Allometry of reproduction, weapon size, and colony size in social shrimp: A comparative analysis of four eusocial species in genus Synalpheus

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Allometry of reproduction, weapon size, and colony size in social shrimp: A comparative analysis of four eusocial species in genus *Synalpheus*

A thesis submitted in partial fulfillment of the requirement for the degree of Bachelors of Science in Biology from The College of William and Mary

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Williamsburg, VA
April 12, 2013
Abstract

Eusociality is one of the most highly developed forms of social behavior in which groups of individuals show overlap of generations, strong reproductive skew, and cooperative care of young. Eusociality is thought to have evolved in several animal groups as a response to ecological challenges. Within the diverse tropical sponge-dwelling marine crustacean genus *Synalpheus*, multiple species display eusocial behavior, a trait that is not found in any other marine organisms. The eusocial species of the genus *Synalpheus* form large colonies often with only one reproducing female among tens to hundreds of individuals. These reproducing females, or queens, strongly influence the growth and success of a colony as they appear to be the primary source of direct recruits. In addition, the success of a eusocial *Synalpheus* colony is highly dependent on its ability to retain and defend its host sponge. This necessary combination of reproduction and defense presents a potential for trade-offs between the allocation of energy and resources for the queen and the colony. Because both defense and reproduction are key factors in the evolution of eusociality, I have compared the allometry of reproductive capacity and defensive weaponry to colony characteristics in queens of four eusocial *Synalpheus* species. Bivariate regressions and structural equation modeling were used to characterize relationships between queen fecundity, size of the major chela (fighting claw), and colony size, shedding light on the relationship between individual success and social organization in sponge-dwelling shrimp. The individual allometry of reproducing females was relatively consistent across species with body mass having strong positive effects on both major chela mass and egg number. In addition, the relationship between chela mass and egg number, or fecundity and weaponry, was negative indicating a tradeoff between
reproduction and defense. Furthermore, the relationship between colony size and major chela mass was also negative indicating a buffer effect between number of cohorts in a colony and the necessity of a major chela for queen personal defense. Finally, the effect of individual allometry on colony size varied dramatically indicating that while queen allometry did significantly affect colony size, other factors outside the sphere of this study are also involved.

I. Introduction

The shift from solitary life to group living represents a key transition in the evolution of social behavior. The conditions and characteristics that favor this social development are varied and have long been debated (Wilson 2005; Foster et al 2006). Eusociality, the most extreme form of social organization, presents an enigma for evolutionary theory in that most members of eusocial colonies forgo individual fitness in order to rear the offspring of others instead. Eusociality is typically recognized in groups of organisms that display three key characteristics: overlap of generations, cooperative broodcare, and non-reproducing or sterile worker castes (Wilson 1971; Andersson 1984). Despite the evolutionary enigma, eusociality has evolved multiple times in a wide variety of taxa. These taxa include the well-known social insects, primarily Hymenoptera (wasps, bees, and ants) and Isoptera (termites) as well as several other groups of insects (Choe & Crespi 1997), two species of mole rats (Jarvis & Bennett 1993), and finally, multiple species of the marine shrimp genus Synalpheus (Duffy 2007).
The evolution of eusociality involves both genetic and ecological factors. Although they vary between taxa, factors suggested to promote eusocial organization include genetic relatedness within colonies, ecological advantages such as food-shelter coincidence (Hamilton 1964), and strong selection for defense (Crespi 1994; Karsai & Wenzel 1998; Duffy et al. 2002). Central to most explanations are that kin selection and inclusive fitness are the driving forces in eusociality (Hamilton 1964) with the benefit of helping raise close relatives outweighing the loss of individual reproduction. More recently, some have emphasized the importance of ecological factors as a major determinant (Fletcher et al. 2005; Wilson 2005). Despite different emphases, it seems clear

Figure 1. A Bayesian consensus tree based on morphological characters (Hultgren & Duffy 2012). Underlined species display eusocial organization with the 4 target species of this study in red.
that multiple factors, behavioral and ecological, contribute to the development of social organization.

The genus *Synalpheus*, specifically the *gambarelloides* species group, is commonly known as snapping shrimp. Within this genus there are at least five known species that display the characteristics of eusocial organization such as overlap of generations, reproductive skew and cooperative broodcare. Eusocial organization has evolved at least three distinct times within the genus and is found in no other marine organisms (Duffy 2007). My thesis focuses on four of the eusocial species: *Synalpheus brooksi*, *S. chacei*, *S. filidigitus*, and *S. regalis* (Figure 1). All four species form large colonies with one to a few reproducing females, known as queens, and tens to hundreds of non-reproducing individuals (*S. brooksi* being the only species in which more than two females are typically present within one colony). Body size varies across and within species with *S. brooksi* being the largest (carapace length of ~3-6mm) and *S. chacei* and *S. filidigitus* being the smallest (carapace length of ~2-3mm). The name snapping shrimp actually refers to all members of the alpheid family and is derived from the presence of a large snapping claw. Present on one side of the body, this claw, or major chela, produces a powerful jet of water and a loud audible snap when closed rapidly, and is used in aggressive interactions and defense (Duffy 1996; Duffy et al 2002; Toth & Duffy 2005). This combination of eusocial colonial living and cooperative defense brings to light questions such as the influence of individuals on colony behavior and dynamics.

The monophyletic *gambarelloides* group within the genus *Synalpheus* consists of around 40 species of coral-reef dwelling shrimp (Figure 1). Diagnostic characteristics of the *gambarelloides* group include a distinctive setal brush on the minor first chela.
(Darveau 1984; Duffy & Macdonald 1999) in addition to the habit of residing within the canals of certain species of sponges demonstrating a parasitic (Duris et. al. 2011) or possibly mutualistic relationship. Body sizes across the gambarelloides group vary considerably, ranging from < 3 mm to > 30 mm in length (Figure 2). Distinction between the species is determined using unique, and often minute, morphological characteristics (Duffy 1996, Darveau 1984). One striking difference in morphology across the eusocial species is the lack of a major chela in reproductive females of S. filidigitus (Figure 2.c). In contrast, S. brooksi (Figure 2.a) has the largest chela (~3-5mm) while S. chacei (Figure 2.b) and S. regalis (Figure 2.d) have smaller chela (~1-4mm and 2-3.5mm, respectively). These variations in major chela size and presence could be linked to a tradeoff between reproduction and defense indicating that the reproductive females potentially invest in reproduction or defense depending on certain factors. One factor would be colony size, or the number of cohorts found within a colony, which would indicate the defense ability of the colony and the queen.

The genus Synalpheus presents an ideal study group for examining the origin and evolution of these reproductive adaptations. The images (Figure 2) show mature reproductive females or “queens.”
of eusocial behavior in that it displays three key conditions: 1) varied forms of social organization among the species, ranging from heterosexual pairs to large eusocial colonies, 2) relatively small number of species, (~40) within the clade, and 3) similarities in general morphology and ecology such as a symbiotic lifestyle (Duffy & MacDonald 1999; Duffy et al 2000). In addition, many of the ecological conditions suggested to foster eusociality, such as fortress-defense (Queller & Strassmann 1998) and food-shelter coincidence (Hamilton 1964), are present within eusocial Synalpheus species. Host specificity among Synalpheus species and their host sponge species is generally strong (Macdonald et.al. 2006); in general it is thought that the sponges provide both food (Duris et. al. 2011) and shelter for the colony (Duffy et al 2000). This sedentary lifestyle categorizes the shrimp as species that live in relatively predictable and valuable environments, allowing for dense populations as well as strong competitive pressure. As theorized by the habitat saturation hypothesis (Selander 1964; Emlen 1982), valuable habitat resources are highly sought after and so are often completely inhabited with few to no available sponges for new colonization. In this case, the sponges are the highly sought after resource. The necessity and limited availability of these sponges along with the high levels of competition would not only promote selection for defense among Synalpheus species but also potentially provide an advantage to cooperative living and colony formation. In addition to selection for defense, limited availability of sponges inhibits the potential success of individuals looking to leave the colony and establish a territory of their own. This raises a key question posed in this study which could explain factors which lead to social evolution. Is the selection for defense that results from inhabiting highly valuable and rare resources linked to a tradeoff with reproduction? This
trade-off might represent a shift in the allocation of both individual and communal resources between defense and reproduction.

Given the relatively similar sedentary and symbiotic life style of almost all Synalpheus species, why has eusocial behavior evolved only within a few species? This raises questions of the evolutionary advantage of eusocial colony formation. If non-reproducing individuals invest nothing in reproduction, their direct fitness is zero. However, genetic relatedness of colony members is key in determining the relative advantage of eusocial living. Members of Synalpheus eusocial colonies are often full siblings (Duffy 1996; D.R. Rubenstein et al. unpublished data), meaning that all non-reproducing individuals are the offspring of the same parents. In this case, forgoing individual reproduction does not end the furthering of the genetic lineage because full siblings are on average as closely related as parents and offspring and so raising siblings should result in a similar genetic payback to raising personal offspring.

One key characteristic that distinguishes the eusocial species of Synalpheus from species with nonsocial organization is the life history trait of direct-development (crawling larva). The life history of most alpheid shrimp species includes a planktonic larval form (swimming larva) which promotes high dispersal capability and lessens the likelihood of kin to aggregate (Duffy & Macdonald 2010). In contrast, several Synalpheus species have direct-development, which results in crawling larva with limited mobility and low dispersal potential (Dobkin 1965; Dobkin 1969). The ability of species with crawling larvae to accumulate in kin groups is supported by the genetic evidence of close relatedness among colony members in these species. Moreover, eusociality occurs in three subclades of Synalpheus which display direct development but occurs in none
that produce swimming larvae (Duffy & Macdonald 2010), supporting the idea that direct development is a key requirement for producing the kin aggregations which are key to eusocial evolution (Hamilton 1964).

One set of factors that is relatively unexplored in the genus Synalpheus involves the reproductive capacity of the social species. Reproductive capacity will depend on resource and energy allocation by reproducing females and potentially the helping and/or defense ability of other colony members. Trade-offs occur when a finite amount of energy or resources cannot be invested in more than one aspect of life. Such trade-offs are key facets of eusocial colonies where one reproducing female bears all of the reproductive pressure and might increase reproduction by limiting her investment in other aspects such as defense or foraging. In turn, other individuals within the colony do not invest in reproduction and so can invest in other duties such as the defense of the colony. Given the link between reproduction/larval development and the presence of eusociality, reproductive investment will be vital in exploring the many facets of eusocial behavior.

Reproduction depends on many characteristics such as the growth of an individual, and on individual allometry, such as body mass and fecundity. Allometry can be defined as biological scaling relationships whether they be morphological or ecological traits. For example, the relationship between body mass, egg number and colony size scales with body size because larger females have the ability to produce more eggs and so could produce a larger colony faster. In addition, major chela mass is an allometric variable that could potentially influence fecundity because in some individuals it makes up a large portion of their total mass. If a reproducing female is either small in body mass or is the queen of a small colony, she may invest more in defense (major
chela) and so limit her fecundity until the colony grows larger with more members for protection or until she grows large enough to defend herself. In this case, the aggregation of a larger colony allows for cooperative defense in which intruding shrimp are confronted with a coordinated attack by colony members (Toth & Duffy 2005). Producing a large colony takes time, and thus will depend on the age of the female. In other words, the older the female/colony, the more generations of cohorts have stayed within the colony. However, age is not easily measured and so body mass, chela mass, and fecundity are the variables I used in comparisons of colony size for this study. By studying the allometry of reproduction and investment in weaponry by reproducing queens in eusocial *Synalpheus* colonies, light can be shed on questions about the relationship between individual reproduction and social organization.

II. Objectives

The objectives of this study are:

(1) Determine whether any social shrimp exhibit a trade-off between investment in reproduction and defense.

(2) Determine if and why individual allometry such as body size and fecundity are good predictors of colony size.

(3) Determine whether differences in these relationships exist among the four social shrimp species and whether they might be explained by differences in ecology.

In order to study the basics of reproduction in the four eusocial species studied here, I compared the individual allometry of the reproducing females, or queens. I measured the relationships between body size, major chela size, and egg/embryo characteristics, and
colony characteristics such as colony size, and number of reproductive females. I predicted that chela mass and egg number would scale with body mass as well as that colony would increase with egg number but negatively influence queen chela mass. This last relationship is the key aspect of the trade-off which I hypothesize would occur in larger colonies. Within the four species studied, individual allometry as well as colony characteristics varied across species. For example, *S. brooksi* has relatively large body mass with relatively small colony size, whereas *S. filidigitus* and *S. chacei* have similarly low body masses but larger colony size. I took advantage of variation among species to explore whether individual level allometry or colony level characteristics are the driving factors for reproduction in eusocial organisms.

III. **Materials and Methods**

In order to quantify the effect of individual reproduction and allometry on colony level characteristics, reproducing females from each species were collected and measured and colony data were recorded. Field collections varied over years and locations so the following is a brief summary of field collection protocol. The following methods detail the protocol for field collection, specimen choice and measurement, calculations and statistical analysis.

III.1. **Specimen collection:**

The specimens used for this study were collected over a period from 1988-2012 from two Caribbean locations; San Blas, Panama (latitude 9.497487, longitude -78.917885) and Carrie Bow Cay, Belize (16.80602,-88.082714). Collections in early
years (1988-1995) were opportunistic and unsystematic. I participated in field collections in the summer of 2012. Quantitative sampling methods varied slightly across the years but the general collection method was as follows.

Each sampling area visited was visually assessed for the potential target habitat: dead coral rubble patches. Patches of dead coral harbor the cryptic sponge species in which eusocial *Synalpheus* species live in colonies. If sufficient rubble patches were present then the area was named and marked with a GPS point. Collection areas were surveyed using either snorkel or SCUBA depending on the depth of the reef. The often cryptic nature of the target sponges made affirmation of their presence difficult and often times required the careful prying apart of the coral rubble. Singular sponges and pieces of coral rubble found to contain sponges were then placed in large mesh bags along with other pieces from the same patch. All rubble pieces from each patch were placed into buckets for transportation. All items collected from one specific area of the reef consisted of one quantitative sample.

All sponge and rubble samples were transported to the wet lab and were placed under constant flowing seawater until they could be analyzed. The rubble pieces were dissected in order to remove the sponges which were in turn delicately dissected and all fauna removed from the internal canals. All sponges, regardless of shrimp presence, were provisionally identified and labeled. Each shrimp specimen found was identified down to species, sexed, and preserved in 95% EtOH and/or formalin. Females carrying eggs and rare species were preserved only in EtOH as formalin degrades morphological characteristics. Every effort was made to collect the whole group of shrimps (i.e., the
colony) present within a sponge so that colony size (number of individuals) could be measured as precisely as possible.

III.2. Choosing female specimens:

The four eusocial shrimp species targeted for this study are *Synalpheus brooksi*, *S. chacei*, *S. filidigitus*, and *S. regalis*. Of the members of the genus displaying eusocial behavior, these four species are the most abundant within the available collection. In order to study the reproductive and colony characteristics of the four species, preserved females from each species were chosen from the collection located at the Marine Biodiversity Lab at the Virginia Institute of Marine Science (VIMS). The individuals were chosen through a set of selection criteria which are as follows:

- Collection location either Carrie Bow Cay, Belize or San Blas, Panama
- Host specimen *Spheciospongia vesparium* (*S. brooksi*), various spp. (*S. filidigitus*, *S. chacei*, *S. regalis*)
- Measurements taken only from ovigerous (egg-bearing) females.

The choice of various locations, years, and host species are due to the varying sample locations and times (i.e. Belize was not visited during some of the target years), as well as the host specificity of certain species.

III.3. Photographing and measuring specimens:
Individual allometric variables of the reproducing females were determined using photographic measurements. These variables include carapace length, chela length, and egg dimensions. The carapace was photographed dorsally as flat as possible with the rostrum visible. Carapace length was measured, to the nearest millimeter, from the center point between the valleys on either side of the rostrum to the center of the edge of the carapace (Figure 3.a). The major chela was removed from the specimen as close to the body as possible to be photographed. The major chela was photographed and measured from the tip of the fixed finger to the opposite dorsal end of chela segment (Figure 3.b).

<table>
<thead>
<tr>
<th>Stage</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Early blastoderm</td>
</tr>
<tr>
<td>2</td>
<td>Large blastoderm, gastrulation</td>
</tr>
<tr>
<td>3</td>
<td>Minute eye visible</td>
</tr>
<tr>
<td>4</td>
<td>Large eyes, outline of abdomen</td>
</tr>
<tr>
<td>5</td>
<td>Large eyes, long abdomen separated from head</td>
</tr>
<tr>
<td>6</td>
<td>Hatched larvae or if no larvae, empty egg capsules</td>
</tr>
</tbody>
</table>

**Figure 4.** Development stage determination using visible morphology derived from Meredith (1952) and Oh & Hartnoll (2004). Though egg development stage varied within one clutch, each clutch was assigned one stage according to which stage described the majority of the eggs.
For the purpose of this thesis, the measure of reproductive output is the number and mass of embryos produced by queens. For the purpose of this thesis, I am labeling these embryos as eggs and clutch size will be referred to as egg number. Eggs were removed gently to avoid damaging other aspects of morphology. All eggs from one female were photographed and counted. Egg length and width were measured for five randomly selected eggs from each clutch. If a clutch contained fewer than 5 eggs, all eggs in that clutch were measured. In addition, development stage was determined through methods derived from Meredith (1952) and Oh & Hartnoll (2004). Eggs were assigned a development stage from 1 to 6 depending on visible morphological characteristics (Figure 4.). Development stage varied within one clutch but often by no more than one stage. In these cases, the development stage that appeared most often for all eggs in the clutch was assigned.

III.4. Individual Allometry Calculations

In order to quantify reproductive capacity, a combination of individual morphological variables and colony-level characteristics were calculated. For individual queens I measured carapace, chela, and egg length. From these, trunk mass, chela mass, and whole body mass were calculated (All formulas used were derived from Duffy & Macdonald 2010):

$$\text{Trunk mass} = 0.5986 \times e^{(0.4892 \times \text{Carapace Length})}$$

$$\text{Major chela mass} = 0.3135 \times e^{(0.4268 \times \text{Major Chela Length})}$$

$$\text{Whole body mass} = \text{Trunk mass} + \text{Major chela mass}$$
Egg length and width measurements were used to calculate both egg mass and volume. Among individual females of a species, the clutch size (egg number) varied considerably (1 to 73 over all specimens) so average individual egg mass and volume per female were calculated by averaging the calculations for 5 eggs from each clutch. Total egg mass and volume were then calculated by multiplying average egg mass/volume by clutch size.

\[
\text{Egg Volume} = \frac{4}{3} \times 3.14 \times \text{Egg length} \times \text{Egg width}^2
\]

\[
\text{Egg Mass} = 0.0299 + 0.0103 \times \text{Egg Volume}
\]

\[
\text{Total egg volume or mass} = \text{Egg volume or mass} \times \text{clutch size}
\]

Calculated variables include fecundity, colony size, and relative chela mass. When compared, these variables can show trends in reproductive output as well as potential trade-offs between individual reproduction and colony defense.

\[
\text{Relative reproductive investment} = \frac{\text{Total egg mass}}{\text{Whole body mass}}
\]

\[
\text{Relative chela mass} = \frac{\text{Major chela mass}}{\text{Whole body mass}}
\]

**III.5. Colony level Variables**

The target variable examined on the colony level was colony size.

\[
\text{Colony size} = \text{Total number of individuals found within a colony}
\]

**III.6. Statistical Analysis**

In order to determine the allometric relationships among individual queen reproductive and defensive capacity and between those characteristics and colony level...
characteristics, four variables were used: 1) Queen body mass, 2) Queen chela mass, 3) log Queen clutch size (number of eggs carried by the queen), and 4) log Colony size. Variables not displaying a normal distribution were log transformed which succeeded in approximating a normal distribution.

In order to initially examine potential relationships, simple bivariate regressions were run between the four variables. The initial regressions included all possible data, with no possible relationships omitted except in the case of absent data (i.e. chela data for *S. filidigitus*). These regressions were used to explore the direct relationships between pairs of variables but do not take into account the compounding effects of all other variables.

To explore the network of compound relationships between variables, I used structural equation modeling (SEM) (an outgrowth of path analysis, Grace 2006). Using the statistical package laavan in program R, SEM was used to determine simultaneous causal relationships between the four variables. In this case, SEM was used as both a confirmatory and exploratory method. Relationships between individual allometry variables were based on clear expectations and so SEM served as a confirmatory method.
to test hypotheses, whereas relationships between allometry and colony are unknown and
so SEM served an exploratory mode to characterize these relationships.

The direction of hypothesized causality among variables was proposed *a priori* in
a saturated structural model (Figure 5) in which all potential relationships, or pathways
are given. Pathway direction and sign of the hypothesized model were based on
assumptions from general allometry. For example, I assumed that body mass directly
influences both chela mass and fecundity and that female fecundity can have an impact of
colony size. Queen body mass was the only exogenous variable and the other variables
being endogenous, meaning that queen body mass only had outward directional effects
and was only affected by variables external to the model. All other variables had at least
one incoming pathway. This suggests that variance in queen body mass is determined by
variables outside of our consideration.

A two-step process was used to first determine the overall fit of the model using a
chi-square statistic which examines the difference between the observed covariance
matrix and the model covariance matrix. If the model was found to fit the data (if the chi-
square was found to be not significant indicating that the covariance matrices were
acceptably similar), then the individual paths were analyzed using t-tests (Grace 2006).
Due to the inability to calculate model fit (chi-squared) for a saturated model where the
observed covariance and model covariance matrices are identical, I estimated all path
coefficients from the saturated model and then removed the one with the weakest effect
and calculated fit of this reduced model with a chi-squared test. If two pathways showed
similarly weak and not significant coefficients, then models omitting each of the paths in
question were compared using AIC in order to choose between the alternative models.
I was unable to fit the same base model for all of the four species for multiple reasons. First, in *S. filidigitus*, the lack of a major chela across all reproducing females (Duffy & Macdonald 1999) eliminated that variable from the model. In addition, for *S. brooksi*, after careful consideration, the colony variable was removed from the SEM analysis. This was due to the occupancy of very large host sponges by *S. brooksi* such that individuals of this species were collected from only a portion the sponge, not the

**Figure 6.** *A priori* structural models for each species consisting of 4 possible variables; queen body mass, major chela mass, log queen egg number, and log Colony size. a) *S. brooksi* b) *S. chacei* c) *S. filidigitus* and d) *S. regalis*. 

19 Bornbusch
entire sponge, so the recorded colony size only represents a portion of the potential entire colony. Because of this, the true colony size is unknown. In addition, *S. brooksi* differs from the other three species because instead of having a single reproducing female per colony, *S. brooksi* colonies often have multiple reproducing females. The number of individuals sampled in *S. brooksi* was larger than the other 3 species in order to account for the fact that a group of females represented one colony instead of one *S. brooksi* female individual. However, *S. brooksi* colony data was included in the initial bivariate regression analysis. Despite being incomplete, I decided that the inclusion of colony data would at least act as a proxy in order to explore basic relationships between colony and individual characteristics in *S. brooksi*.

*A priori* models for each species (Figure 6) were fitted using structural equation modeling. As mentioned above, missing pathways are due to either insufficient data or removal after calculation of AIC determined model fit. Unstandardized and Standardized path coefficients were calculated to determine the pathway coefficients. The reasons for using both unstandardized and standardized were to allow for analysis of relationships both within and among models and species. Unstandardized coefficients are presented in the original units of the variable and therefore allow for comparison of the same path among different models and species. Standardized coefficients, which standardize the units of all paths within one model, allow for comparison of the strength of pathways within one model/species where variables are measured in different units.

IV. Results
Of the 191 individual shrimp queens sampled, 47 were *S. regalis*, 39 *S. filidigitus*, 43, *S. chacei*, and 62 *S. brooksi*. The number of individuals for *S. brooksi* is larger due to the high number of females per colony. The 62 individual *S. brooksi* females represent 33 colonies.

**IV.1. Bivariate Allometry**

Bivariate regressions were performed on all measured variables to characterize allometric relationships and to decide which variables should be used as target variables. The variables for which regressions were run but which were not chosen as target variables include carapace length, chela length, relative chela mass (chela mass/body mass), fecundity (egg number/body mass) and total egg mass (Appendix 1).

For the 4 target variables (Queen body mass, queen major chela mass, log egg number and log colony size) the simple regressions were initially used to determine characteristics of the relationships (Table 1, Figures 7-12). Allometric relationships studied include Queen body mass vs. major chela mass, Queen body mass vs. log egg number, and Major chela mass vs. log egg number (Figures 7 - 9). *S. filidigitus* was excluded from all comparisons with major chela due to the lack of a major chela in ovigerous females of this species.
Queen body mass was positively related to chela mass and log egg number in all species (Figures 7, 8, Table 1) confirming that these variables scale to body mass with a roughly linear allometry. There was no clear relationship between chela mass and egg number in *S. brooksi* *S. chacei* and *S. regalis* (Figure 9).

Table 1. Results from bivariate linear regression analysis. Values shown include Estimate (Unstandardized coefficient), \( \beta \) (slope of intercept), R-squared, and P-value.

<table>
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<tr>
<th></th>
<th>Estimate (Unstd. Coeff)</th>
<th>R-squared</th>
<th>P-value</th>
</tr>
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<tbody>
<tr>
<td><em>S. brooksi</em></td>
<td></td>
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</tr>
<tr>
<td>body mass -&gt; major chela mass</td>
<td>0.146</td>
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<tr>
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<td>egg number -&gt; colony size</td>
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<td>0.445</td>
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Figure 7. Queen major chela mass (mg) in relation to Queen body mass (mg). Body and chela mass vary across species so scales differ. $R^2$ values are included.

Figure 8. Queen body mass (mg) in relation to the log of egg number. $R^2$ values are included.

Figure 9. Queen major chela mass (mg) in relation to log10 egg number. Body mass varies across species so x-axis scales differ. $R^2$ values are included.
Figure 10. Queen body mass in relation to log of colony size. *S. brooksi* have characteristically large body masses and small colonies and so Plot a) has a different axes scales. $R^2$ values are included.

Figure 11. Queen egg number in relation to the log of Colony size. $R^2$ values are included.

Figure 12. Queen major chela mass in relation to the log of colony size. *S. filidigitus* is morphologically lacking a major chela and so is not included in this comparison. $R^2$ values are included.
The relationship between queen body mass and log colony size (Figure 10) was positive for *S. chacei*, *S. filidigitus* and *S. regalis*, though *S. regalis* showed a barely positive relationship (slope of linear trendline = 0.0003). *S. brooksi* showed a negative relationship between queen body mass and log colony size. Though the colony data for *S. brooksi* is incomplete, it is possible that these relationships stay relatively similar across the scale of colony size. Major chela mass and log colony size (Figure 11) showed a positive relationship for *S. brooksi*, *S. filidigitus*, and *S. regalis*, thought *S. regalis* again showed a barely positive relationship (slope of linear trendline = 0.0006). Finally, the relationship between egg number and log colony size (Figure 14) was highly positive for *S. chacei*, *S. filidigitus*, and *S. regalis*. The relationship was negative for *S. brooksi* indicating that because both body mass and egg number have a negative relationship with colony size, *S. brooksi* may have other factors affecting colony size not included in this study.

**IV.2. Multivariate Structural Equation Modeling**

Because many of the variables might interact in complex and multivariate ways, simple regression analysis was insufficient. Therefore, structural equation modeling was used to illustrate the complex causal relationships between the target variables (Table 2). Figures 13 & 14 display the SEM results for each species with the unstandardized coefficients and the standardized coefficients, respectively.
IV.2.a. *Synalpheus brooksi*]

Due to the unavailability of complete colonies, the analysis of *S. brooksi* focused solely on individual allometry (Figure 13a. 14a). Queen body mass significantly and positively affected both major chela mass and log queen egg number (P < 0.001. Table 2), with the effect of queen body mass on major chela mass and egg number being comparable (standardized coefficients, Figure 14a). The relationship between queen egg number and major chela mass was negative but not significant (standardized pathway coefficient = -0.001, P-value = 0.112).
IV.2.b. Synalpheus chacei

Including the pathway between log queen egg number and log colony size resulted in a much poorer model fit (the chi-squared dropped from 0.791 to 0.003) so the path was omitted from the model using AIC to determine the best alternative model. All other pathways were significant at the \( P < 0.05 \) level. Queen body mass positively affected major chela mass, log queen egg number and log colony size with all pathways being significant (all \( P < 0.001 \)). The effects of queen body mass on log...
queen egg number and major chela mass were comparable and somewhat stronger than the effect of queen body size on colony size (Figure 14.b). The relationship between major chela mass and log queen egg number was negative and significant (standardized pathway coefficient = -0.737 and P-value = 0.002), supporting the possibility of a trade-off between investments in these two variables. There was a weak effect but nevertheless significant negative relationship between log colony size and major chela mass with a pathway standardized coefficient of -0.209 (P = 0.050).

![Diagram showing structural equation modeling results for each species.](image)

**Figure 14.** Structural equation modeling results included on structural models for each species. Standardized pathway coefficient for are included for each pathway and arrow thickness is scaled to represent pathway strength. Solid arrows indicate a significant relationship while dotted lines represent not significant pathways. Arrow direction indicate direction of causation and arrow color indicates the sign of the causation (black = positive, red = negative).
IV.2.c. *Synalpheus filidigitus*

The lack of a major chela in *S. filidigitus* queens required the removal of that variable from the model. In addition, because queen body mass is the sum of queen trunk mass and major chela mass, queen trunk mass was used for *S. filidigitus* instead of queen body mass. The resulting model showed a significant positive effect of queen trunk mass on log egg number, as expected (P < 0.001). Log egg number was strongly positively related to log colony size with a standardized pathway coefficient of 0.746 and a P value < 0.001. The effect of queen trunk mass on log colony size not significant (P = 0.685).

IV.2.d. *Synalpheus regalis*

*S. regalis* demonstrated significant pathways from queen body mass to major chela mass and log egg number (P values < 0.000). Queens from larger colonies tended to have relatively smaller major chela although this effect was not statistically significant. All other pathways were found to be positive and not significant.

V. **Discussion**

Statistical analysis using simple regressions and structural equation modeling gave insight into the allometric relationships of body size to fecundity and defensive weaponry as well as to colony size. In all species, queen body mass positively affected both egg number and major chela mass, confirming my original hypotheses that chela mass and fecundity scale positively with body mass. In addition, in species where the queen has a
major chela (i.e. excluding \textit{S. filidigitus}) there was a tendency toward a negative relationship between chela mass and egg number though this was only significant in \textit{S. chacei}. This indicates that there is a possible trade-off between investment in egg production (reproductive capacity) and chela mass (defense ability). This is a key point as queens from larger colonies tended to have smaller chela indicating the buffer effect of many colony members which lessens the queens reliance on her own fighting claw. The correlations between allometry and colony size differed across all species with \textit{S. regalis} showing no significant effects on colony size and \textit{S. chacei} and \textit{S. filidigitus} showing significant pathways from queen body mass and egg number to colony size, respectively.

\textbf{V.1. Species specific allometry and colony level comparison}

The four eusocial \textit{Synalpheus} species showed somewhat different relationships between individual allometric variables and colony size. This sheds light on the fact that there are varying types of social organization even among the eusocial shrimp, in addition to different factors which affect it. Within each species, correlations between allometric variables remained predictable while their relationships with colony size varied. Standardized pathways (Figure 14) were used to compare strengths of relationships within one species.

\textbf{V.1.a. \textit{Synalpheus brooksi}}

\textit{S. brooksi} was unique among the four species in that only individual level allometric variables were statistically analyzed. Queen body mass significantly affected both major chela mass and queen egg number with the coefficient of the effect varying by
only 0.108). The coefficient was higher in the relationship between body mass and egg number suggesting a higher investment in reproduction.

Despite solely analyzing allometric data, *S. brooksi* demonstrates unique colony characteristics among *Synalpheus* eusocial species that warrant discussion. As mentioned before, *S. brooksi* is the only species where multiple reproducing females inhabit a single sponge. The *S. brooksi* colonies I studied were found within the sponge species *Spheciospongia vesparium*, the Loggerhead sponge, a large barrel-shaped species.

Because of this, the entire sponge was not able to be collected, leading to the partial samples seen in the majority of *S. brooksi* colony data. These large sponges could allow for large colony formation, making them extremely valuable resources. In *S. brooksi*, the presence of multiple reproducing females could indicate either of two possible situations; 1) a single colony with multiple reproducing females, or 2) multiple smaller colonies inhabiting a single sponge. In the first situation, multiple females reproducing for a single colony would allow for faster colony growth and in turn, sponge defense. If the cohorts of multiple females stayed within a single colony, the high rate of colony growth would provide a competitive advantage when inhabiting large or highly sought after sponges. Given the negative relationship between chela mass and egg number, this high level of reproduction would mean a decrease in necessity and mass of chela for the queen. And in contrast, a decrease in fecundity could be explained by a higher number of reproducing females which releases the reproductive pressure on each individual. However, of the four eusocial species, *S. brooksi* possess the largest major chela even thought their body mass is relatively similar to *S. regalis*. This would suggest that the second situation, that multiple smaller colonies inhabit a single large sponge, could be plausible. In this case,
cooperation between multiple colonies would allow for defense and retention of valuable sponge habitat. However, cooperation among colonies would require a sort of recognition of conspecific foreigners versus conspecific nestmates, which means that despite cooperation across groups, the likelihood of territorial behavior and conflict between adjacent colonies within a sponge would favor retention of the larger chela. A solution to this question would require extensive complete colony testing in addition to genetic testing.

V.1.b. *Synalpheus chacei*

*S. chacei* was the only species with statistically significant pathways for all relationships. The pathway which was excluded, between queen egg number and log colony size, was the only not significant effect and was omitted in order to preserve the fit of the model. Queen body mass positively and strongly influenced both chela mass and egg number, confirming allometric assumptions common to all four species (i.e. body mass positively and directly affects chela mass and fecundity). In addition, queen body mass showed a positive highly significant effect on colony size. Because body mass and not egg number was the only significant factor affecting colony size, a possible explanation is that the colony size depends more on the queen age, that is to say the number of generations of cohorts that the queen has to produce to create the colony. In younger colonies with fewer members, the female’s egg number or reproductive investment may have a clearer effect on overall colony size. Moreover, the negative effect of colony size on chela mass and of chela mass on egg number demonstrates a potential tradeoff between reproduction and defense. If we can infer that colony size depends on
queen age, as a queen ages and more generations of cohorts accumulate within the colony, there would be a buffer effect between the queen and potential danger. This allows her to minimize the investment in her major chela which in turn significantly increases her ability to produce eggs.

V.1.c. *Synalpheus filidigitus*

Because *S. filidigitus* queens lack major chelae, reproduction was the focus of the analysis for this species. The highly significant relationship between queen body mass and queen egg in combination with the lack of a major chela indicating no investment in defense number suggests that *S. filidigitus* invests highly in reproduction. *S. filidigitusi* presents an extreme example of a case where the queen has come to fully rely on defense by other colony members in that she has shed her major chela entirely. In addition, the almost equally strong relationship between egg number and colony size shows that *S. filidigitus* queens fecundity is tightly correlated with colony size.

V.1.d. *Synalpheus regalis*

Allometric relationships between body mass, chela mass and egg number were all significant and positive as in the other 3 species. However, *S. regalis* is the only species to show no significant relationship between colony size and any individual level variable. Because neither body mass nor egg number significantly affects colony size, variation in colony size could be due to variables not included in this model such as environmental factors like sponge size and availability.
V.1.e. Across species comparisons

When comparing pathways across different models and species, standardized pathway coefficients were used (Figure 13). Within the allometric correlations, the standardized effect of queen body mass on egg number was comparable to the effect on chela mass for all species, suggesting fairly tight allometric constraints on these variables. I also found evidence of possible trade-offs between investment in reproduction and defense, and that other members of the colony might help alleviate the trade-off. This is particularly evident in *S. filidigitus*, who have no chelae and demonstrate a strong relationship between queen body mass and egg number as well as the strongest pathway coefficient from egg number to colony size across all species. For *S. regalis*, who have the largest colonies of the four species, it is possible that they invest more in defense. Furthermore, because *S. regalis* shows no significant effects on colony size from any variables, it is possible that other factors outside those studied here, such as habitat availability and competition, affect *S. regalis* colony size, perhaps emphasizing their need for retention and defense of such environmental resources. However, it is interesting to see that in *S. regalis* and *S. filidigitus*, the two species who display eusocial organization in the strictest sense (i.e. largest colonies with highest reproductive skew), the chela seems to play a very minor role (or absent in the case of *S. filidigitus*) in the relationships between individual allometry and colony size. This illustrates that as colonies become larger and the queen becomes increasingly outnumbered by non-reproducing members, she no longer needs to invest in her protection and so the major chela becomes a less significant predictor of individual investment and colony characteristics.
S. chacei, is the only species who showed significant relationships for all pathways in addition to the strongest pathways for all included pathways (unstandardized pathway coefficients Figure 13). Not only are the correlations between individual allometric relationships the highest, but S. chacei is the only species to demonstrate a direct significant effect of queen body mass on colony size. This suggests that perhaps S. chacei is less affected by factors outside the sphere of this study and so the relationships between allometry and colony size are clear.

In contrast, for S. brooksi, even though only individual-level variables were considered, the relationships shown were some of the lowest across the four species. Perhaps this is due to the presence of multiple females within one sponge, which if all individuals in one sponge were a single colony, would potentially release individual females from some reproductive pressure and allow them to invest more in say body size via foraging or other unconsidered factors. This possibility is emphasized by S. brooki’s comparatively large body mass.

For those species with chela present, all pathways between chela mass and egg number were negative, despite only S. chacei being significant. This suggests a tradeoff in investment. For S. chacei, this relationship indicates a clear tradeoff between queen egg number and chela mass. The bidirectional pathway between chela mass and egg number is intended to indicate that the directionality of the relationship between colony size reproduction, and defense are not clearly known and require further study.

Though the allometric relationships were relatively predictable across all four species, their relationship to colony size was highly unpredictable. There was seemingly no conformity among species in the affect of reproducing individuals on colony size,
including when taking into account phylogenetic relatedness. This suggests that the four species demonstrate variations of eusociality that depend on multiple factors, some of which were not included in this study. Environmental factors, such as host specificity and habitat availability could contribute highly to varying levels of eusociality.

V.2. Future Recommendations

In order to address the questions arising from this study, there are a few aspects which would require improvement. Firstly, sampling methods for field collections would need to be standardized across all locations. Seeing as the specimens used in this study were taken from a collection spanning 25 years, there was inevitable variation across sampling methods. This led to inconsistencies in specimen preservation as well as a lack of data for certain variables and species. If further studies are to be produced on whether colony level characteristics are affected by individual allometry, there will be a necessity for more data to be gathered concerning both allometry and colony level variables. This includes allometry, genetic relatedness, and indications of sex and caste for non reproducing individuals. Furthermore, the addition of environmental factors such as sponge availability and size would add another level of analysis that could assist in explaining variations in colony characteristics.

V.3. Conclusions and Implications

Explanations for the eusociality paradox have greatly benefitted from studies of *Synalpheus* species. Explorations of the eusocial species in this genus have shown that both ecological factors and kinship are major factors in the evolution of eusociality.
(Duffy & Macdonald 2010). In addition, *Synalpheus* studies have established that many elements that are key to understanding the development of eusociality are dependent on reproduction. These include larval development and dispersal capability (Dobkin 1945, Duffy & Macdonald 2010) as well as inclusive fitness (Queller 1996) and kinship (Hamilton 1964). This study attempts to clarify a few of the allometric and colony-level processes that influence the success of both individuals and colonies. The data presented here suggest that individual allometry and colony size feedback into each other through the influence of both reproduction and colony defense. In addition, the intensity and direction of this feedback loop varies across species. In *S. chacei* and *S. filidigitus*, the role of colony size and defense and its influence on individual allometry, specifically fecundity, seems to be the clearest. These two species have the smallest chela of the four species (with *S. filidigitus* exhibiting no chela) in addition to the strongest relationship between queen body mass and egg number indicating a tradeoff. However, because colony size appears to be most strongly influenced by different factors in these two species (queen body mass for *S. chacei* and egg number for *S. filidigitus*), it suggests that there are multiple different pathways of influence from individual allometry to colony size. In contrast, factors affecting colony size are relatively unknown for *S. brooksi* and *S. regalis* and so could be linked more strongly to environmental factors. These data indicate the possibility of multiple pathways affecting the aspects of eusociality such as colony characteristics, cooperative defense, and selective breeding. However, much more extensive research and data collection is needed to unravel the complexities of the relationships between individuals and colonies, as well as reproduction and defense.
Acknowledgments

I would like to thank everyone who helped make this research possible. I am grateful to everyone at the VIMS Marine Biodiversity Lab especially my advisor Emmett Duffy, and my mentor Rachael Blake. I would like to thank the College of William and Mary, including the Roy R. Charles Center and Ted Dintersmith who made funding this research possible. For their funding and support, I would like to specifically thank the Scion Natural Science Association and Montserrat Gorina-Ysern at the Healthy Children-Healthy Oceans Foundation.
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Appendix

Plots in this appendix show simple regressions between variables other than the four target variables. These were used in order to compare and determine which variables would best serve as target variables. In addition, Tables 1A and 2A show regression statistics for all measured variables as well as a complete data table with original data.

**Figure A.1.** Queen carapace length (mm) in relation to the log of colony size.

**Figure A.2.** Queen fecundity (egg mass/whole body mass) in relation to relative major chela mass (major chela mass/whole body mass). *S. filidigitus* is morphologically lacking a major chela and so does not appear in this comparison.
**Figure A.3.** Queen fecundity (egg mass/body mass) in relation to the log of Colony size. *S. brooksi* has relatively small colonies and so has a different x-axis scale.

**Figure A.4.** Queen relative chela mass (major chela mass/body mass) in relation to the log of colony size. *S. filidigitus* is morphologically lacking a major chela and so is not included in this comparison.
Figure A.6. Queen chela length in millimeters in relation to Queen queen carapace length in millimeters.
Queen carapace length vs log10colony size

Figure A.5. Queen Carapace length (mm) in relation to the log of Colony size.
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| CBC96-301   | <em>filidigitus</em>   | 0.000 | 1.589  | 4  | 2 | 0.136 | 13 |
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| CBC97-01    | <em>filidigitus</em>   | 0.000 | 1.775  | 3  | 3 | 0.127 | 48 |
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| CBC98-3901  | <em>filidigitus</em>   | 0.000 | 2.022  | 5  | 1 | 0.190 | 2  |
| CBC99-9001  | <em>filidigitus</em>   | 0.000 | 1.931  | 7  | 3 | 0.175 | 21 |
| CBC012107   | <em>regalis</em>       | 0.988 | 4.387  | 18 | 4 | 0.737 | 111|
| CBC012203   | <em>regalis</em>       | 1.035 | 3.997  | 14 | 1 | 0.612 | 100|
| CBC014303   | <em>regalis</em>       | 1.116 | 4.691  | 43 | 2 | 1.549 | 204|
| CBC015103   | <em>regalis</em>       | 0.916 | 4.388  | 29 | 2 | 0.962 | 164|
| CBC01608    | <em>regalis</em>       | 1.147 | 4.930  | 44 | 3 | 1.895 | 198|
| CBC017003   | <em>regalis</em>       | 1.132 | 4.707  | 53 | 1 | 2.308 | 188|
| CBC017703   | <em>regalis</em>       | 0.814 | 2.634  | 8  | 2 | 0.390 | 46 |
| CBC021833   | <em>regalis</em>       | 0.801 | 2.785  | 0  |   | 0.189 |    |
| CBC022404   | <em>regalis</em>       | 1.170 | 3.816  | 21 | 3 | 0.534 | 122|
| CBC031502   | <em>regalis</em>       | 1.009 | 3.021  | 0  |   | 0.48  | 48 |
| CBC034429   | <em>regalis</em>       | 1.089 | 4.536  | 25 | 4 | 1.332 | 195|
| CBC034525   | <em>regalis</em>       | 1.069 | 4.891  | 38 | 2 | 1.552 | 153|
| CBC03704    | <em>regalis</em>       | 0.953 | 4.025  | 15 | 3 | 0.711 | 96 |
| CBC037302   | <em>regalis</em>       | 0.866 | 3.791  | 1  | 4 | 0.045 | 77 |
| CBC037602   | <em>regalis</em>       | 0.889 | 2.813  |   |   | 0.28  |    |
| CBC04-101   | <em>regalis</em>       | 1.047 | 3.892  | 26 | 1 | 0.468 | 28 |
| CBC04-2201  | <em>regalis</em>       | 0.814 | 3.431  | 23 | 3 | 0.589 | 67 |
| CBC04-2302  | <em>regalis</em>       | 1.063 | 4.217  | 39 | 5 | 1.544 | 7  |
| CBC04-2902  | <em>regalis</em>       | 0.938 | 3.758  | 11 | 5 | 0.420 | 1  |
| CBC04-601   | <em>regalis</em>       | 0.849 | 3.468  | 18 | 1 | 0.636 | 7  |
| CBC05-1501  | <em>regalis</em>       | 1.037 | 3.894  | 31 | 4 | 1.278 | 140|
| CBC05-1601  | <em>regalis</em>       | 1.254 | 4.882  | 31 | 1 | 1.041 | 105|
| CBC05-1701  | <em>regalis</em>       | 0.861 | 3.040  | 21 | 1 | 0.660 | 49 |
| CBC05-2301  | <em>regalis</em>       | 1.023 | 4.469  | 35 | 1 | 1.172 | 137|
| CBC05-2401  | <em>regalis</em>       | 0.884 | 3.145  | 23 | 2 | 0.898 | 91 |
| CBC05-2801  | <em>regalis</em>       | 1.078 | 4.539  | 25 | 1 | 0.749 | 17 |
| CBC05-2901  | <em>regalis</em>       | 0.816 | 3.026  | 13 | 1 | 0.340 | 18 |
| CBC05-3201  | <em>regalis</em>       | 0.966 | 3.402  | 17 | 1 | 0.521 | 66 |</p>
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