0.0683 | 1.0008 | -0.0760 |
| | Latency to first cross midline | 0.2525 | 0.7793 | 0.1388 |
| | Duration in shelter post-startle | 0.9781 | 0.0301 | -0.0427 |
| | Latency to obtain food post-startle | 0.9566 | 0.0320 | 0.0337 |

**Table 9.** Variance of the included behaviors which is explained by each factor.

Round 1:

| Factor | Variance | % | Cumulative % |
|---|---|---|---|
| Startle recovery | 2.016 | 33.60 | 33.60 |
| Pre-startle | 1.659 | 27.65 | 61.25 |
| Exploration | 1.509 | 25.16 | 86.41 |

Round 2:

| Factor | Variance | % | Cumulative % |
|---|---|---|---|
| Startle recovery | 2.480 | 41.33 | 41.33 |
| Exploration | 1.997 | 33.29 | 74.62 |
| Pre-startle | 2.055 | 34.25 | 108.87 |

**Table 10.** Factor scores of each individual calculated through factor analysis. (R1 = Round 1, R2 = Round 2)

| | Boldness (Startle Recovery) | | Boldness (Pre-Startle) | | Exploration | |
|---|---|---|---|---|---|---|
| ID# | R1 | R2 | R1 | R2 | R1 | R2 |
| 1 | 0.544 | 0.297 | 0.817 | -0.578 | -0.348 | 0.447 |
| 3 | -0.360 | -0.285 | 0.424 | 0.043 | 0.807 | 0.432 |
| 8 | -0.397 | -0.466 | 0.225 | -0.224 | 0.445 | 0.472 |
| 9 | -0.395 | -0.577 | -0.798 | -0.586 | 0.552 | 0.410 |
| 10 | -0.386 | -0.568 | -1.262 | -0.329 | 0.539 | -0.203 |
| 12 | -0.508 | -0.911 | -0.778 | 0.564 | -0.631 | -0.767 |
| 13 | -0.536 | -0.528 | -0.113 | -1.108 | -0.684 | 0.437 |
| 14 | 0.049 | 0.867 | 0.536 | 1.015 | 0.672 | 0.456 |
| 15 | -0.039 | 0.673 | -0.194 | -0.607 | 0.086 | 0.379 |
| 16 | -0.335 | 0.423 | -1.157 | -0.537 | 0.541 | 0.431 |
| 18 | -0.406 | -0.585 | 0.598 | -0.874 | 0.593 | 0.407 |
| 19 | 0.281 | -0.523 | -0.205 | -0.443 | -3.094 | -3.388 |
| 20 | -0.546 | -0.563 | 2.652 | 2.469 | -0.556 | 0.208 |
| 21 | 3.428 | 3.071 | 0.292 | 1.637 | 0.537 | 0.406 |
| 22 | -0.395 | -0.324 | -1.036 | -0.442 | 0.542 | -0.127 |

# VITA

Jillian Blenderman graduated from Klein High School in 2012 and began attending Stephen F. Austin State University that fall, declaring a major in Biology and minor in Psychology. In May of 2016, she graduated with honors as a University Scholar and received the degree of Bachelor of Science.

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Literature citations follow the format of the journal Behavioral Ecology.

This thesis was typed by Jillian Blenderman.