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# Individual Movement Rates Are Sufficient To Determine And Maintain Dynamic Spatial Positioning Within UCA Pugilator Herds

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INDIVIDUAL MOVEMENT RATES ARE SUFFICIENT TO DETERMINE AND  
MAINTAIN DYNAMIC SPATIAL POSITIONING WITHIN *UCA PUGILATOR*  
HERDS

By

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Bachelor of Science  
University of Rhode Island, 2013

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Submitted in Partial Fulfillment of the Requirements

For the Degree of Master of Science in

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College of Arts and Sciences

University of South Carolina

2016

Accepted by:

Blaine Griffen, Director of Thesis

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Lacy Ford, Senior Vice Provost and Dean of Graduate Studies

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## DEDICATION

This work is dedicated to my parents, Timothy Knotts and Bethelena Weston-Knotts, and my siblings, Jake, Sierra, and Kiralee Knotts, without the support of whom I would not be where I am today. Their constant encouragement and inspirational conversations motivate me every day to achieve to best of my ability.

## ACKNOWLEDGEMENTS

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## ABSTRACT

Spatial location within aggregations (i.e. periphery, central) is of biological significance to gregarious animals. Because these positions are a potential consequence of consistent individual behavioral differences, or personality, a better understanding of potential mechanisms concerning personality is central to predicting an individuals' location. To determine the effects of individual personality on the dynamic spatial positioning of *Uca pugilator* while herding, field data collection and agent-based modeling were employed. Individuals were assayed to establish their personalities and returned to the field for observation as a means of identifying location preference within selfish herds. There was a significant difference between the extreme personalities and the proportion of time spent on the edge of the herd. The active individuals were at the periphery ~50% more of the time than less active individuals. An individual-based model qualitatively replicated these field results by applying the mechanism of activity level as an indicator of individual personality. This suggests that differences in personality-dependent movement are sufficient to explain the spatial positioning of individuals within selfish herds. This study enhances our understanding of the possible mechanisms that govern group movement, and has implications for modeling population dynamics that can be influenced by individual personality.

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## CHAPTER 1

### INTRODUCTION<sup>1</sup>

Consistent individual variation in behavior (i.e. animal personality) has been documented across a wide range of phyla, including animals with various levels of complexity (Bell and Sih 2007, Briffa et al. 2008; Briffa and Weiss 2010; Kurvers et al. 2010; Briffa and Greenaway 2011; Ducatez et al. 2012). This behavioral variation can have repercussions for individuals, populations, and communities (Smith and Blumstein 2008; Dingemanse et al. 2010; Schuett et al. 2010; Briffa and Greenaway 2011). Wolf and Weissing (2012) provide a comprehensive inventory of these consequences of individual variation; for example, individual personality can influence life history parameters and fitness through differential use of resources and environment, community structure through cascading effects originating from species interactions, and the distribution of individuals or populations within habitats through differential movement patterns inducing spatial formations.

Several taxa that are known to display individual personalities make use of social grouping (e.g., herding, shoaling, flocking) and personality can yield different individual consequences within these groups (Cote et al. 2012). For instance, personality influences the level of activity within the larger group, such as movement, affecting spatial position and thereby possible foraging success or predation risk (Hirsh 2007; Wolf et al. 2007).

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<sup>1</sup> Knotts ER, Griffen BD. 2016. *Behavioral Ecology and Sociobiology*. 70:639-46. Reprinted here with permission of publisher.

This in turn can result in personality-specific fitness (Dingemanse et al. 2004; Stamps et al. 2007; Smith and Blumstein 2008; Wilson et al. 2010; Cote et al. 2012).

Individual movement within social groups is generated by dispersal decisions or interactions at the individual scale (Couzin and Krause 2003; Clobert et al. 2009; Cote et al. 2010). Further, an individual's location within a group carries with it specific costs and benefits (Hirsh 2007). For example, according to the selfish herding theory (Hamilton 1971), aggregations form to reduce the likelihood of being captured by a predator because risk is spread among more individuals. Hamilton (1971) considered individuals at the periphery of the group to be at the highest risk of "marginal predation" (Vine 1971; Viscido et al. 2001; Viscido and Wetthey 2002). Theoretical and empirical evidence demonstrate peripherally located individuals in a variety of system (e.g. spiders, mussels, shoaling fish, beetles, tadpoles) are at greater risk (Okamura 1986; Rayor and Uetz 1990; Bumann et al. 1997; Hirsh and Morrell 2011; Morrell et al. 2010). For example, Romey et al. (2008) used bass and goldfish predation on either whirligig beetles or tadpoles to empirically demonstrate that, even with predators moving in three-dimensional space and prey in two dimensions, predators were significantly more likely to attack the periphery. Therefore, if herding behavior reflects solely an attempt to reduce predation risk, all individuals may be expected to maximize the number of conspecifics between themselves and the potential attackers by seeking a position in the center of the group (Hamilton 1971; Vine 1971; Morrell et al. 2010). However, benefits such as resource acquisition are also highest at the periphery of a herd (Krause 1994; Hirsh 2007). Given that personality affects individual traits, such as risk-aversion or

movement, an alternative expectation is that location within a herd will be personality-dependent (Smith and Blumstein 2008; Cote et al. 2010).

Available evidence from a variety of systems appears to support personality-dependent positioning within groups, with a result that personality can play an important role in determining group spatial dynamics and structure (Dyer et al. 2009; Cote et al. 2010; Cote et al. 2012; Keiser et al. 2014). For instance, personality influences individual spatial distribution in sheep (Michelena et al. 2009; Sibbald et al. 2009), geese (Kurvers et al. 2010), and fish (Cote et al. 2012). Bold individuals are more likely to split from the group and explore the environment while shy individuals have a higher tendency to remain close to one another (Kurvers et al. 2010; Michelena et al. 2009; Sibbald et al. 2009). As a consequence, individual personality may yield emergent group properties, such as bold individuals leading the group with shy individuals following (Dyer et al. 2009; Harcourt et al. 2009).

The use of behavior rules that guide decision making has been widely examined empirically (Viscido and Wethey 2002; Viscido et al. 2005; Ballerini et al. 2008b) and assumed in theoretical studies of animal movement and group dynamics (Couzin et al. 2002; Couzin and Krause 2003; Sumpter 2006; Ballerini et al. 2008a; Giardina et al. 2008). Two deficiencies exist when trying to use these behavior rules to understand group dynamics influenced by individual personality. First, existing collective behavior models employ a limited set of rules used by all individuals equally: do not collide with the nearest neighbors, move in the same direction as the nearest neighbor, and remain near conspecifics (Couzin et al. 2002). Models have demonstrated various movement rules capable of being used during collective herding as a function of predation risk

(Viscido et al. 2002; James et al. 2004; Reluga and Viscido 2005), and Morrell et al. (2010) used these model frameworks to demonstrate the effectiveness of those movement rules in reducing predation risk for specific spatial positions (i.e. central, peripheral). However, none of these models demonstrating movement rules include personality-dependent behavior rules. Second, because personality-dependent behavior rules have not been used, the mechanisms leading to personality-dependent spatial positioning remains unclear. Does this positioning reflect active decision making (e.g., do individuals with certain personality types choose to remain on the periphery of a group), or is spatial position an emergent property of movement rules that is independent of active choice?

In this study, we examine the effects of personality on individual spatial dynamics of *Uca pugilator*, the sand fiddler crab. *U. pugilator* is common in sandy and muddy marsh habitats along the east coast of North America (Crane 1975). It exhibits selfish herding, where individuals bunch more closely together when threatened (Morrell et al. 2010; Viscido and Wethey 2002). This reduces an individual's own theoretical predation risk, but creates unequal protection, with increased risk at the periphery of a herd when predators attack from the outside (Viscido et al. 2001; Viscido and Wethey 2002; Morrell et al. 2010). Common predators of *U. pugilator* include feral hogs (Wood and Roark 1980), clapper rails and willets (Viscido et al. 2001), raccoons (Whitten 2014), and the fiddler crab *Uca minax* (Pratt et al. 2002). Each of these predator species attacks by running swiftly at herding fiddler crabs from the outside. Thus, predation risk should be greater for fiddler crabs on the periphery of a herd than for those in the center.

Individual personality can be measured by various traits (e.g. sociability, exploration/activity level, boldness). Activity level and boldness are often positively

correlated within individuals (Fraser et al. 2001; Wilson and McLaughlin 2007; Pintor et al. 2008; Wilson and Godin 2009; Cote et al. 2010; Wilson et al. 2010; Cote et al. 2013), leading some researchers to use activity level or exploratory behavior as a proxy for boldness (Leblond and Reebbs 2006; Reale et al. 2007; Wilson et al. 2010). In our study system, individual crabs are consistently bold in their willingness to take risk and are consistent in their activity levels, however, these two personality traits (boldness and activity level) are not correlated within the same individual crab (Decker and Griffen 2012). While either of these personality traits could conceivably influence spatial positioning within a herd, we focus in this study on activity level, as we reasoned that it was the aspect of personality that was most likely to yield personality-dependent movement rules that could govern spatial location within a herd.

The purpose of this study was to investigate the spatial positioning of individual personalities in *U. pugilator* herds, and to assess whether individual placement in a herd can be explained without relying on active choice by individuals. We tested the hypothesis that active individuals will be found more frequently on the periphery and less active individuals will be found more frequently within the interior of a group. We also tested the hypothesis that this expected pattern does not rely on conscious choice of individual crabs regarding their spatial location in a herd, but that it can be produced as an emergent property of individual differences in activity level alone. We tested these hypotheses using a combination of lab measurements of personality type (i.e., activity level), field observations of the locations of marked and released individuals within a herd, and computer simulation modeling.

## CHAPTER 2

### MATERIAL AND METHODS

#### 2.1 STUDY SITE AND FIELD COLLECTIONS

This study was conducted between June and August 2014 in North Inlet Estuary (33°19'36.83"N, 79°12'23.76"W) in Georgetown, South Carolina, USA. It was not possible to record data blind because our study involved focal animals in the field. *U. pugilator* generally aggregates into herds to deposit-feed on sediments during low tide (Pratt et al. 2002). Herds are commonly mixed-sex and can be hundreds to thousands of individuals in size. *U. pugilator* were sampled by walking quickly toward the aggregations of crabs located low down on the shore, some distance away from their burrows (thus eliminating any chance that they could escape by entering burrows), and scooping individuals into plastic buckets. This approach was repeated from opposite directions in order to prevent differential escape by sex or size (Pratt et al. 2002).

#### 2.2 LAB BEHAVIORAL ASSAYS

We followed previously methods that have previously been used to quantify activity levels in this species (Decker and Griffen 2012), as well as in other aggregating species, including sheep (Sibbald et al. 2009) and fish (Cote et al. 2013). Behavioral tests were administered within 24 hours of collecting the individual to ensure that the physiological/energetic state was not substantially altered. An open field test (Archer

1973) was employed to assay activity or exploratory behavior in a novel environment on a single individual at a time. This assessment commonly uses an enclosed arena with marked grids to develop a quantitative measure of general exploration activity. For our study, the enclosure was a rectangle glass aquarium [55x30x35cm] with sides covered with opaque plastic to discourage any external visual influence on the behavior of the individual.

We first removed the organic content of the sediment by placing it into a furnace at 550°C for 5 hours in order to discourage any influence of foraging on the exploratory behavior. The bottom of the aquarium was covered with a uniform distribution of sediment approximately 2cm thick in which eight equal size quadrats (area  $\approx 206\text{cm}^2$ ) were marked. Filtered seawater was then added because fiddler crabs require sediment with high water content for natural functioning (Reinsel and Rittschof 1995).

*U. pugilator* were released independently (n=224) into the aquarium underneath an opaque plastic cup for ten minutes to ensure acclimation. After the allotted time, the cup was raised remotely using a rigged pulley system to guarantee no disruption to the animal's behavior by an observer. The assessment extended for ten minutes during which a video camera was used to collect movements between quadrats. Through video analysis, a searching space was acquired as the quantitative measure of an individual's general exploratory behavior. Searching space was defined as the number of quadrats entered by the crab's full body with allowance for re-entry. Therefore, a crab could have a quadrat count larger than the eight quadrats present in the aquarium if the individual actively explored the novel environment. For each individual, we also noted the sex and



measured its size in carapace width. Carapace width ranged from 11.4mm to 21.3mm and sex counts were equivalent.

These searching space trials were conducted on separate individuals, with 8-16 crabs tested per day (crabs tested on the same day were treated as a block, total of 25 daily blocks). From this daily group, we retained the individuals with the upper and lower 25% of searching space values as representative of the active and less active extreme personalities, respectively (n=51 of each personality extreme). Crabs were marked on the carapace using nail polish (e.g. different colors for active and less active personalities). A preliminary study indicated that nail polish did not alter the behavior of *U. pugilator* (paired sample t-test comparing observations of no-polish and polish-treatments:  $p=0.071$ ; equivalence test using two one-sided test (TOST) approach: null hypothesis is not rejected; there was a non-significant increase in activity levels on the second observation that may have resulted from familiarity with the chamber) (Knotts, *unpubl. data*). These retained crabs were then used to assess the impacts of personality on spatial positioning in a herd as explained below.

### 2.3 FIELD SPATIAL POSITIONING

*U. pugilator* (those with the daily upper and lower extremes of searching space as measured above) were returned to the field within 24 hours of the first interactions during low tide, and were released into pre-existing herds of conspecifics that were foraging on the exposed mudflats.

All individuals on a given day were released back onto the mudflat at the same moment by placing them all under a single cover and then raising this cover up remotely. After disturbing the herds during initial setup, we remained motionless until fiddler crabs

within the herd resumed their feeding behavior prior to lifting the cover to release the marked crabs (2-10 minutes, personal observation) (McLain et al. 2005). The number of released crabs in one session ranged from four to six fiddler crabs. Following release, we assessed the location of each marked crab within the herd by observing the crabs using binoculars from a stationary point that was initially 2-3 meters from the nearest edge of the herd, so as not to disturb the herd. Proximity to the herd varied throughout the observation period depending on herd movement. An individual was tracked using its sex and carapace color as indicators for specific crab identification. The location assessment of the marked crab was characterized by the individual's position (edge vs. center) within the herd. Animal groupings often exhibit distinct patterns such as sharply defined edges, shape, and spacing between individuals (Viscido et al. 2005). Natural *U. pugilator* herds are often characterized by densely packed individuals in the middle with thinning towards the edge, but still remaining near each other as a cohesive group. Using this information, the crab was considered to be on the edge of a herd if there were less than four other individuals within three body lengths of the focal crab and/or at the edge of a densely packed herd. Otherwise, the individual was considered to be in the interior of the herd. These observations took place every three minutes for one hour or until all marked *U. pugilator* were lost from sight (38.71 min  $\pm$  9.39 min, mean  $\pm$  SD).

Analyses were conducted with the statistical program R, v.3.1.0. We analyzed the data using a generalized linear model (binomial distribution with logit link function) with the proportion of observations for each crab where it was observed on the edge of a herd as the response variable, and with the following fixed factors: activity level, carapace width, and sex, and with the number of observations made during the field session as a

weighting factor. We initially included release date as a random blocking factor in a generalized linear mixed-effects model (Bates et al. 2015); however, this term had no effect on model results (determined using AIC) and so data were pooled across all sampling dates to produce the generalized linear model described above. We selected these fixed factors because they characterize phenotypic variation that has previously been found to explain spatial population structure and large-scale organization (Clobert et al. 2009, Michelena et al. 2009). Initially, a full model was developed to include all main effects and interactions. This model was then simplified using the `step` function of R, which is based on Akaike information criterion (AIC) in order to produce the best-fit and most parsimonious model.

## 2.4 MODEL TO EXPLORE MECHANISM

We conducted an individual-based simulation model to explore the potential mechanistic link between an individual's personality type and its spatial location within a herd. The model description below follows the ODD (overview, design concepts, and details) protocol for describing agent-based models (Grimm and Railsback 2005, Grimm et al. 2006). The model was implemented in NETLOGO v. 5.0.5 (Wilensky 1999).

*-Purpose.* This model was not meant to quantitatively reflect field conditions, but was designed to evaluate qualitatively whether differences in spatial position within a herd could emerge from differences in individual movement associated with active personalities independent of a conscious choice about location within a herd by individuals. The explored mechanism was that active individuals advanced a greater distance than less active individuals, consistent with our laboratory observations.

*-Entities, State Variables, and Scales.* The entities of the model were individuals of varying exploratory behaviors/personalities that followed simple selfish-herding rules within herds that moved through a uniform habitat. Movement distance of individuals was dictated by their personality variable as described below. State variables of each modeled individual included its personality, the herd group they belonged to, and herdmates they followed. These last two variables were used in the model to direct herding behavior of individuals as described below. Spatial and temporal aspects of the model were not specified since this model was generic. Simulations were run for 1000 time steps with a population of 200 individuals.

*-Process Overview and Scheduling.* At each time step, modeled individuals moved towards the closest herd. This simple procedure yielded dynamic herds that were similar to natural herds in the field, with individuals packed densely in the middle of the herd, and the density of individual thinning towards the edge of a herd. This pattern was exploited at each time step to assess whether each modeled individual was on the edge or in the middle of a herd. Specifically, after movement during each time step was complete, individuals were considered to be on the edge of a herd if there were less than four other individuals within a two-unit radius of the focal individual. Otherwise, it was considered to be in the middle of the herd. A sensitivity analysis found that model output was qualitatively similar if other radii (i.e. unit-radius=1.5, 4, 8, 12) were used to define edge vs. center.

*-Design Concepts.*

**Interaction** – Modeled individuals interacted simply by directing their movement towards groups of other individuals. Previous work with flocking birds has shown that

individuals remain in a group by tracking the location of just 6-7 closest neighbors (Ballerini et al. 2008a). Each modeled individual here therefore adjusted its bearing at each time step towards the mean of the seven closest individuals that were within its vision radius (set to 20 model cells). Unless the vision radius was set the extreme value of 1-2 model cells, varying the vision radius did not alter the results.

**Stochasticity** – Crabs were placed at random locations when the model was initialized. Additionally, the orders in which crabs readjusted their headings and moved was randomly shuffled each time step to avoid bias from the advantage of moving first.

**Observation** – Outputs used for analysis from each of the 1000 simulations included the proportion of highly exploratory crabs and proportion of non-exploratory crabs at the edge of a herd, as well as a histogram of the crab personality distribution. The proportions of extreme behavior types were determined by taking the 25% upper and lower activity levels, the same as in the field.

*-Initialization.* Simulations were conducted with 200 individuals. The personality of each individual was assigned randomly using a value drawn from an exponential distribution with a mean of 6.5, mimicking the distribution of personality types observed from our lab measurements described above (Wilcoxon Ranked-Sum test for comparison observed actual distribution and modeled distribution means:  $p=0.083$  and F-test for comparison of variance of distributions:  $p=0.085$ ). This assignment simulated a spectrum of different personality types from which the upper and lower 25% of the distribution were analyzed in order to be consistent with methods used in collection of lab/field data described above.

-*Input Data.* The environment was assumed to be constant. Therefore, the model had no input data.

## CHAPTER 3

### RESULTS

#### 3.1 LAB BEHAVIOR ASSAYS

Using the lab behavioral assessment (n=224), we found that *U. pugilator* personalities were skewed toward less active individuals with a long tail, suggesting relatively few very active or exploratory individuals (Fig. 3.1).

#### 3.2 FIELD SPATIAL POSITIONING

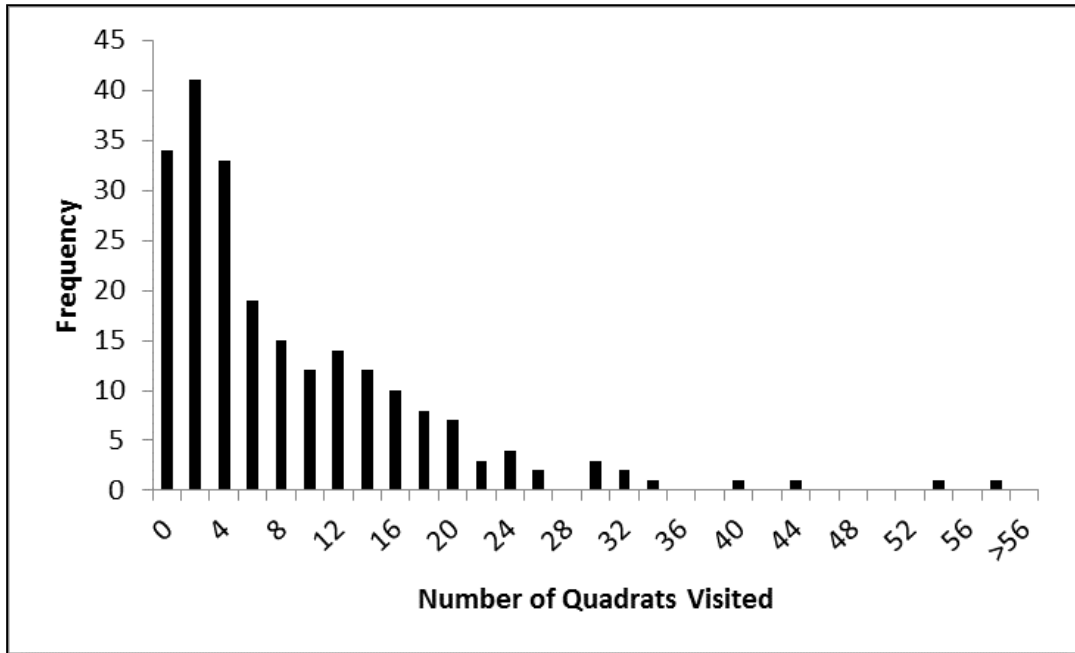
Model simplification based on AIC indicated that the proportion of time spent at the edge of a herd by marked crabs was best explained using personality as the only explanatory factor (Table 3.1). Specifically, there was a significant difference between the extreme personalities in the proportion of time spent on the edge of the herd ( $p < 0.001$ , null deviance = 183.12 with 101 degrees of freedom and residual deviance = 124.32 with 100 degrees of freedom, Fig. 3.2). Active individuals were at the periphery about 50% more of the time than less active individuals.

#### 3.3 MODEL TO EXPLORE MECHANISM

The model based on personality-dependent movement rates qualitatively replicated observed field patterns: highly active individuals spent a higher proportion of time at the periphery of the herd than less active individuals (Fig. 3.3). Quantitative results varied with parameter values (e.g., the visual field of the modeled individuals, the initial population, the number of neighbors that modeled individuals tracked, the radius

used to define center versus edge), but this did not change the overall pattern of active individuals being at the edge more than less active individuals.



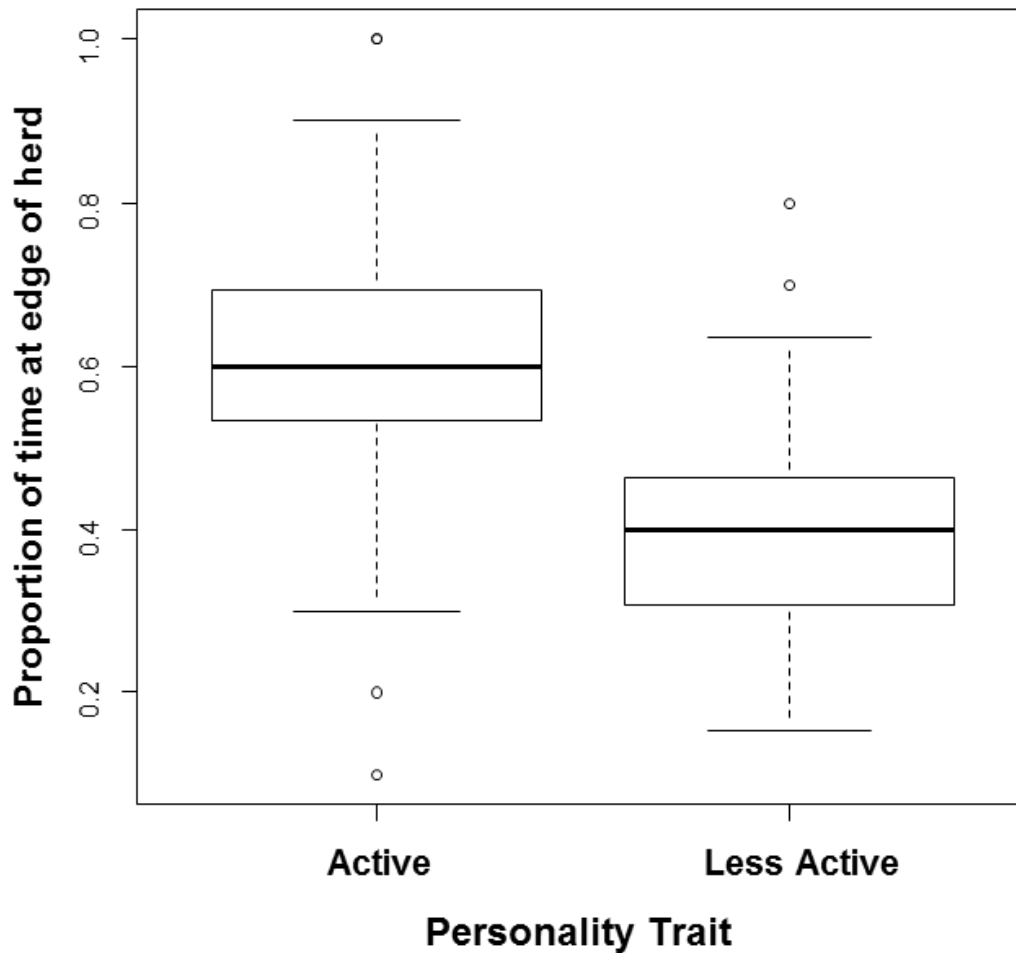


**Figure 3.1** Frequency distribution of the searching space (i.e. number of quadrats visited) *Uca pugilator* explored during the lab behavior assessment (n=224).

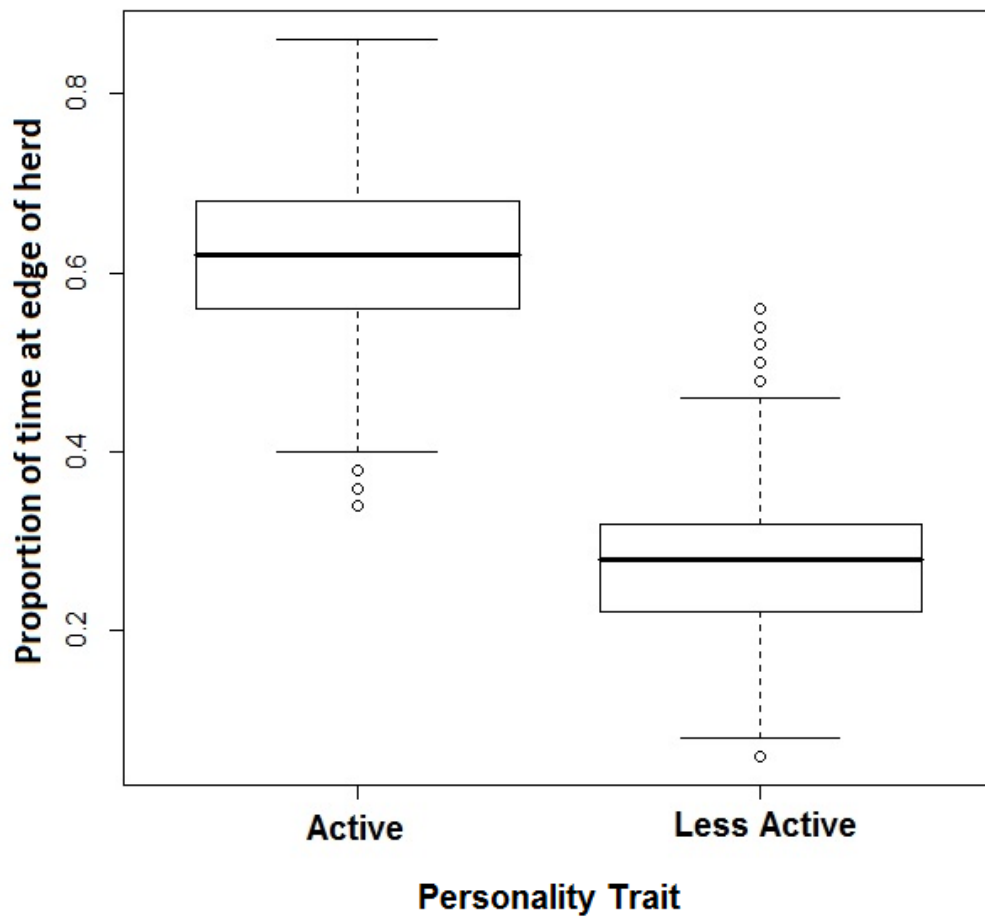
**Table 3.1** Model selection analysis for the effects of activity level (i.e. activity), carapace width, and sex on the proportion of time spent at the edge of a herd (i.e. Prop Location).

a) Stepwise-selection approach for model selection based on AIC using the `step` function of R. The best-fit and most parsimonious model is bolded. The colon (:) represents an interaction between the parameters it is linking. All main effects were included in models containing interactions. b) Output from the best-fit model. The asterisk (\*\*\*) represents <0.001 significance

<b>a) Information theoretic approach for model selection</b>			
<b>Model Type</b>	<b>General Model</b>		<b>AIC</b>
Null Model	Prop Location~1		474.89
Generalized Mixed-Effects Model	Prop Location~Activity:Carapace Width:Sex:(1 Date)		428.50
Generalized Linear Model	Prop Location~Activity:Carapace Width:Sex		427.68
Generalized Linear Model	Prop Location~Activity:Carapace Width +Activity:Sex + Carapace Width:Sex		425.69
Generalized Linear Model	Prop Location~Activity:Sex + Carapace Width:Sex		423.69
Generalized Linear Model	Prop Location~Activity + Carapace Width:Sex		421.70
Generalized Linear Model	Prop Location~Activity + Carapace Width + Sex		419.99
Generalized Linear Model	Prop Location ~ Activity + Carapace Width		418.12
<b>Generalized Linear Model</b>	<b>Prop Location~Activity</b>		<b>418.53</b>
<b>b) Model Output for best-fit model</b>			
<b>Parameter</b>	<b>Estimate</b>	<b>Standard Error</b>	<b>p Value</b>
Activity	-0.83886	0.113	<0.001 ***



**Figure 3.2** Boxplot showing the proportion of time at the edge of the herd for the two extreme behavior types of *Uca pugilator* (n=102; 51 per personality). The horizontal line is the median, with the box including the upper and lower quartiles of the data. The whiskers encompass 95% of the data, and the individual data points indicate outliers.



**Figure 3.3** Boxplots showing proportion of time at the edge of the herd for the two extreme behavior types of modeled individuals within the individual-based simulation model (replication=1000).

## CHAPTER 4

### DISCUSSION

We have demonstrated that active individuals are significantly more prone to be found on the periphery of *U. pugilator* herds while less active individuals tend to be found in the interior. Our model demonstrated that such positioning within a herd can be explained by simple differences in activity levels among individuals. Therefore, spatial positioning does not necessarily reflect active choice of relative location.

Personality distribution is an important factor to evaluate within a population because of its potential to influence dispersal (Dyer et al. 2009; Clobert et al. 2009; Cote et al. 2010; Cote et al. 2012; Keiser et al. 2014) and other population processes. As studied here, the personality distribution of the North Inlet *U. pugilator* herds were greatly shifted toward less active individuals. This is consistent with previously documented personality distributions at this same site (Decker and Griffen 2012). The predominance of less active individuals could reflect greater predation on periphery (i.e. more active) crabs during each generation, if predation was intense enough. For *U. pugilator*, predators (e.g. crabs, birds) frequently target members at the periphery of the group (Hamilton 1971; McLain et al. 2003; personal observation). Alternatively, the observed distribution may reflect the natal distribution of personalities and may therefore be an evolved population characteristic. Future studies could further examine whether predation shifts the distribution of personality-types by quantifying predation risk

experienced by individuals with different activity levels and that are located at different spatial positions within a herd.

The relative abundance of active and less active individuals within herding populations may be a factor contributing to herd size. Herd size is capable of being linked to multiple factors including local population density and structure of landscape (Gerard and Loisel 1995). The amount of time spent on the periphery of a herd could influence the behavior of an individual. As a result, this could potentially establish a positive feedback that helps to maintain animal personalities (Sih et al. 2015). As herd size varies, the amount of area on the periphery vs. in the center of the herd varies. More specifically, the periphery:center ratio is inversely related to herd size. Thus, it may be expected that the greater the proportion of low exploratory individuals, the larger will be the selfish herd; whereas if the personality distribution were shifted towards active individuals, herd size may be expected to decrease on average. This would be consistent with previous findings that bold sheep split into subgroups with smaller group sizes (Michelena et al. 2009).

Results of our model simulation illustrate how complex patterns can emerge from simple behavioral rules when these rules depend on personality type. Previous work shows that group properties and spatial dynamics in gregarious species can emerge from dynamics associated with individual personality (Couzin et al. 2005; Dyer et al. 2009; Harcourt et al. 2009; Cote et al. 2010; Cote et al. 2012; Keiser et al. 2014). Our field sampling supports these previous findings. However, our model demonstrates that complex patterns can emerge when individuals have personality-dependent behavior rules, and that complex patterns need not depend on active choice by individuals. Many

previous studies have employed simple or complex movement rules to model selfish herding (Viscido et al. 2002; James et al. 2004; Reluga and Viscido 2005; Morrell et al. 2010), but these models did not incorporate personality into the behavioral rules. Identifying personality-specific behavioral rules and building these rules into ecological theory may therefore enhance our ability to understand not only group dynamics such as selfish herding, but also ubiquitous ecological processes such as foraging or predator avoidance.

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