8-2013

INDIVIDUAL BEHAVIORAL VARIATION OF JUVENILE SPINY LOBSTER (*Panulirus argus*) DENNING BEHAVIORS AND THE ROLE IT PLAYS IN SHELTER COMPETITION DURING HABITAT LOSS

Katherine Heldt
Clemson University, kheldt@g.clemson.edu

INDIVIDUAL BEHAVIORAL VARIATION OF JUVENILE SPINY LOBSTER
(*Panulirus argus*) DENNING BEHAVIORS AND THE ROLE IT
PLAYS IN SHELTER COMPETITION DURING HABITAT LOSS

_____

A Thesis
Presented to
the Graduate School of
Clemson University

_____

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Biological Sciences

_____

by
Katherine A Heldt
August 2013

_____

Accepted by:
Dr. Michael J. Childress, Committee Chair
Dr. Margaret B. Ptacek
Dr. William C. Bridges Jr.
Dr. Rodney D. Bertelsen

ABSTRACT

       Variation in juvenile spiny lobster (*Panulirus argus*) aggressive and gregarious behaviors may play an important role in structuring population level interactions. Since aggressive and gregarious behaviors were not repeatable and were found to be highly correlated with size, these behaviors were found to be largely driven by a combination of behavioral plasticity and ontogeny. Although larger individuals were found to be the most aggressive and least gregarious individuals, often occupying crevice shelters by themselves, they did not exclude smaller, less aggressive lobsters from crevice shelters. Surprisingly, in shelter limited situations, small, less aggressive individuals were more likely to use dens and remain in dens, while large, more aggressive individuals were more likely to remain outside of dens and disperse. In general, larger individuals are able to walk longer distances in less time and are less likely to be preyed upon while away from shelter, suggesting that vulnerability may play an important role in the decision to share dens or disperse. Effects of prior experiences in natural shelter-rich or natural shelter-poor habitats were also found to influence denning behaviors with individuals from natural shelter-poor habitats better responding to sudden shelter loss. Therefore, prior experiences may also play an important role in denning behavior. This thesis provides evidence for behavioral ontogeny and plasticity in juvenile spiny lobster social behavior and is an important first step in understanding the role of individual behavioral variation in shelter competition and behavioral mitigation of habitat loss.

DEDICATION

This thesis is dedicated to my loving parents, Mark and Debra Heldt, who have supported and encouraged me to chase my dreams and aspirations. It is said that "life's roughest storms prove the strength of our anchors" (author unknown). My parents have guided me throughout my life, provided me with the means to overcome challenges that cross my path, and acted as my anchor when I have drifted; for this I will be forever grateful.

ACKNOWLEDGMENTS

TABLE OF CONTENTS

Table of Contents (Continued)

LIST OF TABLES

LIST OF FIGURES

List of Figures (Continued)

CHAPTER ONE

THE CARIBBEAN SPINY LOBSTER AND FLORIDA BAY STUDY SYSTEM

Summary

Behavioral plasticity, or the ability of animals to change behaviors in response to changes in the environment (Dewitt and Scheiner 2004), may be a way for populations to mitigate habitat loss (Crispo 2007). Animals can show behavioral plasticity by utilizing new habitat (Kramer-Schadt et al. 2011), using existing habitat in new ways (Macreadie et al. 2010), or increasing dispersal to remaining habitat (Robertson and Butler 2009). Studies across many taxa including dark-eyed juncos, western spadefoot toads, African antelope, European wild rabbits, red foxes, red squirrels, meadow voles, spackled wood butterfly, etc.(cited in Banks et al. 2007; Denver et al. 1998; Yeh and Price 2004) show that animals can exhibit behavioral plasticity during habitat loss events. For example, Robertson and Butler (2009) found that, in patchy habitats, Caribbean spotted spiny lobsters (*Panulirus guttatus*) were more likely to disperse to larger reefs than smaller reefs.

In Florida Bay, recent mass mortalities of seagrass and sponges have severely reduced the availability of protective crevice shelters for juvenile Caribbean spiny lobsters (*Panulirus argus*) (Butler et al. 1995; Childress and Bouwma in prep). Such a decrease in the availability of essential shelters may cause a decline in these species through increased predation (Smith and Herrnkind 1992; Childress and Herrnkind 1994), shelter competition (Childress

and Herrnkind 1997; Childress and Bouwma in prep) and/or disease transmission (Behringer et al. 2006; Behringer and Butler 2010). However, for species such as the Caribbean spiny lobster, behavior variation and plasticity in den sharing has the potential to mitigate this habitat decline through changes in patterns of shelter utilization (Childress and Herrnkind 1997; Childress and Bouwma in prep).

Previous studies have found that artificial shelters can mitigate the loss of natural shelters, but that lobsters rarely use these structures to their full capacity (Eggleston and Lipcius 1992; Herrnkind et al. 1997). Despite potential benefits from conspecific denning, in Florida Bay, nearly half of all juvenile lobsters are found in shelters alone (Davis and Dodrill 1982; Childress and Herrnkind 1997). Even after the recent mass sponge mortality dramatically decreased the number of crevice shelters available, the average number of lobsters per shelter remained constant and far below the maximum capacity of each shelter (Herrnkind et al. 1997; Childress and Bouwma in prep). These observations raise an important question about the variability of gregariousness among individuals. Do some spiny lobsters share dens more than others, and if so, what influences individual variation in patterns of den sharing and dispersal?

Since Caribbean spiny lobsters disperse and aggregate, understanding whether juvenile spiny lobsters can mitigate habitat loss may be particularly important (Durant 1998; Dobson and Poole 1998). An individual's response to stochastic events can vary greatly (Robinson et al. 1992), and in particular, post-

settlement movement can play a large role in population dynamics and community structure (Dayton 1971). By examining the individual behavioral variation of juvenile spiny lobster den sharing and dispersal, I was able to examine post-settlement behavior and determine the impacts of habitat loss on population dynamics and benthic community structure. By using field sites that have experienced sponge loss events (Butler et al. 1995; Fourqurean and Robblee 1999), I was able to gather valuable data on the juvenile life stage of an important fisheries species (Hunt 1994) without having to manipulate the natural environment.

Understanding the role of behavior in species survival is imperative for conservation and management plans (Caro 1998). By understanding the behavioral mechanism by which lobsters use and share crevice shelters, I can better predict the consequences of habitat loss in the Florida Bay nursery. In addition to understanding individual variation in denning behaviors, I also measured how patches of artificial structures influenced natural dispersal of individuals. McGregor and Peake (1998) noted the importance of identifying individuals in a population in conservation studies since individuals may vary behaviorally, and Sutherland et al. (1994) found that individual behavior can determine population structure and affect the response of a population to stochastic events. Since individuals within a population have the ability to vary behaviorally, predicting the consequences of habitat loss may be difficult, yet an important step in species conservation.

In this thesis, I examined the role of behavioral variation (temperaments, ontogeny, and plasticity) in aggressive and gregarious behaviors of juvenile Caribbean spiny lobsters to better understand the dynamics of den sharing under normal and reduced shelter conditions. I analyzed patterns of den sharing and dispersal for individuals from natural shelter-rich and natural shelter-poor habitats to determine whether spiny lobsters can behaviorally compensate. My proposed research involved interrelated laboratory and field experiments that examined behavioral variation. I hypothesized that spiny lobster social behavior (gregariousness and aggression) would be predicted by internal characteristics (such as sex, injury, size, molt history, etc.), and that variation in patterns of denning behavior (including den use, den sharing, and den fidelity) and dispersal would be the result of behavioral temperaments, behavioral ontogeny, and/or behavioral plasticity. I (1) characterized individual variation in aggression and gregarious behaviors in relation to internal characteristics, (2) experimentally examined den competition by determining the patterns of den use, den sharing, and den fidelity before and after a simulated shelter loss event, and (3) tracked individually marked juveniles in the field to estimate natural patterns of denning behavior and dispersal. By better understanding behavioral variation in juvenile spiny lobsters before and after habitat loss events, I will be able to better predict the impacts of habitat loss and examine possible restoration techniques, which is especially important for this economically and culturally important species.

Life History of the Caribbean Spiny Lobster

Caribbean spiny lobsters, *Panulirus argus*, are one of the most important commercially exploited species in the Caribbean (Hunt 1994). Their large size, fast growth, and wide range of habitats contribute to their extraordinary success in the face of strong fishing pressure (Forcucci et al. 1994). Their life history involves an alteration of stages from a long-lived planktonic phyllosoma larva (6-9 months) to a short-lived puerulus post-larva (1-2 weeks) that uses vertical migration behavior timed with incoming tides to actively seek shallow-water habitat for metamorphosis into the benthic juvenile stage (Herrnkind and Butler 1986; Butler et al. 2006). Newly settled juvenile lobsters are solitary and rely on crypsis while hiding in dense macroalgae to avoid predators (Andree 1981; Marx and Herrnkind 1985b). As these juveniles grow older (15-20 mm), they utilize the odor cues of conspecifics to help them transition to crevice shelters under sponges, corals, and soft corals (Childress and Herrnkind 1996; 2001a). Shelter choice depends on several factors including conspecific density (Mintz et al. 1994), predation levels (Eggleston and Lipcius 1992), the number and size of shelters (Eggleston et al. 1992), and the behavioral interactions between individuals (Berrill 1975; Childress and Herrnkind 1996; 1997; 2001a).

In the Florida Keys, spiny lobster settlement occurs primarily in the sponge-dominated hardbottom habitats of Florida Bay (Butler et al. 2006; Zito-Livingston and Childress 2009). One important factor that has altered the community structure of spiny lobster habitats has been the loss of juvenile

habitat, especially seagrass, soft corals, and sponges, and natural shelters (Butler et al. 1995). In the Middle Keys, Herrnkind et al. (1997) have shown that fewer lobsters used sponges as shelters after the 1993 sponge die-off than before and that lobsters were more likely to use artificial blocks and solution holes as shelters after the sponge die-off. It has also been shown that the shelter provided by seagrass and/or hardbottom habitats may protect early benthic lobsters from predation and is important to survival (Smith and Herrnkind 1992).

As spiny lobsters shift to hard-bottom habitat, they begin to aggregate and opportunities for conspecific interactions begin to arise (Marx and Herrnkind 1985a). Aggregation appears to be mediated by attraction to conspecific odors (Nevitt et al. 2000; Ratchford and Eggleston 2000). Thus, the presence of a conspecific in a shelter can serve as an attractant to other lobsters (Childress and Herrnkind 2001a; 2001b). Attraction to conspecific odors leads to the sharing of crevice shelters (Herrnkind et al. 1975; Berrill 1975; Childress and Herrnkind 1996) but does not necessarily mean that den sharing has a direct benefit (Childress and Herrnkind 2001a).

There are three ways that lobsters may potentially benefit from aggregation. First, lobsters may benefit by a reduction in exposure time while moving from one shelter to the next (Smith and Herrnkind 1992; Childress and Herrnkind 2001a). This guide effect hypothesis may be most important early on when juvenile lobsters are small and unable to coordinate their defenses against

predators (Childress and Herrnkind 2001b). Second, when sufficiently large, juvenile lobsters may benefit by coordinated group defense against potential predators that attack a den (Butler et al. 1999). Third, lobsters in dense aggregations may also benefit by a reduction in the per capita probability of successful attack (the dilution effect). Mintz et al. (1994) found that lobsters tethered in large shelters with many other lobsters have higher survival than lobsters tethered in large shelters with fewer than five conspecifics.

As abiotic and biotic conditions change, there can be differences within and between aggregations. Juvenile lobsters living in hardbotttom habitat spend most of the time during the day denning in shelters, while at night they forage (Herrnkind et al. 1975). Aggregations are formed during the day via denning behavior, during the night via foraging in the same habitat patches, and also during migratory queues (Herrnkind 1969). During denning, on average, two lobsters are seen per den (shown experimentally; Nevitt et al. 2000), but overall, a general Poisson distribution is followed for number of individuals per den (Childress and Herrnkind 1997; Herrnkind et al. 2001). These variations in aggregation behavior suggest that aggregations can be highly variable, with as many as 50% of juvenile lobsters in the Florida Bay nursery being found alone in shelters (Davis and Dodrill 1982; Childress and Herrnkind 1997).

As Caribbean spiny lobsters mature, they make their way from shallow water nursery habitat to patch reefs and eventually the reef tract (Kanciruk 1980). Other than the extensive work on the cues influencing the spectacular single-file

7

migration of adult lobsters with the approach of winter (Kanciruk and Herrnkind 1972; Herrnkind et al. 1972) very few studies have examined the daily and seasonal movement of adults on the reef tract. An acoustic tagging study of adult Caribbean spiny lobsters in the Western Sambo Ecological Reserve has shown that individual lobsters show high variability in their movement patterns, but overall tend to be most active at dawn and dusk and exhibit more movement at night than day (Bertelsen and Hornbeck 2009; Bertelsen 2013). Along with daily movement patterns, adult spiny lobsters also exhibit homing ability (Boles and Lohmann, 2003) and often return to the same foraging grounds (Bertelsen and Hornbeck 2009; Bertelsen 2013).

Decline of the Florida Bay Lobster Nursery

One of the greatest concerns for conservation biologists is the rate at which habitat loss is occurring. Habitat loss due to environmental stochasticity (storm events, pollution, predation, disease, habitat fragmentation, invasion, etc.) is a major contributor to the loss of genetic and species diversity of both plant and animal taxa (Scott 1988; Tews et al. 2004; Allendorf and Luikart 2007). Human activities have directly altered or indirectly impacted more than half of the earth's land and nearly all of the world's shallow marine habitats (UNEP 2002). For shallow-water marine communities, loss of habitat complexity is a major conservation concern (Airoldi et al. 2008; Thrush and Dayton 2002). This is particularly true for communities where corals (Nagelkerken et al. 2000) and

sponges (Bell 2008) serve as essential habitat for a majority of fish and invertebrate species. In the marine environment, studies on coral reefs (Graham et al. 2006) and coastal habitats (Wen et al. 2010) have shown that environmental stochasticity can result in at least one of the following: local extinctions, reduced species richness, loss of habitat complexity, and changes in functional group or community dynamics.

Predicting the consequences of habitat loss on species that utilize natural structure is not always easy. Impacts include not only the loss of physical structure through urbanization, agricultural erosion, and dredging of channels (UNEP 2002) but also the loss of key species that provide structure to entire communities such as redwoods (Cobb et al. 2012), kelp beds (Estes and Duggins 1995), and coral reefs (Moberg and Folke 1999). Many individuals such as cavity dwelling birds (Hagan et al. 1996), tropical forest insects (Golden and Crist 1999), and coral reef fishes (Wilson et al. 2006) often show remarkable resistance to the impacts of habitat loss, and the key to this resistance is often the behavioral variation of individuals in their habitat use (Agrawal 2001).

The primary nursery habitat for juvenile Caribbean spiny lobsters in Florida Bay (Butler et al. 2006) has been impacted by both anthropogenic and natural changes. Since juvenile spiny lobsters den in the hardbottom habitats of Florida Bay (Childress and Herrnkind 1996; 1997), it is important to understand whether lobsters can mitigate anthropogenic and natural impacts. Anthropogenic changes began when the Florida East Coast Railroad was built in the Florida

9

Keys during the period from 1905 -1930 and have continued in lower Florida by

the damming and altering of water flow entering and exiting the Everglades

system (Davis and Ogden 1997). For example, it has been estimated that Shark

Slough, a major contributor of freshwater entering Florida Bay, has experienced

almost a 59% decrease in water flow due to engineered flood control (Smith et al.

1989). These changes in water flow have most likely resulted in increased

salinities in Florida Bay, and since Florida Bay is especially shallow (<3 m), it

may be more easily impacted by future natural and anthropogenic changes. For

spiny lobsters, factors such as a lack of nursery habitat and hypersaline water

can limit post larval recruitment and overall habitat use (Field and Butler 1994).

Natural changes that have caused fluctuations in water clarity and quality of

Florida Bay in the past include temperature, storm intensity, amount of

precipitation, and nutrient levels (Fourqurean and Robblee 1999), and along with

overall altered water properties, specific habitats in Florida Bay have also been

negatively affected (Boesch et al. 1993).

Many natural habitats of Florida Bay, including mangrove, hardbottom,

coral reef, and seagrass, are being impacted by natural and anthropogenic

changes. Changes in climate, loss of species, increased nutrients, depletion of

natural habitat, and exploitation of resources have all negatively impacted

various regions of Florida Bay. Seagrass die-offs began in 1987 (Zieman et al.

1988), and algal blooms and increased turbidity between the fall of 1991 and the

summer of 1993 were proposed to be the cause of almost 100% mortality of

sponges in the genera *Speciospongia, Ircinia, Hippiospongia, Spinosella,* and *Vergangia* (Butler et al. 1995, Fourqurean and Robblee 1999). Coral bleaching began to occur in the 1980's (Jaap 1985; Williams et al. 1987), and along with disease impacts (Porter and Meier 1992), it resulted in a 13-29% decline in species richness (Porter and Meier 1992). During their time spent in hardbottom habitats, juvenile lobsters rely on natural shelters such as sponges and corals (Childress and Herrnkind 1996; 1997; Butler et al. 2006), and few studies have examined individual behavioral variation of juveniles and the impacts of habitat loss on their denning and dispersal behaviors. As vital ecological processing systems, the negative impacts on Florida Bay and its inhabitants are of concern. Since it is unlikely that natural and anthropogenic impacts will lessen, it is important understand the potential impacts of these environmental changes, and by understanding how spiny lobsters utilize nursery habitat, we may be able to better protect this species from experiencing a population decline.

Behavioral Variation and Hypotheses

       In general, species from across a wide range of taxa have been shown to exhibit variation in individual behavior (Dall et al. 2004), suggesting that individuals may be able to respond to environmental change in different ways. Individual variation in behavior can arise in several ways. First, behaviors may differ between individuals at the same life history stage (Sih et al. 2010). These fixed differences in individual behavior are often called behavioral temperaments

or personalities (Sih et al. 2010; Sih et al. 2004a). They may arise by frequency

dependent selection that favors different temperaments in different contexts (e.g.

foraging, predator avoidance, mating, etc.) (Sih et al. 2004b). For example, it

has been shown that great tits (*Parus major*) show individual differences in

exploration behavior (Dingemanse et al. 2002), and that fast explorers are more

aggressive towards conspecifics than slow explorers (Dingemanse et al. 2004).

Artificial selection of great tits has also shown that these behavioral syndromes

are heritable (Dingemanse and Reale 2005), and field studies have found that

environmental conditions between wet and dry years favor different behavioral

types (Dingemanse 2004). Second, behaviors may change during the

development of animals as they grow and mature (West-Eberhard 2005).

Variation due to behavioral ontogeny is often shaped by natural selection

favoring different behavioral strategies at each life history stage (Cole, 1954).

For example, bluegill sunfish (*Lepomis macrochirus*) and colonial web-building

spiders (*Metepeira incrassate*) exhibit ontogenetic behavioral changes as they

grow larger, shift in habitat use, and gain size refuge from predation (Rayor and

Uetz 1993; Werner and Hall 1988). Finally, behaviors may vary among

individuals in response to changes in environmental conditions (West-Eberhard

2005; Ghalambor et al. 2010). This behavioral plasticity occurs when individuals

alter their behaviors in response to changes in the environment (Ghalambor et al.

2010). For example, three-spined stickelbacks (*Gasteroseus aculeatus*) exhibit

behavioral plasticity in the amount of 'zigzag' dancing that is performed, and

when cannibalistic foraging groups are present, the amount of dancing is reduced (Foster 1995). Often these behavioral changes are favored by changes in the strength of selection (Ghalambor et al. 2010).

My thesis addressed several related hypotheses examining whether individual behavioral variation in patterns of lobster denning behavior and dispersal are a result of behavioral temperaments, behavioral ontogeny, and/or behavioral plasticity. Overall, I hypothesized that there would be variation in juvenile spiny lobster behavior (aggression and gregariousness). I expected that an individual's behavior would differ after environmental change (habitat loss) and could be predicted by internal characteristics (such as sex, injury, size, molt history, etc.). I predicted that, along with size and habitat loss, injury and molt status would be predictors of social behavior. Specifically, I predicted that injury would be a predictor of social behavior, with uninjured individuals being more gregarious than injured individuals since previous research has shown that individuals avoid sharing shelters with injured conspecifics (Parsons and Eggleston, 2005; Briones-Fourzan et al. 2008). I also predicted that molt history would be a predictor of social behavior, with recently molted individuals being less aggressive than unmolted individuals, since recently molted individuals are more vulnerable to injury (Lipcius and Herrnkind 1982). Three hypotheses and predictions associated with behavioral temperaments (repeatability), ontogeny (size), and plasticity (habitat type) then followed (Figure 1.1).
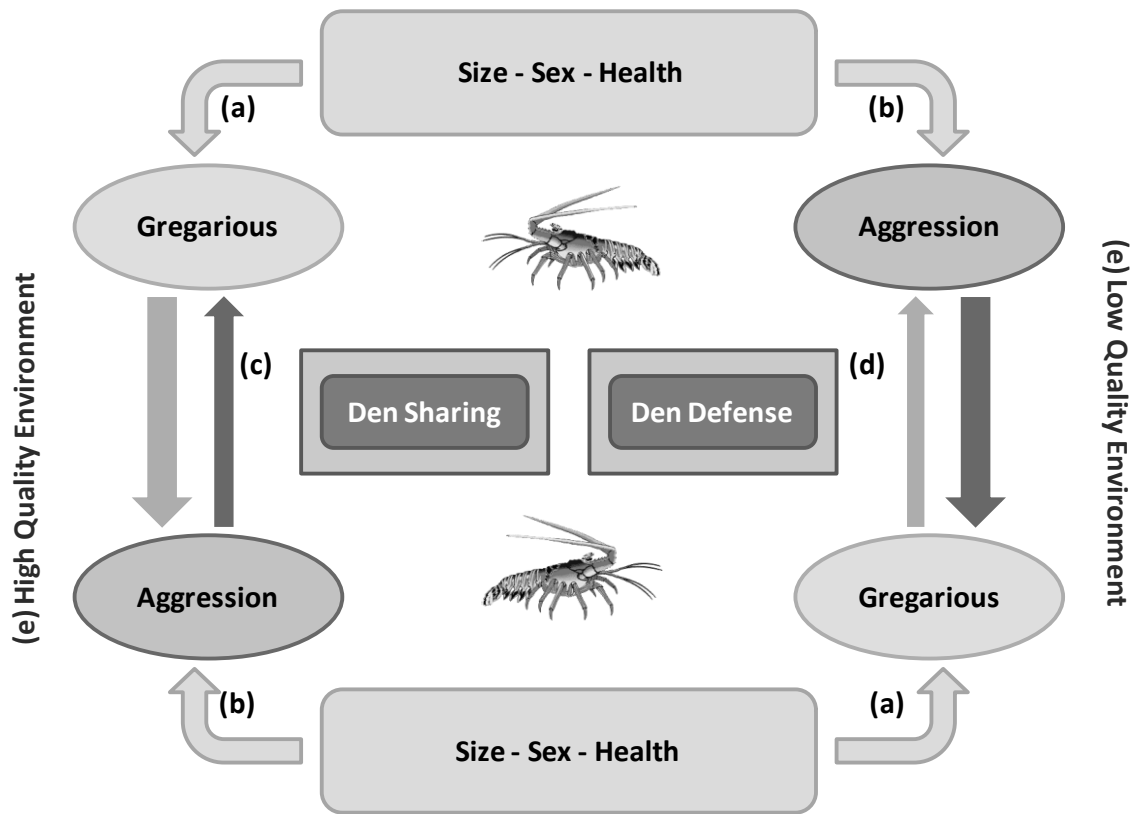
Figure 1.1: Predicted interactions of individual characteristics and social behavior. Individual characteristics, such as size, sex, injury, and molt history may impact the levels of (a) gregariousness and (b) aggression, which then impacts the final decision to (c) share dens or (d) defend dens. (e) Habitat quality or loss of shelters may also impact levels of aggression and gregariousness.

My first hypothesis is that variation in denning behavior and/or dispersal is the result of behavioral temperaments. A behavioral temperament occurs when individuals show consistent differences in their behaviors across situations and contexts (Sih et al. 2004a). For example, some individuals may consistently express higher aggression than other individuals in the population (Figure 1.2a). Although behavioral temperaments can constrain behavioral ontogeny and behavioral plasticity, they do not always do so (Sih et al. 2010). Behavioral expression can still change throughout ontogeny or across different environments so long as the individuals are consistent in their relative expression when compared to others in the population. When the slope of the reaction norm is zero and relative expression compared to others in the population is maintained, this behavior is considered canalized (Ghalambor et al. 2010), and the behavior is fixed across different environments (Figure 1.2a). Following this hypothesis, I predicted that individuals would have distinct levels of gregariousness and/or aggression. Specifically, I expected that variation in social behavior would be explained by time, size, and habitat type, such that aggression and gregariousness would be fixed through time, for individuals of different sizes, and for individuals from different habitat types. Individuals with fixed behaviors would favor distinct levels of aggression and gregariousness that would result in repeatable den defense and den sharing behaviors.
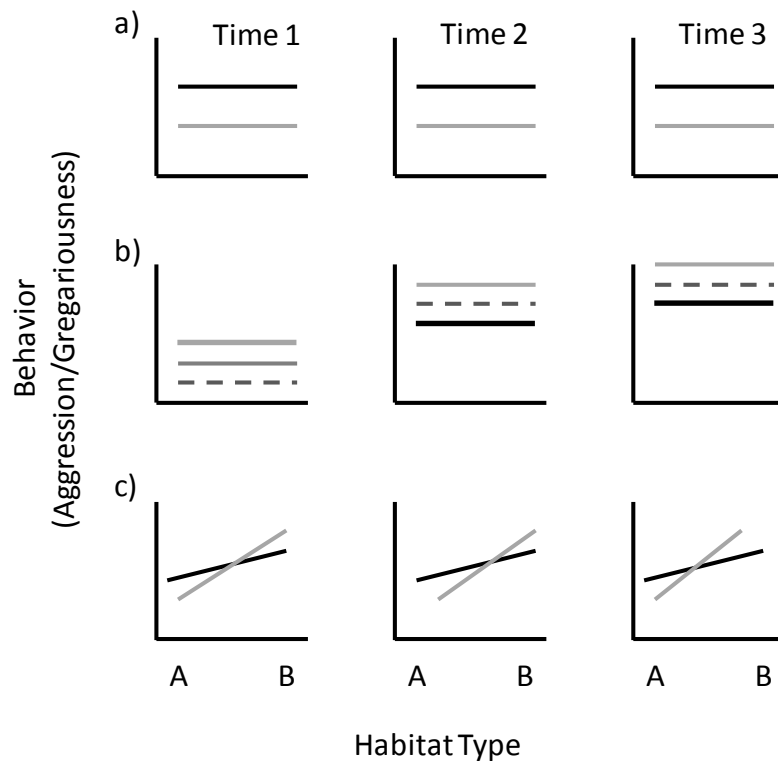
Figure 1.2: Reaction norm plots across time and habitat types.

(a) Individual variation that is repeatable among individuals across different habitat types represents behavioral temperaments. (b) Individual variation that changes across time represents behavioral ontogeny. (c) Individual variation that varies across different habitat types represents behavioral plasticity. These are not mutually exclusive as behaviors may vary in all three ways.

Figure 1.2: continued.

Traditionally, a reaction norm framework exhibits the quantitative response of an individual (or genotype) to changes in the environment, allowing one to look for genotype (G), environment (E), and genotype X environment (G X E) interactions (Stearns 1992). Here, individual variation in behaviors is illustrated by reaction norm plots or graphical representations of individual phenotypes (represented by the black, dark gray, and light gray lines) across time (time 1, 2, and 3) and in different habitat types (condition A and B) (Ghalambor et al. 2007).

My second hypothesis is that variation in denning behavior and/or dispersal is the result of behavioral ontogeny. Behavioral ontogeny occurs when behaviors change for individuals through time. For example, a behavior that is rarely expressed when individuals are young increases in expression with age (Stamps 2003). Behavioral ontogeny can constrain the expression of behavioral temperaments (Sih et al. 2010) or behavioral plasticity (Ghalambor et al. 2010), but it does not always do so (Figure 1.2b). For example, individuals with distinct behavioral temperaments may also show behavioral ontogeny as expression increases with age (Bell and Stamps 2004). Following this hypothesis, I predicted that individuals would have different levels of gregariousness and/or aggression that are size or age related. Specifically, I expected that variation in social behavior would be explained by the size of the individual, with larger individuals being more aggressive than smaller individuals. Large size would favor aggressive individuals resulting in increased den defense and decreased den sharing while small size would favor gregarious individuals resulting in decreased den defense and increased den sharing.

My third hypothesis is that variation in denning behavior and/or dispersal is the result of behavioral plasticity. Behavioral plasticity is often an adaptive response in which different behaviors are expressed in different environments. Such plastic responses are driven by natural selection favoring different optimal behaviors in different environments. Following this hypothesis, I predicted that individuals would have different levels of gregariousness and or aggression that

are habitat related. Specifically, I expected that variation in social behavior would be explained by habitat type regardless of ontogenetic differences, with individuals from natural shelter-rich habitats exhibiting increased gregariousness and individuals from natural shelter-poor habitats exhibiting increased aggression. High quality habitat, that is rich in natural crevice shelters, would favor gregarious individuals, and low quality habitat, that is lacking natural crevice shelters, would favor aggressive individuals. Decreased den sharing and increased den defense would occur when gregarious individuals are favored, and increased den sharing and decreased den defense would occur when aggressive individuals are favored. Plasticity can evolve when the environment is variable, environmental cues are reliable, each environment favors a different phenotype, and no phenotype has the highest fitness across all environments (Ghalambor et al. 2010) (Figure 1.2c). Behavioral plasticity has been found in many species (Miner et al. 2005), and individuals that are plastic can still exhibit behavioral temperaments or behavioral ontogeny.

In the remainder of this thesis, I present two experiments that examined behavioral variation in juvenile Caribbean spiny lobsters. In the second chapter, I present an experiment that examined whether variation in juvenile spiny lobster social and denning behavior is due to behavioral temperaments and/or behavioral ontogeny. Here, I examined behavioral temperaments and ontogeny by determining whether behavior is repeatable and/or influenced by size respectively. In the third chapter, I present an experiment that examined whether

variation in juvenile spiny lobster social behavior, denning behavior, and

dispersal is due to behavioral temperaments, ontogeny, and/or plasticity. The

presence of behavioral temperaments and/or plasticity was determined by

examining individual behavioral variation before and after a simulated shelter

loss events, and the presence of behavioral ontogeny was determined by

examining individual behavioral variation by size. In this chapter, I also

determined which characteristics (such as sex, habitat type, injury, size, molt

history, etc.) best explain social behavior, denning behavior, and dispersal before

and after a shelter loss event.

References

Agrawal, AA. 2001. Phenotypic plasticity in the interactions and evolution of species. Science 294(12): 321-325.

Airoldi, L, D Balata, and MW Beck. 2008. The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. Journal of Experimental Marine Biology and Ecology 366: 8-15.

Allendorf, FW and G Luikart. Units of conservation. In: Conservation and the Genetics of Populations. Blackwell Publishing, USA pp 380-420.

Andree, S. 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobster, *Panulirus argus*. Science thesis, FL State University.

Banks, SC, MP Piggott, AJ Stow and AC Taylor. 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology 85(10): 1065-1079.

Behringer, DC and MJ Butler. 2010. Disease avoidance influences shelter use and predation in Caribbean spiny lobster. Behavioral Ecology and Sociobiology 64: 747-755.

Behringer, DC, MJ Butler, JD Shields. 2006. Avoidance of disease by social lobsters. Nature 441: 421.

Bell, JJ. 2008. The functional role of marine sponges. Estuarine, Coastal, and Shelf Science 79(3): 341-353.

Bell, AM and JA Stamps. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. Animal Behaviour 68: 1339-1348.

Berrill, M. 1975. Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (crustacea:decapoda). Bulletin of Marine Science 25(4): 515-522.

Bertelsen, R. 2013. Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. Fisheries Research. In press.

Bertelsen, R and J Hornbeck. 2009. Using acoustic tagging to determine adult spiny lobster (*Panulirus argus*) movement patterns in the Western Sambo Ecological Reserve (Florida, United States). New Zealand Journal of Marine and Freshwater Research 43: 35-46.

Boesch, DF, NE Armstrong, CF D'elia, NG Maynard, HW Paerl, SL Williams. 1993. Deterioration of the Florida bay ecosystem: an evaluation of the scientific evidence. National Fish and Wildlife Foundation, National Park Service, South FL Water Management District: 1-32.

Boles, LC and KJ Lohmann. 2003. True navigation and magnetic maps in spiny lobsters. Nature 421: 60-63.

Briones-Fourzan, P, E Ramirez-Zaldivar, E Lozano-Alvarez. 2008. Influence of conspecific and heterospecific aggregation cues and alarm odors on shelter choice by syntopic spiny lobsters. Biological Bulletin 215(2): 182-190.

Butler, MJ, JH Hunt, WF Herrnkind, MJ Childress, R Bertelsen, W Sharp, T Matthews, JM Field, and HG Marshall. 1995. Cascading disturbances in Florida bay, USA: Cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 129: 119-125.

Butler, MJ, AB MacDiarmid, and JD Booth. 1999. The cause and consequenes of ontogenetic changes in social aggregations in New Zealand spiny lobsters. Marine Ecology Progress Series 188: 179-191.

Butler, MJ, RS Steneck, and WF Herrnkind. 2006.Juvenile and adult ecology. In: Lobster Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, UK pp 263-309.

Caro, T. 1998. The significance of behavioral ecology for conservation biology. In: Behavioral Ecology and Conservation Biology. Oxford University Press, NY pp 3-26.

Childress, MJ and PE Bouwma. In preparation. Assessing the impact of mass sponge mortality on a guild of shelter-dwelling commensals in Florida bay.

Childress, MJ and WF Herrnkind. 1994. The behavior of juvenile Caribbean spiny lobster in Florida bay: seasonality, ontogeny and sociality. Bulletin of Marine Science 54(3): 819-827.

Childress, MJ and WF Herrnkind. 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. Animal Behaviour 51: 675-687.

Childress, MJ and WF Herrnkind. 1997. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? Marine and Freshwater Research 48: 751-758.

Childress, MJ and WF Herrnkind. 2001a. The guide effect influence on the gregariousness of juvenile spiny lobsters. Animal Behaviour 62:465-472.

Childress, MJ and WF Herrnkind. 2001b. The influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. Marine and Freshwater Research 52: 1077-1084.

Cobb, RC, JAN Filipe, RK Meentemeyer, CA Gilliagan, and DM Rizzo. 2012. Ecosystem transformation by emerging infectious disease: loss of large tanoak from California forests. Journal of Ecology 100: 712-722.

Cole, LC. 1954. The population consequences of life history phenomena. The Quarterly Review of Biology 29(2): 103-137.

Crispo, E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. Evolution 61(11): 2469-2479.

Dall, SR, AI Houston, and JM McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7:734-739.

Davis, GE and JW Dodrill. 1982. Recreational fishery and population dynamics of spiny lobsters, *Panulirus argus*, in Florida bay, Everglades National Park, 1977-1980. Bulletin of Marine Science 44: 78-88.

Davis, SM and JC Ogden. 1997. Everglades: the ecosystem and its restoration. St. Lucie Press, FL.

Dayton, PK. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 361-389.

Denver, RJ, N Mirhadi, and M Phillips. 1998. Adaptive plasticity in amphibian metamorphosis: response of *Scaphiopus hammondii* tadpoles to habitat desiccation. Ecology 79(6): 1859-1872.

Dewitt, TJ and SM Scheiner. 2004. Phenotypic variation from single genotypes. In: Phenotypic Plasticity: Functional and Conceptual Approaches. Oxford University Press, NY pp 1-9.

Dingemanse, NJ. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society, Biological Sciences 271(1541): 847-852.

Dingemanse, NJ, C Both, PJ Drent, and JM Tinbergen. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. Proceedings of the Royal Society B 271: 847-852.

Dingemanse NJ, C Both, PJ Drent, K van Oers, and AJ van Noordwijk. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. Animal Behaviour 64: 929–937.

Dingemanse NJ and D Reale. 2005. Natural selection and animal personality. Behavior 142: 1159-1184.

Dobson, A and J Poole. 1998. Conspecific aggregation and conservation biology. In: Behavioral Ecology and Conservation Biology. Oxford University Press, NY pp 193-208.

Durant, S. 1998. A minimum intervention approach to conservation: the influence of social structure. In: Behavioral Ecology and Conservation Biology. Oxford University Press, NY pp 105-129.

Eggleston, DB and RN Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73(3): 992-1011.

Eggleston, DB, RN Lipcius, DL Miller, and L Coba Cetina. 1992. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Marine Ecology Progress Series 62: 79-88.

Estes, JA and DO Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs 65(1): 75-100.

Field, JM and MJ Butler. 1994. The influence of temperature, salinity, and postlarval transport on the distribution of juvenile spiny lobsters, *Panulirus argus* (Latreille, 1804), in Florida bay. Crustaceana 67(1): 26-44.

Forcucci, D, MJ Butler, and JH Hunt. 1994. Population-dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida bay, Florida. Bulletin of Marine Science 54(3): 805-818.

Foster, SA. 1995. Understanding the evolution of behaviour in threespine stickleback: the value of geographic variation. Behaviour 132: 1107-1129.

Fourqurean, JW and MB Robblee. 1999. Florida bay: a history of recent ecological changes. Estuaries 22(2B): 345-357.

Ghalambor, CK, LM Angelom, and SP Carroll. 2010. Behavior as phenotypic plasticity. In: Evolutionary Behavioral Ecology. Oxford University Press, NY pp 90-107.

Ghalambor, CK, JK McKay, SP Carroll, and DN Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21: 383-389.

Golden, DM and TO Crist. 1999. Experimental effects of habitat fragmentation on old-field canopy insects: community, guild and species responses. Oecologia 118(3): 371-380.

Graham, N, SK Wilson, S Jennings, N Polunin, JP Bijoux, and J Robinson. 2006. Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Sciences of USA 103(22): 8425-8429.

Hagan, JM, M Vander Haegen, and PS McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10(1): 188-202.

Herrnkind, WF. 1969. Queuing behavior of spiny lobsters. Science 164: 1425-1427.

Herrnkind, WF and MJ Butler. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 34: 23-30.

Herrnkind, WF, MJ Butler, and JH Hunt. 1997. Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. Marine and Freshwater Research 48(8): 759-769.

Herrnkind, WF, MJ Childress, and KL Lavalli. 2001. Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behaviour. Marine and Freshwater Research 52: 1113-1124.

Herrnkind, W, P Kanciruk, J Halusky, and R McLean. 1972. Descriptive characterizatoin of mass autumnal migrations of spiny lobster, *Panulirus argus*. Proceedings of the Gulf and Caribbean Fisheries Institute: 79-98.

Herrnkind, W, J Van Derwalker, and L Barr. 1975. Population dynamics, ecology, and behavior of spiny lobster, *Panulirus argus*, of St. John, U. S. Virgin Islands: Habitation and patterns of movements. Science Bulletin. Natural History Museum Los Angeles Co. 20(2): 31–45.

Hunt, JH. 1994. Status of the fishery for *Panulirus argus* in Florida. In: Spiny Lobster Management: Current Situation and Perspectives.Blackwell Scientific, Oxford, England pp158-168.

Jaap, W. 1985. An epidemic zooxanthellae expulsion during 1983 in the lower Florida Keys: Hypothermic etiology. 5th International Coral Reef Symposium 6: 143-148.

Kanciruk, P. 1980. Ecology of juvenile and adult Palinuridae (spiny lobsters). In: The biology and management of lobsters. London Academic Press, NY. pp 59-92.

Kanciruk, P and WF Herrnkind. 1972. Preliminary investigations of the daily and seasonal locomotor activity rhythms of the spiny lobster, *Panulirus argus*. Marine Behaviour and Physiology 1: 351-359.

Kramer Schadt, S, TS Kaiser, K Frank, T Wiegand. 2011. Analyzing the effect of stepping stones on target patch colonization in structured landscapes for Eurasian lynx. Landscape Ecology 26: 501-513.

Lipcius, RN and WF Herrnkind. 1982. Molt cycle alterations in behavior, feeding and diel rhythms of a decapods crustacean, the spiny lobster *Panulirus argus*. Marine Biology 68: 241-252.

Macreadie, PI, JS Hindell, MJ Keough, GP Jenkins, and RM Connolly. 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013-2021.

Marx, J and WF Herrnkind. 1985a. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. Journal of Crustacean Biology 5(4): 650-657.

Marx, J and WF Herrnkind. 1985b. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bulletin of Marine Science 36(3): 423-431.

McGregor, P and T Peake. 1998. The role of individual identification in conservation biology. In: Behavioral Ecology and Conservation Biology. Oxford University Press, NY pp 31-55.

Miner, BG, SE Sultan, SG Morgan, DK Padilla, and RA Relyea. 2005. Ecological consequences of phenotypic plasticity. TRENDS in Ecology and Evolution 20(12): 685-692.

Mintz, JD, RN Lipcius, DB Eggleston, and MS Seebo. 1994. Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance. Marine Ecology Progress Series 112: 255-266.

Moberg, F and C Folke. 1999. Ecological goods and services of coral reef ecosystems. Ecological Economics 29: 215-233.

Nagelkerken, I, G van der Velde, MW Gorissen, GJ Meijer, T van't Hoff, and C den Hartog. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science 51: 31-44.

Nevitt, G, ND Pentcheff, KJ Lohmann, and RK Zimmer. 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. Marine Ecology Progress Series 203: 225-231.

Parson, DM and DB Eggleston. 2005. Indirect effects of recreational fishing on behavior of the spiny lobster *Panulirus argus*. Marine Ecology Progress Series 303: 235-244.

Porter, JW and OW Meier. 1992. Quantification of loss and change in Floridian reef coral populations. American Zoology 32(6): 625-640.

Ratchford SG and DB Eggleston. 2000. Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. Animal Behaviour 59: 793-799.

Rayor, LS and GW Uetz 1993. Ontogenic shifts within the selfish herd-predation risk and foraging trade-offs change with age in colonial web-building spiders. Oecologia 95(1): 1-8.

Robertson, DN and MJ Butler. 2009. Variable reproductive success in fragmented populations. Journal of Experimental Marine Biology and Ecology 377(2): 84-92.

Robinson, GR, RD Holt, MS Gaines, SP Hamburg, ML Johnson, HS Fitch, and EA Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. Science 257: 524-526.

Scott, ME. 1988. The impact of infection and disease on animal populations: implications for conservation biology. Conservation Biology 2: 40-56.

Sih, A, A Bell, and J Chadwick Johnson. 2004a. Behavioral syndromes: an ecological and evolutionary review. TRENDS in Ecology and Evolution 19: 372-378.

Sih, A, AM Bell, J Chadwick Johnson and RE Ziemba. 2004b. Behavioral syndromes: an integrative overview. The Quarterly Review of Biology 79(3): 241-277.

Sih, A, A Bell and J Chadwick Johnson. 2010. Behavioral syndromes. In: Evolutionary Behavioral Ecology. Oxford University Press, NY pp 516-530.

Smith, TJ, HJ Hudson, MB Robbless, GN Powell and PJ Isdale. 1989. Freshwater flow from the Everglades to Florida bay: a historical reconstruction based on fluorescent banding in the coral *Solenastrea bournoni*. Bulletin of Marine Science 44(1): 274-282.

Smith, KN and WF Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. Journal of Experimental Marine Biology and Ecology 157: 3-18.

Stamps, J. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. Animal Behaviour 66:1-13.

Stearns, SC. 1992. Quantitative genetics and reaction norms. In: The Evolution of Life Histories. Oxford University Press, UK pp 39-71.

Sutherland, WJ and PM Dolman. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. Proceedings of the Royal Society London B 255: 133-138.

Tews, J, U Brose, V Grimm, K Tielborger, MC Wichmann, M Schwager and F Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31: 79-92.

Thrush, SF and PK Dayton. 2002. Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. Annual Review of Ecology and Systematics 33: 449-473.

UNEP. 2002. State of the environment and policy retrospective 1972-2002. In: Global Environmental Outlook 3. UN Publications, NY pp 62-89.

Wen, CK, MS Pratchett, KT Shao, KP Kan, and BK Chan. 2010. Effects of habitat modification on coastal fish assemblages. Journal of Fish Biology 77:1674-1687.

Werner, EE and DJ Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecological Society of America 63(5): 1352-1366.

West-Eberhard, MJ. 2005. Developmental plasticity and the origin of species differences. Proceedings of the National Academy of Sciences 102:6543-6549.

Williams, EC, C Goenaga, and V Vicente. 1987. Mass bleachings on Atlantic coral reefs. Science 238:877-878.

Wilson, SK, N Graham ,MS Pratchett, GP Jones, and N Polunin. 2006. Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient. Global Change Biology 12: 2220-2234.

Yeh, PJ and TD Price. 2004. Adaptive phenotypic plasticity and the successful colonization of a novel environment. American Naturalist 164(4): 531-542.

Zieman, JC, JW Fourqurean, MB Robblee, M Durako, P Carlson, L Yarbro, and G Powell. 1988. A catastrophic die-off of seagrasses in Florida bay and Everglades National Park: Extent, effect and potential cruises. Eos 69(44):1111.

Zito-Livingston, AN and MJ Childress. 2009. Does conspecific density influence the settlement of Caribbean spiny lobster *Panulirus argus* postlarvae? New Zealand Journal of Marine and Freshwater Research 43: 313-325.

CHAPTER TWO

INFLUENCE OF ONTOGENTY AND PLASTICITY ON SOCIAL BEHAVIOR IN
JUVENILE CARIBBEAN SPINY LOBSTERS

Introduction

It is well known that individuals vary in their behaviors (Darwin, 1859), but
often far less than the range of variation expressed in the population as a whole
(Dall et al. 2012). Behavioral specialization occurs when individuals respond to
environments and situations in different ways (Dall et al. 2004). In general,
variation in behavior can arise from genetic, environmental, or genetic by
environmental interactions and has been shown to vary by characteristics such
as sex, size, age, morphotype, etc. (Dall et al. 2012). The relationship between
physical or life history traits and behavior can be highly correlated or relatively
plastic depending on differences in variation among and within individuals and
can play an important role in species interactions (Sih et al,. 2004).

Current research suggests that individual behavioral variation plays an
important role in ecological and evolutionary processes. Wolf and Weissing
(2012) provide fourteen implications of intraspecific variation, suggesting that
maintaining intraspecific variation may be key in ecological and evolutionary
processes and that there may be both positive and negative consequences to
reduced behavioral variation. Sih et al. (2004a) express that consistent individual
differences in behavioral may impact ecological and evolutionary factors such as
individual fitness, species distribution, response to environmental change, and

speciation rates. The study of behavioral variation and behavioral differences is an essential part of many studies, in a variety of scientific fields (including animal psychology, behavioral genetics, pharmacology, animal husbandry, behavioral ecology, etc.), and is vital for understanding the ecological and evolutionary consequences of behavior (Reale et al. 2007).

Since social behavior is complex, as it involves the interaction of two or more individuals, it may be best understood when examined in various social contexts (mating, feeding, migrating, etc.) or situations (e.g. predator present, predator absent). Examining individual traits across multiple contexts and situations allows for better understanding of the role that temperaments, ontogeny, and/or plasticity play in explaining behavioral variation (Sih et al. 2004). For example, cannibalistic isopods (*Thermosphaeroma thermophilum*) were found to vary in levels of precannibalistic aggression based on their social partner (Bleakley et al. 2013), and individual phenotypes of group-living cichlids (*Neolamprologus plucher*) have been found to influence group dynamics and variation among social groups (Hamilton and Ligocki 2012).

Overall, species interactions rely on the ability of individuals to gather social information (Bonnie and Earley 2007). Social information may be communicated in a variety of ways, including through vocalizations, vibrations, chemical transmission, touch, visual displays, etc. (Herberholz 2007), and it is suggested that natural selection will favor individuals that are closely co-evolved in order to better receive and send information (Schaefer and Ruxton 2012). In

many studies, chemical odor cues have been shown to play a large role in social interactions (Hay 2009), and in crustaceans, odor cues that are released can impact decisions involving foraging, mating, aggression, and gregariousness (Herberholz 2007). At shelters, odor cues are utilized in order to mediate before fight and after fight interactions between individuals and reduce potential costs accrued during fighting (Atema and Cobb 1980). For spiny lobsters (*Panulirus argus*), odor cues also decrease the search time for shelter by guiding individuals towards dens and may ultimately result in decreased predation (Childress and Herrnkind 2001a). Exuded as a byproduct in their urine (Horner et a. 2006; Shabani et al. 2009), odors cues are often honest signals that have the potential to send information about the signaller (size, sex, age, social status, etc.) along with an indication of habitat quality by the presence of conspecific(s) (Atema and Steinbach 2007, Moore 2007, Childress 2007).

As a highly social species, both gregarious and aggressive behaviors are exhibited by Palinurid lobsters (Childress 2007). It has been shown that size (*Jasus lalandii*; Fielder 1965, *P. interruptus*; Roth 1972), sex (*P. interruptus*; Roth 1972), and body condition (*P. cygnus*; Atema and Cobb 1980) impact levels of aggression, suggesting that aggressive behaviors may be variable among individuals as well as between species. Gregarious behaviors in *P. argus*, such as aggregations during the day in shelters, at night for foraging and avoiding predation, and during long distance migratory cues, vary during the lifespan of Caribbean spiny lobsters (Herrnkind et al. 1975; Herrnkind 1969; Childress and

Herrnkind 1996). For example, postlarval lobsters live in isolation in macroalgae, but as benthic juveniles, they exhibit more gregariousness by sharing crevice shelter habitat (Andree 1981; Childress and Herrnkind 1994; Forcucci et al. 1994; Childress and Jury 2006).

Variation in behavior can lead to individual niche specialization and ultimately alter population and community level interactions (Bolnick et al. 2003; 2011). Gherardi et al (2012) suggest that few studies have examined behavioral consistency in crustaceans, and social behavior for *P. argus* has been previously described in detail for adults, but little documentation of juvenile behavior has been reported. Therefore, it is important to understand whether behavior is repeatable for *P. argus* (behavioral temperaments) and how behavior varies throughout the lifespan of an individual (behavioral ontogeny).

There are several potential explanations for why behavioral variation may arise and be maintained in spiny lobsters. First, spiny lobsters may have fixed differences in behavior between individuals at the same life history stage. These fixed differences in individual behavior, often called behavioral temperaments or personalities (Sih et al. 2010; Sih et al. 2004a), occur when individuals show repeatable differences in their behaviors across situations and contexts (Sih et al. 2004a). Repeatable behavior exists for example, when some individuals in a population are consistently more aggressive than other individuals in the population. Although behavioral temperaments can constrain behavioral ontogeny (or vice versa), they do not always do so (Sih et al. 2010), and

behavioral expression can still change throughout ontogeny or across different environments so long as the individuals change behavior in a consistent manner (Bell and Stamps 2004).

Second, behaviors may change during the ontogeny of an animal as they grow and mature (West-Eberhard 2005). Behavioral ontogeny occurs when behaviors change for individuals through time, and the relative expression of behavior differs when compared to others in the population (Stamps 2003). For example, an individual may exhibit low levels of aggression at a young age or small size and may exhibit high levels of aggression at a old age or large size. Natural selection may shape behavioral ontogeny as different behavioral strategies are favored at each life history stage (Cole, 1954). *P. argus* exhibits ontogenetic behavioral changes by altering habitat preferences from algae, to hard bottom habitat, then ultimately coral reef habitat (Herrnkind and Butler 1986; Butler et al. 2006; Andree 1981; Marx and Herrnkind 1985b; Childress and Herrnkind 1996; 2001a). Recently, it has become important to examine behavioral differences among individuals in order to determine the role of within and between individual variation, and it is a necessary step in examining whether behavioral variation among individuals is the result of behavioral temperaments and/or ontogeny (Dingemanse and Dochtermann 2013).

This study will address several related hypotheses regarding individual behavioral variation in aggressive and gregarious behaviors of juvenile spiny lobsters. Overall, I hypothesize that there is variation in juvenile spiny lobster

social behavior (aggression and gregariousness) and make two predictions. If variation in aggressive and gregarious behavior is the result of behavioral temperaments, I predict that individuals will have distinct levels of gregariousness and/or aggression that are repeatable through time. If variation in aggressive and gregarious behavior is the result of behavioral ontogeny, I predict that individuals will have different levels of gregariousness and/or aggression that are size or age related.

Methods

Collection and Housing

During 2010-2012, three "collections" of juvenile *P. argus* (Table 2.1) were taken from Florida Bay (Figure 2.1) by hand net and shipped to Clemson University Aquatic Facilities, Clemson, SC. I recorded each lobster's size (mm CL), sex, and molt stage (premolt, intermolt, and postmolt; Forcucci et al. 1994) and examined each lobster for presence of injuries (missing legs, antennae, telson damage). Each individual received a uniquely-coded cable tie ID tag that was placed around the base of either the right or left antennae. Pairs of similar-sized lobsters (+/- 2 mm CL) were assigned a 150 liter housing tank with a single artificial crevice shelter and allowed to acclimate for one week. Lobsters housed together in the same housing tank were designated "familiar" lobsters, while lobsters housed in separate housing tanks were designated

Table 2.1: "Collection" parameters. Information for three "collections" of juvenile spiny lobsters. KML 1, KML3, and KML4 "collections" were collected within the Florida Keys National Marine Sanctuary either in the fall or spring seasons. Each individual measured (CL mm), sexed, and checked for injury and disease.

"collection"	Site	n	Season	Size Range (+/- SE)	Sex Ratio (M:F)
KML1	KML	16	Fall	39.4 (+/-1.597)	1.29
KML3	MTM/PNT	10	Fall	36.76 (+/-0.497)	1.5
KML4	KML/BPT	20	Spring	39.11 (+/-0.899)	1.67
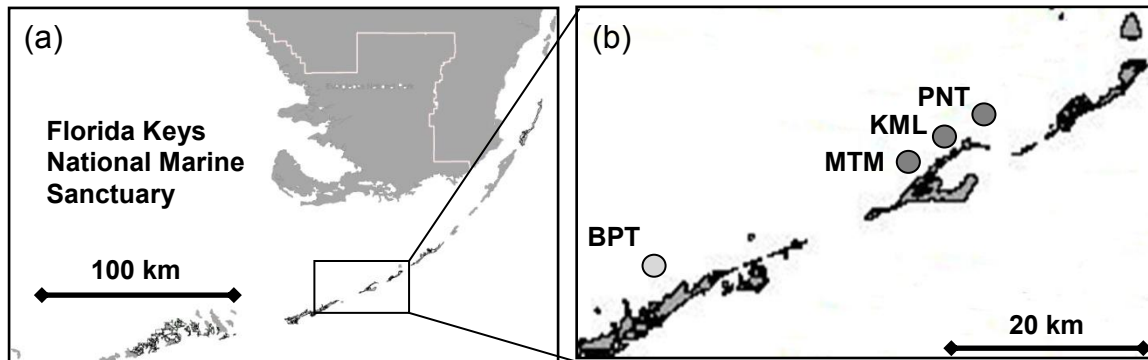
Figure 2.1: Map of collection sites. (a) All individuals were collected from within the Florida Keys National Marine Sanctuary. (b) The three collection locations were PNT, MTM, KML, and BPT. Gregarious and aggressive behaviors were examined for each "collection" gathered.

"unfamiliar". Any lobsters that exhibited a chalky-white hemolymph were assumed to be infected with PaV1 (Shield and Behringer 2004) and were excluded from this study. Pairs were assigned without consideration of sex since it has been shown that sheltering behavior is not sex-specific (Zimmer-Faust et al. 1985). Salinity was kept at 35 ± 2 ppt. using artificial seawater (Instant Ocean®), and the room temperature was maintained between 19-21ºC. For initial observational purposes (of "collection" KML), the room lighting was phase-shifted six hours, and a 12 h:12 h light:dark cycle was maintained. After initial observations, all other lobsters (of "collection" PNT and BPT) were kept in a greenhouse under natural lighting conditions via South Carolina's light:dark cycle, and the room temperature was allowed to fluctuate between 25-35 ºC. This wide temperature range was a result of daily temperature fluctuations in the greenhouse which are similar to daily temperature fluctuations for Clemson, SC. All "collections" and room combinations were statistically examined for as a block design in the analyses. Lobsters were fed frozen shrimp daily. All molting events were recorded, and after molting, lobsters were retagged and remeasured.

Behavioral Measures of Aggression

Aggressive behaviors were measured for two "collections" of juvenile spiny lobsters (KML1 and KML3). To measure the frequency of aggressive acts (antennae whips, antennae pushes, body pushes; Bouwma 2006), lobsters were

observed once a day, at night, for ten minutes using a focal animal sampling rule and a continuous observation recording rule (Martin and Bateson 1993). Observations were completed for seven days. All aggressive acts were summed across the seven days, and the average number of aggressive acts that occurred per day was calculated. The aggression levels of each individual were measured once after entering the lab (time 1) then again after a molting event or 3 months, whichever occurred first (time 2). Linear regressions were used to examine the influence of time and size on aggressive behavior, and ANOVAs were used to examine model terms for significance (JMP 10). The average number of aggressive acts was the dependent variable and time, "collection," and size were independent variables. To meet the assumptions of normality, aggression data were square root transformed. Repeatability for aggression was determined by dividing between-individual variation by the total variation (sum of between-individual and within-individual variation) from the ANOVA analysis.

Behavioral Measures Gregariousness

As one measure of gregariousness, den sharing was determined for two "collections" of juvenile spiny lobsters (KML1 and KML3). The proportion of time spent in the den was recorded twice a day (once in the morning and once at night) by determining the location of each individual within the aquarium. Individuals utilizing the den at the same time were considered sharing dens. Individuals utilizing the den alone or not utilizing the den at all were considered

not sharing dens. Den sharing was recorded for a total of seven days (14

observations), and to determine average den sharing, morning and night

observations were summed and divided by the total number of observations.

Linear regressions were used to examine the influence of time and size on den

sharing behavior, and ANOVAs were used to examine model terms for

significance (JMP 10). Average den sharing was the dependent variable and

time, "collection," and size were independent variables. Repeatability for

gregariousness was determined by dividing between-individual variation by the

total variation (sum of between-individual and within-individual variation) from the

ANOVA analysis.

As an additional measure of gregariousness, three "collections" of juvenile

spiny lobsters (KML1, KML3, and KML4) were tested in a Y-maze to determine

odor preference. Lobsters that molted were allowed three days to recover before

being used in Y-maze trials. Y-maze trials were randomized with each Y-maze

trial containing an emitting lobster and a choosing lobster. For KML1 and KML3,

single choice tests (odor/no odor) were completed between pairs of familiar

lobsters and unfamiliar lobsters. For example, a choosing lobster completed

three y-maze trials, one that contained a familiar odor cue and two that contained

a single unfamiliar odor cue. For KML4, single choice tests (odor/no odor) were

completed between a pair of home aquaria. For example, a choosing lobster

completed two y-maze trials, one with odor cues from a home aquarium that

contained one familiar lobster and another with odor cues from a home aquarium that contained two unfamiliar lobsters.

For "collections" KML1 and KML3, the emitting lobster (unfamiliar or familiar) was removed from its housing tank with a hand-net and was placed in the back compartment of the maze (Box 1 or 2; Figure 2.2). For "collection" KML4, a small aquatic pump was placed into the emitting lobster's home aquarium (unfamiliar or familiar), and the odor cue was pumped into the back compartment of the maze. The emitting lobster or odor cue tube was randomly placed in the left/right box of the maze. Then, the choosing lobster was removed from its tank with a hand-net and placed into a tray that retained water and floated in its home tank for ten minutes. The tray containing the choosing lobster was placed in the gated area of the maze, and the lobster was slowly released to avoid stressful responses (such as tail flipping). After five minutes of acclimation, the gate was removed.

All trials were time lapse recorded (one frame/30sec) at night under red light. Previous research has shown that lobsters do not see red lighting and use of red lighting is preferred for nocturnal animals (Weiss et al. 2006). All video was analyzed using Adobe Premier Elements 3.0, the Noldus Observer program and a frame reader (Contour® shuttlexpress). The proportion of time spent in each side of the Y-maze across 12 hours and final den choice was recorded. The proportion of time spent in each side of the maze was determined by adding the amount of time spent in each side and den of the maze and dividing by the

41
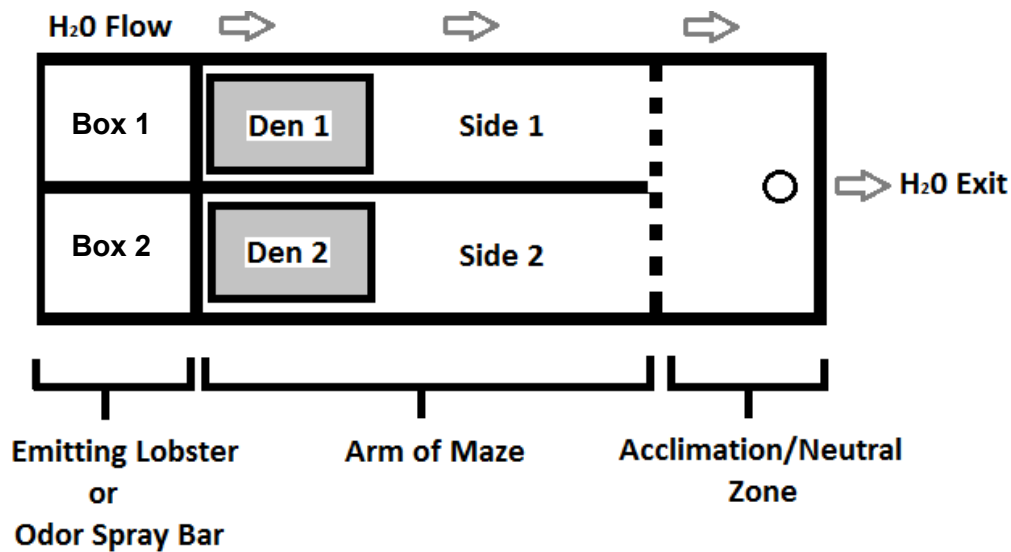
Figure 2.2: Diagram of the Y-maze. An overhead view of the 1.21 m x 0.34 m Y-maze that was used to determine odor preference in juvenile spiny lobsters. Emitting lobsters were placed or pumped odor cues were released into box 1 or 2 and choosing lobsters were placed in the acclimation zone. Each side of the Y-maze contained a den so that denning behavior could be observed. For KML1 and KML3 "collections", the water exited the mechanical filter, entered the maze above the emitting lobster boxes, flowed through the maze and out to the reservoir (75 gallons) and was re-circulated back into the filter. For the KML4 "collection", odor cues were dripped into the back of the maze via an aquatic pump (MiniJet404 at 106gph) and flowed through the maze and out to the reservoir without re-circulation.

total trial time. For example, if the odor was emitted from box 1, then the proportion of time spent in the odor side of the maze was a sum of the amount of time spent in side 1 plus den 1 of the maze, and this sum was then divided by the total trial time (Figure 2.2). Final den choice was determined by recording which den the individual was located in at the end of the trial. After completing trials with "collection" KML1, preliminary data suggested that 1 hour trials were representative of 12 hour trials, and odor preference for the remainder of individuals was determined across 1 hour. All Y-maze trials were completed for each individual once after entering the lab (time 1) and once after a molting event or after 3 months, whichever occurred first (time 2). Linear regressions were used to examine the influence of time and size on odor preference, and ANOVAs were used to examine model terms for significance (JMP 10). Average odor preference was the dependent variable and time, "collection," and size were independent variables. To meet the assumptions of normality, den sharing was arcsine square root transformed. Repeatability for odor preference was determined by dividing between-individual variation by the total variation (sum of between-individual and within-individual variation) from the ANOVA analysis.

Results

Growth

Most individuals exhibited normal signs of growth during captivity (Figure 2.3a). Significant "collection" x time interactions ($F_{1,2}=4.578$, $p=0.016$) were found for

Figure 2.3: Effect of time on size, aggression, den sharing, and odor preference. The (a) size, (b) aggression, (c) den sharing and (d) odor preferences for individuals in three spiny lobster "collections" across time. KML1 is represented by circles, KML3 by squares and KML4 by triangles. The average size, behavior, and slope is represented by a solid line (KML1), dashed line (KML3), and dotted line (KML4). *Data were square root transformed to meet the assumptions of normality. **Data were arc sine square root transformed to meet the assumptions of normality

Table 2.2: Examination of repeatability in size, aggression, and gregariousness. "Collection" level and time effects and their interactions were examined for size and aggressive and gregarious behaviors. The F-ratio and p-value are reported along with measures of repeatability (reported as a 95% confidence level).

Source	Size		Aggression		Den Sharing		Odor Preference	
df	(1,2)		(1,1)		(1,2)		(1,2)	
	F	P	F	P	F	P	F	P
"Collection"	0.326	<0.001**	1.255	0.274	43.550	<0.001**	4.324	0.020*
Time	91.384	<0.001**	0.415	0.536	0.327	0.572	0.394	0.534
P x T	4.578	<0.001**	49.158	<0.001**	0.012	0.913	0.842	0.438

Variances	Size	Aggression	Den Sharing	Odor Preference
Between-Individual	16.964	0.023	0.005	0.031
Within-Individual	3.059	0.063	0.041	0.155
Repeatability (95% CI)	0.847	0.267	0.109	0.167
(Upper 95% CI)	0.454	-0.149	-0.288	-0.451
(Lower 95% CI)	1.240	0.678	0.518	0.471

size, and time was highly significant ($F_{1,2}$=91.384, p=<0.001). Overall, size increased through time, and repeatability was high for growth (Table 2.2).

Behavioral Measures of Aggression

There was a significant "collection" x time interaction ($F_{1,1}$=49.158, p=<0.001), and average aggression for KML1 increased through time while average aggression for KML3 decreased through time (Figure 2.3b). Variation seen within the individual was higher than variation seen between individuals, and repeatability was low (Table 2.2). Average aggression was higher for larger individuals than smaller individuals (Figure 2.4a). Aggression was significantly correlated with size for "collections" KML1 ($F_{1,30}$=5.560, p=0.025) and KML4 ($F_{1,18}$=4.860, p=<0.041) but not KML3 (Table 2.3).

Behavioral Measures of Gregariousness

A significant "collection" difference was found for average den sharing ($F_{1,2}$=43.550, p=<0.001;Figure 2.3c). Average den sharing was significantly higher for KML1 than KML3 and did not significantly change through time. Between-individual variation in average den sharing was lower than within-individual variation, and repeatability was low (Table 2.2). Average den sharing was higher for larger individuals than smaller individuals (Figure 2.4b), and average den sharing was significantly correlated with size only for "collection" KML 4 ($F_{1,18}$=5.891, p=0.026; Table 2.3).

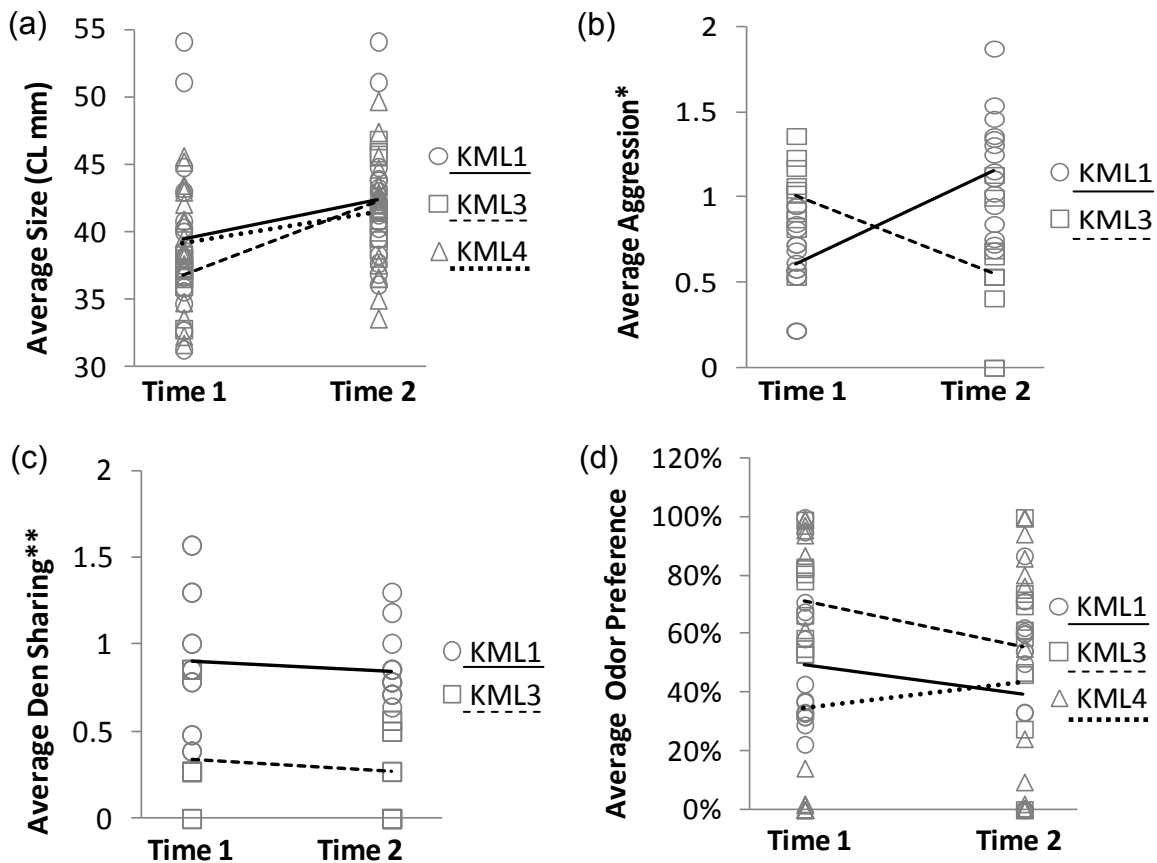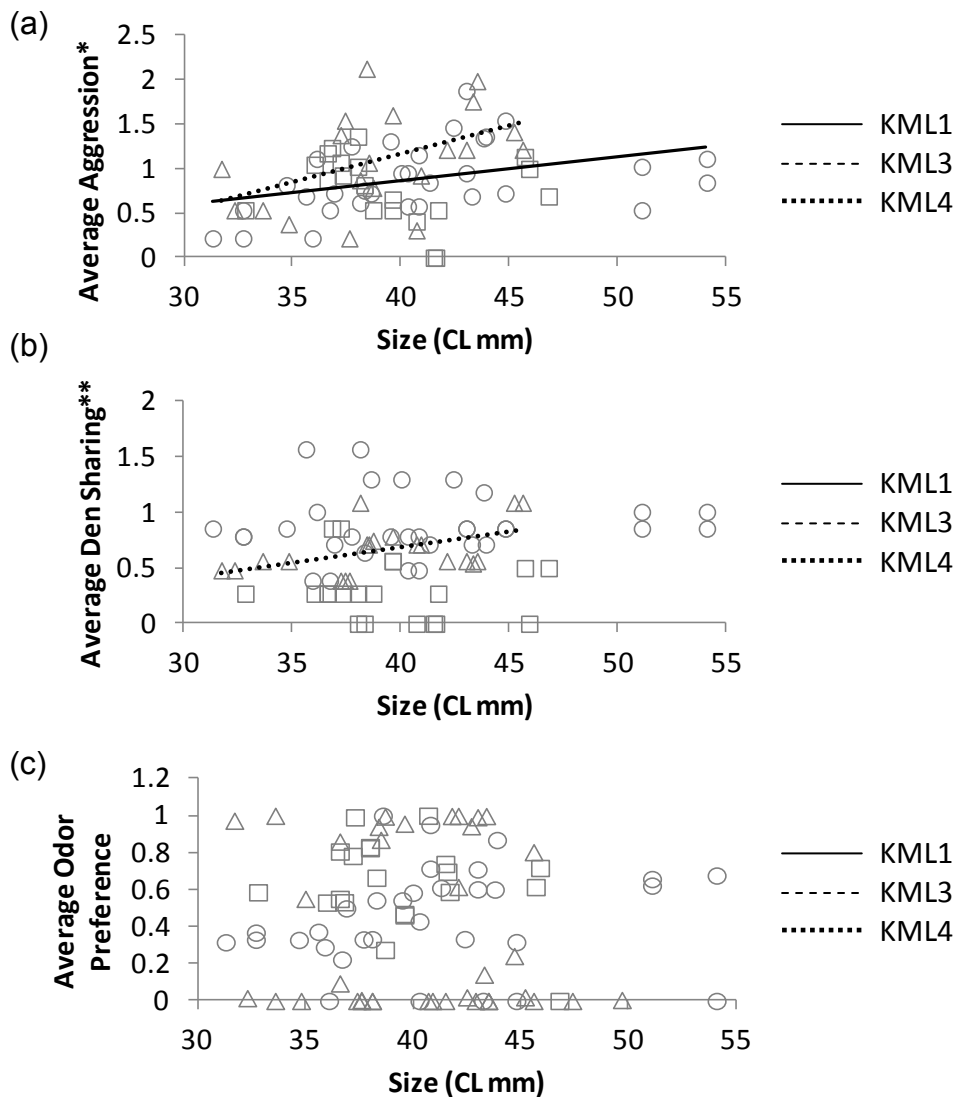**Figure 2.4: Effect of size on aggression, den sharing, and odor preference.**

The (a) aggression, (b) den sharing, and (c) odor preferences for individuals in

three spiny lobster "collections" compared by size. KML1 is represented by

circles, KML3 by squares and KML4 by triangles. Significant correlations are

represented by a solid line (KML1), dashed line (KML3) or dotted line (KML4).

Table 2.3: ANOVAs for aggressive and gregarious behavior. ANOVAs were used to determine the effects of size on three behaviors (aggression, den sharing and odor preference). Time was not likely to be a significant factor that influenced behavior, so data were pooled from time 1 and time 2.

Behavior	"collection"	df	F-value	P-value
Aggression	KML1	1,30	5.560	0.025*
	KML3	1,18	0.779	0.389
	KML4	1,18	4.860	0.041*
Den Sharing	KML1	1,30	0.149	0.703
	KML3	1,18	0.256	0.620
	KML4	1,18	5.891	0.026*
Odor Preference	KML1	1,30	0.633	0.433
	KML3	1,18	1.441	0.246
	KML4	1,35	0.545	0.465

No effects of familiarity were found, and therefore, all Y-maze odor preference trial data were combined for analyses. Proportion of time spent in the side of the Y-maze was highly correlated with final den choice ($R^2=0.619$; $p<0.001$); Therefore, proportion of time was used for further gregariousness analyses. Average odor preference was highest for KML3 and was significantly different by "collection" ($F_{1,2}=4.324$, $p=0.020$; Figure 2.3d). Time did not significantly influence average odor preference. Between-individual variance for average odor preference was again lower than within-individual variance, and repeatability was low (Table 2.2). Average odor preference was not correlated with size for any "collections" (Figure 2.4c and Table 2.3).

Discussion

I examined whether or not juvenile Caribbean spiny lobsters exhibit individual behavioral variation in social behavior, and whether variation in social behavior is the result of behavioral temperaments and/or behavioral ontogeny. To determine whether aggressive and gregarious behaviors were the result of behavioral temperaments, behavioral ontogeny, or a combination of both, I examined both the influence of time and size, respectively, on these related behaviors. Variation in aggressive and gregarious behaviors of juvenile spiny lobsters was found, and individuals differed greatly in their levels of aggressive and gregarious behaviors through time. Given the variation in behavioral responses within a "collection", aggressive and gregarious behaviors were not

highly repeatable across time and it is unlikely that individuals exhibited behavioral temperaments.

Although no prior studies examining repeatability in juvenile spiny lobster behavior exist, a few studies on other crustaceans have found evidence for repeatable behavior across time. Studies on hermit crabs, fiddler crabs, crayfish, and crabs have shown that behaviors are repeatable (cited in Gherardi et al. 2012). Hermit crabs have been particularly well studied and have been shown to exhibit behavioral temperaments in a variety of situations and contexts (Gherardi et al. 2012). For example, for hermit crabs, it has been shown that 1) relative expression of startle behavior when compared to others in the population remains the same across situations (Briffa et al. 2008), 2) individuals exhibit repeatability in startle responses across high and low-risk situations (Briffa and Bibost, 2009), and 3) individuals retain their boldness levels regardless of shell conspicuousness (Briffa and Twyman, 2011). More recent studies have also shown that higher levels of aggression in hermit crabs are also correlated with boldness and exploratory behavior across situations suggesting that, in hermit crabs, behavioral temperaments are a result of a suite of traits (Mowles et al. 2012). Although hermit crabs exhibit behavioral temperaments, evidence for behavioral plasticity has also been found, since behavior varies with predation risk (Briffa et al. 2008). For juvenile spiny lobsters, I found no evidence for repeatable behavior suggesting that, unlike hermit crabs, juvenile lobsters are not

50

consistent in behavior, and rather, the differences in behavior found seem to be explained by behavioral ontogeny or effects of size.

I found that variation in social behavior (aggression and den sharing) was the result of behavioral ontogeny. It was not surprising to find evidence for behavioral ontogeny in social behavior since distinct ontogenetic habitat shifts and associated shifts in behavior are exhibited throughout the lifespan of *P. argus* (Andree 1981; Marx and Herrnkind 1985a; Kanciruk 1980; Bertelsen and Hornbeck 2009; Bertelsen 2013). Smaller juveniles (15-20 CL mm) have recently migrated from algal beds and have experienced recent shifts in behavior from an asocial to social lifestyle (Andree 1981; Marx and Herrnkind 1985b; Childress and Herrnkind 1996; 2001a) while larger individuals (~45 mm CL), on the other hand, are about to enter adulthood which is associated with shifts towards coral reef habitat and deep-water migrations (Kanciruk 1980; Kanciruk and Herrnkind 1972; Herrnkind et al. 1972; Bertelsen and Hornbeck 2009; Bertelsen 2013). It has been suggested that maintaining behavioral variation may be important for ontogenetic niche shifts (Childress and Herrnkind 2001b), and since Caribbean spiny lobsters exhibit distinct shifts in habitat use, maintaining behavioral variation may be helpful for surviving habitat transitions, especially in a changing environment (Schlaepfer et al. 2010).

Specifically, I found that larger individuals were more aggressive and more likely to share dens than smaller individuals. Conspecific interactions throughout the lifespan of *P. argus* may partially explain the variation seen in social behavior

and why this variation in behavior is related to size. Post algal lobsters are more active in presence of conspecifics (Childress and Herrnkind 1994), suggesting that gregarious and aggressive interactions may change with social group dynamics. Work by Enquist and Leimar (1983) suggests that the size of individuals interacting during fights may play an important role in determining fighting strategies. Hence, there may be some adaptive value for smaller individuals that are less aggressive and more gregarious, and for crustaceans, it is well known that size plays an important role in the decision to fight an opponent (Briffa and Sneddon, 2007). For *P. argus*, a highly social crustacean, aggressive behavior may also play a role in den sharing, since larger, more aggressive individuals have the potential to exclude smaller, less aggressive individuals from sharing shelters.

Although one measure of gregariousness, den sharing, was correlated with size, a second measure of gregarious behavior, odor preference, was not explained by behavioral ontogeny. Overall, odor preference was highly unpredictable and fell much lower than prior measures of odor preference. Briones-Fourzan et al. (2008) found that ~80% of individuals tested in y-maze trials were attracted to conspecific odor cues, and Ratchford and Eggleston (1998) found that ~85% of individuals tested in y-maze trials were attracted to conspecific odors cues from larger lobsters. Studies completed using the same experimental procedures at Clemson University facilities have shown that after seven years, odor preference has decreased (Sercy 2005; Appendix A).

Previous studies have shown between ~75% preference for dens emitting odor (Sercy 2005) in Y-maze trials, while recent odor trials suggest that odor preference has significantly decreased to less than 50%. Variation in attraction in odors may be important for dealing with environmental changes and supports the adaptive value of maintaining variation in aggressive and gregarious behaviors.

As a first look at behavioral variation in juvenile spiny lobsters, this study provides evidence showing that aggressive and gregarious behaviors are not consistent through time and that aggressive and gregarious den sharing behaviors are related to size. This study finds a lack of evidence for behavioral temperaments, and rather, suggests that behavioral ontogeny may best explain variation among individuals for aggressive and gregarious behaviors in juvenile spiny lobsters. The differences between "collections" coupled with ontogenetic effects and low repeatability measures suggest that prior experiences may influence aggressive and gregarious behaviors and that some individuals may be more plastic in their behavioral responses than others. If behavioral plasticity is the driving force for behavioral variation among juvenile spiny lobsters, I would predict that individuals would have different levels of gregariousness and or aggression that are habitat related suggesting that individuals experiencing different habitat types may behave differently. Although behavioral plasticity has been found in many species (Miner et al. 2005), it is not the only factor playing a role in behavioral variation, and individuals that are plastic can still exhibit

behavioral temperaments or behavioral ontogeny (Sih et al. 2010). To better understand the relationship between behavioral ontogeny and plasticity, future studies examining juvenile Caribbean spiny lobster individual behavioral variation across various contexts and situations will be important.

Evidence suggests that individual behavioral variation has become increasingly important in understanding how species will adapt to habitat changes. Since variation in behavior can impact population structure and population responses, it is important to identify the responses of individuals within a population as single entities (McGregor and Peake 1998; Sutherland and Dolman 1994) in order to better predict the consequences of habitat change. Examining the ecological and evolutionary role of individual behavioral variation in the life history strategies of species may be imperative for the conservation, management, and overall survival of species, especially in disturbed environments. As an economically and culturally important species, understanding behavioral differences in the Caribbean spiny lobster will allow us to better understand whether this species has the potential to mitigate environmental change.

References

Andree, S. 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobster, *Panulirus argus*. Science thesis, FL State University.

Atema, J and JS Cobb. 1980. Social behavior. In: The Biology and Management of Lobsters. London: Academic Press, NY pp 409-450.

Atema, J and MA Steinbach. 2007. Chemical communication and social behavior of the lobster, *Homarus americanus*, and other decapod Crustacea. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 115- 144.

Bell, AM and JA Stamps. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. Animal Behaviour 68: 1339-1348.

Bertelsen, R. 2013. Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. Fisheries Research. In press.

Bertelsen, R and J Hornbeck. 2009. Using acoustic tagging to determine adult spiny lobster (*Panulirus argus*) movement patterns in the Western Sambo Ecological Reserve (Florida, United States). New Zealand Journal of Marine and Freshwater Research 43: 35-46.

Bleakley, BH, SM Welter, K McCauley-Cole, SM Shuster, and AJ Moore. 2013. Cannibalism as an interacting phenotype: precannibalistic aggression is influenced by social partners in the endangered Soccorro isopod (*Thermosphaeroma thermophilum*). Journal of Evolutionary Biology 26: 832-842.

Bolnick, DI, R Svanback, JA Fordyce, LH Yang, JM Davis, CD Hulsey and ML Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. The American Naturalist 161(1): 1-28.

Bolnick, DI, P Amarasekare, MS Araujo, R Burger, JM Levine, M Novak, VHW Rudolf, SJ Schreiber, MC Urban, and DA Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26(4): 183-192.

Bonnie, KE and RL Early. 2007. Expanding the scope for social information use. Animal Behaviour 74(2): 171-181

Bouwma, PE. 2006. Aspects of antipredation in *Panulirus argus* and *Panulirus Guttatus*: behavior, morphology, and ontogeny. Electronic Theses, Treatises and Dissertations. Paper 3466.

Briffa, M and A Bibost. 2009. Effects of shell size on behavioural consistency and flexibility in hermit crabs. Canadian Journal of Zoology 87: 597-603.

Briffa, M, SD Rundle, and A Fryer. 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab Pagurus bernhardus. Proceedings of the Royal Society B 275: 1305-1311.

Briffa, M and LU Sneddon. 2007. Physiological constraints on contest behavior. Functional Ecology 21: 627-637.

Briffa M and C Twyman. 2011. Do I stand or blend in? conspicuousness awareness and consistent behavioral differences in hermit crabs. Biological Letters 7: 330-332.

Briones-Fourzan, P, E Ramirez-Zaldivar, and E Lozano-Alvarez. 2008. Influence of conspecific and heterospecific aggregation cues and alarm odors on shelter choice by syntopic spiny lobsters. Biological Bulletin 215(2): 182-190.

Butler, MJ, RS Steneck, and WF Herrnkind. 2006.Juvenile and adult ecology. In: Lobster Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, UK pp 263-309.

Childress, MJ. 2007. Comparative sociobiology of spiny lobsters. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 271-293.

Childress, MJ and WF Herrnkind. 1994. The behavior of juvenile Caribbean spiny lobster in Florida bay: seasonality, ontogeny and sociality. Bulletin of Marine Science 54(3): 819-827.

Childress, MJ and WF Herrnkind. 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. Animal Behaviour 51: 675-687.

Childress, MJ and WF Herrnkind. 2001a. The guide effect influence on the gregariousness of juvenile spiny lobsters. Animal Behaviour 62:465-472.

Childress, MJ and WF Herrnkind. 2001b. The influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. Marine and Freshwater Research 52: 1077-1084.

Childress, MJ and SH Jury. 2006. Chapter 3: Behaviour. Lobsters: Biology, Management, Aquaculture and Fisheries: 78-112.

Cole, LC. 1954. The population consequences of life history phenomena. The Quarterly Review of Biology 29(2): 103-137.

Dall, SR, AM Bell, DI Bolnick and FL Ratnieks. 2012. An evolutionary ecology of individual differences. Ecology Letters 15: 1189-1198.

Dall, SR, AI Houston, and JM McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7:734-739.

Darwin, C. 1859. On the origin of species. Clowes and Sons, London.

Dingemanse NJ and NA Dochtermann. 2013. Quantifying individual variation in behavior: mixed effect modeling approaches. Journal of Animal Ecology 82:39-54.

Enquist M and O Leimar. 1983. Evolution of fighting behavior: decision rules and assessment of relative strength. Journal of Theoretical Biology 102: 387-410.

Fielder, DR. 1965. The spiny lobster, *Jasus lalandei* (H. Milne-Edwards), south Australia. Australian Journal of Marine and Freshwater Research 15: 133-144.

Forcucci, D, MJ Butler, and JH Hunt. 1994. Population-dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida bay, Florida. Bulletin of Marine Science 54(3): 805-818.

Gherardi, F, L Aquiloni, and E Tricarico. 2012. Behavioral plasticity, behavioral syndromes and animal personality in crustacean decapods: an imperfect map is better than no map. Current Zoology 53(4): 567-579.

Hamilton, IM and IY Ligocki. 2012. The extended personality: indirect effects of behavioural syndromes on the behaviour of others in a group-living cichlid. Animal Behaviour 84: 659-664.

Hay, ME. 2009. Marine chemical ecology: chemical signals and cues structure marine populations, communities, and ecosystemros. Annual Review of Marine Science 1: 193-212.

Herberholz, J. 2007. The neural basis of communication in crustaceans. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 71-89.

Herrnkind, WF. 1969. Queuing behavior of spiny lobsters. Science 164: 1425-1427.

Herrnkind, WF and MJ Butler. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 34: 23-30.

Herrnkind, W, P Kanciruk, J Halusky, and R McLean. 1972. Descriptive characterizatoin of mass autumnal migrations of spiny lobster, *Panulirus argus*. Proceedings of the Gulf and Caribbean Fisheries Institute: 79-98.

Herrnkind, W, J Van Derwalker, and L Barr. 1975. Population dynamics, ecology, and behavior of spiny lobster, *Panulirus argus*, of St. John, U. S. Virgin Islands: Habitation and patterns of movements. Science Bulletin. Natural History Museum Los Angeles Co. 20(2): 31–45.

Horner, AJ, SP Nickles, MJ Weissburg, CD Derby. 2006. Source and specificity of chemical cues mediating shelter preference of Caribbean spiny lobsters (*Panulirus argus*). Biological Bulletin 211: 128-139.

Kanciruk, P. 1980. The biology and management of lobsters: ecology of juvenile and adult Palinuridae (spiny lobsters). Academic Press, NY. 2: 59-92.

Kanciruk, P and WF Herrnkind. 1972. Preliminary investigations of the daily and seasonal locomotor activity rhythms of the spiny lobster, *Panulirus argus*. Marine Behaviour and Physiology 1: 351-359.

Martin, P and P Bateson. 1993. Recording methods. In: Measuring Behavior an Introductory Guide. Cambridge University Press, pp 84-100.

Marx, J and WF Herrnkind. 1985a. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. Journal of Crustacean Biology 5(4): 650-657.

Marx, J and WF Herrnkind. 1985b. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bulletin of Marine Science 36(3): 423-431.

McGregor, P and T Peake. 1998. The role of individual identification in conservation biology. In: Behavioral Ecology and Conservation Biology. Oxford University Press, NY pp 31-55.

Miller, SD. 2012. Effects of disease and ocean acidification on the den sharing behavior of juvenile Caribbean spiny lobster, *Panulirus argus*. Clemson University Calhoun Honors Undergraduate Thesis. Clemson, SC pp 1-55.

Miner, BG, SE Sultan, SG Morgan, DK Padilla, and RA Relyea. 2005. Ecological consequences of phenotypic plasticity. TRENDS in Ecology and Evolution 20(12): 685-692.

Moore, PA. 2007. Agonistic behavior in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive encounters and dominance. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 90-114.

Mowles, SL, PA Cotton, and M Briffa. 2012. Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs. Behavioral Ecology and Sociobiology 66: 1087-1094.

Ratchford, SG and DB Eggleston. 1998. Size- and scale-dependent chemical attraction contribute to an ontogenetic shift in sociality. Animal Behaviour 56: 1027-1034.

Reale, D, SM Reader, D Sol, PT McDougall, and NJ Dingemanse. 2007. Integrating animal temperament within ecology and evolution. Biological Reviews 82: 291-318.

Roth, AC. 1972. Agonistic behavior and its relationship to group density, size differences, and sex in the California spiny lobster, *Panulirus interruptus*. M.S. Thesis, San Diego State University, San Diego, California: 1-78.

Schlaepfer, MA, PW Sherman, and MC Runge. 2010. Decision making, environmental change, and population persistence. In: Evolutionary Behavioral Ecology. Oxford University Press, UK pp 506-515.

Schaefer, HM and GD Ruxton. 2012. By-product information can stabilize the reliability of communication. Journal of Evolutionary Biology 25: 2412-2421.

Sercy, K. 2005. Towards an understanding of the proximate and ultimate mechanisms of the interspecific variation in spiny lobster gregariousness. Calhoun Honors Thesis Clemson University: 1-29.

Shabani, S, M Kamio, and C Derby. 2009. Spiny lobsters use urine-borne olfactory signaling and physical aggressive behaviors to influence social status of conspecifics. Journal of Experimental Biology 212: 2464-2474.

Shield,JD and DC Behringer. 2004. A new pathogenic virus in the Caribbean spiny lobster, *Panulirus argus*, from Florida. Diseases of Aquatic Organisms 59: 109-118.

Sih, A, A Bell, J Chadwick Johnson. 2004a. Behavioral syndromes: an ecological and evolutionary review. TRENDS in Ecology and Evolution 19: 372-378.

Sih, A, A Bell, and J Chadwick Johnson. 2010. Behavioral syndromes. In: Evolutionary Behavioral Ecology. Oxford University Press, NY pp 516-530.

Sutherland, WJ and PM Dolman. 1994. Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. Proceedings of the Royal Society London B 255: 133-138.

Stamps, J. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. Animal Behaviour 66:1-13.

Weiss, HM, E Lozano-Alvarez, P Briones-Fourzan, and F Negrete-Soto. 2006. Using red light with fixed-site video cameras to study the behavior of the spiny lobster, *Panulirus argus*, and associated animals at night and inside their shelters. Marine Technology Society Journal 40(3): 86-95.

West-Eberhard, MJ. 2005. Developmental plasticity and the origin of species differences. Proceedings of the National Academy of Sciences 102: 6543-6549.

Wolf, M and FJ Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology and Evolution 27(8): 452-461.

Zimmer-Faust, RK, JE Tyre, and JF Case. 1985. Chemical attreaction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. The Biological Bulletin 169: 106-118.

CHAPTER THREE

THE ROLE OF JUVENILE SPINY LOBSTER DENNING BEHAVIOR IN
SHELTER COMPETITION AND MITIGATION OF HABITAT LOSS

Introduction

Habitat selection theory predicts that individuals will choose the most
suitable habitat and that this optimal choice may ultimately impact survival and
overall fitness (Grinnell 1917; Jones 2001). When choosing a habitat, animals
must not only consider factors such as habitat quality, predation risk, and prey
availability, but they must also consider the impacts of conspecific interactions
(Valone 2007). But what happens when preferred habitats are suddenly
degraded due to natural or anthropogenic disturbance? Do animals remain in
sub-optimal habitat, disperse to seek habitats that are less impacted, and/or alter
behavior to mitigate negative consequences?

Individuals impacted by habitat loss have the potential to fall into
ecological traps, as cues become decoupled from habitat quality, resulting in
poor decisions that may impact overall fitness (Schlaepfer et al. 2010). An
ecological trap occurs when poor habitat (associated with negative population
growth rate) is preferred over resource-rich habitat (associated with positive
population growth rate) as a result of sudden habitat changes that alter the
reliability of cues that indicate resource quality or the ability of organisms to
disperse to more suitable habitats (Gilroy and Sutherland 2007). Selection of
poor-quality habitat may result in decreased survival, reduced ability to produce

offspring, and local population extinction (as seen in birds; Gilroy and Sutherland 2007). Individuals that are closely evolved to their surrounding habitat or individuals that exhibit fixed behaviors may be unable to adapt to sudden and rapid habitat changes (Gilroy and Sutherland 2007), and several studies have shown the negative impacts of ecological traps, especially in birds and arthropods (Kokko and Sutherland 2001). Species that fall into ecological traps may be further impacted via behaviorally-mediated Allee effects resulting in decreased population growth (Kokko and Sutherland 2001).

Not all animals, however, fall into an ecological trap during sudden loss of habitat. In fact, it has been shown that animals can be rescued from ecological traps via natural selection and/or adaptations such as phenotypic plasticity (Kokko and Sutherland 2001). A recent focus of research has been on examining the ability of animals to recognize and choose between combinations of altered, novel, or familiar environmental conditions and determining the possible consequences of habitat change (Robertson & Hutto, 2006). In evolutionary biology, natural selection is the process by which variation in traits are maintained and produced across generations (Fox and Westneat 2010). Natural selection occurs, for example, when populations move towards new habitat preferences and these preferences are maintained in future generations. In contrast, biological adaptation is the result of change within a generation. These "short-term" adaptations (phenotypic plasticity) allow for changes in gene expression depending on environmental conditions (Fox and Westneat 2010).

Since natural selection is a "long-term" process, adaptation in individual behavior and social behavior may be important when dealing with environmental change.

Modification of individual behavior via adaptation may be a result of behavioral plasticity, or the ability of animals to change behaviors in response to changes in the environment (Dewitt & Scheiner 2004). Behavioral plasticity may be another way for individuals to mitigate habitat change or loss (Crispo 2007). Animals can exhibit behavioral plasticity by utilizing new habitats (Kramer-Schadt et al. 2011), using existing habitats in new ways (Macreadie et al. 2010), or increasing dispersal to remaining habitats (Robertson et al. 2009). For example, nesting behavior in birds has been shown to be plastic, and in high-risk predation areas, birds alter their behavior by nesting in more concealed areas (Eggers et al. 2006; Peluc et al. 2008). Studies across many taxa, including insects, crustaceans, amphibians, birds and mammals, show that animals can exhibit behavioral plasticity in response to habitat loss events (Banks et al. 2007).

Another potential mechanism of response to sudden habitat loss is change in social behavior. Due to spatial and temporal changes in individual habitat use, intraspecific variation within social systems may develop, as seen in mice (Schradin and Pillay 2005) and freshwater trout (Alanara et al. 2001), resulting in altered behavioral interactions (Lott 1984). For example, in South African striped mice (*Rhabdomys pumilio*), spatial changes in habitat use have altered levels of sociality and reproductive ability (Schradin and Pillay 2005). Specifically, social striped mice that live in the succulent karoo have been shown

to exhibit group living with populations that contain sexually mature individuals that do not reproduce. This is in stark contrast to territorial mice that have been shown to live solitarily in the grasslands with home ranges up to ten times larger than social mice, and in grassland populations, social interactions occur only during mating (Schradin and Pillay 2005). For brown trout (*Salmo trutta*), temporal changes in habitat use have led to decreased resource competition, and dominant trout were found to be more likely to feed at dusk (when resources were rich), while subordinate trout were more likely to feed at other (resource poor) times (Alanara et al. 2001). Interestingly, these temporal changes in resource use were also found to be plastic, suggesting that as environmental parameters change (e.g. temperature), so too can behavioral interactions.

Shallow water marine communities are just as vulnerable to sudden loss of habitat as human-inhabited terrestrial communities, and recent changes in water quality of Florida Bay, FL have led to sudden loss of shallow-water marine habitats (Fourqurean and Robblee 1999). Salinity and nutrient fluxes due to drought, altered freshwater input, and tropical storms have caused widespread loss of seagrasses (Zieman et al. 1988), blooms of cyanobacteria (Phlips et al. 1999), and widespread loss of sponges (Butler et al. 1995). This complex mosaic of seagrass and sponge-dominated hardbottom communities was once rich with marine invertebrates, fishes, sea birds, and marine mammals (Fourqurean and Robblee 1999). However, the loss of these habitats has had negative consequences on the abundance and/or distribution of shrimp (Ehrhardt

and Legault. 1999), fishes (Thayer et al. 1999), and spiny lobsters (Butler et al. 1995; Herrnkind et al. 1997).

Caribbean spiny lobsters, *Panulirus argus*, are one of the most important commercially exploited species in the Caribbean (Hunt 1994). Florida Bay is the largest US nursery for *P. argus*, supporting a multi-million dollar commercial fishery in the Florida Keys (Davis and Dodrill 1982; Forcucci et al. 1994; Butler et al. 2006). Postlarval lobsters are transported into Florida Bay during flood tides and settle in dense beds of macroalgae (*Laurencia* spp) and seagrass (Marx & Herrnkind 1985a; Herrnkind and Butler 1986). After approximately three months of being solitary and hidden in macroalgae, juvenile lobsters (~15-25 mm CL) begin to seek crevice shelters under sponges, sea whips, corals, and solution holes (Andree 1981; Childress and Herrnkind 1994; Forcucci et al. 1994; Childress and Jury 2006).

These post-algal juvenile lobsters are the first ontogenetic stage to show conspecific attraction (Childress and Herrnkind 1996; Ratchford & Eggleston 2000) and begin to aggregate in clumps of algae or crevice shelters (Andree 1981; Childress and Herrnkind 1997; 2001b). Den sharing by juvenile spiny lobsters has long been thought to be an adaptation against predation (Atema and Cobb 1980; Butler et al. 1999), since lobsters sharing dens could potentially benefit by group defense against predators (Eggleston and Lipcius 1992) or simply by the dilution effect (Mintz et al. 1994). However, Childress and Herrnkind (2001a) found that juvenile lobsters tethered together in sponge

crevices had no higher survival than solitary lobsters tethered in sponge crevices. Furthermore, nearly 50% of all juvenile lobsters in the Florida Bay nursery are found in shelters by themselves (Davis and Dodrill 1982; Childress and Herrnkind 1997) and when attacked by predators, juvenile lobsters disperse rather than clump together (Childress 1995). These observations suggest that lobster den sharing might simply be a consequence of conspecific attraction. Lobsters searching for a crevice shelter are three times more likely to find one if a conspecific is already present in the shelter, thus, gaining a significant reduction in exposure time to predators (Childress and Herrnkind 2001a). The aggregation cue appears to be a water-born olfactory cue (Zimmer-Faust et al. 1985; Nevitt et al. 2000; Ratchford & Eggleston 2000) released in urine (Horner et al. 2006; 2008), and once arriving at the source of the odor, the intruder may either occupy a nearby crevice or attempt to enter the shelter of the resident. Den sharing is not as egalitarian as it might seem, as juvenile lobsters will often push, jostle, or whip approaching conspecifics (Berrill 1975).

In the field and laboratory, aggressive interactions have also been noted between individuals sharing shelters (Childress personal observation). Aggressive acts, including threatening postures and physical strikes, may be exhibited by spiny lobsters during mating, foraging, and den sharing, and aggression exhibited within the den can result in the formation of short-term dominance hierarchies (Berill 1975; 1976). Factors including size, sex, and molt status most likely impact aggressive behaviors (Atema & Cobb 1980), and

through varying levels of aggression and gregariousness, individuals have the potential to exclude or include others from den sharing respectively. Whether or not these aggressive acts will prevent individuals from sharing shelters is currently unknown, and if habitats become limited, decreased sheltering opportunities have the potential to result in increased competition for dens. These observations raise an important question about the variability of gregariousness and aggression among individuals. Do some spiny lobsters share dens more than others, and if so, what influences individual variation in patterns of den sharing and dispersal?

In the winters of 1991-1992 and 1992-1993, cyanobacteria blooms occurred in a significant portion of the Florida Bay hardbottom/seagrass community north of Long Key, FL (Butler et al. 1995). As a result, many of the sponge shelters occupied by juvenile Caribbean spiny lobsters were lost (Herrnkind et al. 1997). Even though 70% of all juvenile lobsters were found utilizing sponge shelters prior to the bloom, the abundance of juvenile lobsters post-bloom was mostly unchanged. There are several possible explanations for this result. First, juvenile lobsters may have switched to using alternative sources of crevice shelters such as sea whips, solution holes, coral heads, and artificial shelters (concrete blocks) (Childress and Herrnkind 1997). Second, the frequency of den sharing may have increased such that each remaining shelter housed more lobsters. And finally, increased post-larval settlement during the year that the sponges were lost may have offsetting the loss of post-algal

juveniles that were left without shelters, resulting in no net change in juvenile

lobster abundance.

In 2005, sixteen 25 X 25 m nearshore sites were established bayside of

the middle Keys for a study of juvenile recruitment and den use with both natural

and artificial block shelters (Zito-Livingston and Childress 2009). In the fall of

2007, another massive cyanobacteria bloom smothered and killed all large,

crevice-filled sponges from eight of these sixteen sites (Childress and Bouwma in

prep). Even after the recent mass sponge mortality dramatically decreased the

number of crevice shelters available, the average number of lobsters per shelter

remained constant and far below the maximum capacity of each shelter

(Childress & Bouwma in prep). This unfortunate natural shelter-loss event

created an opportunity to study the impact of shelter loss on the behavioral

variation of juvenile spiny lobsters occupying both natural shelter-rich and natural

shelter-poor habitats.

In this study, I examined which characteristics (e.g. size, habitat type, sex,

injury, molt history, etc.) best explained denning behavior, whether these

characteristics could predict denning behavior, and whether habitat loss events

influence which variables best explain and/or predict denning behavior. I aimed

to (1) determine the influence of habitat type, sex, size, and body condition on

aggressive and gregarious behaviors (2) experimentally examine the patterns of

den use, den sharing and den fidelity before and after shelter loss by simulating a

shelter loss event and (3) track individually-marked juveniles in the field to

estimate patterns of dispersal in natural shelter-rich and natural shelter-poor habitats. I hypothesized that spiny lobster denning behavior would be explained by individual characteristics and that variation in aggressive and gregarious individuals would result in specific patterns of den sharing and dispersal. More specifically, I predicted that size and habitat type would best explain an individual's level of aggressive and gregarious behavior. Further, I predicted that when shelter was limited, resulting in increased den competition, large, aggressive individuals would exclude smaller individuals from entering dens. Therefore, for larger individuals, I expected to see an increase in den use, den fidelity, and dispersal, and a decrease in den sharing.

Methods

Sixteen sites (25 m x 25 m) located in the upper and lower middle Keys within the Florida Keys National Marine Sanctuary (Figure 3.1a,b) were mapped such that all known crevice shelters, natural and artificial, could be censused by a diver (Figure 3.1c). A total of eight natural shelter-poor (without natural sponge crevices) and eight natural shelter-rich (with intact natural sponge crevices) sites provided replicate "collections" of lobsters experiencing similar shelter availability. The eight sites east of the Long Key landfill (MTM, SBM, MAT, LIG) lost all large sponges during a cyanobacteria bloom in 2007, and thus, were considered natural shelter-poor sites (Figure 3.1b). The eight sites west of the Long Key landfill (ODR, GRA, BPT, BAM) remained abundant in sponges, offered

69
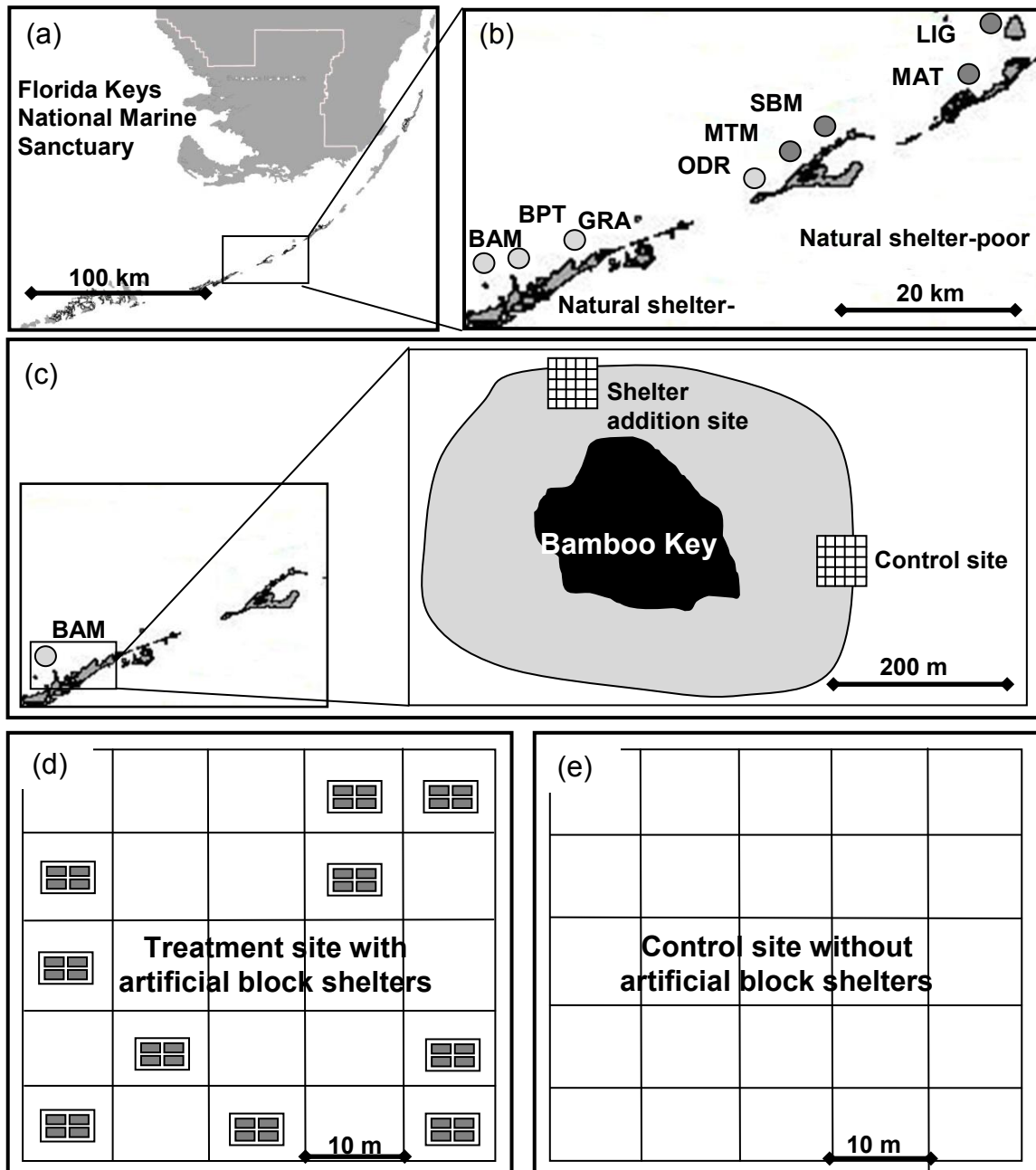
Figure 3.1: A detailed map and grid of 16 sites located in the Florida Keys National Marine Sanctuary. (a) The location of my sixteen sites (eight stations). All locations are within the boundaries of the Florida Keys National Marine Sanctuary.

Figure 3.1: continued. (b) A magnification of Fig. 3.1a. Four of the stations were natural shelter-poor (LIG, MAT, SBM, MTM), and four of the stations were natural shelter-rich (ODR, GRA, BPT, BAM). (c) An example of one of my stations (BAM-Bamboo Key). Each station consisted of one artificial shelter treatment and one control site. (d) A representation of the 25m x 25m grids placed on the artificial shelter treatment sites. Each artificial treatment site (natural shelter-poor with artificial shelters and natural shelter-rich with artificial shelters) contained ten artificial shelter blocks. (e) A representation of the 25m x 25m grids placed on control sites (natural shelter-poor and natural shelter-rich). Control sites did not contain artificial shelter blocks.

alternative natural shelter, and thus, were considered natural shelter-rich sites (Figure 3.1b). These site differences allowed me to examine the influence of habitat type on social (aggression and gregariousness) and denning behavior.

Juvenile *P. argus* (15-48 mm carapace length; n=320) were collected by hand net from each of the 16 field sites. At the time of collection, all sites contained ten artificial block shelters, each with four sheltering holes, from a prior study (Zito-Livingston and Childress 2009). A "collection" of twenty lobsters was gathered from each natural shelter-rich and natural shelter-poor site, in order to test the effect of habitat type on behavior. After collection, artificial block shelters were removed from four of the natural shelter-poor and four of the natural shelter-rich sites. This further divided the sites into two habitat type control sites (natural shelter-poor and natural shelter-rich; Figure 3.1d) and two artificial shelter treatment sites (natural shelter-poor with artificial shelter and natural shelter-rich with artificial shelter; Figure 3.1e). These control and treatment sites allowed me to examine the influence of habitat type and artificial shelter treatment on dispersal behavior.

Each individual collected was measured (mm CL), sexed, staged (premolt, intermolt, and postmolt), and checked for injuries (missing legs, antennae, and telson damage) (see methods in Forcucci et al. 1994). Each individual received a uniquely-coded cable tie ID tag that was placed around the base of either the right or left antennae. Lobsters that exhibited a chalky-white hemolymph were considered infected with PaV1 (Shield & Behringer 2004) and were not used in

this study. All molting events were recorded, and after molting, lobsters were retagged and their carapace length was measured. Individuals with a soft carapace when collected were considered as having molted during experimentation, since post-molt behavior has previously shown to differ from unmolted animals (Lipcius and Herrnkind 1982).

Behavioral Measures of Aggression and Gregariousness

Experiments examining aggression and gregariousness were completed at the Florida Keys Marine Laboratory in Long Key, FL (Table 3.1). Animals were housed in outdoor facilities under normal light conditions with fresh sea water (33± 3 ppt) continuously filtered into each aquarium and water temperatures of 24-31 ºC. Each "collection" (n=16) was segregated so that aggression and gregariousness was measured for individuals from a single site, and the procedure listed below was completed for each "collection".

Pairs of similar-sized lobsters (30.8 +/- 6.4 SD mm CL) from the same "collection" (n=320) were assigned to a 40 liter housing tank with a single artificial crevice shelter (10 x 20 x 40 cm) that contained two separate sheltering holes so that each individual had the option of denning alone. Pairs were assigned without consideration of sex since it has been shown that sheltering behavior is not sex-specific (Zimmer-Faust et al. 1985). Animals were housed in aquaria for one week to determine levels of aggression and gregariousness, and lobsters

Table 3.1: Timeline of experiments. Three experiments in total were used to examine behaviors of individual juvenile spiny lobsters (n=320). Aquarium and mesocosm experiments occurred at the Florida Keys Marine Lab in Long Key, FL, and field experiments were completed at sites (n=16) located within the Florida Keys National Marine Sanctuary. Each experiment was completed across a one week time frame.

Week	Location	Behavior Measured	Days Observed
1	Aquarium	Aggression and Gregariousness	Seven
2	Mesocosm	Denning Behaviors	Seven
3	Field	Dispersal	Four*

*Observations were conducted one, five, six, and seven days after initial release.

were fed frozen shrimp each night after behavioral observations to simulate nocturnal feeding conditions.

The number of aggressive acts by each individual, including antennae whips, antennae pushes, and body pushes, was recorded for one week. Observations were taken nightly for ten minutes using a focal animal sampling rule and a continuous observation recording rule (Martin and Bateson 1993). All aggressive acts were summed across the seven days, and to determine average aggression, the average number of aggressive acts that occurred per day was calculated. To measure gregariousness, the proportion of time spent in the den was recorded twice a day (once in the morning and once at night) by determining the location of each individual within the aquarium. Individuals utilizing the shelter at the same time were considered sharing dens, and individuals that remained outside of the shelter were considered not sharing dens. Individuals sheltering alone were considered to be using the shelter but not sharing the shelter. Den sharing was recorded for a total of seven days (14 observations). To calculate average gregariousness, the number of times den sharing was exhibited was divided by the number of times the den was used and shared, and the morning and night observations were averaged. Data were square root transformed to meet the assumptions of normality and analyzed using student's t-test and ANOVA (JMP 10) with average aggression and gregariousness as dependent variables and size and habitat type (from which they were collected) as independent variables. Multiple regression models were also used to

determine the relative influences of habitat type, size, sex, injury, and molt history on aggressive and gregariousness behaviors.

Denning Behavior Measures and Habitat Loss

After one week in captivity, experiments examining denning behavior and the influence of habitat loss on denning behavior were completed at the Florida Keys Marine Laboratory in Long Key, FL (Table 3.1). Animals were housed in outdoor facilities under normal light conditions with fresh sea water (33± 3 ppt) continuously filtered into a mesocosm and water temperatures of 24-31 ºC. Lobsters were fed frozen shrimp each night to simulate nocturnal feeding conditions.   Each "collection" gathered (n=16) was segregated so that denning behavior was measured for individuals from a single site, and the procedure listed below was completed for each "collection".

Twenty individually-marked juveniles (n=320) from the same "collection" were released into a mesocosm (or a large, oval concrete 40 x 20 x 1.3 m deep raceway with a center island) that contained three mangrove snapper (*Lutjanus griseus*) as 'predators' to maintain 'honest' lobster den-seeking behaviors. The mesocosm was visually divided into a total of twelve similarly sized sections for data recording purposes and contained concrete block artificial shelters (n=10), each with four sheltering holes, resulting in a shelter capacity of >10 juvenile lobsters. Before release into the mesocosm at night, each individual received two additional colored cable ties to facilitate individual identification. Every day,

just after sunrise, the position of all individuals was recorded (see methods in Childress & Herrnkind 1997). Molted lobsters were captured, identified, measured, retagged, and returned to the shelter where they were captured. After four days, half of the artificial shelters (n = 5) were removed, by taking every other shelter out of the mesocosm, and daily monitoring continued for three additional days.

A total of three behaviors (den use, den sharing, and den fidelity) were examined. Den use was defined as an individual residing within an artificial shelter. Den sharing was defined as an individual residing within an artificial shelter along with one or more conspecifics. Den fidelity was defined as the number of consecutive days an individual remained in the same artificial shelter. For example, if an individual was using a shelter (on day 1) and remained in the shelter the next day (on day 2), it received a den fidelity score of one. Each behavior was calculated by taking a sum of the number of times the behavior occurred, and average den use, den sharing, and den fidelity per day was calculated before the shelter loss event and after the shelter loss event.

Data were analyzed using student's t-test and ANOVA (JMP 10) to compare the frequency of den use, den sharing, and den fidelity before and after the shelter loss event. A comparison of forward step-wise regression models using minimum AIC criteria was used to determine what combination of characteristics could best explain den use, den sharing and den fidelity. Size and habitat type were considered *a priori* explanatory variables, and other

characteristics of interest such as sex, injury, molt history, aggression and gregariousness were also included in the model. Changes in the patterns of den use were also examined for each "collection" by comparing random den choice (known from prior research as the Poisson expected; Herrnkind et al. 2001) to observed distributions using log-linear G tests and Chi-square analyses (JMP 10). Observed distributions were calculated by determining, on average, the number of times a den contained one, two, three, etc. (up to 11) conspecifics.

Dispersal Measures and Habitat Loss

After the mesocosm experiment and two weeks in captivity, all surviving individuals were released into the field (back onto the site from which they were collected) and were resighted daily for four days to examine the relationship between dispersal and behavioral characteristics of individual lobsters and the effect of habitat type on dispersal (Table 3.1). Individually-marked juveniles from the mesocosm study were released onto the field site from which they were collected (Figure 3.1a). Recall that artificial shelter blocks were removed from half of the sites resulting in two control sites (Figure 3.1e; natural shelter-poor and natural shelter-rich) and two treatment sites (Figure 3.1d; natural shelter-poor with artificial shelters and natural shelter-rich with artificial shelters). Individuals were randomly released within the site with the primary choice of placement being in an artificial shelter (if present) or the best possible natural shelter. All resident individuals were also tagged with an antennae tag and

resighted for comparison with those that had been returned to the site. Four times, one, five, six, and seven days after initial release, just after sunrise, the position of tagged and untagged individuals was recorded by snorkelers via direct observation. Search time was limited to one hour. Any individuals that needed to be removed from shelters to identify antennae tags were released back into the shelter from which they were removed.

All released individuals were classified as either resighted or not resighted. Resighted individuals were those that had been resighted at least once during the week census period. Individuals that were not resighted were those that were never resighted during the week census period. I then analyzed this binary outcome by habitat type and artificial shelter treatment (natural shelter-poor with artificial shelters and natural shelter-rich with artificial shelters) vs. control (natural shelter-poor and natural shelter-rich) sites using a logistic regression model (JMP 10) with individual characteristics of size, sex, injury, molt history, aggression, and gregariousness as covariates.

Results

Behavioral Measures of Aggression and Gregariousness

On average, females were significantly more aggressive than males ($F_{1,318}$=3.029, p=0.083), but no effect of habitat type was found ($F_{1,318}$=1.609, p=0.206) on levels of aggression (Figure 3.2). Average aggression of individuals significantly increased with size of the individual ($F_{1,318}$=50.450, p=<0.001), while

(a)

(b)
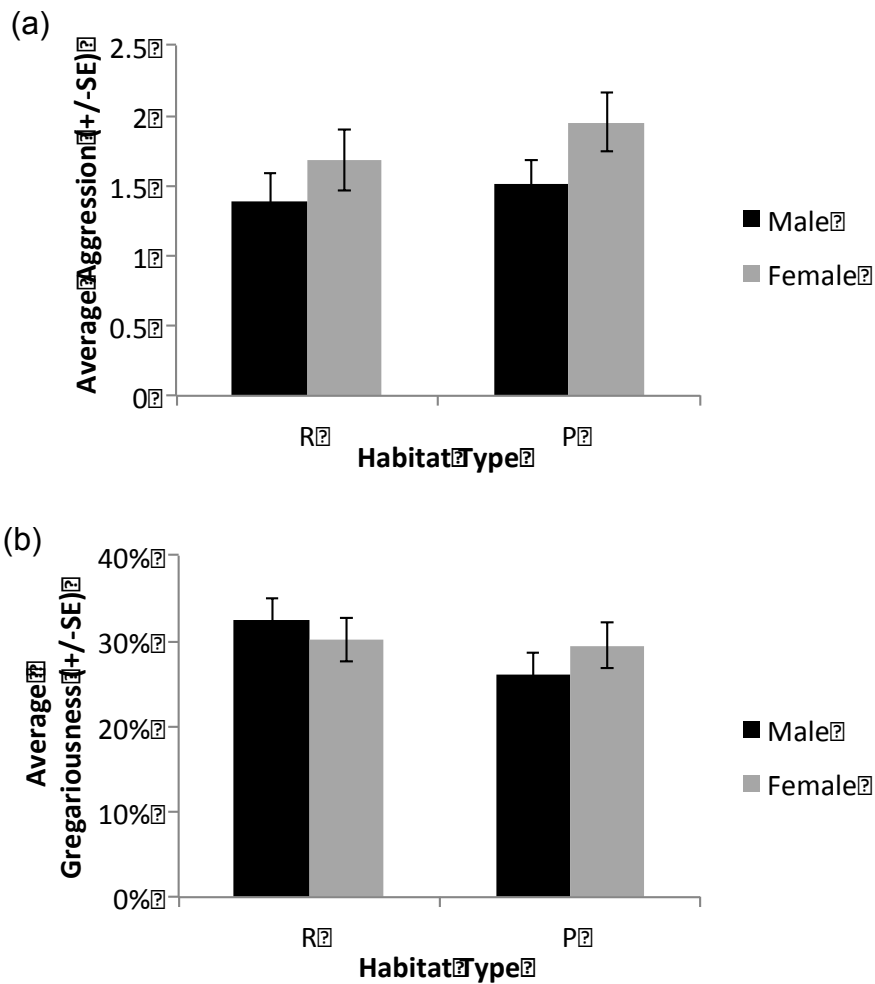
Figure 3.2: Effect of habitat type (natural shelter-rich/natural shelter-poor) on aggressive and gregarious behavior. The (a) average aggression and (b) percent gregariousness exhibited by juvenile spiny lobsters from natural shelter-rich (R) and natural shelter-poor (P) environments. Black bars represent males and gray bars represent females. Error bars are represented by standard error.
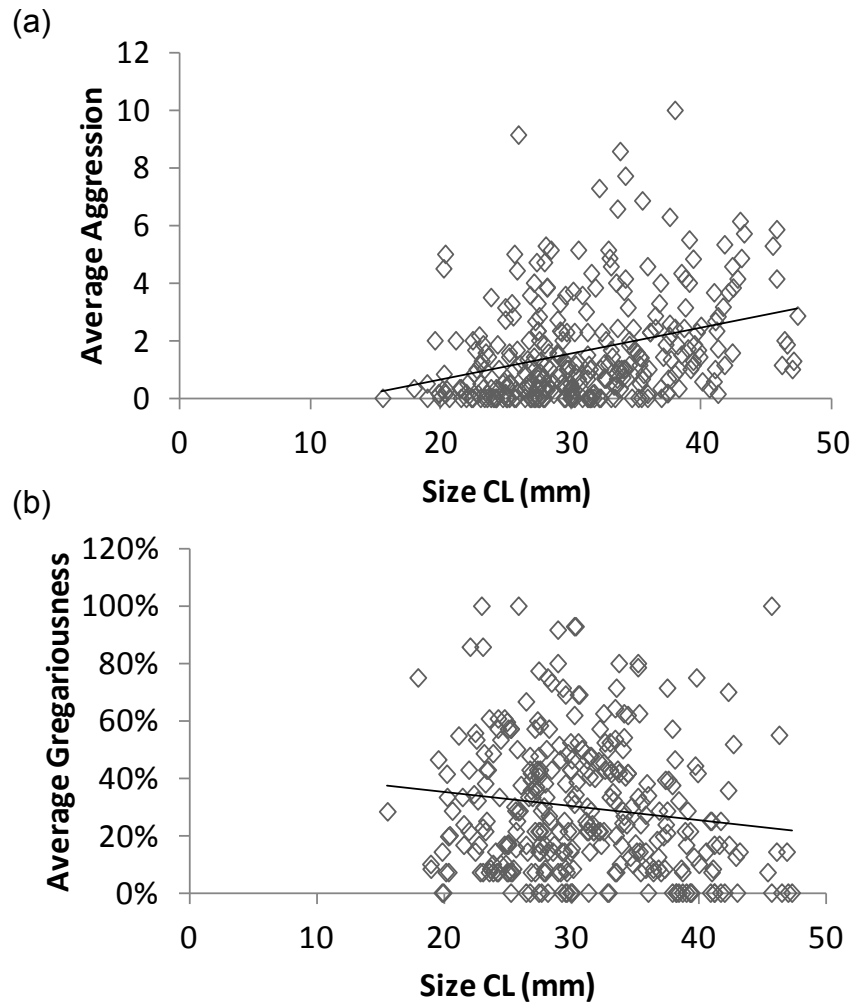
(a)

(b)

Figure 3.3: Effect of size on aggressive and gregarious behavior. The

(a) average aggression and (b) percent gregariousness exhibited by various

sizes (CL mm) of juvenile spiny lobsters. A best fit line was added to show

general trends.

average gregariousness of individuals significantly decreased with size of the individual ($F_{1,318}$=11.635, p=<0.001) (Figure 3.3). Average gregariousness was not significantly influenced by sex ($F_{1,318}$=0.266, p=0.607) but did differ significantly by habitat type ($F_{1,318}$=6.150, p=0.014). Individuals from natural shelter-rich sites exhibited higher levels of gregariousness than individuals from natural shelter-poor sites. Fully fit regression models suggest that size, molt history, and injury best explained levels of aggression and that size alone best explained levels of gregariousness (See Table 3.2).

Measures of Denning Behavior and Effects of Habitat Loss

Prior to the removal of shelters, the average observed distribution of individuals within a den did not differ from expected Poisson values (X^2=1.454, p=0.228; Figure 3.4; Table 3.3). However, habitat type was found to significantly influence den use ($F_{1,301}$=<34.265, p=<0.001) and den sharing ($F_{1,301}$=31.091, p=<0.001). Individuals from natural shelter-rich habitats were more likely to use dens and share dens than individuals from natural shelter-poor habitats. Den fidelity was not significantly influenced by habitat type ($F_{1,283}$=0.395, p=0.530). Den use ($F_{1,301}$=0.073, p=0.787), den sharing $F_{1,301}$=0.150, p=0.703), and den fidelity ($F_{1,283}$=1.043, p=0.412) did not significantly differ by size of the individual. Best fit forward step-wise regression models suggested that habitat type best explained den use and den sharing, while habitat type and size together best explained den fidelity (See Table 3.3).

Table 3.2: Multiple regression models for social behavior. The fully fit regression models for gregariousness and aggression behavioral measures. The F-ratio and p-value are reported for each characteristic. Habitat type represents natural shelter-rich (R) and natural shelter-poor (P) sites.

Behavior	Source	df	F-ratio	p-value
Aggression				
	Size (CL mm)	1	45.739	<0.001**
	Habitat Type (R/P)	1	0.092	0.762
	Sex (M/F)	1	2.256	0.134
	Injury (Y/N)	1	16.373	<0.001**
	Molting (Y/N)	1	5.764	0.017
Gregariousness				
	Size (CL mm)	1	8.252	0.004*
	Habitat Type (R/P)	1	3.417	0.281
	Sex (M/F)	1	0.313	0.576
	Injury (Y/N)	1	1.168	0.281
	Molting (Y/N)	1	0.174	0.677

  * p-value ≤ 0.01
** p-value ≤ 0.001

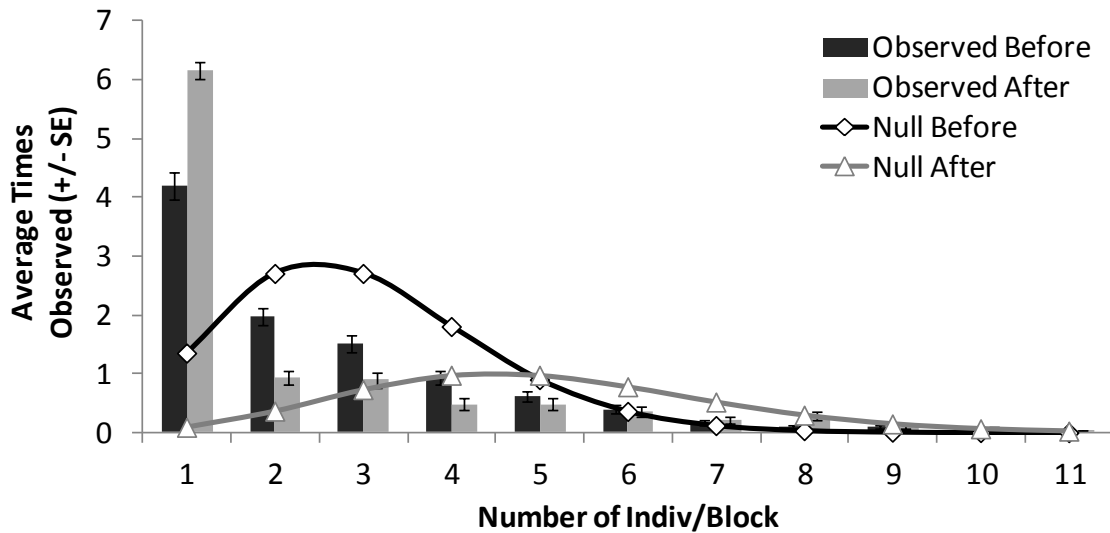**Figure 3.4: The expected and observed den sharing distributions before and after shelter loss.** The expected Poisson distribution of den sharing plotted against observed values before and after a shelter loss event. The expected null distribution represented by lines (black before and gray after) and the observed data represented by bars (black before and gray after). Error bars are represented by standard error.

Table 3.3: Comparison of expected and observed den sharing distributions

before and after shelter loss. Chi-square analyses comparing expected

Poisson den sharing distributions to observed den sharing distributions. Analyses

were completed before and after the shelter loss event.

Treatment	X^2 Value	P-value
Before	1.454	0.228
After	0.552	<0.001**

  * p-value ≤ 0.05
** p-value ≤ 0.01

After shelter removal, the average observed distribution of individuals within a den significantly differed from expected Poisson values (X^2=0.552, p=<0.001; Figure 3.4; Table 3.3). This significance was primarily due to a higher number of individuals denning alone and in pairs than expected resulting in a lower number of individuals denning in groups of four, five, and six. The shelter removal treatment had a significant effect on denning behavior, and after a shelter loss event, den use ($F_{1,574}$=6.473, p=0.011) significantly decreased while den fidelity significantly increased ($F_{1,536}$=8.010, p=0.005). Den sharing was not significantly influenced by the shelter removal treatment ($F_{1,558}$=0.033, p=0.857).

Both habitat type and size were found to significantly influence denning behavior after shelter loss. Individuals from natural shelter-rich habitats exhibited significantly lower den use after a shelter loss event than individuals from natural shelter-poor habitats ($F_{1,298}$=23.298, p=<0.001), while individuals from natural shelter-poor habitats exhibited similar amounts of den use ($F_{1,274}$=0.482, p=0.488). After shelter loss, den sharing significantly decreased for individuals from natural shelter-rich habitats ($F_{1,298}$=5.695, p=0.018) and significantly increased for individuals from natural shelter-poor habitats ($F_{1,258}$=5.255, p=0.023). Den fidelity increased for individuals from both natural shelter-rich ($F_{1,279}$=3.040, p=0.082) and natural shelter-poor habitats ($F_{1,255}$=4.998, p=0.026) after shelter loss (Figure 3.5). With further analysis, it was found that size of the individual greatly influenced the frequency of den use ($F_{1,270}$=6.434, p=0.012) and den fidelity ($F_{1,250}$=18.546, p=<0.001) after a shelter loss event but not den
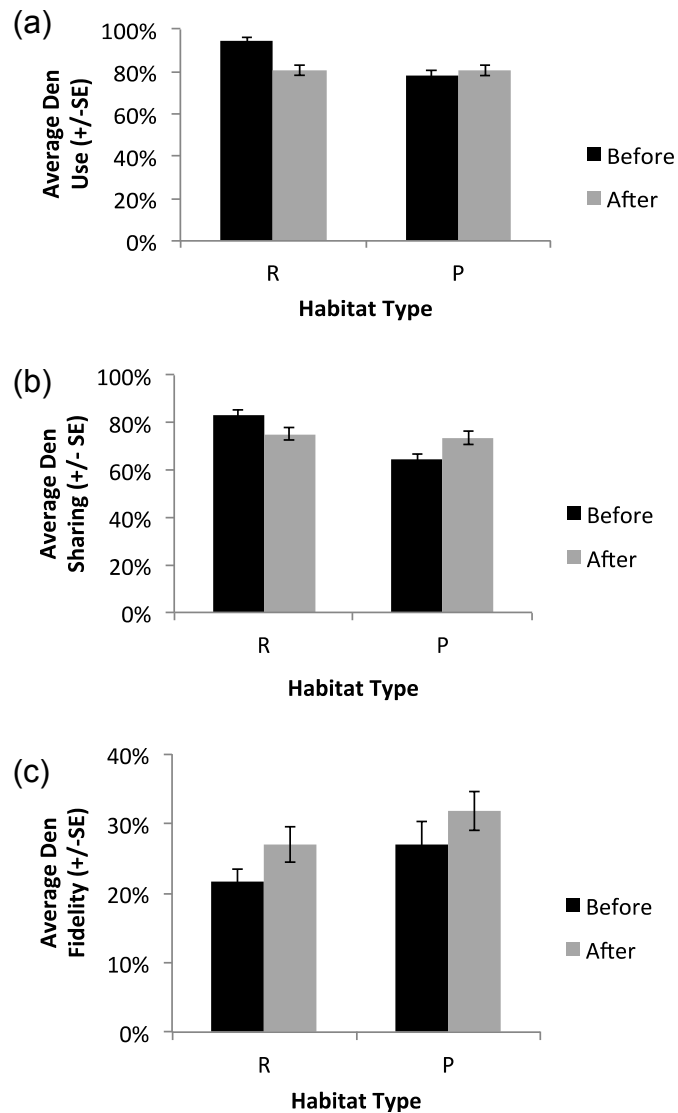
Figure 3.5: Effect of habitat type (natural shelter-rich/natural shelter-poor) on denning behavior before and after shelter loss. The average percent (a) den use, (b) den sharing, and (c) den fidelity before and after a shelter loss event by habitat type (natural shelter-rich (R) and natural shelter-poor (P)). Black bars represent data before the shelter loss event, and gray bars represent data after the shelter loss event. Error bars are represented by standard error.
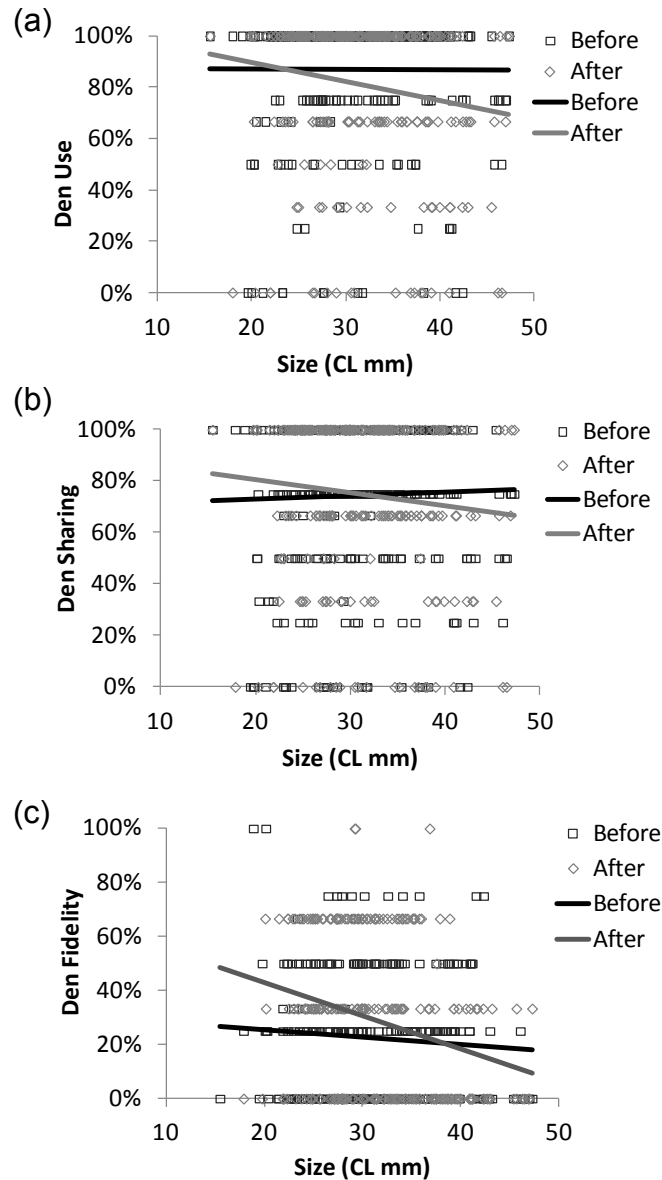
Figure 3.6: Effect of size on denning behavior before and after shelter loss.

The percent (a) den use, (b) den sharing, and (c) den fidelity before and after a

shelter loss event analyzed by size of the individual (CL mm). Black diamonds

represent data before the shelter loss event, and gray squares represent data

after the shelter loss event. A black and gray linear best fit line reflect trends

before and after the shelter loss event respectively.

sharing ($F_{1,254}$=2.519, p=0.114). When fewer shelters were present, larger, more aggressive individuals were less likely to reside within a shelter and had lower levels of den fidelity than smaller individuals (Figure 3.6). According to best fit forward step-wise models, the shelter removal treatment significantly explained den use but not den sharing and den fidelity. Shelter removal treatment interactions with habitat type, size, and average aggression most explained den use. Den sharing was best explained by shelter removal treatment by habitat type and shelter removal treatment by size interactions. Both shelter removal treatment by size, and shelter removal treatment by injury interactions best explained den fidelity after habitat loss (See Table 3.4).

Measures of Dispersal and Effects of Habitat Loss

Overall, resight values were somewhat low, with only 73 of the 261 (~28%) released individuals being resighted. The average percent of individuals resighted across four days was not different between habitat types ($F_{3,257}$=1.381, p=0.249), although natural shelter-poor sites without artificial shelters had the lowest resight values (Figure 3.7). Individuals that were smaller on average, were more likely to be resighted than larger individuals (t_{107}=5.008, p=<0.001). Fully fit logistic regression models found that size best explained dispersal behavior (Table 3.5).

89

Table 3.4. Best fit forward step-wise regression models for denning behavior. The best fit stepwise regression models with minAIC for den use, den sharing and den fidelity. The F-ratio and p-value are reported for each. Habitat type represents natural shelter-rich (R) and natural shelter-poor (P) sites, and treatment represents the effect of removing shelter blocks from the mesocosm.

Behavior	Source	df	F-ratio	p-value
Den Use				
	Habitat Type (R/P)	1	11.987	<0.001**
	Size (CL mm)	1	1.068	0.302
	Sex (M/F)	1	3.665	0.056
	Injury (Y/N)	1	3.306	0.070
	Aggression	1	1.034	0.210
	Treatment (T)	1	5.648	0.018
	Habitat x T	1	16.661	<0.001**
	Size x T	1	4.472	0.035
	Aggr x T	1	4.472	0.035
Den Sharing				
	Habitat Type (R/P)	1	17.122	<0.001**
	Size (CL mm)	1	0.021	0.886
	Injury (Y/N)	1	5.932	0.015
	Molt (Y/N)	1	3.604	0.058
	Treatment (T)	1	0.078	0.780
	Habitat x T	1	13.910	<0.001**
	Size x T	1	5.489	0.020

Table 3.4: continued.

Behavior	Source	df	F-ratio	p-value
Den fidelity				
	Habitat Type (R/P)	1	4.833	0.028
	Size (CL mm)	1	20.257	<0.001**
	Molt (Y/N)	1	4.347	0.038
	Size x T	1	7.399	0.007*
	Injury x T	1	10.463	0.001**

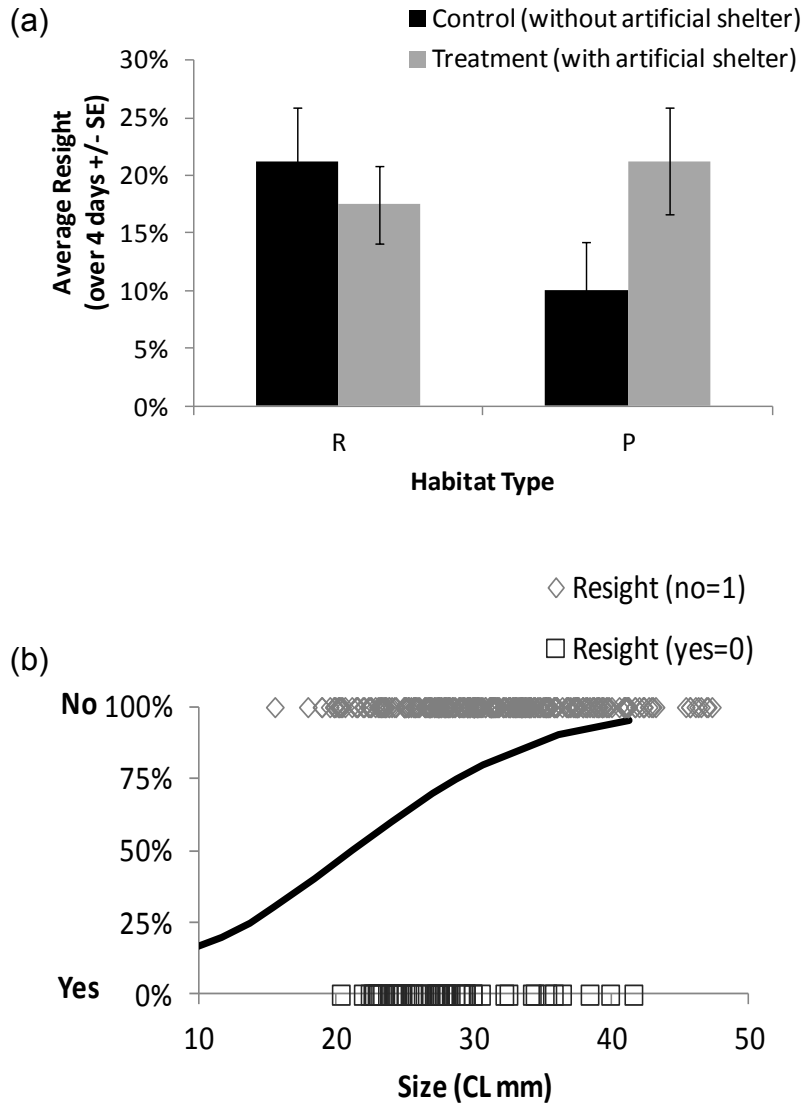 * p-value ≤ 0.01
** p-value ≤ 0.001

Figure 3.7: Effect of habitat and size on dispersal. (a) The average percent resight of juvenile spiny lobsters over four days by habitat type (natural shelter-rich (R), natural shelter-rich with artificial shelters, natural shelter-poor (P) and natural shelter-poor with artificial shelters. (b) The average size CL (mm) and probability curve of resight for individuals resighted at least once and individuals never resighted. Black squares represent individuals that were resighted and gray diamonds represent individuals that were not resighted.

Table 3.5: Logistic regression model for dispersal. The full logistic

regression model for dispersal. The F-ratio and p-value are reported for each

characteristic. Habitat type represents natural shelter-rich (R) and natural

shelter-poor (P) sites, and treatment represents the effect of having artificial

shelter blocks on sites.

Behavior	Source	df	F-ratio	p-value
Dispersal				
	Habitat Type (R/P)	1	0.331	0.416
	Size (CL mm)	1	23.971	<0.001**
	Sex (M/F)	1	0.275	0.600
	Injury (Y/N)	1	0.249	0.618
	Molt (Y/N)	1	0.099	0.794
	Aggression	1	0.614	0.433
	Gregariousness	1	0.878	0.349
	Treatment	1	<0.001	0.988
	Habitat x T	1	2.620	0.105
	Size x T	1	1.380	0.240
	Sex x T	1	0.036	0.849
	Injury x T	1	0.128	0.721
	Molt x T	1	1.157	0.282
	Aggr x T	1	1.681	0.195
	Greg x T	1	2.127	0.145

  * p-value ≤ 0.01
** p-value ≤ 0.001

Discussion

In this study, I examined individual variation in social (aggression and gregariousness) and denning behaviors (den use, den sharing, and den fidelity) in relation to various characteristics (including size, sex, injury, molt history, etc.) before and after a shelter loss event. I found that large, uninjured individuals were the most aggressive and that small individuals were the most gregarious, which supported my prediction that size of the individual would be strongly correlated with these behaviors. The influence of body size on aggression has been studied in other crustaceans including clawed lobsters (Atema and Steinbach 2007), crayfish (Moore 2007), and crabs (Pedetta et al. 2010). A review by Atema & Cobb (1980) on various Palinuridae species, suggested that size is the best predictor of aggression levels in lobsters (*J. lalandii* Fielder 1965, *P. interruptus* Roth 1972), that males are more aggressive than females (*P. interruptus* Roth 1972), and that newly molted individuals are less likely to exhibit aggressive acts that post-molt individuals (*P. cygnus* Atema and Cobb, 1980). Although aggressive behaviors have been described for spiny lobsters, few studies have clearly demonstrated how these behaviors impact competition for resources.

Surprisingly, the patterns of den use, den sharing and den fidelity after shelter loss conditions did not match my prediction that large, aggressive individuals would exclude smaller individuals from entering and sharing dens. While some large, aggressive individuals chose to occupy crevice shelters by

94

themselves, many others chose not to occupy crevice shelters at all. This allowed smaller, less aggressive individuals to occupy crevice shelters. As a consequence, smaller lobsters exhibited increased den use, den sharing, and den fidelity after a shelter loss event. Another consequences was that smaller lobsters were resighted more often than larger lobsters during the mark-recapture study. These results suggest that, although aggression may play a role in intraspecific interactions, competition for dens may not be as intense as predicted, even when shelter is limited. Rather than den competition, vulnerability may be a more important factor in determining sheltering behavior with respect to size and aggression. I hypothesize that larger juvenile lobsters, with their greater ability to disperse, can decrease their predation risk by dispersing when shelters are limited. This hypothesis is supported by tethering experiments that have shown greater predation of smaller tethered juveniles than larger tethered juveniles (Andre 1981; Eggleston et al. 1992; Smith and Herrnkind 1992).

Although my ability to estimate dispersal was limited by the somewhat low number of individuals resighted in the field (~28% of released lobsters were resighted), I did find that habitat type (specifically natural shelter-poor with artificial shelter sites) and size influenced dispersal. Additional pilot studies utilizing acoustic telemetry techniques (Bertelsen and Hornbeck 2009; Bertelsen 2013) suggest that juvenile lobsters (n=3) can be resighted for at least seven days after being tagged (Appendix C). In general, smaller individuals were less

likely to disperse (therefore more likely to be resighted), supporting prior conclusions based on their vulnerability to predation when outside of shelters (Andre 1981; Eggleston et al. 1992; Smith and Herrnkind 1992). Providing artificial shelters on natural shelter-poor sites resulted in a similar percentage of resighted juveniles (~18%) as those released onto natural shelter-rich sites (~17%) and natural shelter-rich sites with artificial shelters (~15%). Since juveniles had a lower percent of resightings on natural shelter-poor sites without added artificial shelters (~9%), providing artificial shelters may be one method for mitigating habitat loss. However, supplementation may be an unnecessary step in conservation of this species given the ability of juveniles to naturally compensate after habitat loss events via changes in behavior, such as increased dispersal or increased den sharing depending on the size of the individual.

Variation in Caribbean spiny lobster social and denning behaviors may provide a mechanism for dealing with habitat loss and has the potential to be influenced by the presence of conspecifics, risk of predation, and resource availability. The degree of shelter competition among juvenile spiny lobsters may vary depending on the presence of conspecific odor cues and social interactions. Studies by Shabani et al. (2009) have shown that odor cues are urine-borne, and the release of odor cues in adult *P. argus* reflect the social status of individuals, with dominant individuals releasing increased amounts of odor cues. The release of odor cues from dominant individuals along with increased aggressive acts also produces avoidance behavior by subordinate individuals. Overall,

aggressive acts may be a key factor in defining dominance status in juvenile

lobsters, and odor cues may be less effective in defining status if they are

decoupled from aggressive acts. During this study, establishment of dominance

status was seen in pairs of familiar juvenile lobsters during aquarium

observations of aggression (Appendix B) but was not found to directly influence

denning or dispersal behaviors in mesocosm or field environments. Shabani et

al. (2009) suggest that the highly gregarious nature of spiny lobsters may explain

why the release of urine is not always related to aggressive interactions, and

rather, may lead to increased levels of gregarious behaviors, such as

aggregating under shelter. It is also important to point out that dominant

individuals have been known to remove subordinate individuals from shelters

(Wilson, 1975; Martin and Moore, 2008). Contrary to previous research, I found

that in shelter limited situations larger, aggressive and more dominant individuals

are less likely to exclude smaller individuals from vital resources because they

utilize shelters less.

In addition to direct competition among juveniles for crevice shelters,

predators can indirectly and directly influence the degree of shelter competition.

For example, the release of alarm cues, via hemolymph of injured individuals,

can indirectly result in the avoidance of conspecifics (Shabani et al. 2008). I

found that injured individuals exhibited decreased levels of aggressive and lower

levels of den sharing than uninjured individuals. Aggressive acts come at an

energetic cost (Briffa and Sneddon, 2007), and injured individuals may be less

likely to fight uninjured conspecifics. Injured individuals are also less likely to be

in shelters with other individuals because uninjured individuals have been shown

to avoid shelters that contain injured conspecifics (Parsons and Eggleston, 2005;

Briones-Fourzan et al. 2008). As a consequence of sheltering alone, injured

lobsters may experience reduced aggressive and gregarious interactions with

conspecifics. Parsons and Eggleston (2005) found that injured conspecifics were

more likely to be predated upon and hypothesized that increased predation could

be a result of hemolyph released into surrounding waters (which is known as a

chemical attractant to predators), reduced defense via inability to escape

predation, and/or reduced benefits of group defense (as a consequence of

conspecific avoidance). The direct presence of predators can also influence

denning behaviors, resulting in decreased den sharing due to escape responses

(Childress 1995; Childress and Herrnkind 1997). Shabani et al. (2008) suggests

that alarm cues, along with escape responses, may have evolved to reduce the

risk of predation, supporting the idea that avoiding predation is important. As a

result, avoiding predation has the potential to impact levels of shelter competition

such that individuals under indirect and/or direct predation risk may exhibit

decreased shelter competition. Since predation results in decreased survival, the

cost of remaining in a shelter with an injured conspecific or near a predator

should be high, regardless of whether the habitat is shelter-rich or shelter-poor.

Finally, the abundance of resources in an area may influence shelter

competition between conspecifics. For example, in post-puerulus larvae of *P.*

longipes, aggression is more likely to occur when individuals are competing for limited shelter or food (Berrill 1976). In a shelter-rich environment, I found that habitat type played an important role in den use and den sharing, with individuals from natural shelter-poor habitats exhibiting lower den use and den sharing than individuals from natural shelter-rich habitats. In a shelter-poor environment, the decrease in den use and den sharing was driven primarily by the size of individuals rather than whether a lobster previously lived in a natural shelter-rich or natural shelter-poor habitat. Although aggressive encounters were seen, gregarious behaviors were still exhibited suggesting that the relationship between aggression, gregariousness, and denning behaviors may be complex.

For juvenile spiny lobsters, the decision to share shelters requires cooperation between two or more individuals and appears to be strongly influenced by the social environment (habitat type and size distribution of juveniles in the group) making it difficult to predict. I found that if juvenile spiny lobsters had previously experienced mass shelter loss prior to collection, these lobsters exhibited a decreased response to subsequent shelter loss, suggesting adaptation to shelter limited environments. This behavioral response of juvenile spiny lobsters during shelter loss suggests that behavioral plasticity in den use and den sharing behaviors may be important. Since shelter loss is likely to increase vulnerability to predation, smaller individuals altered their denning behavior by remaining in the same den longer, while larger individuals decreased den use and den sharing. Larger individuals most likely experience less

pressure from predation (Andre 1981; Eggleston et al. 1992; Smith and Herrnkind 1992), and therefore, were more likely to remain outside the den and disperse to alternative shelters/habitats. These changes in denning behavior suggest that spiny lobsters may be able to compensate for shelter loss via plasticity in their behavior.

By determining how animals utilize their natural habitat, we can better predict the impacts of environmental change on habitat use. As a commercially important species (Hunt 1994 cited in Forcucci et al. 1994), understanding potential influences of habitat change on spiny lobster abundances is vital for the survival of this fishery. Here, I show that although larger individuals exhibited higher levels of aggression, aggression did not predict denning behaviors. In fact, after a shelter loss event, which should have led to increased competition for shelter, I found that large, aggressive individuals were less likely to use dens, share dens, and remain in dens for consecutive days than smaller, less aggressive individuals. For this gregarious species, these results suggest that individuals may be plastic in their behavior and that perhaps there is some cost associated to den sharing that larger individuals are less willing to pay when shelter is limited. Understanding the role of habitat selection in a species can play a large role in monitoring, management, and conservation of animals and their surrounding habitat (Jonzen 2008), and this study is an important first step in evaluating the role of individual behavioral variation in influencing den competition and behavioral mitigation of habitat loss.

References

Alanara, A, MD Burns and NB Metcalfe. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. Journal of Animal Ecology 70(6): 980-986.

Andree, S. 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobster, *Panulirus argus*. Science thesis, FL State University.

Atema J and JS Cobb. 1980. Social behavior. In: The Biology and Management of Lobsters. Blackwell Publishing, UK pp 409-450.

Atema, J and MA Steinbach. 2007. Chemical communication and social behavior of the lobster, *Homarus americanus*, and other decapod Crustacea. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 115-144.

Banks, SC, MP Piggott, AJ Stow, and AC Taylor. 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. Canadian Journal of Zoology 85: 1065-1079.

Berrill, M. 1975. Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (Crustacea:Decapoda). Bulletin of Marine Science 25(4): 515-522.

Berrill, M. 1976. Aggressive behaviour of post-puerulus larvae of the Western Rock Lobster *Panulirus longipes* (Milne-Edwards). Australian Journal of Marine and Freshwater Research (27): 83-88.

Bertelsen, R. 2013. Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. Fisheries Research. In press.

Bertelsen, R and J Hornbeck. 2009. Using acoustic tagging to determine adult spiny lobster (*Panulirus argus*) movement patterns in the Western Sambo Ecological Reserve (Florida, United States). New Zealand Journal of Marine and Freshwater Research 43: 35-46.

Briffa, M and LU Sneddon. 2007. Physiological constraints on contest behavior. Functional Ecology 21: 627-637.

Briones-Fourzan, P, E Ramirez-Zaldivar, E Lozano-Alvarez. 2008. Influence of conspecific and heterospecific aggregation cues and alarm odors on shelter choice by syntopic spiny lobsters. Biological Bulletin 215(2): 182-190.

Butler, MJ, JH Hunt, WF Herrnkind, MJ Childress, R Bertelsen, W Sharp, T Matthews, JM Field, and HG Marshall. 1995. Cascading disturbances in Florida bay, USA: Cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Marine Ecology Progress Series 129(1-3): 119-125.

Butler, MJ, AB MacDiarmid, JD Booth. 1999. The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. Marine Ecology Progress Series 188: 179-191.

Butler, MJ, RS Steneck, and WF Herrnkind. 2006.Juvenile and adult ecology. In: Lobster Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, UK pp 263-309.

Childress, MJ. 1995. The ontogeny and evolution of gregarious behavior in juvenile Caribbean spiny lobster, *Panulirus argus*. Ph.D. Thesis, Florida state University, Tallahassee, FL.

Childress, MJ and PE Bouwma in preparation. Assessing the impact of mass sponge mortality on a guild of shelter-dwelling commensals in Florida bay.

Childress, MJ and WF Herrnkind. 1994. The behavior of juvenile Caribbean spiny lobster in Florida bay: seasonality, ontogeny and sociality. Bulletin of Marine Science 54(3): 819-827.

Childress, MJ and WF Herrnkind. 1996. The ontogeny of social behaviour among juvenile Caribbean spiny lobsters. Animal Behaviour 51: 675-687.

Childress, MJ and WF Herrnkind. 1997. Den sharing by juvenile Caribbean spiny lobsters (*Panulirus argus*) in nursery habitat: cooperation or coincidence? Marine and Freshwater Research 48: 751-758.

Childress, MJ and WF Herrnkind. 2001a. The guide effect influence on the gregariousness of juvenile spiny lobsters. Animal Behaviour 62:465-472.

Childress, MJ and WF Herrnkind. 2001b. The influence of conspecifics on the ontogenetic habitat shift of juvenile Caribbean spiny lobsters. Marine and Freshwater Research 52: 1077-1084.

Childress, MJ and SH Jury. 2006. Behaviour. In: Lobsters: Biology, Management, Aquaculture and Fisheries. Blackwell Publishing, UK pp 78-112.

Crispo, E. 2007. The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. Evolution 61(11): 2469-2479.

Davis, GE and JW Dodrill. 1982. Recreational fishery and population dynamics of spiny lobsters, *Panulirus argus*, in Florida bay, Everglades National Park, 1977-1980. Bulletin of Marine Science (44): 78-88.

Dewitt, TJ and Scheiner. 2004. Phenotypic variation from single genotypes: a primer. In: Phenotypic Plasticity: Functional and Conceptual Approaches. Oxford University Press, NY pp 1-9.

Eggers, S, M Greisser, M Nystrand, and J Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian jay. Proceedings of the Royal Society London B 273: 701-706.

Eggleston, DB and RN Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. Ecology 73(3): 992-1011.

Eggleston, DB, RN Lipcius, DL Miller, and L Coba Cetina. 1992. Shelter scaling regulates survival of juvenile Caribbean spiny lobster *Panulirus argus*. Marine Ecology Progress Series 62: 79-88.

Ehrhardt NM, and CM Legault. 1999. Pink shrimp recruitment variability as an indicator of Florida bay dynamics. Estuaries 22:471-483.

Fielder, DR. 1965. The spiny lobster, *Jasus lalandei* (H. Milne-Edwards), south Australia. Australian Journal of Marine and Freshwater Research 15: 133-144.

Forcucci, D, MJ Butler, JH Hunt. 1994. Population-dynamics of juvenile Caribbean spiny lobster, *Panulirus argus*, in Florida bay, Florida. Bulletin of Marine Science 54(3): 805-818.

Fourqurean, JW and MB Robblee. 1999. Florida bay: a history of recent ecological changes. Estuaries 22(2B): 345-357.

Fox, CW and DF Westneat. 2010. Adaptation. In: Evolutionary Behavioral Ecology. Oxford University Press, UK pp 16-31.

Grinnell, J. 1917. Field tests of theories concerning distributional control. The American Naturalist 51(602): 115-128.

Gilroy, JJ and WJ Sutherland. 2007. Beyond ecological traps: perceptual errors and undervalued resources. TRENDS in Ecology and Evolution 22(7): 351-356.

Heatwole, DW, JH Hunt, FS Kennedy Jr. 1988. Catch efficiencies of live lobster decoys and other attractants in the Florida spiny lobster fishery. Florida Department of Natural Resources 44.

Herrnkind, WF and MJ Butler. 1986. Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Marine Ecology-Progress Series 34: 23-30.

Herrnkind, WF, MJ Butler, and JH Hunt. 1997. Role of physical refugia: implications from a mass sponge die-off in a lobster nursery in Florida. Marine and Freshwater Research 48(8): 759-769.

Herrnkind, WF, MJ Childress, and KL Lavalli. 2001. Cooperative defence and other benefits among exposed spiny lobsters: inferences from group size and behavior. Marine Freshwater Research 52: 1113-1124.

Horner, AJ, SP Nickles, MJ Weissburg, CD Derby. 2006. Source and specificity of chemical cues mediating shelter preference of Caribbean spiny lobsters (*Panulirus argus*). Biological Bulletin 211: 128-139.

Horner, AJ, MJ Weissburg, CD Derby. 2008. The olfactory pathway mediates sheltering behavior of Caribbean spiny lobsters, *Panulirus argus*, to conspecific urine signals. Journal of Comparative Physiology A-Neuroethology Sensory Neural and Behavioral Physiology 194: 243-253.

Hunt, JH. 1994. Status of the fishery for *Panulirus argus* in Florida. Spiny Lobster Management: Current Situation and Perspectives: 158-168.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. The Auk. 118(2):557-562.

Jonzen, N. 2008. Habitat selection: implications for monitoring, management, and conservation. Israel Journal of Ecology and Evolution 54 (3-4): 459-471.

Kokko, H and WJ Sutherland 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evolutionary Ecology Research 3: 537-551.

Kramer Schadt, S, TS Kaiser, K Frnak, T Wiegand. 2011. Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. Landscape Ecology 26: 501-513.

Lipcius, RN and WF Herrnkind. 1982. Molt cycle alterations in behavior, feeding and diel rhythms of a decapods crustacean, the spiny lobster *Panulirus argus*. Marine Biology 68: 241-252.

Lott, DF. 1984. Intraspecific variation in the social systems of wild vertebrates. Behaviour 88: 266-325.

Macreadie, PI, JS Hindell, MJ Keough, GP Jenkins, and RM Connolly. 2010. Resource distribution influences positive edge effects in a seagrass fish. Ecology 91:2013-2021.

Martin, P and P Bateson. 1993. Recording methods. In: Measuring Behavior an Introductory Guide. Cambridge University Press, pp 84-100.

Martin, AL and PA Moore. 2008. The influence of dominance on shelter preference and eviction rates in the crayfish, *Oronectes rusticus*. Ethology 114: 351-360.

Marx, J and WF Herrnkind. 1985a. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. Journal of Crustacean Biology 5(4): 650-657.

Mintz, JD, RN Lipcius, DB Eggleston, and MS Seebo. 1994. Survival of juvenile Caribbean spiny lobster: effects of shelter size, geographic location and conspecific abundance. Marine Ecology Progress Series 112: 255-266.

Moore, PA. 2007. Agonistic behavior in freshwater crayfish: the influence of intrinsic and extrinsic factors on aggressive encounters and dominance. In: Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms. Oxford University Press, NY pp 90-114.

Nevitt, G, ND Pentcheff, KJ Lohmann, and RK Zimmer. 2000. Den selection by the spiny lobster *Panulirus argus*: testing attraction to conspecific odors in the field. Marine Ecology-Progress Series 203: 225-231.

Parson, DM and DB Eggleston. 2005. Indirect effects of recreational fishing on behavior of the spiny lobster *Panulirus argus*. Marine Ecology Progress Series 303: 235-244.

Pedetta, S, L Kaczer, and H. Maldonado. 2010. Individual aggressiveness in the crab *Chasmagnathus* influence in fight outcome and modulation by serotonin and octopamine. Physiology and Behavior 101(4): 438-445.

Peluc, SI, TS Sillett, JT Rotenberry, and CK Ghalambor. 2008. Adaptive phenotypic plasticity in island songbird exposed to a novel predation risk. Behavioral Ecology 19: 830-835.

Phlips, EF, S Badylak, TC Lynch. 1999. Blooms of the picoplanktonic cyanobacterium synechococcus in Florida bay, a subtropical inner-shelf lagoon. Limnology and Oceanography 44(4): 1166-1175.

Ratchford, SG and DB Eggleston. 2000. Temporal shift in the presence of a chemical cue contributes to a diel shift in sociality. Animal Behaviour 59: 793-799.

Robertson, DN and MJ Butler. 2009. Variable reproductive success in fragmented populations. Journal of Experimental Marine Biology and Ecology 377(2): 84-92.

Robertson, BA and RL Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87(5): 1075-1085.

Roth, AC. 1972. Agonistic behavior and its relationship to group density, size differences, and sex in the California spiny lobster, *Panulirus interruptus*. M.S. Thesis, San Diego State University, San Diego, California: 1-78.

Schlaepfer, MA, PW Sherman, and MC Runge. 2010. Decision making, environmental change, and population persistence. In: Evolutionary Behavioral Ecology. Oxford University Press, UK pp 506-515.

Schradin, C and N Pillay. 2005. Intraspecific variation in the spatial and social organization of the African striped mouse. Journal of Mammalogy 86(1): 99-107.

Shabani, S, M Kamio, and C. Derby. 2008. Spiny lobsters detect conspecific blood-borne alarm cues exclusively through olfactory sensilla. The Journal of Eperimental Biology 211: 2600-2608.

Shabani, S, M Kamio, and C Derby. 2009. Spiny lobsters use urine-borne olfactory signaling and physical aggressive behaviors to influence social status of conspecifics. Journal of Experimental Biology 212: 2464-2474.

Shield, JD and DC Behringer. 2004. A new pathogenic virus in the Caribbean spiny lobster, *Panulirus argus*, from Florida. Diseases of Aquatic Organisms 59: 109-118.

Smith, KN and WF Herrnkind. 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. Journal of Experimental Marine Biology and Ecology 157: 3-18.

Thayer GW, AB Powell, and DE Hoss. 1999. Composition of larval, juvenile and small adult fishes relative to changes in environmental conditions in Florida bay. Estuaries 22: 518-533.

Valone, TJ. 2007. From eavesdropping on performance to copying the behavior of others: a review of public information use. Behavioral Ecology and Sociobiology 62(1): 1-14.

Wilson, EO. 1975. Sociobiology. Cambridge, MA: Harvard University Press.

Zieman, JC, JW Fourqurean, MB Robblee, M Durako, P Carlson, L Yarbro, and G Powell. 1988. A catastrophic die-off of seagrasses in Florida bay and Everglades National Park: Extent, effect and potential cruises. Eos 69:1111.

Zimmer-Faust, RK, JE Tyre, and JF Case. 1985. Chemical attraction causing aggregation in the spiny lobster, *Panulirus interruptus* (Randall), and its probable ecological significance. The Biological Bulletin 169: 106-118.

Zito-Livingston, AN and MJ Childress. 2009. Does conspecific density influence the settlement of Caribbean spiny lobster *Panulirus argus* postlarvae? New Zealand Journal of Marine and Freshwater Research 43: 313-325.

APPENDICES

Appendix A: Evolution of Gregariousness

These data provide evidence for a decrease in odor preference and may suggest that spiny lobsters may be less gregarious than in the past (Figure A.1; Table A.1). A study completed by Sercy (2005) found that juvenile spiny lobsters exhibit ~75% odor preference, and using the same experimental methods, I found that juvenile spiny lobsters have ~50% odor preference. I hypothesize that the evolution of gregarious behaviors resulting in decreased odor preference may be a result of 1) environmental degradation, 2) fishing pressures, 3) natural selection or a combination of the three. Currently Y-maze trials completed in various environmental conditions (natural seawater and artificial seawater using Instant Ocean©) suggest that odor preference remains low in both environmental conditions (Figure A.1; Table A.1). Y-maze trials completed in lowered pH also result in low levels of odor preference (~40%; Miller 2012) that do not significantly differ from odor preference found in normal pH. These data suggest that immediate changes to environmental conditions may not influence odor preference. Further examination of all three hypotheses is needed to truly understand the evolution of this highly gregarious behavior.

Table A.1: Chi-square analyses of odor preference by year and by salt water treatment. Chi-square analyses of odor preference by year (2005 and 2012) and by salt water treatment (natural and artificial). The year 2005 and natural salt water treatment were considered expected values, and the year 2012 and artificial salt water treatment were considered observed values.

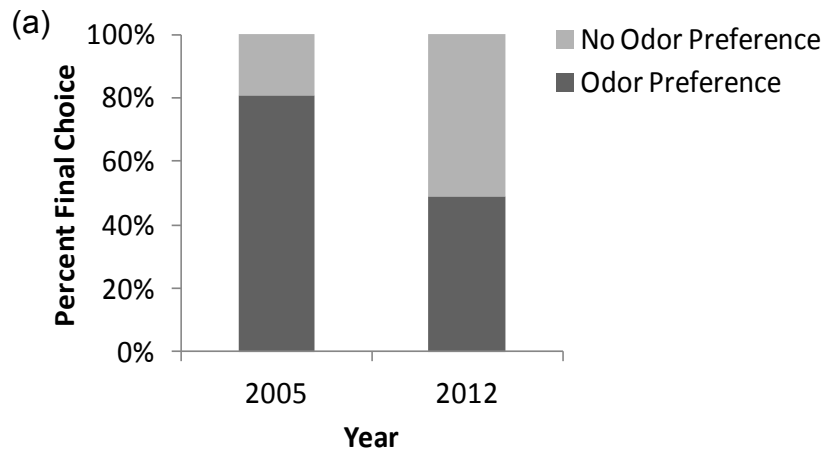| Source	X^2 Value	P-value
Year	6.490	0.011*
Treatment	0.249	0.618
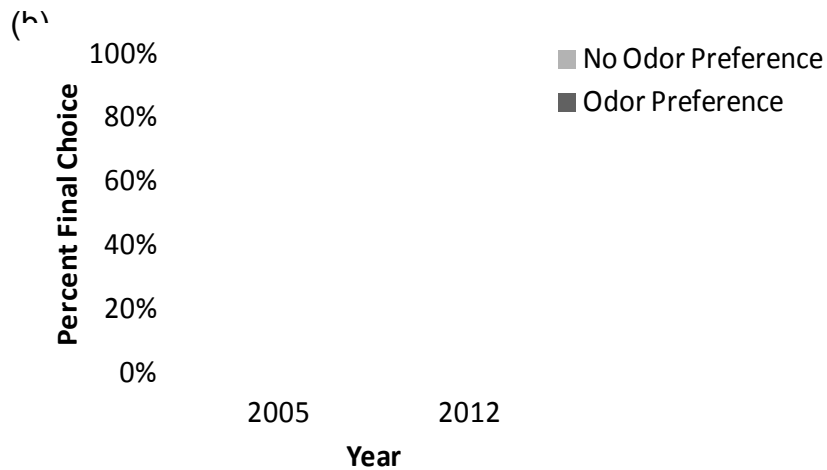
Figure A.1: Effect of year and salt water treatment on odor preference.

Percent odor preference for juvenile lobsters across (a) two years and (b) two salt water treatments. Individuals that spent a higher proportion of time in the odor arm of the y-maze than the no odor arm of the y-maze were considered as havin odor preference. Light gray bars represent no odor preference, and dark gray bars represent odor preference.

Appendix B: Role of Aggression in Defining Status

Y-maze odor preference trials (see Chapter Two) were conducted so that the influence of dominance and familiarity status on juvenile *P. argus* odor preference was able to be examined. In general, I found that, within lobster pairs, dominance status was established, with dominant individuals exhibiting more aggressive acts than subordinate individuals (Figure B.1a; $F_{1,24}=6.670$, $p=0.0163$). In contrast, den sharing was not significantly different by dominance status (Figure B.1b; $F_{1,24}=0$, $p=1.000$). Y-maze odor preference trials found no evidence for preference based on familiarity or dominance status (Figure B.1c). Dominant choosing lobsters were as likely as subordinate lobsters to prefer odors emitted from familiar ($F_{1,24}=0.128$, $p=0.724$), unfamiliar subordinate ($F_{1,24}=0.126$, $p=0.726$), and unfamiliar dominant ($F_{1,24}=0.042$, $p=0.840$) lobsters.
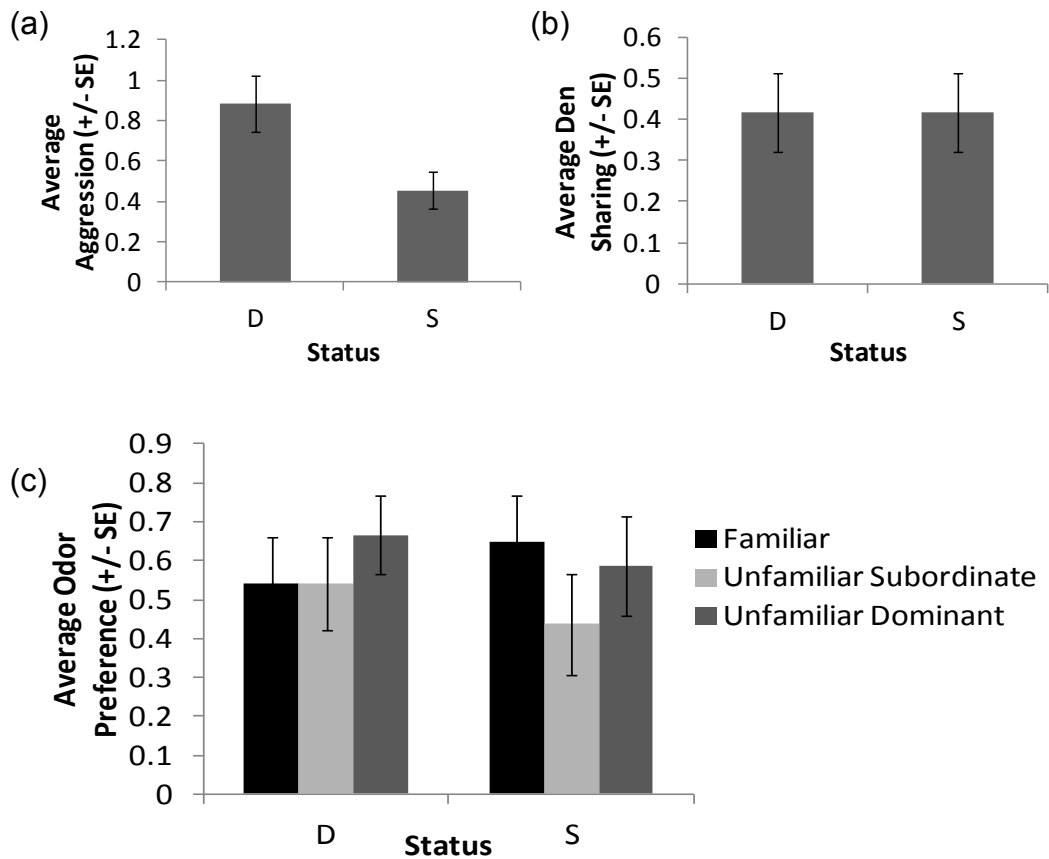
Figure B.1: Influence of status on social behavior. The (a) average

aggression, (b) average den sharing, and (c) average odor preference by

dominant (D) and subordinate status (S). Average odor preference was also

examined by familiarity such that, during a y-maze trial, the emitting lobster was

familiar (black bars), unfamiliar and subordinate (light gray bars), or unfamiliar

and dominant (dark gray bars) when compared to the choosing lobster status.

Error bars are represented by standard error.

Appendix C: Examination of Dispersal via Acoustic Telemetry

Preliminary acoustic telemetry trials show that juvenile spiny lobsters can be tracked in the field for at least one week using Vemco V8 acoustic telemetry tags. Lobsters were tagged (n=3) and released onto a site (MTM2; Figure C.1a) that contained ten receivers in a hexagonal array (Figure C.1b). Geometric methods that were previously developed (Bertelsen and Hornbeck 2009; Bertelsen 2013) were used to determine the location of individuals. All individuals changed locations within the site during the eight day tracking period, and artificial shelter blocks and solution holes were used as shelters. Two individuals (Lob-38116 and Lob-38115) remained on-site, while one individual (Lob-38114) moved off-site and later returned (Figure C.1c). Since the chances of resighting a juvenile lobster after release is low (<25%), using acoustic telemetry may be a much better method for tracking individuals. Obtaining precise and accurate dispersal measures is an important step in understanding juvenile spiny lobster dispersal behavior and the role dispersal plays in mitigating habitat loss. Hence, future research should be directed towards utilizing acoustic telemetry as a means to examine juvenile *P. argus* dispersal behavior.
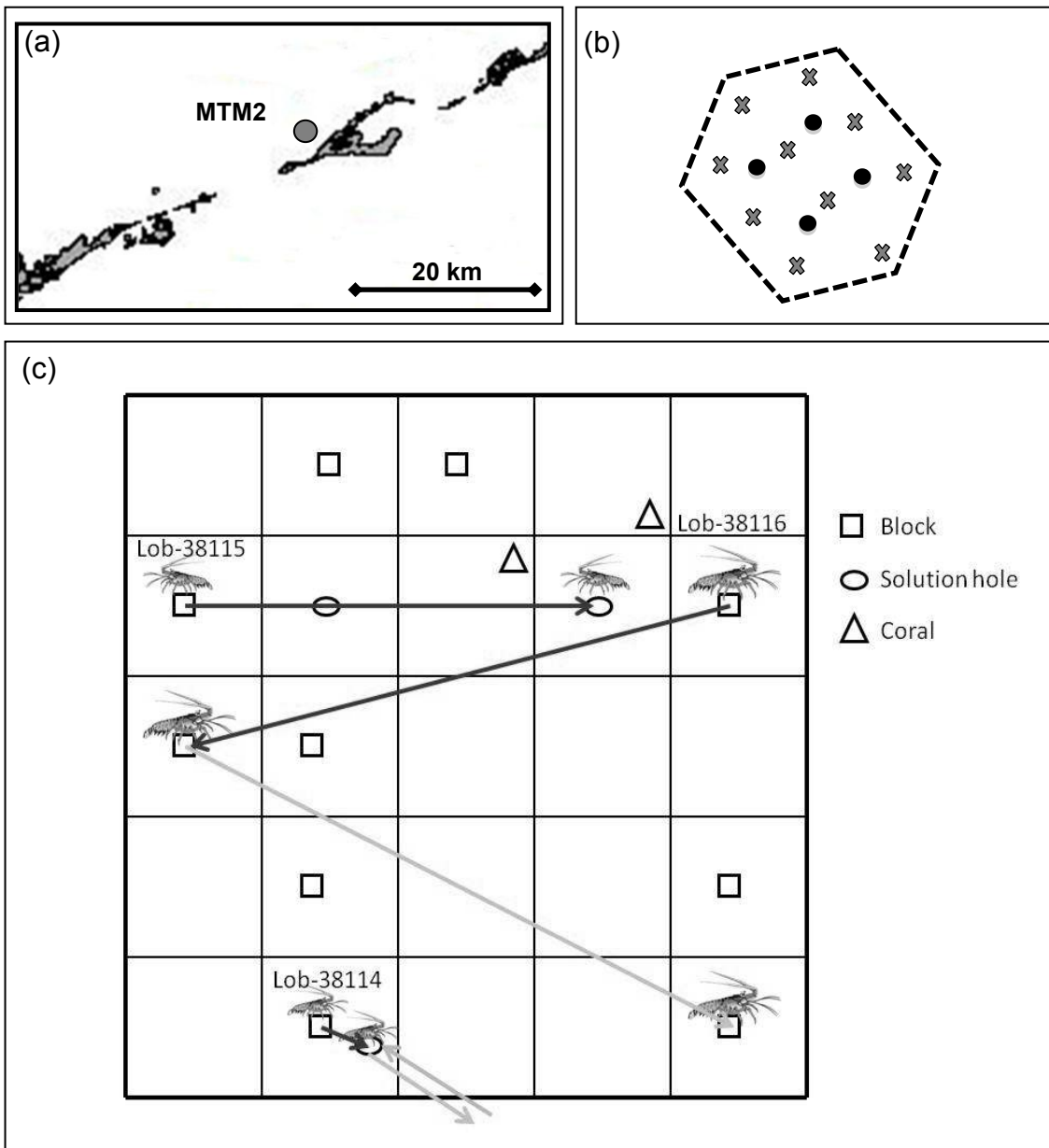
Figure C.1: Aerial and habitat maps of site MTM2 acoustic tagging preliminary study. (a) Map of MTM2 due west of the Keys Marine Laboratory. (b) Arrangement of ten acoustic receivers in a hexagonal grid surrounding the MTM2 site. The black circles mark the four site corners, and the gray X's mark the placement of the ten receivers.

Figure C.1: continued. (c) Habitat map of the MTM2 site showing ten artificial block shelters, two coral heads and three solution hole shelters. Arrows show the path of three acoustically tagged lobsters (Lob-38114, Lob-38115, and Lob-38116) tracked for 8 days. Any directional change in movement is shown by a change in arrow direction or color.