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The Evolution of Social Monogamy and Biparental Care in Stomatopod Crustaceans

By

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Requirements for the degree of

Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee in Charge:

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Professor Eileen Lacey

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ABSTRACT

The Evolution of Social Monogamy and Biparental Care in Stomatopod Crustaceans

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Doctor of Philosophy in Integrative Biology

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Although social monogamy and biparental care have been extensively studied in birds, mammals, and fish, the evolutionary origins and maintenance of these phenomena are not well-understood, particularly in invertebrate taxa. The evolution of social monogamy is of interest because current theory predicts that both males and females will usually gain more fitness from mating with multiple partners. Furthermore, biparental care should only occur when males and females both gain more fitness benefits from providing parental care than from investing time and energy into mate searching. Given these expectations, under what environmental and social conditions will social monogamy and biparental care arise and do the same conditions maintain monogamy and biparental care on an evolutionary time scale? Long-term social monogamy, which occurs when a male and female pair for longer than a single breeding cycle, has been reported in eight genera of Lysiosquilloid stomatopods. Furthermore, the Lysiosquilloidea also contains the only marine crustacean genus (*Pullosquilla*) in which biparental care has been systematically studied. This dissertation examines the evolutionary maintenance and origins of both biparental care and long-term social monogamy in the Lysiosquilloidea, using experimental manipulations, ecological surveys, and comparative, phylogenetically-based methods.

Chapter 1: The maintenance of biparental care

I examined the fitness costs and benefits of biparental care in the stomatopod *Pullosquilla thomassini* using an experimental manipulation of the number and sex of care providers. In the absence of any care, egg clutch survival and growth decreased. However, neither the number, nor the sex of the care providers had a significant effect on changes in egg clutch mass. Parental care treatment did not affect ovary size, the total number of eggs in a clutch, or egg size. Thus, while parental care increases production of offspring, uniparental care by either sex is sufficient to achieve this goal. Males providing uniparental care lost more weight than those providing

biparental care or no care. This may lead to sexual conflict over female desertion. These results suggest that biparental care is not evolutionarily maintained in *P. thomassini* by increasing the number of offspring hatching in an egg clutch. Instead, I hypothesize that biparental care may be evolutionarily maintained in *P. thomassini* by increasing the rate of egg clutch production and facilitating double-clutching.

Chapter 2: The effects of environmental and demographic variation on pairing behaviors

I examined the effects of environmental and demographic variation on pairing behaviors, egg clutch production, and burrow distribution in two sympatric stomatopod crustaceans, *P. litoralis* and *P. thomassini*. These small (<16mm) stomatopods are found as heterosexual pairs in U-shaped burrows in coral patch reef ecosystems. Coral patch reef ecosystems consist of coral heads of varying sizes separated by sand flats; in this heterogeneous environment, the coral heads host high levels of invertebrate and fish diversity and abundance in comparison to the sand flats. I hypothesized that environmental heterogeneity in the coral back reef environment would affect pairing behaviors, egg clutch production, and burrow distribution of *Pullosquilla* species due to gradients in food abundance or predation by fish. I tested this hypothesis on demographic and environmental data collected from a survey of *Pullosquilla* species collected in a patch reef in Moorea, French Polynesia. My findings indicate that proximity to coral heads is an important factor in structuring the demography and pairing behaviors of *P. litoralis*, but not its congener, *P. thomassini*. The directionality of the relationships between proximity to coral heads and several demographic traits suggests that gradients in fish predation are responsible for these patterns in *P. litoralis*. This suggests that selective pressures from fish predation may play an important role in the maintenance of pairing behaviors in *P. litoralis*. Determining the causes of differences in demographic patterns and pairing behaviors of *P. litoralis* and *P. thomassini* may yield a better understanding of the evolutionary maintenance of social monogamy in stomatopod crustaceans.

Chapter 3: The evolutionary origins of long-term social monogamy in stomatopods

I examined two hypotheses for the evolutionary origins of long-term social monogamy in stomatopod crustaceans using comparative, phylogenetically-based methods. One of the most commonly posited explanations for the evolution of social monogamy is that biparental care is required to successfully raise offspring. A prediction of this hypothesis is that biparental care should evolve in a clade before or at the same time as social monogamy. I tested this prediction by reconstructing ancestral states of social monogamy and biparental care on a Maximum Likelihood tree of 66 stomatopod species and found that long-term social monogamy evolved before biparental care in the Lysiosquilloid stomatopods. This indicates that a need for biparental care did not lead to the origin of social monogamy in this clade. Based on my finding that predation influences pairing behaviors in *P. litoralis* (Chapter 2) and the observation that all known socially monogamous stomatopods are sit-and-wait predators, I propose an alternative hypothesis for the origin of social monogamy in stomatopods. Sit-and-wait predation evolves as a strategy to maximize energy intake while minimizing predation risk when a lineage lives in an environment where both prey items and potential predators are abundant. I therefore hypothesized that a suite of behaviors, including burrowing, sit-and-wait predation, and social monogamy, that allowed stomatopods to escape high levels of predation evolved in the Lysiosquilloidea. I tested two predictions of this hypothesis: 1) social monogamy should evolve more often in burrow-dwellers living in soft-bottom substrates and 2) the evolution of long-term social monogamy should be correlated with the evolution of sit-and-wait predation. I tested this

hypothesis on a Maximum Likelihood phylogeny of 66 stomatopod species using ancestral state reconstructions and Pagel's (1994) test of correlated trait evolution and found that burrowing, sit-and-wait predation, and social monogamy evolved sequentially in the Stomatopoda. Long-term social monogamy may have evolved as a way of further maximizing the fitness benefits of the sedentary lifestyle associated with sit-and-wait predation. This novel evolutionary route to long-term social monogamy may be associated with the shallow benthic marine environments that most Lysiosquilloids inhabit.

Conclusions

The findings of my thesis emphasize the importance of studying a diversity of taxa and environments when trying to understand the evolution of important behavioral traits. For example, it is often assumed that when biparental care is widespread in a species, it increases the viability of the current brood of offspring. However, in *P. thomassini* there is no evidence that biparental care increases either the survival or development of embryos (Chapter 1). Additionally, the evolution of social monogamy in many animals is attributed to a need for biparental care. The Lysiosquilloid stomatopods appear to provide a counter-example in which social monogamy likely facilitated the evolution of biparental care and other form of paternal effort (Chapter 3). Instead, my findings support the hypothesis that long-term social monogamy and sit-and-wait predation may have evolved to decrease mortality from predation during foraging and mate searching. The role of the risk of predation during mate searching in the evolution of social monogamy has received relatively little attention in the large body of literature on mating system evolution, but it appears that predation plays an important role in determining pairing behaviors and burrowing distributions in *P. litoralis* (Chapter 2). Taken as a whole, these findings provide compelling justification for studying the evolution of behaviors in a wide diversity of taxa.

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This dissertation is dedicated to Andrew Xavier Dulac. Andrew, you inspire me every day!

Are two parents better than one? Examining the effects of biparental care in a stomatopod crustacean.

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ABSTRACT:

Although social monogamy and biparental care have been extensively studied in birds, mammals, and fish, few studies of these phenomena have been conducted on invertebrate species. Social monogamy is characteristic of several ecologically important marine crustaceans, while biparental care has only been characterized in a single genus of stomatopod crustacean, *Pullosquilla*. This study investigated the fitness costs and benefits of biparental care in the socially monogamous *Pullosquilla thomassini* using an experimental manipulation of the number and sex of care providers. In the absence of any parental care, egg clutch survival and growth decreased. However, neither the number, nor the sex of the care providers had a significant effect on changes in egg clutch mass. Parental care treatment did not affect ovary size, the total number of eggs in a clutch, or egg size. These results suggest that while parental care increases production of offspring, uniparental care by either sex is sufficient to achieve this goal. Males providing uniparental care lost more weight than those providing biparental care or no care. This may lead to sexual conflict over female desertion. We suggest that biparental care may increase fitness in *P. thomassini* by increasing the rate of egg clutch production.

INTRODUCTION:

Biparental care occurs when both the male and the female provide direct care for embryos or young. In most taxa, excepting passerine birds, females provide care more often than males and biparental care is rare. However, biparental and paternal care exist in a diverse range of animals (fish: Mank et al 2005, Goodwin et al 1998; birds: Lack 1968, Cockburn 2006; mammals: Eisenberg 1966, Kleiman and Malcolm 1981, Reynolds et al 2002; invertebrates: Trumbo 2012). Biparental care should be evolutionarily maintained when both sexes gain more reproductive success from providing parental care than from investing time and energy into mate searching (Maynard Smith 1977, 1978). In turn, biparental care may be a selective pressure favoring the evolution and maintenance of social monogamy (Lack 1968, Emlen and Oring 1977, Burley and Johnson 2002). The evolution of social monogamy has long interested researchers because current theory predicts that both males and females will gain fitness from mating with multiple partners (Bateman 1948, Trivers 1972). This raises the question, when will biparental care provide fitness advantages that will make social monogamy advantageous? I investigated the fitness benefits and costs of biparental care in the socially monogamous stomatopod crustacean *Pullosquilla thomassini* to better understand the evolution of this form of biparental care and its role in the maintenance of social monogamy.

In iteroparous species, biparental care is both a form of cooperation and an opportunity for conflict between the sexes (Trivers 1972, Lessells 2006). Energy allocated to present clutches detracts from the production of potential future clutches, so that males and females must individually determine how much care to allocate to each clutch to maximize their lifetime

reproduction (Trivers 1972). Game theory analyses suggest that for biparental care to persist, both males and females must gain greater net lifetime fitness benefits from providing care to offspring than from investing their energy in finding a new mate. These fitness benefits can occur in two ways that are not mutually exclusive: 1) parental care can increase the fitness of individual offspring (i.e. current reproduction) by increasing their survival and/or female fecundity or 2) parental care can increase the rate at which offspring are produced by increasing the resources females can allocate to future clutches (Maynard-Smith 1977, 1978). Thus, to understand why biparental care occurs in a species, it is vital to understand how it affects present and future reproductive success in both sexes.

When one parent from a pair providing biparental care provides less than half of the care or deserts, sexual conflict may ensue. Sexual conflict is defined by Parker (1979) as “a conflict between the evolutionary interests of individuals of the two sexes.” The other parent has several choices: 1) it may try to fully or partially compensate for the lost care, causing a potential cost in future reproductive success, 2) it may not vary the amount of care it provides, or 3) it may desert its young in favor of future reproductive opportunities. Partial compensation by the remaining parent should be the best strategy to evolutionarily enforce biparental care and maximize lifetime reproductive fitness. Although strategies vary between taxa, partial compensation appears to be the most commonly expressed strategy (Harrison et al. 2009). In this study I investigated whether males or females compensate when providing uniparental care at a cost to their future reproductive success.

Although monogamy and biparental care have been extensively studied in birds, mammals, and fish, there are few studies of invertebrate models. Social monogamy is characteristic of several ecologically important marine crustaceans, including fiddler crabs (Detto and Blackwell 2009), alpheid shrimp (Duffy and MacDonald 2009) and mantis shrimps (Wickler and Seibt 1981, Correa and Thiel 2003; Christy and Salmon 1991; Caldwell 1991), while biparental care is known from only one genus of stomatopod crustaceans, *Pullosquilla* (Jutte 1997, Lindstrom 2003).

Based on the natural history of *Pullosquilla*, there are several likely mechanisms of evolutionary maintenance of biparental care that are not mutually exclusive. Biparental care may increase current reproductive success by increasing the number of eggs produced in each egg clutch or by increasing the survival or rate of development of eggs. Biparental care may increase future reproductive success by increasing the frequency at which females can produce egg clutches. Finally, biparental care may facilitate the successful rearing of double-clutches.

I investigated several of these mechanisms by addressing the following questions on *Pullosquilla thomassini* in an experimental study: 1) Does parental care (either uni- or biparental) affect changes in egg clutch size, egg size, and number of eggs per clutch when a single clutch is present in the burrow? 2) Does biparental care provide fitness benefits over uniparental care in these same metrics, as well as in ovary available for future reproduction in the female? I also examined the potential for sexual conflict to occur over parental care in *P. thomassini* by investigating: 1) whether either sex pays a fitness cost when providing uniparental care, rather than biparental care or no care, and 2) whether uniparental care by either sex occurs in the field population from which experimental animals were sampled. In addition to providing the first data regarding the adaptive consequences of biparental care in a stomatopod crustacean, this study yields important insight into the evolutionary maintenance of biparental care by examining it in a comparative model system.

METHODS:

Study System

Among marine crustaceans, only one species of stomatopod, *Pullosquilla litoralis*, has been shown to provide biparental care (Lindstrom 2003). Based on laboratory observations, we suspected that biparental care also occurs in a congener with very similar ecology and behaviors, *Pullosquilla thomassini*. Both *P. litoralis* and *P. thomassini* (Michel and Manning 1971) are small (<16mm) mantis shrimps found throughout the Indo-Pacific. Both male and female *Pullosquilla* aerate eggs extensively with their pleopods, move egg clutches within their burrows, and remove fouled eggs and parasites from egg clutches (Jutte 1997). Laboratory studies indicate that *P. litoralis* males and females spend roughly equal amounts of time caring for eggs (Lindstrom 2003). When food is abundant, pairs may double-clutch by producing a second clutch of eggs before the first clutch has hatched. In this case, males and females expend approximately twice as much time providing care to both clutches of eggs as they do for a single clutch (Lindstrom 2003). *Pullosquilla* is a member of the Lysiosquilloidea, a clade of mantis shrimps that includes at least eight socially monogamous genera (as well as many non-monogamous genera) that primarily provide maternal care. This clade provides an ideal comparative system for asking questions about the fitness benefits of social monogamy and biparental care.

Study Site and Field Collection Methods

A study on seventy-seven pairs of adult *P. thomassini* with egg clutches in early stages of development (evidenced by the lack of eyespots) was performed at Lizard Island Research Station from October– December 2011. Stomatopods were collected by excavating burrows with hand trowels while on SCUBA from Casuarina Beach, a tidal sandflat on Lizard Island, Australia (Figure 1; 55 L 0332697 8376974 UTM). Burrows at depths of 1 – 3 m were scooped into resealable plastic bags underwater and adult *P. thomassini* and egg clutches were removed from sand with a 1 mm sieve. Sieved sand was retained for use in the study

Density and Collection Surveys

To assess the density of *Pullosquilla thomassini* on Cassaurina Beach, a burrow density survey was performed prior to making collections. *P. thomassini* burrows can be easily distinguished from other organisms' burrows on Cassaurina Beach by their size (3-5mm diameter), their well-manicured openings, and their flush construction with the sand. Burrow densities were surveyed along 20-30m transects at the following angles from the northern-most mooring buoy at the site (55 L 0332697 8376974 UTM): 0°, 20°, 40°, 60°, 80°, 180°, 210°, 330°, 345°.

To assess the relative abundance of burrows containing single males, females, pairs, and eggs, 127 burrows were collected along the same transects. Burrows were hand-excavated and sieved as previously described and sorted in the lab to determine their contents (single male or female, pair, eggs). Pairs with eggs clutches in early developmental stages were included in the experiment described below. Other animals were released at Cassaurina Beach.

Parental Care Experiment

To document the adaptive consequences of biparental care, an experiment was performed between October - December, 2011 at Lizard Island Research Station with animals collected during the population survey. After collection from the wild, pairs of *P. thomassini* were allowed

to acclimate to lab conditions overnight in 100 ml cups. They were then randomly assigned to one of four parental care treatments for five days. Animals were housed in approximately 700 mL of their natal aragonite sand, sieved to remove intrafaunal predators and potential food sources, in 1 L clear plastic cups with mesh lids in continuous-flow seawater pumped in from Cassuarina beach. Ambient temperature seawater ranged between 27 and 30 degrees C. Only animals that excavated new burrows in the cups and brought egg clutches into the burrow were used in the experiment. Stomatopod burrows were visible along the sides and bottom of each cup. To determine if the number or sex of parents providing care affected the development and survival of *P. thomassini* eggs, as well as the size of adults, pairs with single egg clutches were randomly assigned to one of four parental care treatments for five days: biparental care, only paternal care, only maternal care, and no care. In the no care treatment, eggs and parents were housed in separate containers, but otherwise kept in identical conditions. At the end of the experimental treatment, animals were removed from the sand with a 1mm sieve and measured as described below.

The following observations were taken immediately before and after treatments. All stomatopods and egg clutches were blotted dry and weighed with a Sartorius TE214S microscale (d=0.1mg). Ventral and dorsal positions of adults and whole egg clutches were photographed with a scale bar with a Canon Powershot SD1200 IS Elph. Individual eggs were photographed at 4.5X on an Olympus dissecting light microscope with full light to measure egg size, assay egg development stage, and detect any fouling organisms. Using ImageJ software, we measured the diameter of 15 eggs from each clutch to examine egg development. Relative ovary size was measured by tracing ovary area and body area in Image J.

Analyses

All analyses were performed in “R” using the *NLME* package (Pinheiro et al. 2009). Data were examined for normality, homogeneity, outliers, and colinearity. Colinearly dependent variables were analyzed separately. The effects of parental care treatment group on changes in mass in males, females, and eggs were analyzed with GLS regression using the methodology of Zurr (2009), with initial male, female, or egg mass as a covariate. Ovary area, total number of eggs, egg size, clutch area, and clutch density were similarly analyzed. Widespread heteroscedasticity in the datasets was corrected using the Aikake Information Criterion (AIC) and ANOVA testing to choose appropriate variance structures (while including all possible explanatory variables and interactions) that were then incorporated into the analysis. After the incorporation of the appropriate variance structure, homogeneity and normality were reassessed using the normalized residuals of the new model.

After the most appropriate variance structure was selected, model simplification was performed by backward elimination of terms. The most complicated version of all models tested followed the same basic form: $\text{gls}(\text{Change in size} \sim \text{Starting size} * \text{treatment}, \text{variance structure})$. The interaction between starting size/weight and treatment group in each analysis was assessed using an F distribution and $\alpha = 0.05$. After final model selection, homogeneity and normality were again assessed.

RESULTS:

Demography

The density of *P. thomassini* burrows at Cassaurina Beach ranged from 0.6 to 2.3 burrows/m, with an average of 1.17 burrows/m (970 m² surveyed). Of the 127 burrows collected during this study, 81 contained pairs, 15 contained single females, and 31 contained single males. A higher percentage of burrows containing pairs (32.89%) also contained egg clutches than burrows containing singles (males: 17.86%, females: 21.43%). Females and males found as pairs in burrows were size-matched (LR: $y=0.716x+0.01$, adjusted $r^2 = 0.481$, DF = 54, F = 51.91, $p < 0.001$). The mass of females found in burrows with egg clutches was positively correlated with the mass of the egg clutches found with them ($y=0.492x$, adjusted $r^2 = 0.358$, DF = 54, F = 31.6, $p < 0.001$).

Variance Structure and Model Selection

Data were highly heterogeneous, so variance structures were incorporated in most GLS models. In most cases, the spread of residuals increased as the numeric covariate increased, which was addressed by incorporating a power of variance covariate or exponent of the variance covariate. In cases where the spread of the residuals differed between factorial treatments, different standard deviations were incorporated into the variance structure model. In cases where both of these forms of heterogeneity existed, a different power of variance covariate was used for each treatment group. (Appendix A)

After incorporating variance structures to address heterogeneity, model selection was used to determine whether to include interactions. The only model that included a significant interaction between the covariate and treatment was:

Percent Change in egg mass ~ Percent change in female mass x Treatment.

Details of this analysis can be found in the appendices; Appendix A shows the variance structures chosen for each model and associated statistics, while appendix B shows the models that were chosen and their associated statistics.

The effects of treatment on changes in egg clutch mass

Initial egg clutch mass, initial female mass, and initial male mass were all correlated with each other, so each covariate was analyzed independently with experimental treatment as a factor. Initial egg mass was significantly negatively related to change in egg mass (-0.396 ± 0.127 , d.f. = 52, $t=-3.120$, $p = 0.003$) and parental care treatment significantly affected the amount of mass change of egg clutches (d.f. = 52, $t=-2.161$, $p = 0.036$). The egg clutches in the treatments receiving parental care experienced equal amounts of mass loss (y-intercept = $7.98E-03 \pm 3.10E-03$), but egg clutches in the treatment receiving no parental care had a significantly lower y-intercept and therefore experienced significantly more mass loss (y-intercept = $1.82E-03 \pm 2.85E-03$, $t=-2.161$, d.f. = 52, $p = 0.036$). There was no significant interaction between starting egg mass and treatment. The same significant trends were observed when the change in egg clutch mass was regressed against starting female mass with parental care treatment as a factor, but not when change in egg clutch mass was regressed against starting male mass with parental care treatment as a factor (Table 1, Figure 2). This suggests that the correlation between female mass and fecundity drives this relationship; male mass is less predictive than female mass of the viability of egg clutches in *P. thomassini*.

The effects of treatment on changes in parental mass and ovary area

Parental care treatment significantly affected the amount of mass change in males (d.f. = 34, $t = -2.063$, $p = 0.048$). Males in both the biparental care and no care treatments gained small amounts of mass and these gains were not statistically different ($t = -0.297$, d.f. = 34, $p = 0.769$). However, males in the male care treatment gained significantly less mass ($-1.34E-03 \pm 6.47E-04$; d.f. = 34, $t = -2.063$, $p = 0.048$). Treatment did not significantly affect the amount of mass change ($F = 0.624$, d.f. = 34, $p = 0.543$) or ovary size in females ($F = 0.650$, d.f. = 31, $p = 0.530$). (Table 2, Figure 3)

Effects of treatment on the relationship between parental weight change and egg clutch mass change

When percent change in egg clutch mass (egg clutch mass change/initial egg mass) was regressed against percent change in female mass (female mass change/initial female mass), parental care treatment significantly affected the percent egg clutch mass change. There was a significant interaction between treatment and percent female weight change ($F = 5.057$, d.f. = 2, $p = 0.0147$). Mass change in females and egg clutches in the no parental care treatment (not housed together) were strongly and significantly positively related (32.236 ± 10.214 , d.f. = 30, $t = 3.156$, $p = 0.004$). In the female care only treatment, the relationship was slightly negative and not significant (17.772 ± 9.393 , d.f. = 30, $t = 1.892$, $p = 0.07$). In the biparental care treatment, the relationship was strongly negative and trended toward significance (-18.611 ± 9.095 , d.f. = 30, $t = -2.046$, $p = 0.052$). The no parental care treatment also had a significantly lower y-intercept than the parental care treatments (-1.461 ± 0.398 , d.f. = 30, $t = -3.667$, $p = 0.001$). These relationships suggest that females are interacting with their egg clutches in ways that change both their own mass and egg clutch mass and that these interactions may differ between parental care treatments. (Table 3, Figure 4)

Percent egg clutch mass change and percent male mass change were not significantly related ($F = 1.628$, d.f. = 30, $p = 0.213$). The parental care treatments did not significantly affect percent egg clutch mass change ($F = 0.078$, d.f. = 30, $p = 0.782$). This indicates that males, unlike females, do not interact with egg clutches in ways that modify both changes in egg clutch mass and their own mass. (Table 3, Figure 5)

Effects of treatment on changes in total eggs, egg size, clutch area, and clutch density

Initial egg clutch area, total number of eggs, and egg density were collinearly related, as were initial egg size and total number of eggs. For this reason, each numeric covariate was considered independently of the others with the experimental treatment as a factor. Egg clutches with greater initial areas gained significantly more area (0.046 ± 0.098 , d.f. = 52, $t = 4.689$, $p < 0.001$). There was a significant negative relationship between initial egg diameter and change in egg diameter (-1.369 ± 0.436 , d.f. = 52, $t = -3.141$, $p = 0.003$). Clutches with higher initial estimates of the total number of eggs lost significantly more eggs (-0.410 ± 0.116 , d.f. = 51, $t = -3.548$, $p < 0.001$). Egg density was reduced significantly more in clutches with higher initial densities of eggs (-0.887 ± 0.191 , d.f. = 47, $t = -4.635$, $p < 0.001$). Treatment did not affect changes in the total number of eggs in a clutch ($F = 0.333$, d.f. = 51, $p = 0.802$), clutch area ($F = 2.440$, d.f. = 52, $p = 0.076$), egg density ($F = 0.961$, d.f. = 47, $p = 0.419$), or egg diameter ($F = 0.961$, d.f. = 47, $p = 0.419$). (Table 4)

DISCUSSION:

In evaluating the effects of both uniparental and biparental care on the survival and development of egg clutches in *Pullosquilla thomassini*, we found that in the absence of any parental care, both egg clutch survival and growth decreased. However, neither the number, nor the sex of the care providers had a significant effect on how much mass an egg clutch lost or gained. These results suggest that while parental care increases individual fitness in terms of current reproduction, uniparental care by either sex is sufficient to achieve this goal. Thus, it is unlikely that biparental care is evolutionarily maintained by increasing the viability of current offspring. Why, then, does biparental care evolutionarily persist in these socially monogamous stomatopods? It is possible that it may increase fitness in *P. thomassini* by increasing the rate of clutching under conditions of high nutrition. Our results also suggest that there are differential fitness costs of parental care to males and females in this system that may cause sexual conflict.

Fitness Benefits of biparental care

Improved offspring survival and faster development, which increase the success of current reproduction, and faster rates of clutch production, which increase success of future reproduction, are commonly attributed as fitness benefits of biparental care. This study finds no evidence of increased egg survival or faster egg development as a result of biparental care in *P. thomassini*. Furthermore, this study provides no support that biparental care increases the amount of ovary available for future reproduction. Thus, these results do not support either of the hypotheses we investigated, that biparental care increases the growth and survival of current single clutches or that biparental care increases the frequency of clutch production or the size of egg clutches. However, because the animals were food deprived so that we could measure changes in mass and size, it is possible that females' energy budgets for future reproduction were altered. Future laboratory experiments that vary parental care and available nutritional resources should be used to further assess these hypotheses.

Although this study found no evidence that biparental care allowed for more ovarian development when stomatopods were food-deprived, it may do so under conditions of nutritional abundance. The frequency of clutching is dependent on the maternal energy budget. Biparental care in a nutritionally rich environment may increase energy available for clutching if females spend less energy on caring for young (moving and aerating eggs) or can gain more energy by spending additional time foraging, away from eggs.

Double-clutching as a fitness benefit?

In the field, *P. thomassini* have been collected in burrows with two clutches at different stages of development, a phenomenon called double-clutching (Lindstrom 2003). Based on this observation and the results of this study that biparental care does not confer benefits on current reproduction, I hypothesize that biparental care is evolutionarily maintained in this population of *P. thomassini* by facilitating double clutching under conditions of high nutrition. This may occur if biparental care either allows females to increase the frequency of clutch production or decreases egg mortality when two clutches are present by providing the physical capacity to care for two clutches simultaneously. I suspect that increased clutching frequency is the primary mode of maintenance because increased clutching frequency is a necessary pre-cursor for the presence of double-clutches and because there is seasonal and geographic variation in whether double-clutches are observed. Future laboratory experiments that vary parental care and

available nutritional resources, as well as experiments that examine the effects of biparental versus uniparental care in the presence of double-clutches may be able to disentangle these hypotheses.

Costs of parental care to future reproduction

We found evidence that uniparental care extracts fitness costs on males, but not females. Males lost more weight when providing uniparental care than when providing biparental care or not providing care, suggesting that males pay an energetic cost for uniparental care that may detract from their future reproductive success. In contrast females gained weight in all parental care treatments and there were no significant differences in weight gain between treatments. There was no evidence of change in gonad area measurements for females in any of the parental care treatments, indicating that the lack of weight loss for females was not because they were allocating increased energy to future reproduction.

In mating systems that include biparental care, sexual conflict may ensue if in the absence of a parent, the other parent partially or fully compensates for the lost care, sacrificing future reproductive opportunities. Sexual conflict over parental care is expected in species with biparental care when there is a cost in current or future fitness for uniparental care; if males are found in the field providing uniparental care for eggs, sexual conflict over female desertion may be occurring. Of the 127 burrows excavated for this experiment, 5 (3.93%) contained single males with eggs. Females may be missing from these burrows due to mortality, desertion, or collection error. Females are very visible because of their bright pink ovaries, making undetected escape during collection unlikely. Thus either female mortality or desertion are the most likely explanations of these single male parents. Densities of *P. thomassini* in the sandy tidal flat of Cassuarina Beach are high, which could facilitate mate switching. However, given the low frequency of male-only care of clutches, potential sexual conflict over female desertion must be relatively low in this population.

Weight gain in females

Although *P. thomassini* in all treatments were subjected to five days of food deprivation, some females and males (with the exception of the uniparental male care treatment) gained weight. Females gained up to 10% of their initial body weight, while two males gained up to 30% of their initial body weight. On average, females gained more weight than males.

This weight gain may be explained in three ways. Stomatopods may be gaining “water weight” without significantly increasing their carbon mass. Future studies could examine this possibility by measuring ash-free dry weights. Alternatively, although the sand used in the experiment was sieved and no food was added to treatments, animals may have been eating very small interstitial food items (i.e. micro-crustaceans, detritus). The very small average weight gain for males and females in the no care treatments (0.001g and 0.002g, respectively) suggests that this hypothesis would only explain a relatively small amount of total weight gain. A more likely weight gain explanation is that stomatopods were eating sections of egg clutches.

The relationship of female mass percent change and egg mass percent change across treatments suggest that females may have been eating their eggs. In the no care treatment, which represents a baseline expectation of how both clutch mass and female mass should change in the absence of interactions between parents and clutches, female mass gain and egg mass gain were strongly positively related. In the female care treatment, egg clutch weight change was highly variable and showed no significant trend. However, in the biparental care treatment, there was a

strongly negative significant relationship between mass change in females and mass change in eggs. In contrast, no significant relationships were observed between male mass gain and egg clutch mass gain. We propose that our findings about female weight gain in the biparental care treatment may be caused by female egg and egg parasite consumption, with females being more likely than males to consume eggs during biparental care.

Egg eating – a source of cooperation or conflict?

Egg eating behavior has been observed in laboratory settings in stomatopods that brood their young (Wright unpublished data, Caldwell personal communication). We often find *P. thomassini* egg clutches in late developmental stages with fewer than 50 eggs in the field, representing a 25%-50% reduction in eggs. These egg clutches include few dead or fouled eggs. Thus, it is likely that eating portions of the egg clutch is a natural behavior of *P. thomassini*. Female stomatopods may selectively eat abnormally developing or fouled eggs and egg parasites to increase the survival of other eggs in a clutch. This would benefit the direct fitness of both sexes. However, in this case, we would expect that males providing uniparental care would eat eggs as well; our data suggests this did not occur. Egg eating may also represent an allocation of energetic resources from current reproduction to future reproduction for the female. If egg eating does not increase the viability of the current egg clutch, but does increase the available energy that a female can allocate to future reproduction, it would only benefit the male under conditions of strict social and genetic monogamy.

Biparental care in crustacea

Most marine crustaceans demonstrate maternal care (Thiel 2003). This may be explained in many crustacean species by biological constraints, including the differential effects of molting on female and male availability for reproduction, as well as the evolution of specialized female body parts for egg brooding in decapods and peracarids. Stomatopods may be freed from such sex-specific constraints because eggs are facultatively carried with the maxillipeds and the ability of females to mate is not dependent on molting. Rather, the only time when females are unavailable for mating is immediately before and after molting.

To our knowledge, biparental care in marine crustaceans has only been suggested in a few species (amphipoda: *Limnoria lignorum*, Henderson 1924, *Limnoria algarum*, Menzies 1957, *Peramphithose stypotrupetes*, Conlan and Chess 1992; Mysidae: *Heteromysis harpax*, Vannini et al 1993; Decapoda: *Synalpheus* spp., Duffy et al. 2003) and has only been systematically studied in *Pullosquilla*. Notably, all of these species burrow, suggesting that burrowing may be associated with the evolution of biparental care in crustacea (Thiel 2007). The evolutionary maintenance of biparental care in crustacea has been best studied in *Hemilepistus reamuri*, a terrestrial isopod, and attributed to a combination of semelparity and extreme environmental conditions that make burrows extremely valuable (reviewed in Linsenmair 2007). Males and females provide extended brood care for their young after hatching for periods of up to 5 months. In contrast, *Pullosquilla* is iteroparous. It can dig a burrow in approximately 30 minutes when displaced (Jutte 1996). It does not provide extended parental care to its young past larval hatching (Jutte 1996, Lindstrom 2003). Thus, despite the commonality of burrowing, it seems likely that very different selective pressures led to the evolution of biparental care in *Pullosquilla*.

Other socially monogamous stomatopods that have been studied in the laboratory do not exhibit biparental care. However, in at least one species (*Lysiosquillina maculata*), males

nutritionally provision their mates (Caldwell 1991). Nutritional provisioning by males represents a high level of indirect paternal effort, which may have been an evolutionary precursor of biparental care in *Pullosquilla* (sensu Hunt and Simmons 2002). Alternatively, extreme size differences between *Lysiosquillina* (>35cm) and *Pullosquilla* (<16mm) may have led to different ecological selective pressures on parental care; the relative abundance of food resources (fish versus zooplankton) and the risks of predation likely differ for the two groups, which may alter the costs and benefits of uniparental versus biparental care. These possibilities may be tested through comparative studies of the relationships between mating system, size, and parental care in the Lysiosquilloidea.

Conclusions and Future Directions

In this study, there were no measurable fitness benefits of biparental care over uniparental care for either sex when *P. thomassini* were caring for a single egg clutch. Our results provided no evidence that biparental care either increased survival and development of eggs or that it increased the frequency or size of egg clutch production. We did find measurable costs to males in terms of weight loss from providing uniparental care. These fitness costs may lead to low levels of sexual conflict over female desertion.

Pairs of *P. thomassini* and *P. litoralis* produce overlapping clutches when nutritional resources are abundant. Future studies will investigate the role of biparental care in facilitating double-clutching to determine if this may be an alternative mode of evolutionary maintenance of biparental care.

WORKS CITED

- Bateman, A.J. (1948). Intrasexual selection in *Drosophila*. *Heredity* 2, 349-368.
- Burley N.T. and K. Johnson. (2002). The evolution of avian parental care. *Philosophical Transactions of the Royal Society, Series B*. 357: 241 – 250.
- Caldwell, R. L. (1991). Variation in reproductive behavior in stomatopod Crustacea. *Crustacean sexual biology*, 67, 90.
- Christy, J. H., & Salmon, M. (1991). Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist*, 31(2), 329-337.
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London, Series B* 273, 1375 – 1383.
- Conlan, K. E., & Chess, J. R. (1992). Phylogeny and ecology of a kelp-boring amphipod, *Peramphithoe stypotrupetes*, new species (Corophioidea: Ampithoidae). *Journal of Crustacean Biology*, 410-422.
- Correa, C., & Thiel, M. (2003). Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Revista Chilena de Historia Natural*, 76(2), 187-203.
- Detto, T., & Backwell, P. R. (2009). Social monogamy in a fiddler crab, *Uca capricornis*. *Journal of Crustacean Biology*, 29(3), 283-289.
- Duffy, J. E. (2003). The ecology and evolution of eusociality in sponge-dwelling shrimp. *Genes, behavior, and evolution in social insects*, 1-38.
- Duffy, J. E., & Macdonald, K. S. (2010). Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), 575-584.
- Emlen, S.T. and Oring L.W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*. 19, 215-223.
- Goodwin, N.B., Balshine-Earn, S., and Reynolds, J.D. (1998). Evolutionary transitions in parental care in cichlid fish. *Proceedings of the Royal Society of London, Series B*. 265, 2265 – 2272.
- Harrison, F., Barta Z., Cuthill, I., and T Szekely. (2009). How is sexual conflict over parental care resolved? A meta-analysis. *Journal of Evolutionary Biology*. 22, 1800 – 1812.
- Henderson, J. T. (1924). The gribble: a study of the distribution factors and life-history of *Limnoria lignorum* at St. Andrews, NB *Contributions to Canadian Biology*, 2(part 1), 309-327.

Hunt, J. and Simmons, L.W. (2002). Behavioural dynamics of biparental care in the dung beetle *Othophagus Taurus*. *Animal Behaviour*. 64, 65-75.

Jutte, P. A. (1997). *The ecology, behavior, and visual systems of Pullosquilla litoralis and P. thomassini, two monogamous species of stomatopod crustacean* (Doctoral dissertation, University of California, Berkeley).

Kleiman, D.G. and Malcolm, J.R. (1981). The evolution of male parental investment in mammals. In D.J. Gubernick and P.H. Klopfer, eds. *Parental Care in Mammals*, pp. 347-387. Plenum, New York.

Lack, D. (1968). Ecological adaptations for breeding in birds. Methuen, London. P. 409.

Lessells, C.M. (2006). The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society, Series B*. 361: 301-317.

Lindstrom, K. S. (2003). *Aspects of the Behavior, Population Genetics, and Phylogeny of Stomatopod Crustaceans* (Doctoral dissertation, University of California, Berkeley).

Linsenmair, K. E. (2007). Sociobiology of terrestrial isopods. *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press, New York, 339-364.

Mank, J. E., Promislow, D.E.L., and Avise, J.C. (2005). Phylogenetic perspectives in the evolution of parental care in ray-finned fishes. *Evolution* 59, 1570-1578.

Maynard Smith, J. (1976). Evolution and the Theory of Games. *American Scientist*. 6, 41-45.

Maynard Smith, J. (1977). Parental investment: a prospective analysis. *Animal Behaviour*. 25, 1-9.

Menzies, R.J. (1957). The marine borer family Limnoridae (Crustacea, Isopoda). Part I. Northern and Central America: systematic, distribution and ecology. *Bull. Mar. Sci. Gulf. And Carib.* 7: 101 – 200.

Parker, G. A. (1979). Sexual selection and sexual conflict. *Sexual selection and reproductive competition in insects*, 123, 166.

Jose Pinheiro, Douglas Bates, Saikat DebRoy, Deepayan Sarkar and the R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

- Reynolds, J.D., Goodwin, N.B., and Freckleton, R.P. (2002). Evolutionary transitions in parental care and live bearing in vertebrates. *Philosophical Transactions of the Royal Society, Series B* 357, 269-281.
- Smiseth, P. T., Dawson, C., Varley, E., & Moore, A. J. (2005). How do caring parents respond to mate loss? Differential response by males and females. *Animal Behaviour*, 69(3), 551-559.
- Thiel, M. (2000a). Population and reproductive biology of two sibling amphipod species from ascidians and sponges. *Marine Biology*, 137(4), 661-674.
- Thiel, M. (2000b). Extended parental care behavior in crustaceans-A comparative overview. *Crustacean Issues*, 12, 211-226.
- Thiel, M. (2003). Extended parental care in crustaceans—an update. *Revista Chilena de Historia Natural*, 76(2), 205-218.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell, ed. *Sexual Selection and the Descent of Man 1871 – 1971*. pp. 139-179. Aldine, Chicago.
- Trumbo, S.T. (2012). Patterns of parental care in invertebrates. In N.J. Royle, P.T. Smiseth, and M. Kolliker, eds. *The Evolution of Parental Care*, pp. 81-100. Oxford, UK.
- Vannini, M., Innocenti, G., & Ruwa, R. K. (1993). Family group structure in mysids, commensals of hermit crabs (Crustacea). *Tropical Zoology*, 6(1), 189-205.
- Wickler, W., & Seibt, U. (1981). Monogamy in Crustacea and man. *Zeitschrift für Tierpsychologie*, 57(3-4), 215-234.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer.

Table 1. GLS statistics of the effects of parental care treatment (biparental care, male care, female care, no care) of the relationships between initial masses of egg clutches, females, and males with changes in egg clutch mass.

Model	Coefficient	Value	SE	t-value	f-value	p-value	DF (total)	DF (residual)
Egg Clutch Mass Change ~ Initial								
Egg Clutch Mass + Treatment	Intercept	7.98E-03	3.10E-03	2.579		0.013	52	47
	Initial egg mass	-0.396	0.127	-3.120		0.003	52	47
	Treatment (no care)	1.82E-03	2.85E-03	-2.161		0.036	52	47
Egg Clutch Mass Change ~ Initial								
Female Mass + Treatment	Intercept	0.012	3.97E-03	2.957		0.005	52	47
	Initial female mass	-0.231	0.089	-2.605		0.012	52	47
	Treatment (no care)	-0.006	2.75E-03	-2.024		0.049	52	47
Egg Clutch Mass Change ~ Initial								
Male Mass + Treatment	Intercept				1.946	0.17	52	47
	Initial male mass				1.786	0.188	52	47
	Treatment				1.322	0.279	52	47

Table 2. GLS statistics of the effects of parental care treatments (biparental care, male care, female care, no care) on changes in male mass (g), female mass (g), and ovary area (mm²).

Model	Coefficient	Value	SE	t-value	f-value	p-value	DF (total)	DF (residual)
Male Mass Change ~ Treatment	Treatment (male)	-1.34E-03	6.47E-04	-2.063		0.048	34	30
Female Mass Change ~ Treatment	Treatment				0.624	0.543	34	30
Percent Ovary Area Change ~ Treatment	Treatment				0.650	0.530	31	27

Table 3. GLS statistics of the effects of parental care treatments (biparental care, male care, female care, no care) on the relationship between percent egg clutch mass change and adult mass change in males and females.

Model	Coefficient	Value	SE	t-value	f-value	p-value	DF (total)	DF (residual)
	Intercept			1.776		0.088	30	24
Percent Egg Clutch Mass Change ~ Percent Female Mass Change x Treatment	Percent female mass change	-18.611	9.095	-2.046		0.052	30	24
	Treatment (none)	-1.461	0.398	-3.667		0.001	30	24
	Percent egg female mass change: Treatment (female)	17.772	9.393	1.892		0.071	30	24
	Percent female mass change: Treatment (none)	32.236	10.214	3.156		0.004	30	24
Percent Egg Clutch Mass Change ~ Percent Male Mass Change + Treatment	Intercept				0.078	0.782	30	26
	Percent Male Weight Change				1.628	0.213	30	26
	Treatment				0.943	0.402	30	26

Table 4. GLS statistics of the effects of parental care treatment (biparental care, male care, female care, no care) on the relationships between initial egg clutch area, initial egg diameter (mm), initial egg count, and initial egg clutch density on changes in egg clutch area, egg diameter (mm), egg count, and egg clutch density, respectively.

Model	Coefficient	Value	SE	t-value	F-value	p-value	DF (total)	DF (residual)
Egg Clutch Area Change ~ Initial Egg Clutch Area + Treatment	Intercept	-10.467	4.590	-2.280		0.027	52	47
	Initial clutch area	0.460	0.098	4.689		0	52	47
	Treatment				2.440	0.076	52	47
Egg Diameter Change ~ Initial Egg Diameter + Treatment	Intercept	0.641	0.151	4.256		<0.001	52	47
	Initial egg diameter	-1.369	0.436	-3.141		0.003	52	47
	Treatment				0.961	0.419	52	47
Egg Count Change ~ Initial Egg Count + Treatment	Intercept			-0.218		0.828	51	46
	Initial egg count	-0.410	0.116	-3.548		<0.001	51	46
	Treatment				0.333	0.802	51	46
Egg Clutch Density Change ~ Initial Egg Clutch Density + Treatment	Intercept			1.103		0.277	47	42
	Initial egg clutch density	-0.887	0.191	-4.635		<0.001	47	42
	Treatment				0.961	0.419	47	42



Figure 1. Lizard Island, Queensland, Australia. A) Cassaurina Beach sandflat where *Pullosquilla thomassini* were collected between Oct. 2011 and December 2011. B) Lizard Island Marine Laboratory (Australian Museum).

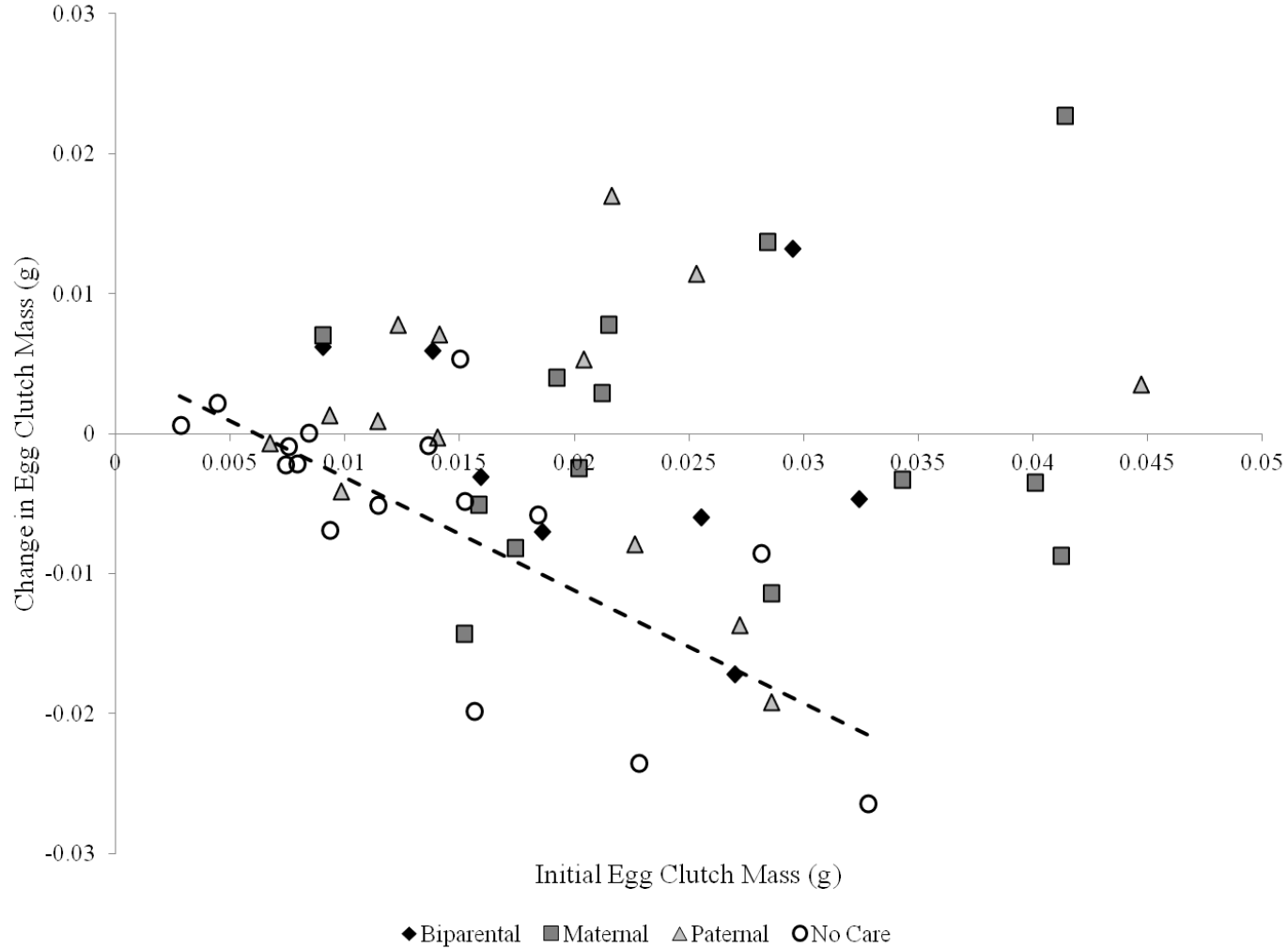


Figure 2. The effect of treatment on the relationship between initial egg clutch mass (g) and change in egg clutch mass (g). The relationship was not significant for any of the treatments receiving parental care. In the no care treatment, there was a significant negative relationship: $y = -0.396x + 1.82E-3$ (see table 1 for full statistics).

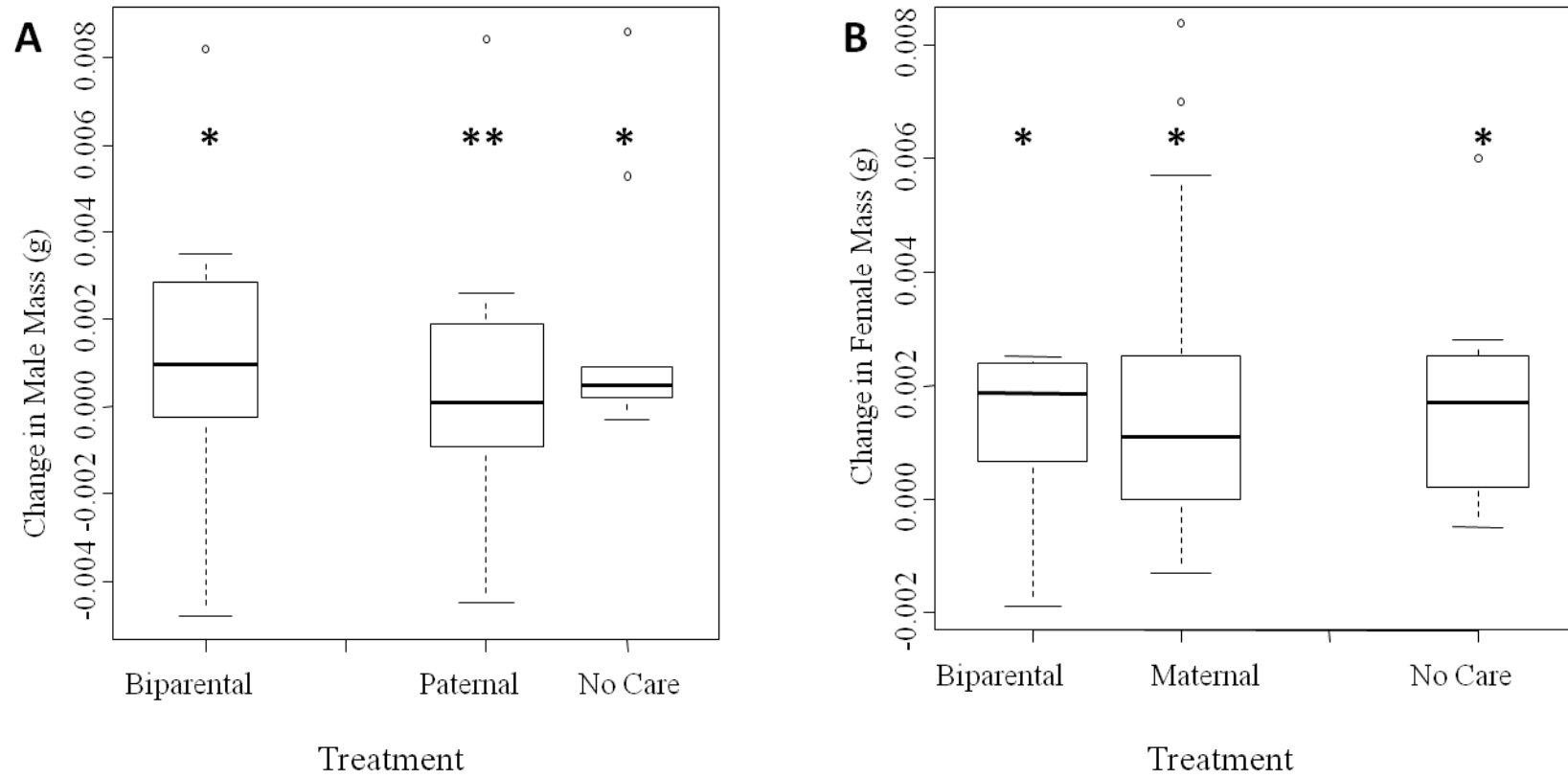


Figure 3. The effects of parental care treatment on A) change in male mass (g) and B) change in female mass (g). Different numbers of stars (*, **) over treatments represent significant differences (see table 2 for full statistics).

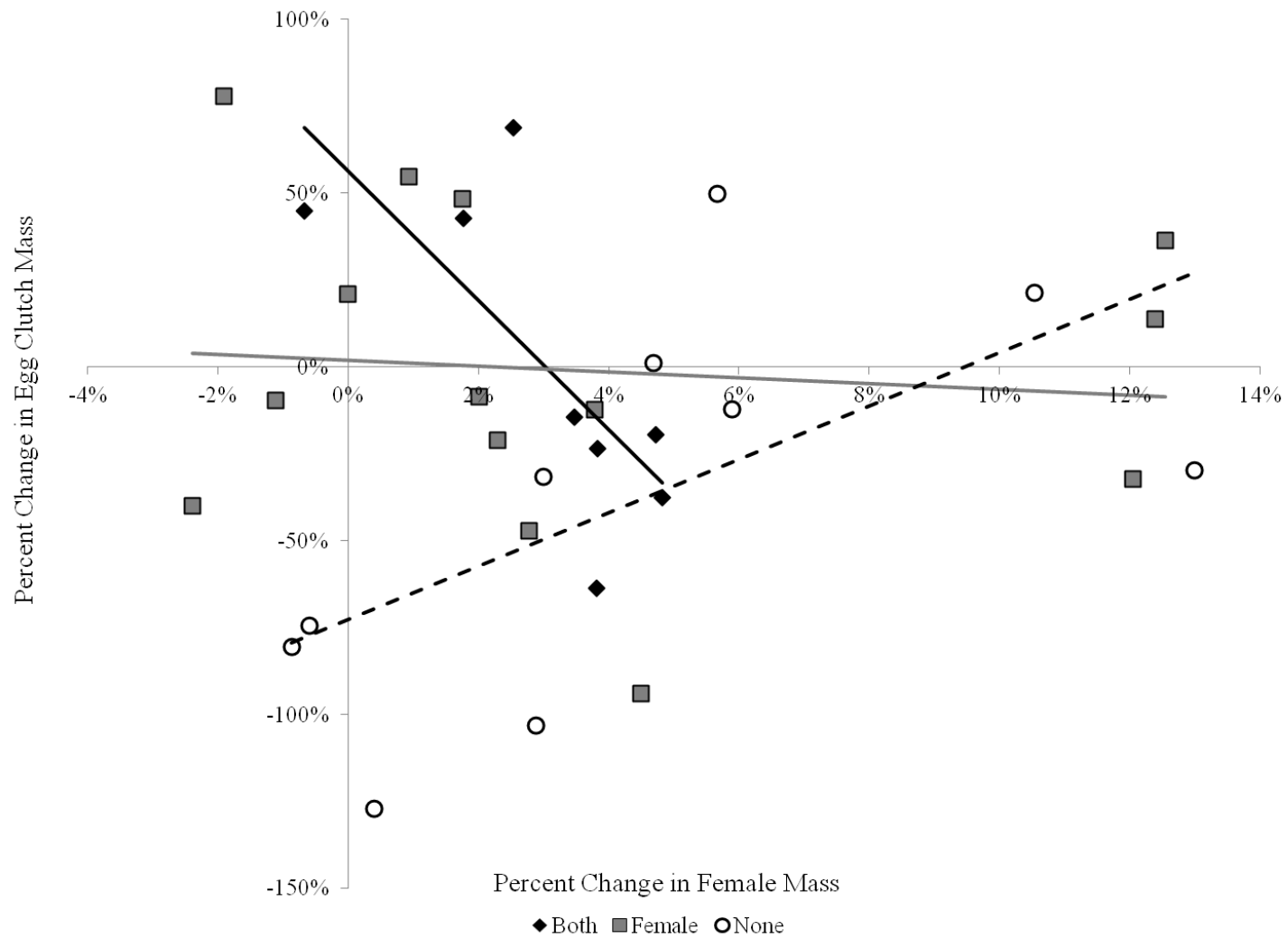


Figure 4. The effects of parental care treatment on the relationship between percent change in female mass and percent change in egg clutch mass. The relationship in the biparental care treatment is $y = -18.61x$. The relationship in the female care treatment is $y = -0.839x$. The relationship in the no care treatment is $13.625X - 1.461$. See table 3 for full statistics.

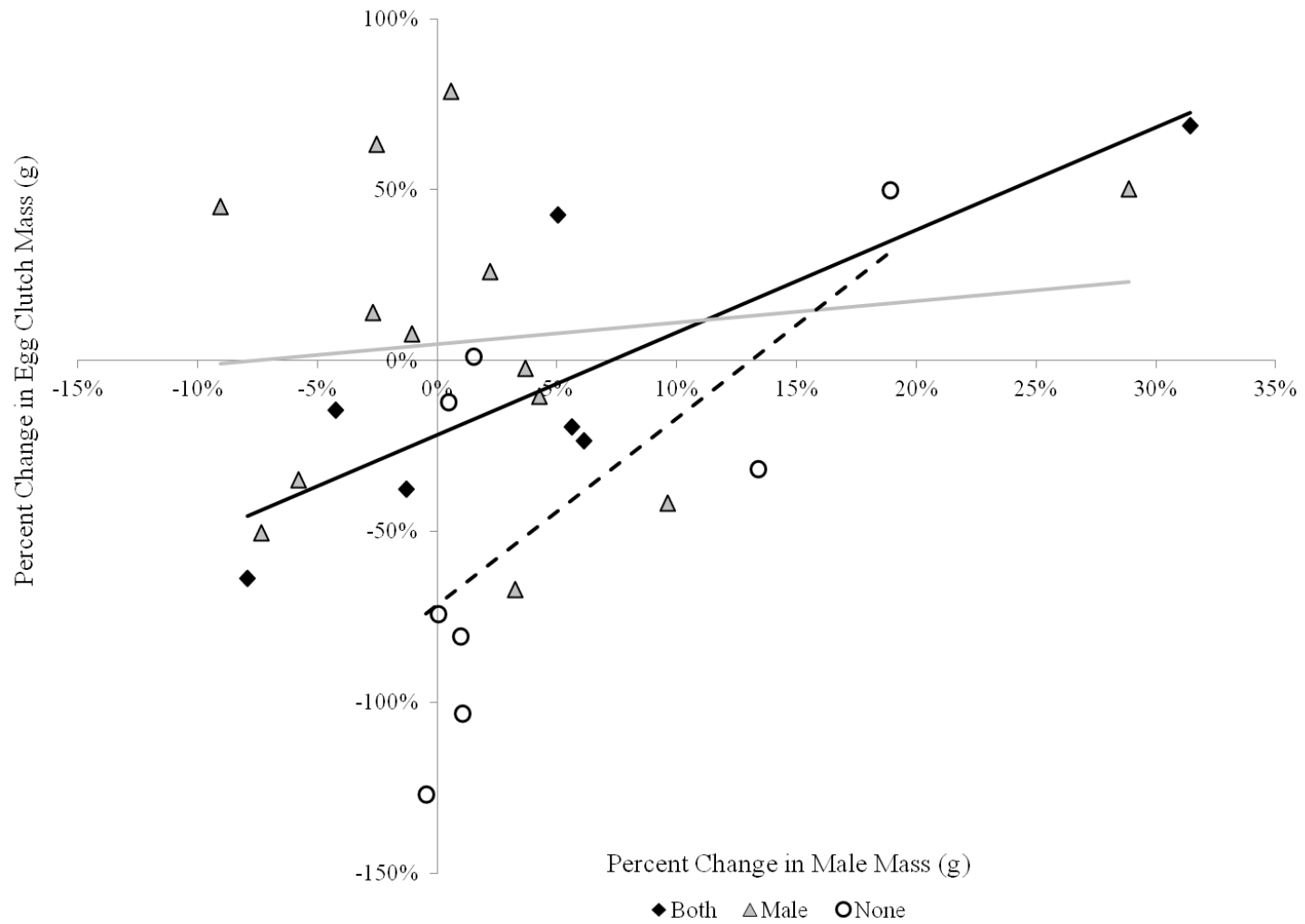


Figure 5. The effects of parental care treatment on the relationship between percent change in male mass and percent change in egg clutch mass. See table 3 for full statistics.

Appendix A

Model Evaluated	Variance Structure (VS)	d.f.	VS AIC	VS Log Likelihood		VS info
				Ratio	VS p-value	
Egg Weight Change ~ Initial Egg Weight x Treatment	Power of variance covariate	10	-303.541	13.696	<0.001	power = 1.181
Egg Weight Change ~ Initial Female Weight x Treatment	Power of variance covariate	10	-286.563	7.313	0.0256	power = 1.668
Egg Weight Change ~ Initial Male Weight x Treatment	None	9	-278.952	na	na	na
Male Weight Change ~ Initial Male Weight x Treatment	Power of variance covariate	8	-252.573	11.581	<0.001	power = 1.777
Female Weight Change ~ Initial Female Weight x Treatment	Power of variance covariate, different strata	10	-266.202	6.594	0.037	female = 0.358, both = 0.559, none = 0.678
Egg Weight Change ~ Initial Female Weight x Treatment	None	7	-25.322	na	na	na
Percent Egg Weight Change ~ Percent Female Weight Change x Treatment	None	7	34.969	na	na	na
Percent Egg Weight Change ~ Percent Male Weight Change x Treatment	Different standard deviations per stratum	9	49.701	14.767	<0.001	male = 1.000, both = 1.018, none = 1.357
Egg Clutch Area Change ~ Initial Egg Clutch Area x Treatment	Power of variance covariate, different strata	13	388.688	-181.344	0.065	power: female = 1.199, male = 1.309, both = 1.324, none = 1.089
Egg Size Change ~ Initial Egg Size x Treatment	None	9	-53.65	na	na	na
Egg Count Change ~ Initial Egg Count x Treatment	Exponential of variance covariate	10	582.818	8.602	0.035	exponent = 3.488x10 ⁻³
Egg Clutch Density Change ~ Initial Egg Clutch Density x Treatment	None	9	303.543	na	na	na

Appendix B

Model Selected	d.f.	AIC	Log Likelihood Ratio	p-value
Egg Weight Change ~ Initial Egg Weight + Treatment	7	-351.357	6.452	0.092
Egg Weight Change ~ Initial Female Weight + Treatment	7	-336.970	5.371	0.147
Egg Weight Change ~ Initial Male Weight + Treatment	9	-328.752	0.866	0.834
Male Weight Change ~ Initial Male Weight + Treatment	6	-307.555	0.578	0.749
Female Weight Change ~ Initial Female Weight + Treatment	8	-321.1120	3.711	0.156
Percent Female Ovary Area Change ~ Initial Female Ovary Area + Treatment	5	-50.3912	0.449	0.799
Percent Egg Weight Change ~ Percent Female Weight Change x Treatment	7	42.727	12.696	0.002
Percent Egg Weight Change ~ Percent Male Weight Change + Treatment	7	52.999	0.335	0.846
Egg Clutch Area Change ~ Initial Egg Clutch Area + Treatment	10	395.957	-187.978	0.359
Egg Size Change ~ Initial Egg Size + Treatment	9	-71.629	2.198	0.532
Egg Count Change ~ Initial Egg Count + Treatment	7	606.641	2.613	0.455
Egg Clutch Density Change ~ Initial Egg Clutch Density + Treatment	6	312.734	3.575	0.312

The effects of environmental and demographic variation on the frequency of pairing in congeneric stomatopod crustaceans *Pullosquilla litoralis* (Michel and Manning 1971) and *Pullosquilla thomassini* (Manning 1978) in a Moorean patch reef

ABSTRACT

Understanding the conditions that lead to the expression of pairing behavior in animals can help to elucidate the selective pressures that allow the evolution and maintenance of social monogamy on a larger scale. This study examined the effects of environmental and demographic variation on pairing behaviors and egg clutch production in two socially monogamous stomatopod crustaceans, *Pullosquilla litoralis* (Michel and Manning 1971) and *P. thomassini* (Manning 1978), living sympatrically in a coral patch reef ecosystem in Moorea, French Polynesia. I hypothesized that environmental heterogeneity of the coral back reef environment would lead to intraspecific variation in demographic traits, pairing behavior, and egg clutch production in *P. litoralis* and *P. thomassini* due to differences in food abundance or predation by fish. I tested this hypothesis on demographic and environmental data collected from a survey of *Pullosquilla* species in a Moorean patch reef. My findings support the characterizations of both *P. litoralis* and *P. thomassini* as socially monogamous and suggest that pairs in both species persist beyond a single breeding cycle. Furthermore, proximity to coral heads appears to be an important factor in structuring the demography and pairing behaviors of *P. litoralis*, but not its congener, *P. thomassini*. The directionality of the relationships between proximity to coral heads and several demographic traits suggests that gradients in predation, rather than food abundance, are responsible for these patterns in *P. litoralis*. Understanding the causes of differences in demographic patterns and pairing behaviors of these two species may yield a better understanding of the evolutionary maintenance of social monogamy in stomatopod crustaceans.

INTRODUCTION

Both males and females are expected to gain fitness benefits from mating with multiple partners (Bateman 1948, Trivers 1972). Given that monogamy will usually limit access to multiple mates, under what environmental and demographic conditions will monogamy be adaptive (i.e. provide fitness advantages)? This question is complicated by the different definitions of monogamy: researchers distinguish between *social monogamy*, when a male and female live in close proximity for at least one breeding episode, *sexual monogamy*, when a male and female mate exclusively for at least one breeding cycle, and *genetic monogamy*, when only a single male sires all of a female's offspring for at least one breeding cycle (Reichard 2003). A broad diversity of animals display social monogamy under at least some conditions (reviewed in Table 1 of Mathews 2002a). However, there is great variation among taxa in the expression and time scale of specific behaviors and abilities associated with pairing (i.e. individual recognition, formation of pair bonds, divorce frequency). Understanding the environmental and demographic conditions that lead to the expression of pairing behaviors in a diversity of animals can help us better understand the selective pressures that allow the evolution and maintenance of social monogamy.

Social monogamy should evolve when the net fitness benefits of living in heterosexual pairs are greater than the net fitness benefits of solitary living and mate searching or living in

polygamous groups (Emlen and Oring 1977, Wickler and Seibt 1981, Grafen and Ridley 1983). In general, conditions that increase mortality during mate searching, such as high levels of predation, extreme environmental conditions, or low population densities, may select for the formation of socially monogamous pairs (Wickler and Seibt 1981, Grafen and Ridley 1983). Other biological, demographic, and environmental conditions may increase the net benefits of living in heterosexual pairs. In terrestrial vertebrates, conditions associated with the evolution of social monogamy include an even spatial distribution of females (Emlen and Oring 1977), the need for biparental care (Lack 1968, Burley and Johnson 2002), an operational sex ratio of close to one (Emlen and Oring, 1977, Schuster and Wade 2003), and mate guarding (Wittenberger and Tilson 1980; Grafen and Ridley 1983). In particular, Emlen and Oring's (1977) hypotheses that biparental care, an even spatial distribution of resources or females, and an even operational sex ratio are the primary factors leading to the evolution of social monogamy have been extensively studied and supported in some birds and mammals (Dobson et al., 2010, Brotherton and Komers, 2003, but see Komers and Brotherton 1997).

In comparison to terrestrial systems, the ultimate causes of social monogamy in invertebrates have been less well-studied. Social monogamy is characteristic of several ecologically and commercially important marine crustaceans, including fiddler crabs (Detto and Blackwell 2009), alpheid shrimp (Duffy and MacDonald 2009) and stomatopod crustaceans (Wickler and Seibt 1981, Correa and Thiel 2003; Christy and Salmon 1991; Caldwell 1991). In crustacean systems, the risk of mortality from predation plays a key role in the two best developed explanations for social monogamy, the mate guarding hypothesis (Wickler and Seibt 1981) and the territorial cooperation hypothesis (Mathews 2002a, Baeza and Thiel 2007). In many decapods and peracarids, the ability of females to mate is strictly linked to the molting cycle. Males may guard females before and after the molt to ensure paternity; when mate searching is costly due to predation, the benefits of extended mate guarding exceed those of mate searching, leading to the evolution of social monogamy (Wickler and Seibt 1981, Grafen and Ridley 1983, Mathews 2002b). The territorial cooperation hypothesis suggests that fitness benefits from pair-formation, such as increased foraging efficiency and more effective territorial defense, along with high fitness costs of mate searching, select for long-term monogamy (Mathews 2002a). More specifically, the shared territorial defense hypothesis has been invoked to explain the evolution of persistent social monogamy in crustaceans inhabiting symbiotic hosts (Baeza and Thiel 2007). It proposes that the relative size, complexity, and abundance of host species coupled with predation risk determine the rates of host guarding and host switching. Social monogamy should occur when hosts or refuges are scarce and less complex and predation risk is high.

There are eight socially monogamous genera of stomatopod crustaceans that are polyphyletically distributed within the Lysiosquilloid superfamily (Porter 2010, Ahyong 2009, Wright Chapter 3). Most stomatopod species are promiscuous (i.e. *Pseudosquilla ciliata*) or serially monogamous (i.e. many Gonodactyloids), sometimes demonstrating male mate guarding (Caldwell 1991). In many species, either males or females leave burrows or cavities to actively search for mates (Caldwell and Dingle 1976, Caldwell 1991). In contrast, the socially monogamous mantis shrimps that have been studied live in long-term heterosexual pairs in U-shaped burrows in sandy or muddy habitats (Caldwell 1991). They are sit-and-wait predators that seldom leave their burrows, preying on zooplankton and fish that swim over them. The Lysiosquilloid genus *Pullosquilla* (Manning 1978) is the only marine crustacean that has been shown to provide biparental care to its embryos (Jutte 1997, Lindstrom 2003, Wright Chapter 1). Phylogenetic analyses indicate that biparental care evolved after social monogamy in the

Lysiosquilloidea (Wright Chapter 3), thus biparental care is not a likely explanation for the origins of social monogamy in this clade. Other explanations, such as predation, territorial cooperation, and resource distribution should be considered when trying to understand the evolution and maintenance of social monogamy in this group.

The time scale of pairing behaviors has important implications for the evolution of social monogamy; long-term pairing may facilitate cooperation over territorial defense and paternal effort (Wright Chapter 3). Understanding the time scale of social monogamy is a major challenge when studying marine crustaceans, particularly small taxa that live in burrows, cavities, or symbiotic hosts (Mathews 2002a, Baeza 2008, 2010, 2011). Mark-recapture studies are impractical (but see Knowlton 1980) and *in situ* observation of pairing behaviors is often impossible. Extraction to assess pairing is usually destructive to the burrow or host species. One goal of this study was to use demographic criteria (Baeza 2008 and Baeza et al. 2011) to assess whether it is likely that *Pullosquilla* spp. forms long-lasting pairs, which may facilitate other behaviors, including biparental care and shared territorial defense.

This study also examined the effects of environmental and demographic variation on pairing behaviors and egg clutch production in *P. litoralis* (Michel and Manning 1971) and *P. thomassini* (Manning 1978) living in a coral patch reef ecosystem in Moorea, French Polynesia. Coral patch reef ecosystems consist of coral heads of varying sizes separated by sand flats (Schroeder and Parrish 2006), which form a highly heterogeneous abiotic and biotic environment (Vroom et al 2005). Within the back reef, coral heads provide a structured, three-dimensional environment, while sand flats are comparatively less complex. Coral heads support higher levels of fish and invertebrate biodiversity than surrounding sand flats (Adams and Ebersole 2002, Schroeder and Parrish 2006, Pante et al. 2006). *Pullosquilla* burrows in the sand flats between coral heads of patch reefs (Manning 1978), experiencing variation in environmental conditions based on coral head proximity. These conditions may include food abundance and predation by fish, as well as abiotic factors such as water movement and substrate composition. This study examines whether variation in the physical structure of the coral back reef is correlated with demographic traits, pairing behaviors, and egg clutch production in either *Pullosquilla* species. It furthermore assesses whether gradients in food abundance or fish predation may be important drivers of patterns in *Pullosquilla* demography and behavior. Although this study focuses primarily on patterns of intraspecific variation, any interspecific differences in demographic and behavioral traits between *P. litoralis* and *P. thomassini* may yield insight into the roles of physiology and the environment on the expression of social monogamy in these species.

Several predictions about spatial patterns of variation of *Pullosquilla* density, animal size, egg clutch production, and pairing behaviors can be made if either food abundance or fish predation drive this variation. Increased food resources should promote higher *Pullosquilla* densities near coral heads and facilitate mate searching and alternative mating tactics, such as satellite behaviors (e.g. Emlen and Oring 1977). Higher food abundance should also increase both growth and fecundity. I therefore expect that if food resource availability is the main driver of *Pullosquilla* distributions, there should be 1) higher *Pullosquilla* densities, 2) larger animals, 3) more egg clutches in burrows, and 4) more burrows containing single individuals closer to coral heads (Table 1). Increased fish predation should lower *Pullosquilla* densities near coral heads. This would increase the costs of mate searching and foraging, leading to both decreased growth and shorter persistence of pairs closer to coral heads. Single individuals should be more vulnerable to predation because they spend more time searching for mates than paired individuals. Therefore, if predation by fish is the main driver of *Pullosquilla* distributions, there

should be 1) lower densities, 2) smaller (more recently settled) animals, 3) fewer burrows with egg clutches, and 4) fewer single individuals than pairs closer to coral heads.

In this study, I conducted a field survey to assess the hypotheses that 1) *Pullosquilla* species demonstrate long-term social monogamy and 2) environmental heterogeneity of the coral back reef environment leads to intraspecific variation in demographics, pairing behavior, and egg clutch production in both *P. littoralis* and *P. thomassini*. By examining the spatial patterns of demographic traits and pairing behaviors of animals collected during the study, I was able to evaluate whether gradients in food abundance or fish predation shaped distributions and pairing behaviors in either species. In addition to providing data on factors affecting pairing behaviors and distributions in *Pullosquilla* species, this study yields new insight into how social monogamy may be evolutionarily maintained in crustacean systems.

METHODS

Study Species

I collected demographic and environmental data on *Pullosquilla* spp. by surveying populations in a Moorean patch reef. *P. litoralis* (Michel and Manning 1971) and *P. thomassini* (Manning 1978) are small (<16mm) spearing mantis shrimps sympatrically distributed throughout the Indo-Pacific. Heterosexual pairs often share U-shaped burrows in sandy substrates (Caldwell 1991, Jutte 1997). Both species are sit-and-wait predators that forage on zooplankton that pass over burrow entrances (Caldwell 1991, Jutte 1997). Despite hundreds of hours of observation underwater, adult *Pullosquilla* have never been observed walking on the sandy surface away from their burrows in the field, although they will briefly leave their burrow to capture a nearby prey item (Wright, unpublished data; Caldwell, personal communication). Males and females share foraging and parental care duties equally (Lindstrom 2003). When food is abundant, pairs may double-clutch by producing a second clutch of eggs before the first clutch has hatched (Lindstrom 2003).

Coral Head and Fish Surveys

A 625 m² quadrant (25m x 25m) was established at the edge of the coral patch reef ecosystem immediately west of Cook's Bay, adjacent to a deep (60m) boating channel (Figure 1). This site is close to the Cook's Bay lagoon site (CL) sampled in Jutte (1997). There was a gradient of depth in the quadrant, ranging from 2m on the side of the reef crest to 3m on the side of the boating channel. All coral heads larger than 1 m² in the quadrant were *Porites* spp.. They were photographed, measured by estimating height, length, width using a transect tape, and their GPS coordinates were taken on the sea surface at the center of each coral head using a Garmin eTrex Vista HCx. Coordinates were collected when error was less than 3 m. Eleven transects between coral heads were randomly selected within the quadrant for assessment.

Fish communities at each coral head were characterized in November 2009 and January 2010. Fish were identified to the lowest possible taxonomic level and counted by an observer on snorkel positioned 2m from each coral head to minimize disturbance. In March 2010, fish surveys were conducted along each transect to further characterize the fish community and to observe fish predation on benthic invertebrates. During these surveys, sections of transect (2m height x 2m width x 1-3 m length) were observed for five minutes. All fish that swam into the surveyed area were identified to the lowest possible taxonomic level; fish that left and returned to the surveyed area were only recorded once. Fish that were ingesting the sandy substrate between coral heads or disturbing the sand with sensory structures (i.e. goatfish) were recorded as preying on benthic invertebrates. A list was compiled of all fish observed in the quadrant during November 2009, January 2010, and March 2010. Fish that potentially prey on benthic crustaceans were identified using the online database FishBase (Froese and Pauly 2011).

Demographic Surveys and Collections

To examine how demography and spatial heterogeneity affected pairing behaviors, we surveyed *Pullosquilla* populations on 11 randomly selected transects between coral heads in the 625 m² quadrant in a coral back reef in Moorea, French Polynesia on SCUBA in March 2010. To assess the density of *Pullosquilla*, burrow density surveys were performed visually on all transects prior to making collections. *Pullosquilla* burrows can be easily distinguished from other

organisms' burrows by their size (3-5mm diameter), their well-manicured openings, and their flush construction with the sand. The exact location of each burrow opening along each transect was recorded ($\pm 0.05\text{m}$). It is not possible to distinguish the burrows of *P. littoralis* and *P. thomassini* without destructive sampling, so density measurements include both species.

To assess the relative abundance of burrows containing single males, females, pairs, and eggs, burrows were collected along the same transects and their exact positions were recorded ($\pm 0.05\text{m}$). Stomatopods were collected by excavating burrows with hand trowels while on SCUBA at depths between 1 m and 3 m. Burrows were scooped into re-sealable plastic bags underwater and adult stomatopods and egg clutches were removed from the sand with a 1 mm sieve at the Richard P. Gump South Pacific Research Station. The process of burrow collection was destructive to surrounding burrows. Therefore, only one burrow was collected along each meter of each transect. Well-established, U-shaped burrows were preferentially collected, which may have caused our sample to be biased toward adult stomatopods.

After collection, all adults collected were identified to species based on the diagnostic trait of the spinulose ventral surface of the telson in *P. thomassini* (absent in *P. littoralis*, Manning 1978) and sexed based on the presence of sperm transfer organs in males. The body length (tip of rostrum to center tip of telson) of each adult was measured to assess whether animals were mating assortatively and to establish the relationship of body size with pairing status, the presence of eggs, and distance to the nearest coral head.

Mapping Burrows

GPS coordinates were determined for each burrow that was counted or collected by incorporating the GPS coordinates of the coral heads, the transect it was on, and the burrow's exact location on the transect into the Pythagorean theorem. The burrows were plotted using *ArcGIS Release 9* (ESRI 2004) and the identity of and distance to the nearest coral head were calculated for each burrow (Figure 2).

Analyses

Density: A linear regression was conducted in *JMP* to examine the effect of distance to the nearest coral head on *Pullosquilla* burrow density. I binned the number of burrow entrances at a given distance from the nearest coral head at 0.1m increments. There were more opportunities to detect burrows at shorter distances because transects varied in length. Therefore, the number of burrow entrances in each bin was divided by the number of times that distance could have been measured along the transects in the quadrant. These density values were log-transformed a priori to regression.

Body Length: To determine whether *P. littoralis* or *P. thomassini* were mating assortatively based on size, the body lengths of males and females collected from the same burrow in heterosexual pairs were regressed against each other in *R*.

To understand the effects of distance to the nearest coral head, sex, and pairing status on the size structure of the population we examined the relationships of these variables with body length for both *P. littoralis* and *P. thomassini*. We used a model testing approach with GLS regression with the *nlme* package in *R* (Zuur 2009, Pinheiro et al. 2013, R Core Team 2013). To address heterogeneity in the datasets in relation to distance to the nearest coral head, we chose a variance structure for each model based on the Aikake Information Criterion (AIC) and visual

examination of normalized residuals graphed against the covariates. This was done using all possible covariates and interactions with REML models. After incorporating the appropriate variance structure, the fixed model was determined by comparing nested Maximum Likelihood models with ANOVAs ($\alpha = 0.05$). The components of the best fixed model were then examined using an ANOVA and t-statistics.

Pairing Status and Presence of Eggs: To understand the effects of sex, body length, and distance to the nearest coral head on both the pairing status of individual stomatopods and whether their burrows contained egg clutches, we used a model testing approach and a series of generalized linear models in the *nlme* package of *R* (Pinheiro et al. 2013, R Core Team 2013) with binomial distributions (paired/single or eggs present/absent) and a logit function linker in both *P. litoralis* and *P. thomassini* (Zuur 2009). Starting with a model of a 3-way interaction between the covariates, AIC values were determined and compared for models as interactions and covariates were systematically excluded from subsequent analyses. All possible models were analyzed and the model with the lowest AIC value was considered to be the best. This model was then examined using t-statistics.

RESULTS

Fish Predation

Thirty fish taxa recorded in the study area were identified as potential predators on *Pullosquilla* (Table 2). Of these fish, 14 were directly observed ingesting sandy substrate or, in the case of goatfish, using sensory structures to disturb the sand (Table 3). Vagabond Butterflyfish (*Chaetodon auriga*), Goatfish (family Mullidae), and Whitebanded Triggerfish (*Rhinecanthus aculeatus*) were most commonly observed predating on benthic invertebrates (Table 3). A pink whiptail stingray (*Himantura fai*) was observed predating along a previously excavated transect and a six bar wrasse (*Thalassoma hardwicke*) ate a *Pullosquilla* while divers were excavating its burrow. Overall, thirty fish predation events were recorded (Table 3).

Density

Density was exponentially positively related to the distance from coral heads (Figure 3; LR of log-transformed density: $y = 0.05689x \pm 0.02$, adjusted $r^2 = 0.125$, $F = 7.856$, d.f. = 47, p -value = 0.007), indicating that stomatopod burrows were most abundant at greater distances from coral heads.

Collections

During this study, 47 *P. littoralis* burrows were collected. Twenty-nine burrows (61.7%) contained heterosexual pairs. Nine of these burrows also contained egg clutches. Nine burrows (19.1%) contained single females, with three containing egg clutches, while eight burrows (17.0%) contained single males, with three containing egg clutches. One burrow contained two females, a single male, and a single egg clutch. (Figure 4A)

Thirty-one *P. thomassini* burrows were collected. Twenty-three burrows (74.2%) contained heterosexual pairs; of these, fourteen contained at least one egg clutch. One pair was collected with two clutches of eggs, one in the early stages of development and one at a later stage. Four burrows (12.9%) were collected containing single females, one of which contained an egg clutch. Three burrows (9.7%) were collected containing single males, one of which contained an egg clutch. One burrow contained two males, a single female, and a single egg clutch. (Figure 4B)

Body length

Heterosexual pairs of both *P. littoralis* and *P. thomassini* were size-matched in body length and females were, on average, longer than their male mates (*P. littoralis*: LR, $y = 0.631x \pm 0.131x + 4.080 \pm 1.665$, adjusted $r^2 = 0.492$, d.f. = 22, $F = 23.26$, $p < 0.001$; *P. thomassini*: LR, $y = 0.636x \pm 0.131x + 4.591 \pm 1.789$, adjusted $r^2 = 0.464$, d.f. = 25, $F = 23.51$, $p < 0.001$). (Figure 5)

To model body length in *P. littoralis*, we incorporated a constant plus power of variance covariate function in the model proportional to the distance to the nearest coral head to address heterogeneity in the dataset (AIC = 190.322, constant = 40.228, power = -1.995). Using a nested model testing approach based on maximum likelihood and AIC values (AIC = 170.897, d.f. = 8, LogLikelihood = 8.760, $p = 0.003$), we determined that the best model for *P. littoralis* body length was:

Body length ~ Sex + Pairing+ Distance from Coral Heads + Distance from Coral Heads*Pairing

Sex significantly influenced body *P. litoralis* body length. Females were larger than males (Figure 6, ANOVA: d.f. = 1, F = 8.221, p = 0.006). There was a relationship between body length and the distance of animals to the nearest coral head (ANOVA: d.f. = 1, F = 8.213, p=0.006), which had a significant interaction with pairing status (Figure 7A, d.f. = 1, F = 12.588, p = 0.001). The relationship between body length and distance from the nearest coral head is positive for paired *P. litoralis* (GLS: $y = 0.378x \pm 0.083x + 11.688 \pm 0.262$, intercept: $t = 44.614$, $p < 0.001$, slope: $t = 4.573$, $p < 0.001$, Residual d.f. = 60), but slightly negative for single *P. litoralis* (GLS: $y = -0.050x \pm 0.116x + 13.021 \pm 0.431$, intercept: $t = 3.095$, $p = 0.003$, slope: $t = -3.693$, $p = 0.001$, Residual d.f. = 60).

To model body length in *P. thomassini*, we incorporated a Power of Variance Covariate proportional to the distance to the nearest coral head in the model (AIC = 172.263, power = -0.111). Using a nested model testing approach based on maximum likelihood and AIC values (AIC = 152.942, d.f. = 4, LogLikelihood = -72.471, p=0.003), we determined that the best model for body length was:

Body Length ~ Sex

However, the relationship between body length and sex was not significant in *P. thomassini* (Figure 6; ANOVA: d.f.=1, F=3.398, p= 0.071).

Ecological and demographic factors affecting pairing status and presence of eggs

Using a generalized linear model testing approach based on AIC values, we determined that the best model for *P. litoralis* pairing status was **Pairing Status ~ Distance from the Nearest Coral Head** (AIC = 72.612, d.f. = 2, DAIC = 1.985). The probability that animals were paired decreased as distance to the nearest coral head increased (Figure 8; GLM, binomial distribution, logit linker, Residual deviance: 68.612 on 63 degrees of freedom; intercept: -2.158 ± 0.592 , $z = -3.649$, $p < 0.001$; slope: 0.379 ± 0.163 , $z = 2.326$, $p = 0.020$). In *P. thomassini*, the best model was **Pairing Status ~ Body Length** (AIC = 45.227, d.f. = 2, DAIC = 0.808). However, there were no significant relationships between pairing status and any of the covariates, including body length.

Using generalized linear model testing approach based on AIC values, there were no significant relationships between presence of eggs and any covariate in *P. litoralis*. In *P. thomassini*, the best model for the presence of eggs was: **Presence of Eggs ~ Body Length** (AIC = 73.959, d.f. = 2, DAIC = 1.266). The probability that eggs were present with an animal increased as body size increased (Figure 9; GLM, binomial distribution, logit linker, Residual deviance: 69.959 on 54 degrees of freedom; intercept: -10.645 ± 4.648 , $z = -2.290$, $p = 0.022$; Size effect: 0.808 ± 0.343 , $z = 2.358$, $p = 0.018$).

DISCUSSION:

These findings support the characterizations of both *P. litoralis* and *P. thomassini* as socially monogamous and suggest that pairs persist beyond a single breeding cycle in both species. Furthermore, it appears that proximity to coral heads is an important factor in structuring the demography of *P. litoralis*, but not its congener, *P. thomassini*, in the coral back reef of Moorea, French Polynesia. The directionality of the relationship between proximity to coral heads and several demographic measurements suggests that gradients in predation, rather than food abundance, are responsible for this pattern in *P. litoralis*. As both *Pullosquilla* species are socially monogamous and proximity to the nearest coral head was associated with pairing in *P. litoralis*, but not *P. thomassini*, these results have important implications on our understanding of the expression and evolutionary maintenance of social monogamy in this genus.

The Timescale of Social Monogamy in *Pullosquilla*

It is difficult to determine the natural time scale of heterosexual pairing in *Pullosquilla* because long-term, noninvasive population monitoring is not practical and the excavation of burrows during population surveys destroys them, disrupting pairs. In a laboratory setting, the animals will form stable pairs for at least four years (Jutte 1996, Lindstrom 2003, Wright unpublished data); however, in all cases they were not housed with extrapair stomatopods. Baeza et al. (2008, 2010, 2011) proposed several criteria that indicate that crustacean pairs are long lasting. Firstly, pairs must be found living together both with and without eggs. Although pairs should form during sexual activity and periods of biparental care in serially monogamous or promiscuous species, they should occur predominantly in the presence of eggs. Secondly, pairs should be size-matched, which suggests long lasting associations between individuals.

Based on these criteria, both *Pullosquilla* species likely form long-lasting pairs. Both species were commonly collected in pairs without eggs. Furthermore, few burrows of either species contained only a single individual and heterosexual pairs of both species were size-matched. Finally, in over 200 daytime hours of bottom time observing and collecting *Pullosquilla*, none were observed on the surface outside of burrows, suggesting that mate searching, at least during daylight hours, is rare in this genus. Since both species likely form persistent heterosexual pairs, it is pertinent to consider selective pressures for social monogamy that would act on longer time scales. Long-term monogamy likely also plays a role in the evolution and maintenance of shared parental care and foraging duties in *Pullosquilla* spp. (Lindstrom 2003, Wright Chapter 1, Chapter 3).

The effects of predation on demographics and social monogamy in *P. litoralis*

It is difficult in natural populations to disentangle the effects of the environment and demography on the expression of pairing behaviors and mating systems (an emergent property of pairing behaviors). The environment may influence demographic patterns, such as density, age structure, and sex ratio, but it may also directly affect the behaviors of organisms. My multivariate model was successful in determining which environmental and demographic factors were associated with pairing behaviors, egg clutch production, body size, and density in *P. litoralis*. However, these results are correlative and are best viewed as suggesting and supporting hypotheses, rather than experimentally evaluating them. I found few associations between pairing behaviors, egg clutch production, body size, density, and environmental factors in *P. thomassini*. There was little variation in pairing behaviors and egg clutch production in *P. thomassini*, so although it is

possible that uninvestigated environmental or demographic factors play an important role in determining the pairing behaviors and distribution of this species, it is also possible that we were simply unable to detect correlations.

I found that proximity to coral heads is an important factor in structuring the demography of *P. littoralis*. This pattern is likely at least partially driven by reef fish predation (Table 1). The exponential increase in *Pullosquilla* density with greater distances from coral heads may be due to higher mortality from fish predation closer to coral heads. This trend probably reflects the distribution of *P. littoralis*, since *P. thomassini* shows no other trends in relation to proximity to coral heads. Differential rates of fish predation on paired stomatopods versus single stomatopods that must attract or search for a mate likely account for the increase of pairing closer to coral heads. Finally, greater survival of pairs farther away from coral heads would explain our observation that paired individuals increase in size farther away from coral heads. Previous research suggests that predation pressure is high: Jutte (1997) found that 25% of *P. littoralis* released into the water column of a Moorean patch reef were consumed by fish within 10 minutes. Future studies to understand how single individuals find or attract mates and to quantify predation risk during mate searching in relation to proximity to coral heads will allow further evaluation of the hypothesis that predation risk is associated with social monogamy in *P. littoralis*.

Although it has often been proposed that predation may play a direct or indirect role in shaping mating systems, this role has not been thoroughly evaluated (Baeza and Thiel 2007). Predation may influence individual behavioral decisions on vigilance, social group size, time spent in refuges, and reproductive behaviors (reviewed in Lima and Dill 1990). In arthropods, the role of predation in mating systems has been considered primarily in the context of its effects on the frequency and duration of male mate searching. Several serially monogamous mate guarding species vary the duration of pairing versus male mate searching with predation risk (amphipoda in Cothran 2004, water striders in Rowe 1994). By influencing individual mating behaviors, predation risk may shape both the overall mating system of a population in these species, as well as individual variation within it (e.g. the water strider *Gerris remigis* in Rowe 1994). It is possible that predation influences pairing behaviors in *P. littoralis* through its effects on mate guarding. However, the reproductive timing of female stomatopods is not constrained by molting, eliminating the extreme selective pressure for mate guarding that has been documented in peracarids (Wickler and Seibt 1981, Cothran 2004). Future studies will be needed to determine if mate guarding occurs in *P. littoralis* and how predation affects pair duration.

Territorial cooperation over defense and foraging, coupled with high predation risk, has been supported as a cause of social monogamy in several shrimp taxa (Alpheids in Knowlton 1980, Caridean shrimp in Baeza 2008, but see Baeza 2011). It may act together with selection from mate guarding, as seen in burrow-dwelling alpheids (Mathews 2002a, 2002b). The benefits acquired from territorial cooperation coupled with the risk of mate searching in high predation environments seems a likely explanation for varied expression of pairing in *P. littoralis*. Although *Pullosquilla* burrows may be constructed in as little as 30 minutes, they are constantly structurally modified and fortified with mucus (personal observation). A “mature” *P. littoralis* burrow is likely costly to construct and maintain and certainly functions as a refuge from predation. Furthermore, paired *P. littoralis* likely obtain fitness benefits in a temporally variable environment by equally sharing foraging duties and storing live zooplankton in their burrows for future consumption (Lindstrom 2003). It is possible that a high cost of mate searching, coupled

with the fitness benefits of shared burrow maintenance and foraging, limits mate searching and enhances pair duration in *P. littoralis* when predation risk is high.

Alternative selective pressures for social monogamy in *P. thomassini*?

There were no relationships between proximity to coral heads and any of the demographic variables that we were able to explicitly measure for *P. thomassini*, suggesting that factors unrelated to the physical structure of the coral patch reef may be structuring the demography and influencing the pairing behaviors of this species. When Jutte (1997) surveyed areas adjacent to my study site, *P. thomassini* were distributed predominantly in the boat channel and sandy lagoon. Perhaps their pairing behaviors do not change with proximity to coral heads because they usually inhabit areas without coral. A higher percentage of *P. thomassini* were paired than *P. littoralis*, suggesting that there may be less variation in pairing behaviors overall in this species due to biological or physiological constraints. However, it is also possible that differences in substrate preferences between the two species may lead to differences in the successful collection of pairs (Jutte 1997, Caldwell personal communication).

There are many possible biological explanations why there is so little variation in pairing behaviors in *P. thomassini* in comparison to *P. littoralis*. These include greater fitness benefits from biparental care, increased mate guarding due to sperm precedence, territorial cooperation in burrow building and foraging, and synchronized female reproductive cycles. While equal proportions of paired and single individuals had egg clutches in *P. littoralis*, far more *P. thomassini* pairs had egg clutches than single individuals, suggesting that pairing may increase the rate of egg clutch production in *P. thomassini*. Furthermore, Wright (2013 Chapter 1) demonstrated that *P. thomassini* males pay a fitness cost for uniparental care. In conjunction, these results suggest that biparental care may be very important in maintaining pairing behaviors in *P. thomassini*. Sperm precedence has not been established in *Pullosquilla* or other stomatopods; however, if sperm precedence occurs in *P. thomassini*, it may lead to mate guarding and social monogamy (Grafen and Ridley 1983, Wickler and Seibt, Matthews 2002b). Finally, synchronized female reproductive cycles associated with extreme tides might lead to the evolution and maintenance of social monogamy in *Pullosquilla thomassini* (Jutte 1997). Greater synchrony in the reproductive cycles of female *P. thomassini* than *P. littoralis* would parsimoniously explain our results because synchrony would constrain the operational sex ratio, allowing less variation in pairing behaviors. There would therefore be a smaller effect of environmental variables (i.e. predation, food abundance) on demographics and pairing behaviors. Further evaluation of these hypotheses is necessary to understand why this population of *P. thomassini* does not demonstrate the same demographic patterns as *P. littoralis*, despite living in the same habitat and having similar biological and ecological characteristics.

The significant relationship between body length and the presence of eggs in the burrow in *P. thomassini* suggests that clutching frequency, and perhaps fecundity, is determined by body size. This is congruent with findings from a population of *P. thomassini* in Lizard Island, Australia, that demonstrated a strong correlation between clutch size and female mass (Wright Chapter 1).

The unknown effects of settlement on demographics and social monogamy

In both *P. littoralis* and *P. thomassini*, the role of settlement in determining demographics and influencing pairing behaviors must be considered. Unfortunately, little is known about settlement

in this genus. Settlement in both species appears to follow a lunar cycle in Moorea and is concentrated during a 3-5 day period (Wright, unpublished data; Caldwell, personal communication). In the final larval stage, *Pullosquilla* are strong swimmers and can actively choose where they settle. Settlement patterns will affect the distribution of individuals and may subsequently affect pairing opportunities. It is possible that either the physical structure of the coral back reef or the density of conspecifics in an area may influence settlement behaviors. Thus, to fully understand the relationship between spatial heterogeneity of the coral back reef and *Pullosquilla* distribution and pairing behaviors, it will be necessary to better understand settlement behaviors and patterns.

Conclusion

Our findings suggest that different factors influence the occurrence of social monogamy in *P. littoralis* and *P. thomassini*. As morphologically similar sympatric species that are both commonly found in heterosexual pairs, these congeners provide exciting opportunities for comparative studies on the fitness benefits and evolutionary maintenance of social monogamy. Further studies comparing biparental care, demographics, mate guarding, and sperm precedence in these species will likely yield a deeper understanding of social monogamy in non-symbiotic marine crustaceans.

WORKS CITED

- Adams, A. J., & Ebersole, J. P. (2002). Use of back-reef and lagoon habitats by coral reef fishes. *Marine Ecology Progress Series*, 228, 213-226.
- Ahyong, S. T., & Jarman, S. N. (2009). Stomatopod interrelationships: preliminary results based on analysis of three molecular loci. *Arthropod Systematics & Phylogeny*, 67(1), 91-98.
- Baeza, J. A., & Thiel, M. (2007). The mating system of symbiotic crustaceans. A conceptual model based on optimality and ecological constraints. *Evolutionary ecology of social and sexual systems. Crustaceans as model organisms*, 249-267.
- Baeza, J. A. (2008). Social monogamy in the shrimp *Pontonia margarita*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Marine Biology*, 153(3), 387-395.
- Baeza, J. A., Bolaños, J. A., Hernandez, J. E., Lira, C., & López, R. (2011). Monogamy does not last long in *Pontonia mexicana*, a symbiotic shrimp of the amber pen-shell *Pinna carnea* from the southeastern Caribbean Sea. *Journal of Experimental Marine Biology and Ecology*, 407(1), 41-47.
- Bateman, A.J. (1948). Intrasexual selection in *Drosophila*. *Heredity* 2, 349-368.
- Brotherton PNM, Komers PE. (2003). Mate guarding and the evolution of social monogamy in mammals. In: Reichard U, Boesch C, editors. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge: Cambridge University Press. P. 42-58.
- Burley N.T. and K. Johnson. (2002). The evolution of avian parental care. *Philosophical Transactions of the Royal Society, Series B*. 357: 241 – 250.
- Caldwell, RL (1991). Variation in the reproductive behavior in stomatopod crustacea. In R.T. Bauer and JW Martin. Eds. *Crustacean sexual biology*. Pp. 67-90. Columbia University Press, New York.
- Caldwell RL and Dingle H. (1976). Stomatopods. *Scientific American*. 234: 80-89.
- Christy JH and Salmon M (1991). Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist*. 31: 329 -337.
- Correa C and Thiel M (2003). Mating systems in the caridean shrimp (Decapoda: Carida) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Rev. chil. Hist. nat.* 76: 187-203.
- Cothran, R. D. (2004). Precopulatory mate guarding affects predation risk in two freshwater amphipod species. *Animal behaviour*, 68(5), 1133-1138.
- Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology*. Wiley-Blackwell.
- Detto T and Backwell P (2009). Social monogamy in a fiddler crab, *Uca Capricornis*. *Journal of Crustacean Biology*. 29: 283-289.

- Dobson FS, Way BM, Baudoin, C. (2010). Spatial Dynamics and the evolution of social monogamy in mammals. *Behavioral Ecology*. 21 (4): **747-752**.
- Duffy, J. E. (2003). The ecology and evolution of eusociality in sponge-dwelling shrimp. *Genes, behavior, and evolution in social insects*, 1-38.
- Emlen, S.T. and Oring L.W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*. 19, 215-223.
- ESRI 2004. ArcGIS Desktop: Release 9. Redlands, Ca. Environmental Systems Research Institute.
- Froese, R. and D. Pauly. Editors. (2011).FishBase. World Wide Web electronic publication. www.fishbase.org, version 12/2012.
- Grafen, A., & Ridley, M. (1983). A model of mate guarding. *Journal of Theoretical Biology*, 102(4), 549-567.
- Jutte, P. A. (1997). *The ecology, behavior, and visual systems of Pullosquilla litoralis and P. thomassini, two monogamous species of stomatopod crustacean* (Doctoral dissertation, University of California, Berkeley).
- Knowlton, N. (1980). Sexual selection and dimorphism in two demes of a symbiotic, pair-bonding snapping shrimp. *Evolution*, 161-173.
- Komers PE, Brotherton, PNM. 1997. Female space use is the best predictor of monogamy in mammals. *Proceedings of the Royal Society of London Series B Biological Sciences*. 264: 1261-1270.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. Methuen, London. P. 409.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619-640.
- Lindstrom, K. S. (2003). *Aspects of the Behavior, Population Genetics, and Phylogeny of Stomatopod Crustaceans* (Doctoral dissertation, University of California, Berkeley).
- Manning, R. B. (1978). *New and rare stomatopod Crustacea from the Indo-West-Pacific region*. Smithsonian Institution Press.
- Mathews, L. M. (2002a). Territorial cooperation and social monogamy: factors affecting intersexual behaviours in pair-living snapping shrimp. *Animal Behaviour*, 63(4), 767-777.
- Mathews, L. M. (2002b). Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)?. *Behavioral Ecology and Sociobiology*, 51(5), 426-432.

- Michel, A and Manning RB (1971). A new austrosquilla (Stomatopoda) from the Marquesas Islands. *Crustaceans*. 20(3): 237-240.
- Pante, E., Adjeroud, M., Dustan, P., Penin, L., & Schrimm, M. (2006). Spatial patterns of benthic invertebrate assemblages within atoll lagoons: importance of habitat heterogeneity and considerations for marine protected area design in French Polynesia. *Aquatic Living Resources*, 19(03), 207-217.
- Pinheiro J., Bates D, DebRoy S, Sarkar D, and the R Development Core Team (2013). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.
- Porter, M. L., Zhang, Y., Desai, S., Caldwell, R. L., & Cronin, T. W. (2010). Evolution of anatomical and physiological specialization in the compound eyes of stomatopod crustaceans. *The Journal of Experimental Biology*, 213(20), 3473-3486.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reichard, U. H. (2003). Monogamy: past and present. *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*, 3-25.
- Rowe, L. (1994). The costs of mating and mate choice in water strider. *Animal Behaviour*, 48, 1049-1056.
- Schroeder, R. E., & Parrish, J. D. (2006). Ecological characteristics of coral patch reefs at Midway Atoll, Northwestern Hawaiian Islands. *Atoll Research Bulletin*, 543, 439-460.
- Schuster SM, Wade MJ (2003). Mating systems and strategies. Princeton (NJ): Princeton University Press.
- Sparkes, T. C., Keogh, D. P., & Pary, R. A. (1996). Energetic costs of mate guarding behavior in male stream-dwelling isopods. *Oecologia*, 106(2), 166-171.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell, ed. *Sexual Selection and the Descent of Man 1871 – 1971*. pp. 139-179. Aldine, Chicago.
- Vroom, P. S., Page, K. N., Peyton, K. A., & Kukea-Shultz, J. K. (2005). Spatial heterogeneity of benthic community assemblages with an emphasis on reef algae at French Frigate Shoals, Northwestern Hawai 'ian Islands. *Coral Reefs*, 24(4), 574-581.
- Wickler W and Seibt U (1981). Monogamy in crustacea and man. *Zeitschrift fur Tierpsychologie*. 57: 215 – 234.
- Wittenberger JF, Tilson RL. 1980. The evolution of monogamy; hypotheses and evidence. *Annual Review of Ecological Systems*. 11: 197-232.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer

Table 1. Predictions of demographic trends for two ecological drivers, food abundance and predation in *Pullosquilla litoralis* and *Pullosquilla thomassini* collected from a coral back reef in Moorea, French Polynesia during March 2010. Supported predictions are highlighted in gray.

Ecological Drivers		
	Food Abundance	Predation
<i>Pullosquilla</i> density	Higher Closer to Coral Heads	Lower closer to coral heads
<i>P. litoralis</i>		
Animal Size	Larger closer to coral heads	Smaller closer to coral heads
Percentage of Burrows with Egg Clutches	Higher closer to coral heads	Lower closer to coral heads
Single/ Paired Burrows	No relationship to distance from coral heads	More pairs closer to coral heads
<i>P. thomassini</i>		
Animal Size	Larger closer to coral heads	Smaller closer to coral heads
Percentage of Burrows with Egg Clutches	Higher closer to coral heads	Lower closer to coral heads
Single/ Paired Burrows	No relationship to distance from coral heads	More pairs closer to coral heads

Table 2. Fish recorded in a 625 m² quadrant in the coral back reef in Moorea, French Polynesia in November 2009, January 2010, and March 2010 that were either directly observed preying on benthic invertebrates or that are known to prey on benthic crustaceans.

Common name	Family	Scientific Name	Observed Preying on Benthic Invertebrates	Known to Prey on Benthic Crustaceans
Orangeband Surgeonfish	Acanthuridae	<i>Acanthurus olivaceus</i>	X	
Convict Surgeonfish	Acanthuridae	<i>Acanthurus triostegus</i>	X	
Yellowfin Surgeonfish	Acanthuridae	<i>Acanthurus xanthopterus</i>	X	X
Brushtail Tang	Acanthuridae	<i>Zebrasoma scopas</i>	X	X
Orangelined Triggerfish	Balistidae	<i>Balistapus undulatus</i>		X
Titan Triggerfish	Balistidae	<i>Balistoides viridescens</i>		X
Whitebanded Triggerfish	Balistidae	<i>Rhinecanthus aculeatus</i>	X	X
Flowery Flounder	Bothidae	<i>Bothus mancus</i>		X
Vagabond Butterflyfish	Chaetodontidae	<i>Chaetodon auriga</i>	X	X
Ornate Butterflyfish	Chaetodontidae	<i>Chaetodon ornatissimus</i>		X
Dotted Butterflyfish	Chaetodontidae	<i>Chaetodon semeion</i>		X
Pink Whiptail Stingray	Dasyatidae	<i>Himantura fai</i>	X	X
Shrimp Goby	Gobiidae	<i>Amblyeleotris</i> spp.		X
Goby	Gobiidae	<i>Gnatholepis</i> spp.	X	X
Axilspot Hogfish	Labridae	<i>Bodianus loxozonus</i>		X
Floral Wrasse	Labridae	<i>Cheilinus chlorourus</i>		X
Bird Wrasse	Labridae	<i>Gomphosus varius</i>		X
Checkerboard Wrasse	Labridae	<i>Halichoeres hortulanus</i>	X	X
Threespot Wrasse	Labridae	<i>Halichoeres trimaculatus</i>	X	X
Violet Line Maori Wrasse	Labridae	<i>Oxycheilinus digrammus</i>	X	X
Sixbar Wrasse	Labridae	<i>Thalassoma hardwicke</i>	X	X
Emperor	Lethrinidae	<i>Lethrinus</i> spp.		X
Goatfish	Mullidae		X	X
Harlequin Snake Eel	Ophichthidae	<i>Myrichthys colubrinus</i>		X
Spotted Sandperch	Pinguipedidae	<i>Parapercis millepunctata</i>		X
Parrotfish	Scaridae	Family Scaridae	X	
Peacock Hind	Serranidae	<i>Cephalopholis argus</i>		X
Hexagonal Grouper	Serranidae	<i>Epinephelus hexagonatus</i>		X
Honeycomb Grouper	Serranidae	<i>Epinephelus merra</i>		X
Camouflage Grouper	Serranidae	<i>Epinephelus polyphkadion</i>		X

Table 3. The number of predation events on benthic invertebrates by fish species during five minute observation periods along all transects in a 625m² quadrant in the coral back reef of Moorea, French Polynesia on March 14, 2010. Starred species were observed predating along transects while performing density or collecting transects on other days of the study.

Common Name	Scientific Name	Number of Observed Predation Events
Vagabond Butterflyfish	<i>Chaetodon auriga</i>	7
Goatfish	Family Mullidae	5
Whitebanded Triggerfish	<i>Rhinecanthus aculeatus</i>	5
Checkerboard Wrasse	<i>Halichoeres hortulanus</i>	2
Convict Surgeonfish	<i>Acanthurus triostegus</i>	2
Parrotfish	Family Scaridae	2
Goby	<i>Gnatholepis spp.</i>	1
Orangeband Surgeonfish	<i>Acanthurus olivaceus</i>	1
Yellowfin Surgeonfish	<i>Acanthurus xanthopterus</i>	1
Brushtail Tang	<i>Zebrasoma scopas</i>	1
Grouper	Family Serranidae	1
*Sixbar Wrasse	<i>Thalassoma hardwicke</i>	1
*Pink Whiptail Stingray	<i>Himantura fai</i>	1



Figure 1. A survey of *Pullosquilla* species was conducted in at 625 m² quadrat of patch reef (A) near Cook's Bay on Moorea, French Polynesia during March 2010. All labwork was performed at the University of California's Gump Biological Station (B).

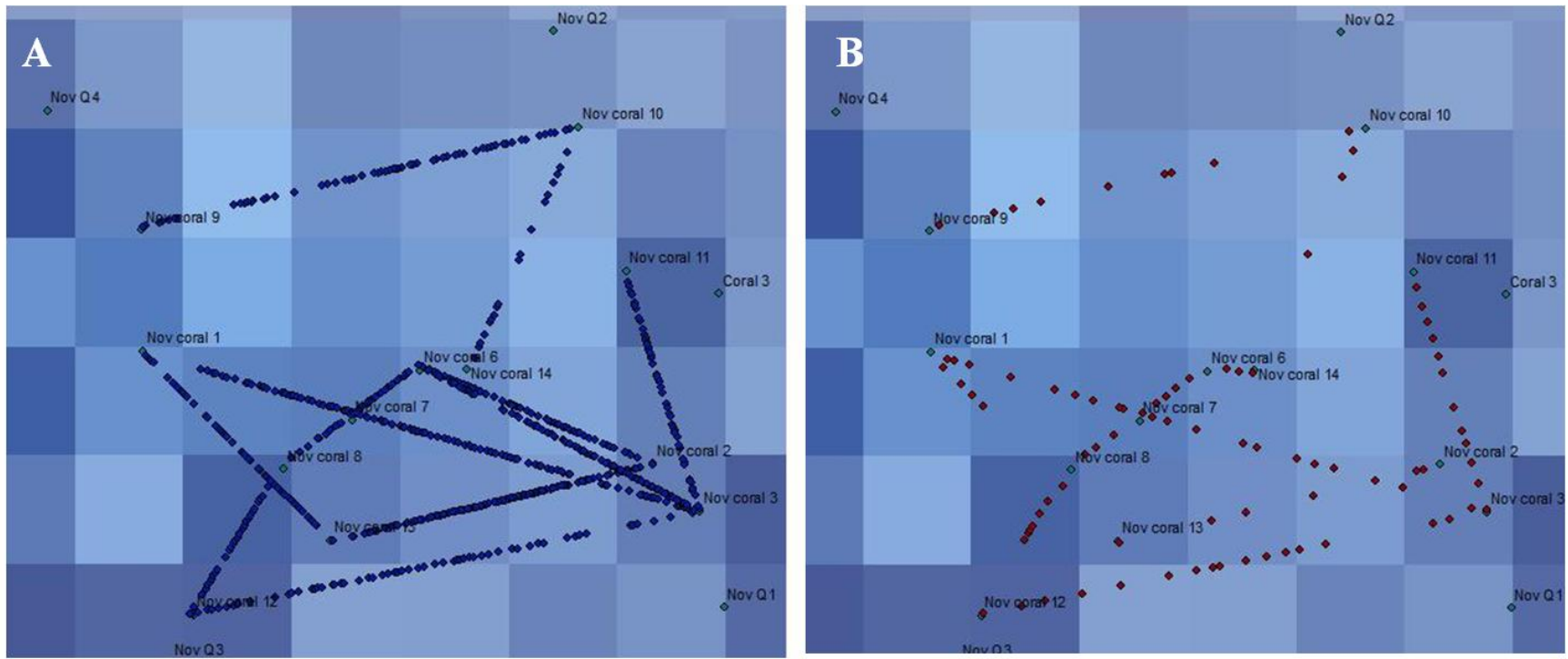


Figure 2. All *Pullosquilla* burrows (A) counted during density transects between coral heads and (B) collected along the same transects in March 2010 during a survey of a 625m² quadrant of coral back reef adjacent to Cook's Bay in Moorea, French Polynesia.

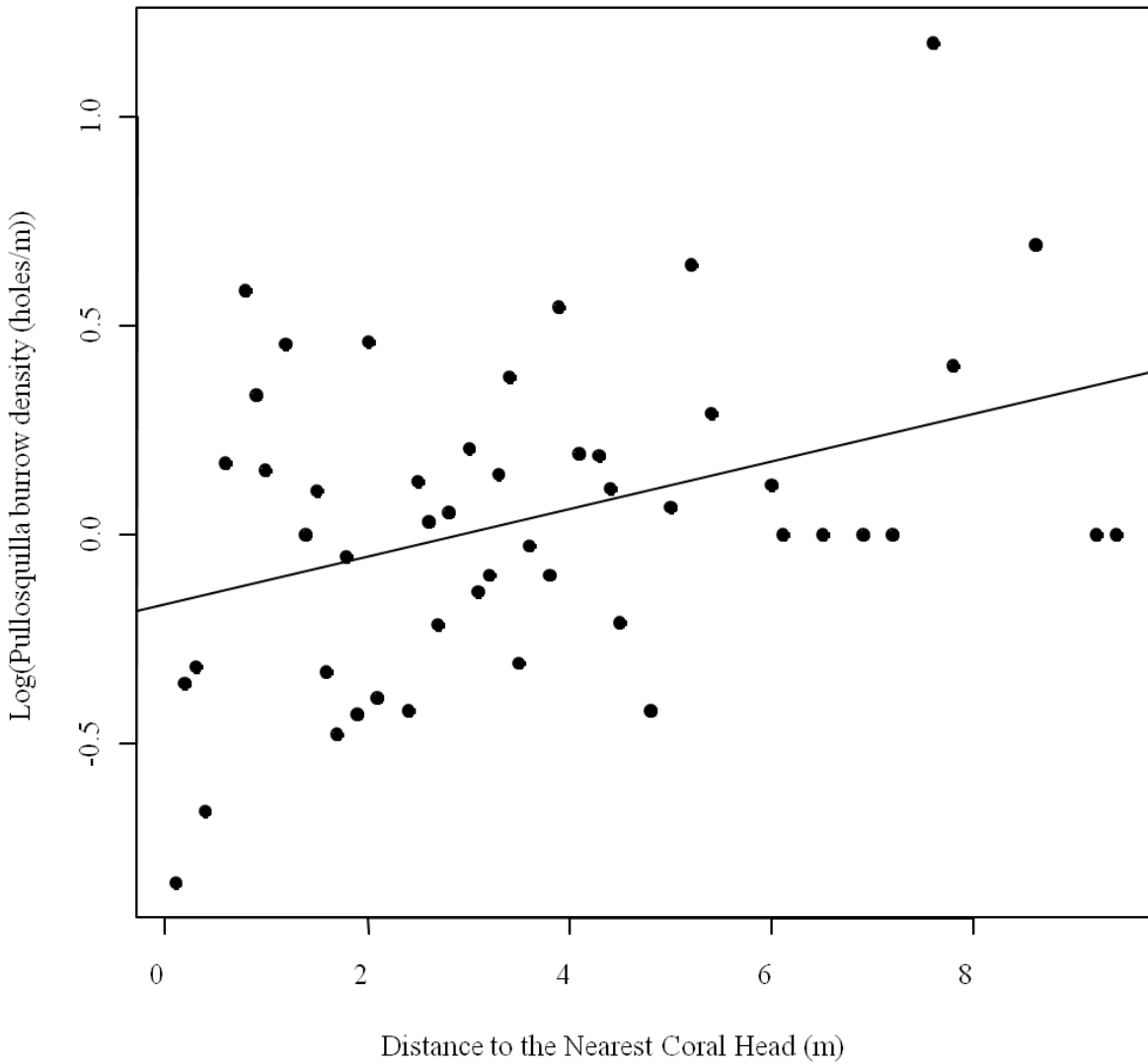


Figure 3. The relationship between logged *Pullosquilla* density (holes/m) and distance to the nearest coral head (m) in a 625m² quadrant of coral back reef west of Cook's Bay, Moorea, French Polynesia studied in March 2010. LR: $y = 0.0569x \pm 0.02$, adjusted $r^2 = 0.125$, $F = 7.856$, d.f. = 47, p-value = 0.007.

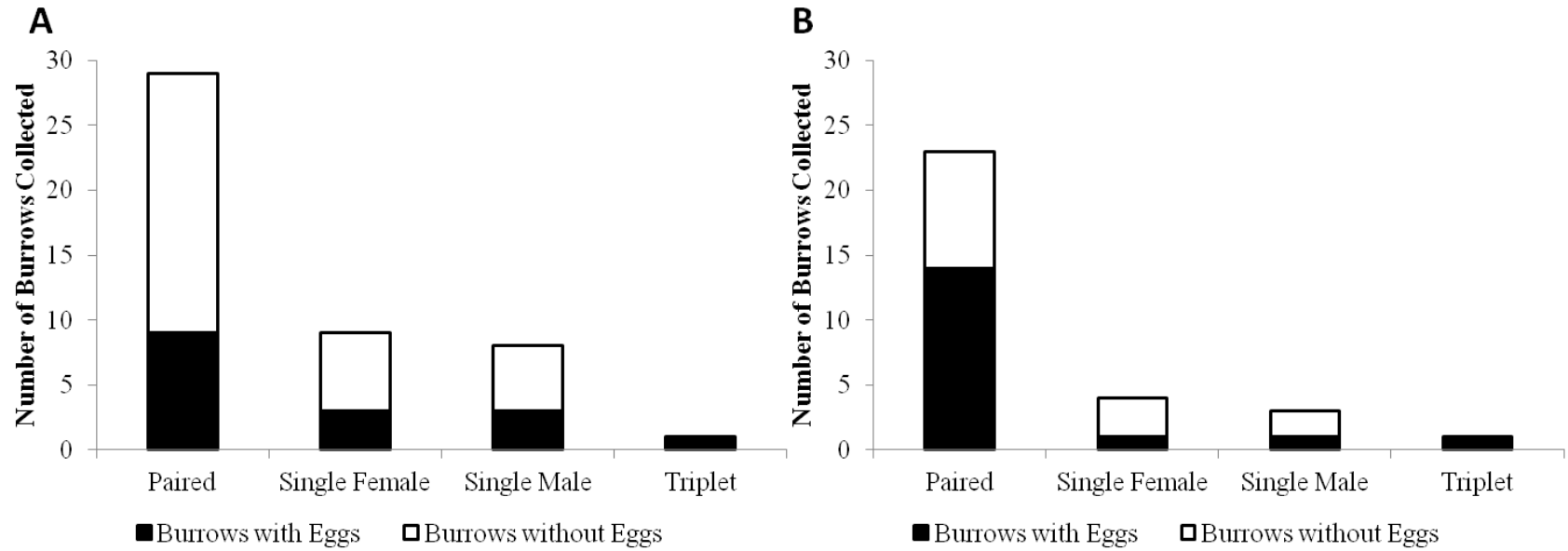


Figure 4. The number of A) *Pullosquilla litoralis* and B) *Pullosquilla thomassini* burrows collected containing heterosexual pairs, single males, single females, or triplets, with (black) and without (white) eggs at a coral back reef site in Moorea, French Polynesia during March 2010.

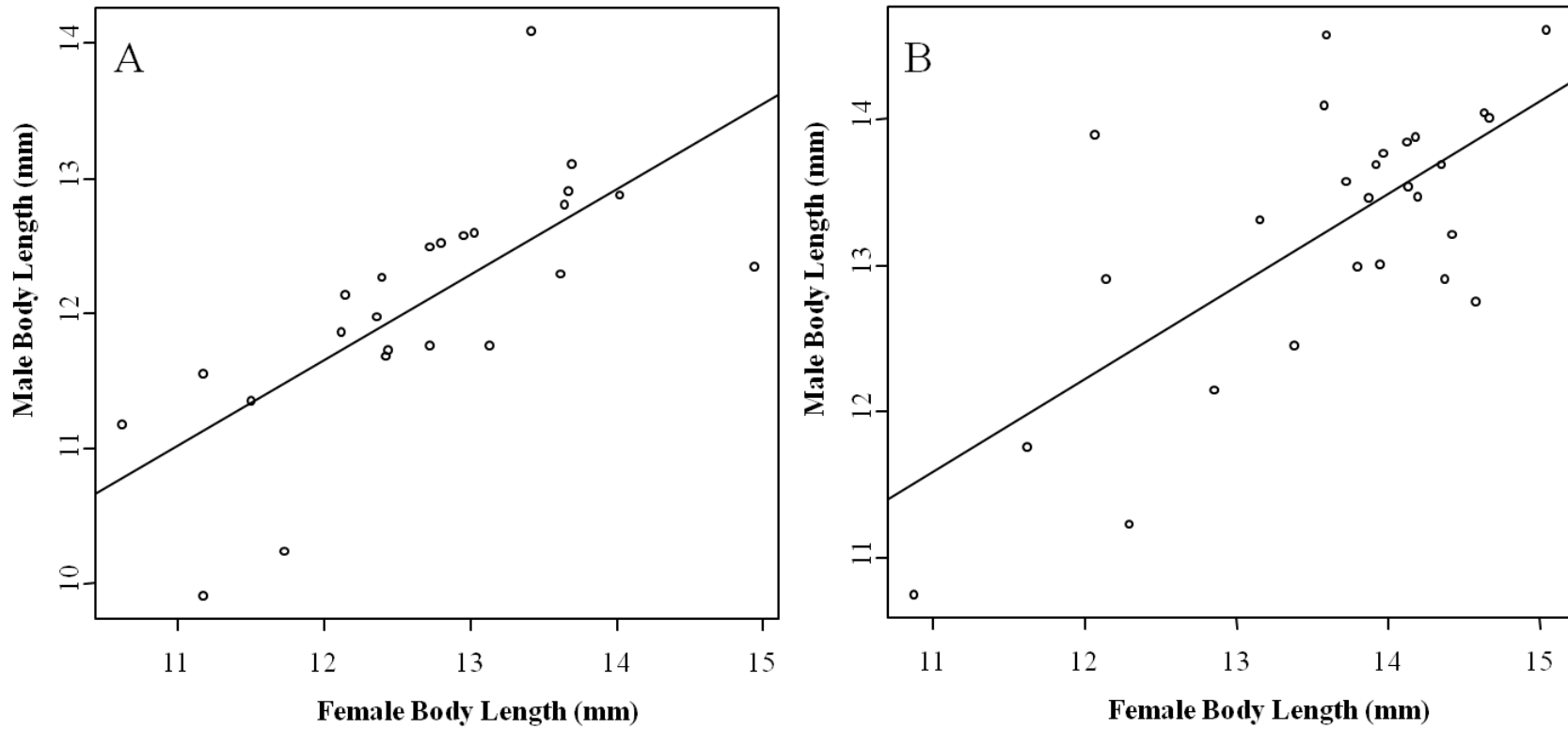


Figure 5. The body lengths (mm) of males and females collected in heterosexual pairs from a coral back reef in Moorea, French Polynesia during March 2010 are size matched in A) *Pullosquilla litoralis* (LR: $y = 0.631x \pm 0.131x + 4.080 \pm 1.665$, adjusted $r^2 = 0.492$, d.f. = 22, $F = 23.26$, $p < 0.0001$) and B) *Pullosquilla thomassini* (LR: $y = 0.636x \pm 0.131x + 4.591 \pm 1.789$, adjusted $r^2 = 0.464$, d.f. = 25, $F = 23.51$, $p < 0.001$).

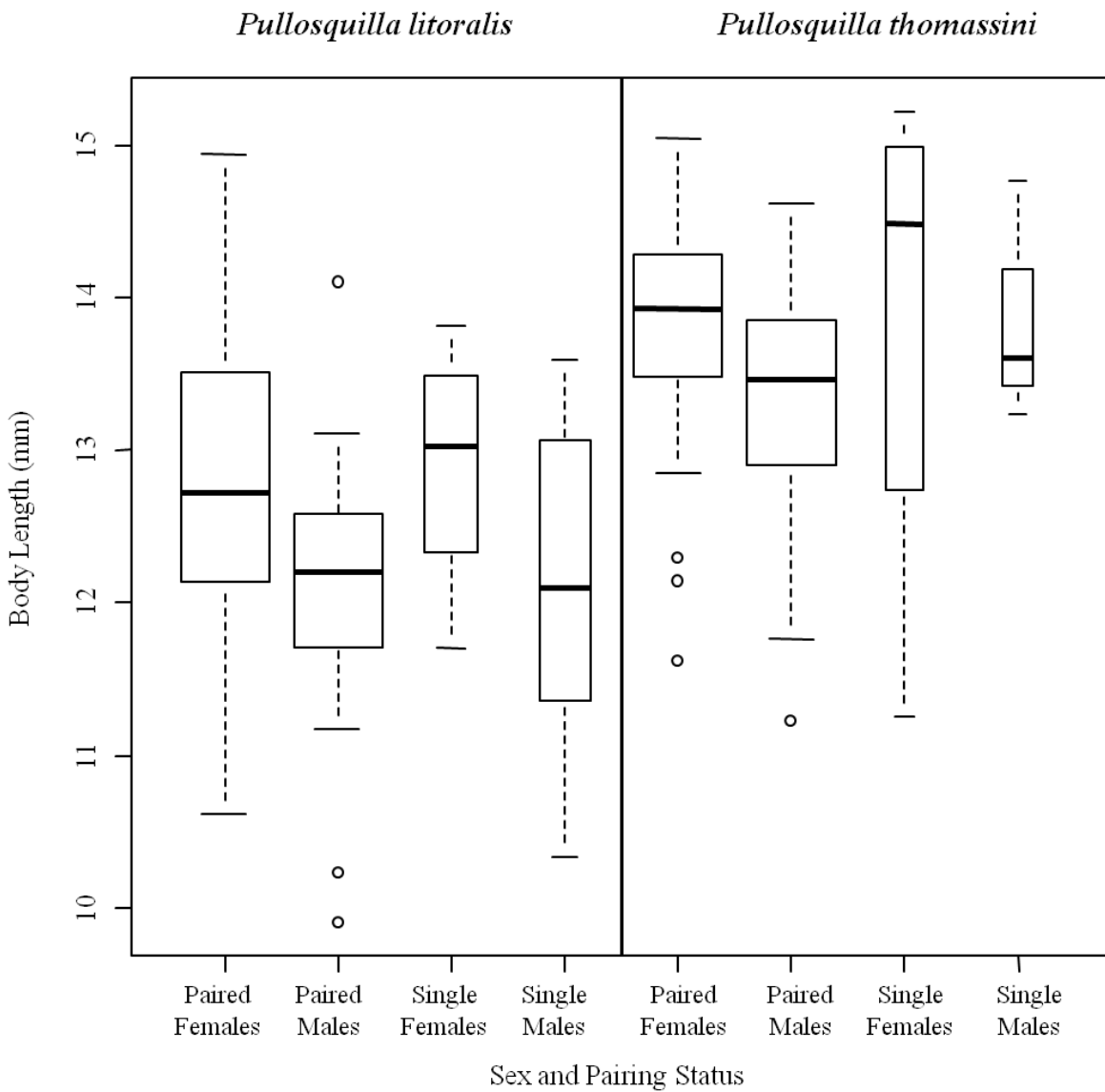


Figure 6. Stomatopod body length of paired versus single males and females for both *Pullosquilla litoralis* and *Pullosquilla thomassini* surveyed in a 625m² quadrant of coral back reef west of Cook's Bay Pass during March 2010. In *P. litoralis*, females were larger than males (ANOVA: d.f. = 1, F=8.221, p=0.006), but there was no differences between single and paired individuals. Neither sex nor pairing status had a significant effect in *P. thomassini*, though similar trends were observed.

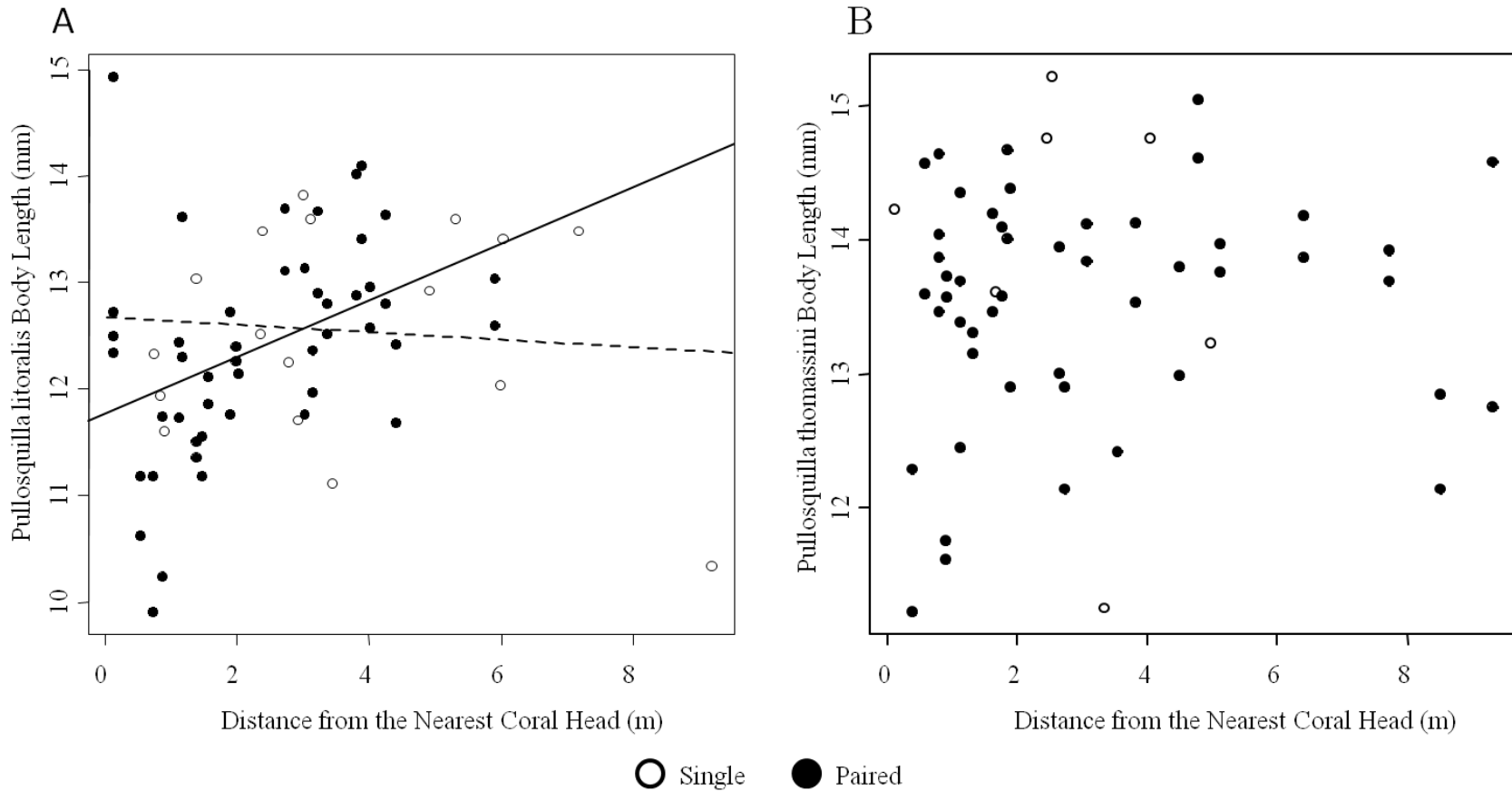


Figure 7. The effects of pairing status and distance from the nearest coral head on the size of A) *Pullosquilla litoralis* and B) *P. thomassini* in a 625m² quadrant of coral back reef west of Cook's Bay, Moorea, French Polynesia during March 2010. Black circles are paired individuals, while open circles are single individuals. The relationship between paired *P. litoralis* body length and distance is positive (GLS: $y = 0.378x \pm 0.083x + 11.688 \pm 0.262$, intercept: $t = 44.614$, $p < 0.001$, slope: $t = 4.573$, $p < 0.001$, Residual d.f. = 60). The relationship between single *P. litoralis* body length and distance is negative (GLS: $y = -0.050x \pm 0.116x + 13.021 \pm 0.431$, intercept: $t = 3.095$, $p = 0.003$, slope: $t = -3.693$, $p < 0.001$, Residual d.f. = 60). The relationship between *P. thomassini* length and distance is not significant based on generalized linear regression analysis.

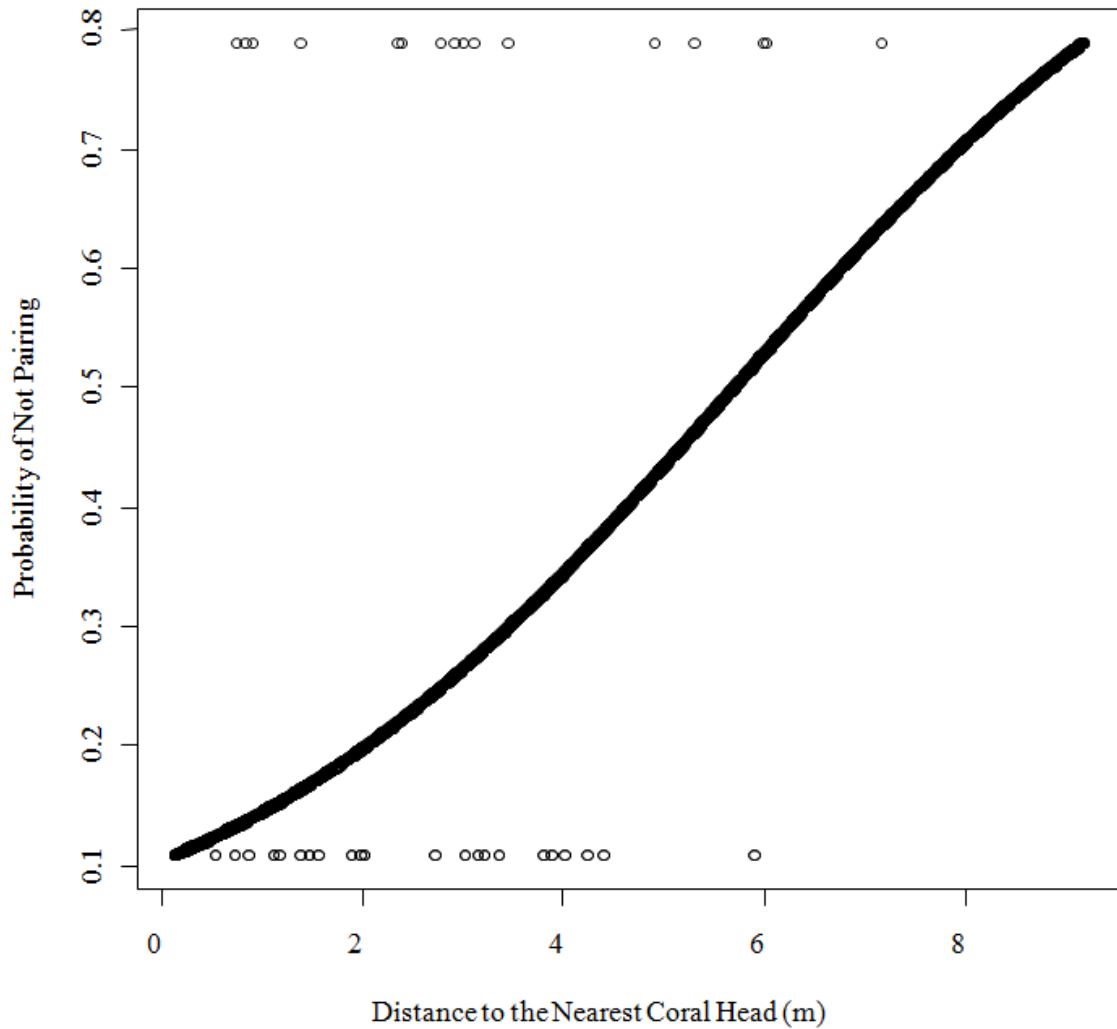


Figure 8. The probability of not pairing increases as distance to the nearest coral head increases in *P. litoralis* studied in a 625m² quadrant of coral back reef west of Cook's Bay, Moorea, French Polynesia in March 2010. (GLM, binomial distribution, logit linker, Residual deviance: 68.612 on 63 degrees of freedom; intercept: -2.158 +/- 0.592, z= -3.649, p<0.001; slope: 0.379 +/- 0.163, z = 2.326, p= 0.020).

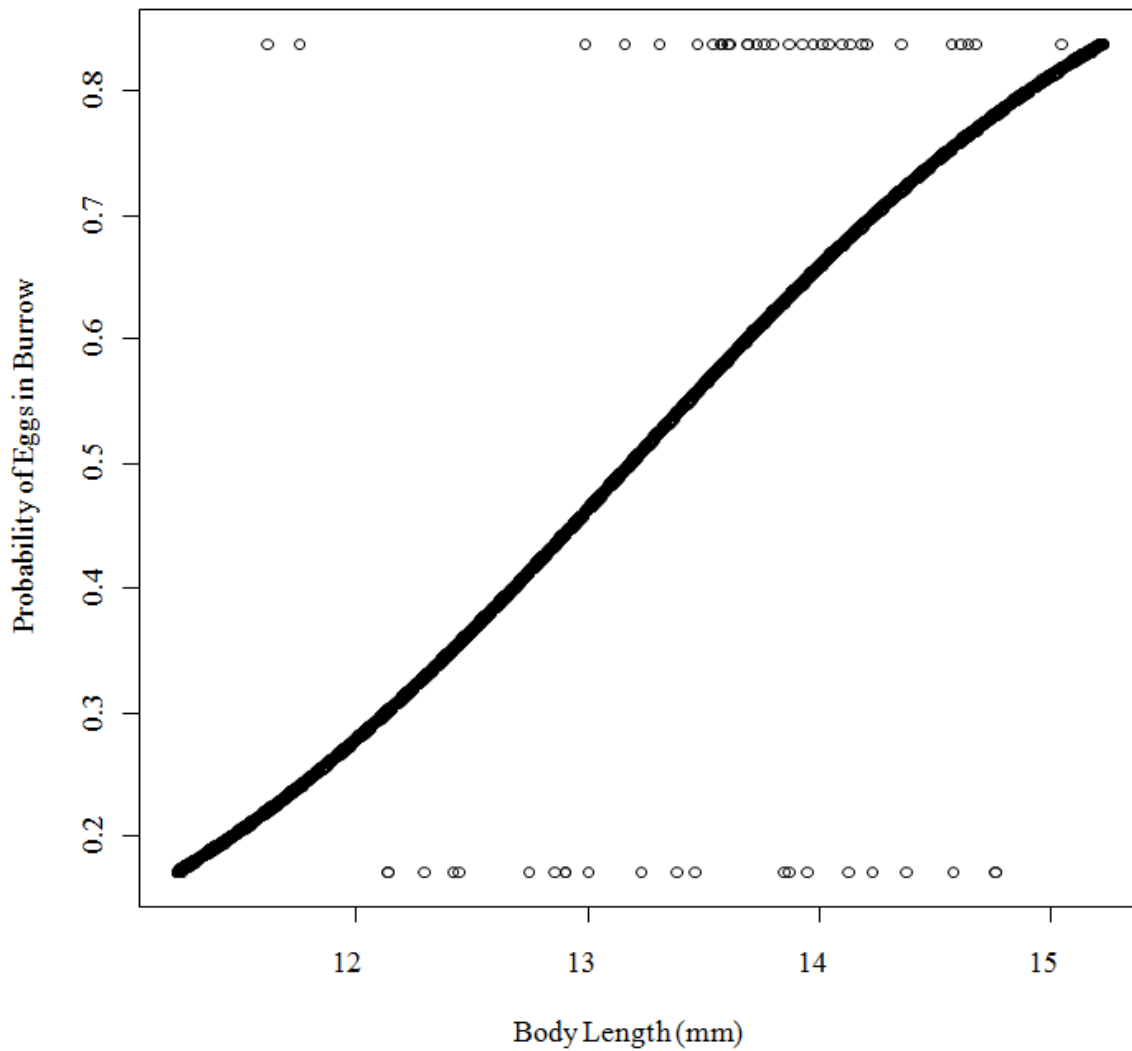


Figure 9. The probability of the presence of eggs in the burrow increases with increasing body length in *P. thomassini* studied in a 625m² quadrant of coral back reef west of Cook's Bay, Moorea, French Polynesia in March 2010. (GLM, binomial distribution, logit linker, Residual deviance: 69.959 on 54 degrees of freedom; intercept: -10.645 +/- 4.648, z= -2.290, p= 0.022; Size effect: 0.808 +/-0.343, z = 2.358, p= 0.0184).

The evolution of a sedentary lifestyle in Lysiosquilloid crustaceans: an evolutionary route to long-term social monogamy through sit-and-wait predation

ABSTRACT

Although social monogamy, when a male and female live together for at least one breeding episode, is characteristic of several ecologically important crustaceans, the evolutionary origins of this form of mating system are not well understood. In Lysiosquilloid stomatopods, long-term social monogamy occurs in eight genera. Members of these genera are sit-and-wait predators that seldom leave their burrows. This sit-and-wait feeding strategy may confer fitness benefits by decreasing vulnerability to predators and increasing energy available for reproduction. However, since foraging and mate searching often occur simultaneously, sit-and-wait predation may decrease mating opportunities, leading to the evolution of social monogamy. To investigate whether the evolution of social monogamy is associated with the evolution of sit-and-wait predation and burrow dwelling in the Lysiosquilloidea, I conducted a comparative, phylogenetically-based study using behavioral and ecological data. I hypothesized that 1) social monogamy would evolve more often in burrow dwellers living in soft-bottom substrates and 2) the evolution of long-term social monogamy would be correlated with the evolution of sit-and-wait predation. I also hypothesized that the evolution of biparental care did not cause the evolution of long-term social monogamy, but instead was facilitated by it. A maximum likelihood tree of 66 stomatopod species was constructed using a concatenated matrix of genetic data. Using phylogenetic comparative analyses, I analyzed the associations between social monogamy, predation strategy, burrowing behavior, parental care, and habitat preference. I found evidence that burrowing, sit-and-wait predation, and social monogamy evolved sequentially in the Stomatopoda. Long-term social monogamy may therefore have evolved as a way of further maximizing the fitness benefits of the sedentary lifestyle associated with sit-and-wait predation. This novel evolutionary route to long-term social monogamy may be associated with the shallow benthic marine environments that most Lysiosquilloids inhabit. I also found evidence that biparental care evolved after long-term social monogamy. This study emphasizes the importance of studying a diversity of taxa and environments when trying to understand the evolution of important behavioral traits such as predation style and mating systems.

INTRODUCTION

The evolutionary origins of social monogamy, when a male and female live in close proximity for at least one breeding episode, have long intrigued researchers. The evolution of monogamy is of interest because current theory predicts that both males and females will usually gain more fitness from mating with multiple partners (Bateman 1948, Trivers 1972). Given this expectation, under what environmental and social conditions will monogamy arise and do these same conditions maintain monogamy on an evolutionary timescale? While many studies have addressed the second question, the evolutionary origins of social monogamy are not well-understood. This study tests a novel hypothesis for the origin of social monogamy in stomatopod crustaceans using comparative phylogenetic methods to relate behavior and environment on an evolutionary timescale.

A host of conditions have been associated with the maintenance of social monogamy, including an even spatial distribution of females (Emlen and Oring 1977), the need for biparental care (Lack 1968, Burley and Johnson 2002), an operational sex ratio of one (Emlen and Oring, 1977, Schuster and Wade 2003), mate guarding (in males: Wittenberger and Tilson 1980; in females: reviewed in Gowaty 1996), and shared territorial defense (Baeza and Thiel 2007). In particular, Emlen and Oring's (1977) hypothesis that biparental care, an even spatial distribution of females, and an even operational sex ratio are the primary factors leading to the evolution of social monogamy has been extensively studied and generally supported in birds and mammals (Brotherton and Komers 2003). It is unclear, however, whether the factors maintaining social monogamy are similar in other animal taxa, particularly in marine invertebrates with very different life histories and ecologies.

It is often assumed that factors selecting for the maintenance of social monogamy are also responsible for its origin. Many studies assess the factors discussed in the previous paragraph by examining their current utility in increasing fitness. However, the current utility of behaviors associated with social monogamy, such as biparental care or territorial cooperation, does not necessarily reflect the role of these behaviors in the origin of social monogamy (Gowaty 1996, Brotherton and Komers 2003). To understand the origins of social monogamy in a clade, it is necessary to understand the behavioral characteristics of the ancestors of the clade. This can be accomplished with both phylogenetic analyses and examinations of the fossil record (Hughes 1998; for examples, see Baeza et al. 2009, Brown et al. 2010). Further, specific predictions about the origin of social monogamy can be tested in a phylogenetic context (Gowaty 1996). Although comparative, phylogenetically-based analyses are dependent on the accuracy of both the species data and the phylogeny used, in taxa with poor fossil records (like the Stomatopoda) and for behavioral traits that do not fossilize, they are the best way to understand the evolutionary origin of traits.

Social and genetic monogamy are characteristic of several ecologically important crustaceans, including fiddler crabs, American lobsters, and mantis shrimps (Wickler and Seibt 1981, Correa and Thiel 2003; Christy and Salmon 1991; Detto and Blackwell 2009). Few studies have taken advantage of this group for the study of the ecology and evolution of monogamy, despite several experimental advantages, such as their diversity, morphological disparity, large population sizes, short generation times, and availability for laboratory culture. Crustaceans offer unique comparative systems in which to test the prevalent hypotheses for the evolution of social systems; recent studies by Baeza et al. (2009) and Duffy and Macdonald (2010) shed light on the evolution of social monogamy in a protandrous simultaneous hermaphroditic clade of Caridean shrimp and eusociality in a clade of alpheid shrimp, respectively.

Most mantis shrimp species are promiscuous (polyandrous/polygynous) or serially monogamous animals that leave burrows and cavities to actively hunt prey (Caldwell 1991, personal communication). In contrast, Lysiosquilloid stomatopod crustaceans include eight genera that form long-term pairs (Ahyong 2001, Porter 2010, Ahyong 2011). These socially monogamous mantis shrimps live in heterosexual pairs in U-shaped burrows in sandy or muddy habitats (Caldwell 1991). Lysiosquilloid genera range in size from 16 mm (*Pullosquilla*) to over 35 cm (*Lysiosquillina*).

Many Lysiosquilloid stomatopods are sit-and-wait predators (as described in Huey and Pianka 1981 and Janetos 1981) that seldom leave their burrows, preying from their burrow-openings on zooplankton and fish that swim over them and benthic animals that approach them. While waiting for prey, they expose only their well-camouflaged eyes and antennal scales so that

they are almost undetectable (Caldwell 1988, Caldwell 1991, Wright personal observation). They can also partially or fully close their burrow entrances with a mucus plug so that it is not apparent to predators (Caldwell 1991). Sit-and-wait predation evolves in a lineage when both its predators and prey items are abundant as a way to maximize energy intake while minimizing mortality from predation (Huey and Pianka 1981, Janetos 1981). The tidal flats and back reef lagoons that most Lysiosquilloids inhabit are flushed daily by tides that carry abundant prey items (i.e. zooplankton and larval fish). They are also home to many fish that prey on stomatopods (Wright Chapter 2, Reaka 1985, Jutte 1997). Thus, it is likely that sit-and-wait predation is a strategy to increase fitness for Lysiosquilloid stomatopods.

Different hypotheses have been proposed to explain the evolution and maintenance of social monogamy in the two best studied Lysiosquilloid genera. In *Pullosquilla*, biparental care and mating synchrony based on tidal cycles may be responsible for the origins and maintenance of social monogamy (Jutte 1997, Lindstrom 2003, but see Wright Chapter 1). However, other Lysiosquilloid species do not provide biparental care for young. Instead, at least one species, *Lysiosquillina maculata*, displays a division of labor in which males forage and provision females (Caldwell 1991). Caldwell (1991) proposed that in large Lysiosquillids, such as *L. maculata*, the cost of constructing extensive, mucus-lined burrows maintains monogamy. Juvenile *Lysiosquillina* are able to build new burrows and are frequently found as single individuals, but if large adults of either sex desert and are unable to find a new mate with a burrow, they are unable to generate enough mucus to build a stable burrow. Smaller socially monogamous stomatopod genera, including *Alachosquilla* and *Acanthosquilla*, do not demonstrate biparental care and are capable of rebuilding burrows as mature adults. It is therefore likely that both biparental care and large burrows are derived traits that evolved after social monogamy and are selecting for its maintenance. The evolutionary origins of long-term social monogamy in the Lysiosquilloidea are therefore ripe for further investigation.

The Lysiosquilloidea may have evolved long-term social monogamy in conjunction with other behavioral traits that facilitated a sedentary lifestyle, allowing stomatopods to escape high levels of predation. I propose the Sedentary Lifestyle Hypothesis: burrow-dwelling stomatopods in the Lysiosquilloidea evolved sit-and-wait predation to decrease their vulnerability to high levels of predation and to increase energy available for reproduction. Because foraging and mate searching often occur simultaneously, sit-and-wait predation may have decreased mating opportunities in Lysiosquilloids. Additionally, animals demonstrating long-term social monogamy do not have to leave their burrow refuge to find new mates, which may have allowed Lysiosquilloids to minimize the costs of mating due to predation (Daly 1978, Lima and Dill 1990). Decreased time spent mate searching because of a sit-and-wait foraging strategy coupled with the high risk of mortality during mate searching may have caused the origin of social monogamy. In this study I use comparative, phylogenetically-based methods to assess the Sedentary Lifestyle Hypothesis. Specifically, I test the following predictions of the hypothesis:

- 1) Sit-and-wait predation evolved after the evolution of burrow dwelling and is associated with sand/mud habitats, and
- 2) Social monogamy evolved after sit-and-wait predation and the evolution of the two traits is correlated.

I also examine the hypothesis that biparental care caused the origin of social monogamy in the Lysiosquilloidea by testing the prediction that biparental care should evolve before social

monogamy in a comparative framework. This study provides new insights into the roles that predation and biparental care may play in the origins of social monogamy.

METHODS:

Character Assignment:

A literature search was performed to determine the habitat preferences, predation styles, burrowing behaviors, mating systems, and parental care behaviors of 66 stomatopod species (Manning 1966, Manning 1968, Manning 1977, Manning 1978, Dingle and Caldwell 1978, Reaka 1981, Manning and Lewinsohn 1986, Moosa 2000, Ahyong 2001, Schram and Muller 2004). Further information on the mating and burrowing behaviors of some species was obtained from Dr. Roy L. Caldwell, who has been studying the behaviors of stomatopods for many years. Stomatopods display high levels of variation in their burrowing behaviors, mating systems, and predation styles. Several of the phylogenetic comparative analyses performed in this study require characters to be binary. Thus, this study focused on three questions when assigning character states to species:

- 1) Does a species live in burrows that they construct themselves or do they live in pre-existing cavities? (Burrowing = 1, Cavity Dwelling = 0)
- 2) Is a species exclusively a sit-and-wait predator, seldom leaving its burrow, or has it been reported to leave its burrow to actively prey on food? (Yes = 1, No = 0)
- 3) Do members of a species live in monogamous pairs for longer than a single breeding cycle in a single burrow or cavity (i.e. long-term social monogamy)? (Yes = 1, No = 0)

Stomatopods live in a diversity of discrete habitats, including mud or sand flats, a variety of rubble environments (rubble, coral rubble, mud rubble), and coral. Habitat was therefore coded as a multistate character. In species where both parents provide direct care for their offspring, parental care was coded as biparental. Male provisioning was attributed to species in which males have been observed to feed females and females are seldom observed foraging. All other species were described as having maternal care. The results and discussion also report examples of stomatopods that are not included on the tree, but demonstrate cavity-dwelling, sit-and-wait predation, or pairing behaviors that are atypical of their superfamily.

Tree Construction:

A maximum likelihood tree of 66 stomatopod taxa was constructed using a concatenated matrix of genetic characters (12S, 16S, 18S, CO1) from *GenBank* (Table 1). This tree includes approximately 10% of known stomatopods: the three stomatopod superfamilies that have been most extensively studied (Lysiosquilloidea, Gonodactyloidea, Squilloidea) are well-represented, but several superfamilies (Bathysquilloidea, Eurysquilloidea, and Parasquilloidea) are under-represented or not included because little is known about these stomatopods and they have not yet been sequenced. The genetic datasets were trimmed and aligned in *Geneious* to create an alignment of 2589 characters. A phylogeny was constructed in PAUP (Swoffard 2002) within *Geneious* using Maximum Likelihood and the GTR+G+I rate model selected by ModelTest. The tree was rooted using the *Hemisquilla* genus as an outgroup (Porter 2010). To better represent the diversity of mating systems in the Lysiosquilloidea, the species *Nannosquilla anomala* was added to the tree as a sister taxa to *Pullosquilla thomassini* phylogeny in *Mesquite* (Maddison and Maddison 2011) based on its Linnean classification and the Ahyong and Harling (2000)

cladogram. It was assigned a branch length of 0.001 to imitate a polytomy while still allowing the tree to be used for maximum likelihood-based comparative analyses.

Comparative Analyses:

A variety of comparative phylogenetic analyses were conducted in *R* (R Core Team 2013) using the packages *Ape* (Paradis et al. 2004) and *Geiger* (Harmon et al. 2009). Ancestral states of ecological and behavioral characters were reconstructed using maximum parsimony (MP) for multistate characters (habitat, parental care) and maximum likelihood (ML) for binary characters (burrowing, predation style, mating system). The Mk1 model of character state evolution was chosen for all ML reconstructions after comparison based on AIC values with a symmetrical rate of change model and a model where all rates varied independently. Pagel's (1994) test of discrete character evolution was performed in *Mesquite* (Maddison and Maddison 2011) to examine the relationships within the behavioral datasets of binary characters.

RESULTS:

Phylogeny of the Stomatopoda

A phylogeny of 66 stomatopod taxa constructed using Maximum Likelihood (Likelihood score = 189799.6) from a concatenated matrix of genetic characters (12S, 16S, 18S, COI) indicated that the Lysiosquilloidea is monophyletic. It supports the Lysiosquillidae as a distinct clade, but suggests that the Nannosquillidae is polyphyletic and encompasses both the Lysiosquillidae and Tetrasquillidae. The internal branching patterns of the Squilloidea are not well-resolved and the Pseudosquillidae is nested within the Squilloidea. (Figure 1)

Ancestral Character State Reconstructions:

The majority of burrowing stomatopods live primarily in sandy or muddy substrates; this was probably the ancestral state of extant stomatopods (Figure 2A). An ancestral state reconstruction of burrowing (figure 2B) indicated that the ancestor of extant stomatopods most likely lived in burrows (0.986 likelihood), rather than coral or rubble cavities (1.393e-02 likelihood). Cavity dwelling evolved in burrowing lineages at least twice on the phylogeny, in the Gonodactyloidea and in the Pseudosquillidae. Cavity dwelling has likely originated at least two other times in the Squilloidea and Lysiosquilloidea, which are not represented in taxa on the phylogeny. The Coronodidae (Lysiosquilloidea) inhabit coral cavities and hardened-mud galleries under rubble (Ahyong 2001, Caldwell personal communication). In the Squillidae, *Meiosquilla lebouri* is a cavity-dweller, while its congeners (*M. dawsoni*, *M. swetti*) live in burrows (Caldwell 1991). Additionally, *Parvisquilla multituberculata*, which has recently been reassigned from the Coronodidae to the Squillidae (Ahyong 2001), lives in coral cavities (Ahyong 2006).

An ancestral state reconstruction of predation style indicated that sit-and-wait predation most likely evolved in the ancestor of the Lysiosquilloidea lineage (Figure 3A). Additionally, sit-and-wait predation is seen in several juvenile cavity-dwelling Gonodactyloids (*G. affinis*, *Haptosquilla*), though the adults of these species are not exclusive sit-and-wait predators, and adult *Echinosquilla guerinii*, which is a sea urchin mimic that seldom leaves its cavity.

An ancestral state reconstruction of long-term social monogamy indicates that social monogamy has been gained or lost at least 3 times in the Lysiosquilloidea (Figure 4A). It most likely had a single origination and several losses within the clade. Low frequencies of pairing have also been reported in the Squilloidea. Caldwell (1991) found 2 out of 96 *M. swettii* burrows and 12 out of 272 *M. dawsoni* burrows contained pairs. This level of pairing suggests serial, rather than long-term, monogamy.

All known stomatopods display maternal care for eggs; the ancestral state of parental care in extant stomatopods was probably maternal care (Figure 5A). Biparental care has evolved once in the Stomatopoda, in the *Pullosquilla* genus. Male provisioning of females, representing increased paternal effort, has evolved once in the *Lysiosquillina* genus. The evolution of social monogamy preceded the evolution of biparental care in the *Pullosquilla* (Figure 5).

Correlations of Burrowing, Predation Style, and Long-term Social Monogamy

Predation Style and Burrowing:

The evolution of sit-and-wait predation style and burrowing in the Stomatopoda were not correlated (Pagel's 1994 test, 1000 iterations, 4-parameter LL = -29.140, 8-parameter LL = -27.677, Difference = 1.462, p-value = 0.269). However, most sit-and-wait predators are burrowers, with the exception of *E. guerinii* (Figure 3).

Predation Style and Long-term Social monogamy:

The evolution of sit-and-wait predation and long-term social monogamy were correlated in the Stomatopoda based on Pagel's (1994) test (Figure 4). Sit-and-wait predation significantly preceded long-term social monogamy (Pagel's test: 1000 iterations, 4-parameter LL = -20.861, 8-parameter LL = -14.106, Difference = 6.755, p-value <0.001).

Long-term Social Monogamy and Burrowing:

The evolution of long-term social monogamy and burrowing were not statistically correlated (Pagel's 1994 test, 1000 iterations, 4-parameter LL = -30.763, 8-parameter LL = -28.543, Difference = 2.221, p-value = 0.064). However, all species displaying long-term socially monogamy do burrow.

These results indicate that all stomatopods with long-term social monogamy are also sit-and-wait predators and burrowers.

DISCUSSION

The findings of this study support the sedentary lifestyle hypothesis. They indicate that burrowing, sit-and-wait predation, and long-term social monogamy evolved sequentially. The common ancestor of extant stomatopods was likely a burrower, while sit-and-wait predation likely evolved in the ancestor of the Lysiosquilloidea. Social monogamy also likely evolved in the ancestor of the Lysiosquilloidea and was subsequently lost in at least twice. The findings of this study furthermore suggest that sit-and-wait predation facilitated the evolution of long-term social monogamy in the Lysiosquilloidea.

Evolutionary Relationships of the Stomatopoda

These findings shed new light on the evolutionary relationships of Lysiosquilloid stomatopods. Our maximum likelihood analysis suggests that the Nannosquillidae family is polyphyletic (Figure 1), which is congruent with the findings of Ahyong and Jarman (2009) and Porter et al. (2010). These findings suggest that the Nannosquillidae should be systematically re-examined. The current Nannosquillidae include both monogamous and non-monogamous taxa; therefore, resolving the relationships of these taxa will be important in understanding the evolution of social monogamy in the Lysiosquilloidea.

The Coronodidae family of the Lysiosquilloidea has smashing raptorial appendages and lives in rubble cavities or galleries associated with rocks (Caldwell and Dingle 1975, Ahyong 2001, Caldwell personal communication). They have not been collected in monogamous pairs. This family is not represented on our phylogeny because it has not yet been sequenced. The relationship of the Coronodidae with other Lysiosquilloid stomatopods will be important in making inferences about the evolution of both sit-and-wait predation and social monogamy.

The Pseudosquillidae are nested within the Squilloidea in our ML tree, which is not congruent with the findings of Ahyong and Harling (2000) that they are members of the Gonodactyloidea or with Porter et al. (2010) that they diverged early from the Stomatopoda and compose a superfamily. Long-branch attraction might account for these inconsistencies, as the branch connecting the Pseudosquillidae to the Squillids is exceptionally long (Figure 1; Felsenstein 1978, Huelsenbeck 1997).

Evolution of behavioral traits

The majority of stomatopods live in sandy or muddy benthic environments and, based on ancestral state reconstruction, the ancestor of extant stomatopods was a burrower. Although ancestral state reconstructions of incomplete phylogenies are not always accurate (Losos 2011, Litsios and Salamin 2012, but see Li et al. 2010), a burrowing stomatopod ancestor is congruent with phylogenetic and fossil evidence. Porter's (2010) phylogeny of the Stomatopoda places two burrowing clades, the Hemisquillidae and the Pseudosquillidae, at the base of the stomatopod tree. Haplocarid fossils in the *Pseudosculda* genus are commonly found on mud or sand substrates and the Aeschronectida, sister group to the Stomatopoda, were benthic filter feeders, suggesting that these animals burrowed in sand and mud (Schram 1969, Watling et al. 2000). Additionally, some Thalassinoides fossils (trace fossils of burrows) from the lower Jurassic that are U-shaped have been attributed to stomatopods (Monaco and Giannetti 2002). Burrowing was likely adaptive in shallow benthic environments replete with fish predators, providing animals a refuge from predation and a safe location for mating, parental care of eggs, and food caching.

Sit-and-wait predation is widespread in the Lysiosquilloidea, with the exception of the Coronodidae. However, the foraging activities of the Coronodidae may be localized to the immediate vicinity of their mud galleries (R.L. Caldwell, personal communication). Sit-and-wait predation occurs when animals are exposed to abundant prey items and high levels of predation (Huey and Pianka 1981, Janetos 1981), conditions that are common in the tidal lagoon ecosystems where many Lysiosquilloids live (Reaka 1985, Jutte 1997, Wright Chapter 2). Sit-and-wait predation may provide stomatopods a variety of fitness advantages, including decreasing the amount of time they are exposed to predation and providing a location to cache food when prey is particularly abundant. Two stomatopod genera of sit-and-wait predators have been observed caching prey items in their burrows in a laboratory setting; *Lysiosquillina maculata* caches fish and shrimp, while the *Pullosquilla* genus (Manning 1978) caches zooplankton, (Wright, unpublished data; Caldwell, personal communication).

Long-term social monogamy appears to have originated or been lost at least three times in the Lysiosquilloidea. It is likely that there are additional losses and gains because several Nannosquillids that were not included in this study, as well as the Coronodidae family, are not socially monogamous. Maximum likelihood ancestral state reconstruction is sensitive to the exclusion of species when there are many losses and gains of a trait (Litsios and Salamin 2012, but see Li et al. 2010), so incorporating more Lysiosquilloids into the analysis may yield different estimates of when long-term social monogamy first originated.

Sit-and-wait predation may facilitate the evolution of long-term social monogamy in stomatopods. Since foraging and mate searching often occur simultaneously, sit-and-wait predation may decrease mating opportunities, leading to the evolution of social monogamy. Social monogamy may increase the fitness benefits of an already sedentary, burrowing lifestyle: heterosexual pairs may be more efficient than single animals at conducting burrow maintenance, guarding burrows from predators, and foraging for prey. Long-term social monogamy also guarantees stomatopods reproductive opportunities and, coupled with sit-and-wait predation, provides extreme protection from predators.

Most stomatopods provide maternal care for their egg clutches, aerating them, guarding them from predators, moving them within the burrow or cavity, and removing dead or fouled eggs (Jutte 1997, Lindstrom 2003, Wright Chapter 1). However, forms of parental care that include paternal effort have evolved twice in the Lysiosquilloidea. *L. maculata* (Lysiosquillidae) displays indirect paternal effort through a sexual division of labor, with males foraging and feeding females, who in turn remain inside the burrow to produce and care for eggs. In contrast, males and females of the *Pullosquilla* genus (Nannosquillidae) share foraging efforts and parental care duties equally. Both biparental care and male provisioning evolved after long-term social monogamy. Thus, long-term social monogamy may facilitate paternal effort by placing males in close proximity to their own developing eggs.

Among the Lysiosquilloidea, all known members of the Lysiosquillidae display long-term social monogamy, while there is more mating system variation within the rest of the clade. It is possible that the sexual dimorphism and large sizes of the Lysiosquillidae constrain mate searching behavior in sexually mature females. *L. maculata*, the best studied Lysiosquillid, is sexually dimorphic in both behavior and morphology (Caldwell 1991). The rostra, eyes, and raptorial appendages of females are reduced in size and they display the division of labor described above (Caldwell 1991, Steves and Wright, unpublished data). This dimorphism may constrain the ability of females to live singly. Furthermore, it may be too costly for sexually

mature males and females to desert and establish a new burrow large and stable enough to accommodate them if they are unable to find a new mate with a burrow (Caldwell 1991).

Evaluation of the Sedentary Lifestyle Hypothesis

This study supports the sedentary lifestyle hypothesis in which both sit-and-wait predation and long-term social monogamy evolved in response to high levels of predation. The sequential evolution of burrowing, sit-and-wait predation, and long-term social monogamy suggests that each behavioral trait may have facilitated the evolution of the next trait, with particularly strong support that sit-and-wait predation facilitated the evolution of long-term social monogamy. Long-term social monogamy may therefore have evolved as a way of further maximizing the fitness benefits of the sedentary lifestyle associated with sit-and-wait predation. It would have provided greater food security through shared foraging (Matthews 2002), allowed animals to better evade fish predators because they could avoid mate searching (Daly 1978, Baeza and Thiel 2007, Magnhagen 1991, Lima and Dill 1990), and allowed for greater paternal effort (Alonzo 2010), potentially increasing both female fertility and offspring survival (but see Wright Chapter 1). Currently the behaviors of only about 10% of extant stomatopods have been characterized and the phylogenetic structure of stomatopod species is not fully resolved (Caldwell 1991). The sedentary lifestyle hypothesis deserves further testing as more behavioral and phylogenetic information becomes available for stomatopods. Although our findings suggest that social monogamy did not evolve because of a need for biparental care to successfully raise young, other alternative hypotheses should also be tested. One intriguing hypothesis is that a high risk of mate searching due to low stomatopod densities may have selected for long-term social monogamy; this could be tested within a comparative framework by examining the average densities of stomatopods on a phylogeny.

Significance

The *Lysiosquilloid* stomatopods appear to have taken a different route in the evolution of long-term social monogamy than other taxonomic groups that have been studied. The most commonly cited causes for the origin of social monogamy include a need for biparental care (Lack 1968, Burley and Johnson 2002), an even distribution of resources in space (Emlen and Oring 1977), a sex ratio close to one (Emlen and Oring 1977, Schuster and Wade 2003), mate guarding (Wittenberger and Tilson 1980; Grafen and Ridley 1983), and territorial cooperation (Matthews 2002a, Baeza and Thiel 2007). While the evolution of long-term social monogamy as described in this study falls loosely under the umbrella of the territorial cooperation hypothesis, most studies examining this hypothesis have focused on the maintenance of social monogamy, rather than the origins of social monogamy (Matthews 2002, Baeza and Thiel 2007, Baeza 2008, 2010, 2011). The *Lysiosquilloid* stomatopods provide an example of how long-term social monogamy may originate through shared territorial cooperation. Furthermore, predation is often discounted as a selective pressure in the study of social monogamy (but see Baeza and Thiel 2007), but predation is likely to be an important selective pressure in the evolution of long-term social monogamy in *Lysiosquilloid* stomatopods because of its selection for a sedentary burrowing lifestyle. Finally, social monogamy evolved before biparental care in the *Lysiosquilloidea*, providing a counter-example to the often cited hypothesis that a need for biparental care causes the evolution of monogamy (Lack 1968, Burley and Johnson 2002).

This novel evolutionary route to long-term social monogamy through sit-and-wait predation may be associated with the shallow benthic marine lagoon environments that most

Lysiosquilloids inhabit. Tidal lagoons are flushed by tides that carry with them abundant zooplankton and larval fish, providing large amounts of food that move directly over stomatopod burrows. Furthermore, lagoon environments often hold large numbers of fish that are potential predators to stomatopods. Stomatopods living in tidal flats may have limited time to actively forage and search for mates because fish predators will be abundant at high tides, while at low tides animals risk exposure and terrestrial predation. The unique selective pressures of this marine environment are ideal for the evolution of sit-and-wait predation and long-term social monogamy. They are not likely to be found often in terrestrial environments, though they may be similar to the conditions experienced by ambush predators of flying insects. The role of predation in the evolutionary origins of sit-and-wait predation and long-term social monogamy in stomatopod crustaceans is difficult to study, but ecological studies suggest that predation plays a role in the evolutionary maintenance of social monogamy at least one stomatopod species (Wright Chapter 2). The findings of this study therefore emphasize the importance of studying a diversity of taxa and environments when trying to understand the evolutionary origins of important behavioral traits such as predation style and mating systems.

WORKS CITED

- Ahyong, S. T. (2001). *Revision of the Australian stomatopod Crustacea*. Sydney: Australian Museum.
- Ahyong, S. T. (2006). Shallow water Stomatopoda of New Caledonia (0-100 m). *Compendium of Marine Species from New Caledonia. Documents Scientifiques et Techniques II*7, 291-293.
- Ahyong, S. T., & Harling, C. (2000). The phylogeny of the stomatopod Crustacea. *Australian Journal of Zoology*, 48(6), 607-642.
- Ahyong, S. T., & Jarman, S. N. (2009). Stomatopod interrelationships: preliminary results based on analysis of three molecular loci. *Arthropod Systematics & Phylogeny*, 67(1), 91-98.
- Alonzo, S. H. (2010). Social and coevolutionary feedbacks between mating and parental investment. *Trends in ecology & evolution*, 25(2), 99-108.
- Baeza, J. A., & Thiel, M. (2007). The mating system of symbiotic crustaceans. A conceptual model based on optimality and ecological constraints. *Evolutionary ecology of social and sexual systems. Crustaceans as model organisms*, 249-267.
- Baeza, J. A. (2008). Social monogamy in the shrimp *Pontonia margarita*, a symbiont of *Pinctada mazatlanica*, off the Pacific coast of Panama. *Marine Biology*, 153(3), 387-395.
- Baeza, J. A., Schubart, C. D., Zillner, P., Fuentes, S., & Bauer, R. T. (2009). Molecular phylogeny of shrimps from the genus *Lysmata* (Caridea: Hippolytidae): the evolutionary origins of protandric simultaneous hermaphroditism and social monogamy. *Biological Journal of the Linnean Society*, 96(2), 415-424.
- Baeza, J. A., Bolaños, J. A., Hernandez, J. E., Lira, C., & López, R. (2011). Monogamy does not last long in *Pontonia mexicana*, a symbiotic shrimp of the amber pen-shell *Pinna carnea* from the southeastern Caribbean Sea. *Journal of Experimental Marine Biology and Ecology*, 407(1), 41-47.
- Bateman, A.J. (1948). Intrasexual selection in *Drosophila*. *Heredity* 2, 349-368.
- Brotherton, P. N., & Komers, P. E. (2003). Mate guarding and the evolution of social monogamy in mammals. *Monogamy: mating strategies and partnerships in birds, humans and other mammals*. Cambridge University Press, Cambridge, 42-58.
- Brown, J. L., Morales, V., & Summers, K. (2010). A key ecological trait drove the evolution of biparental care and monogamy in an amphibian. *The American Naturalist*, 175(4), 436-446.
- Burley N.T. and K. Johnson. (2002). The evolution of avian parental care. *Philosophical Transactions of the Royal Society, Series B*. 357: 241 – 250.
- Caldwell, R. L. (1988). Interspecific interactions among selected intertidal stomatopods. *Behavioural adaptation to intertidal life*. Plenum Press, London-New York, 371-385.

- Caldwell, RL (1991). Variation in the reproductive behavior in stomatopod crustacea. In R.T. Bauer and JW Martin. Eds. *Crustacean sexual biology*. Pp. 67-90. Columbia University Press, New York.
- Caldwell, R. L., & Dingle, H. (1975). Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, 62(5), 214-222.
- Christy JH and Salmon M (1991). Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist*. 31: 329 -337.
- Correa C and Thiel M (2003). Mating systems in the caridean shrimp (Decapoda: Carida) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Rev. chil. Hist. nat.* 76: 187-203.
- Daly, M. (1978). The cost of mating. *The American Naturalist*, 112(986), 771-774.
- Detto T and Backwell P (2009). Social monogamy in a fiddler crab, *Uca Capricornis*. *Journal of Crustacean Biology*. 29: 283-289.
- Dingle, H., & Caldwell, R. L. (1978). Ecology and morphology of feeding and agonistic behavior in mudflat stomatopods (Squillidae). *The Biological Bulletin*, 155(1), 134-149.
- Duffy, J. E., & Macdonald, K. S. (2010). Kin structure, ecology and the evolution of social organization in shrimp: a comparative analysis. *Proceedings of the Royal Society B: Biological Sciences*, 277(1681), 575-584.
- Emlen, S.T. and Oring L.W. (1977). Ecology, Sexual Selection, and the Evolution of Mating Systems. *Science*. 19, 215-223.
- Felsenstein, J. (1978). Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Biology*, 27(4), 401-410.
- Grafen, A., & Ridley, M. (1983). A model of mate guarding. *Journal of Theoretical Biology*, 102(4), 549-567.
- Gowaty, P. A. (1996). Battles of the sexes and origins of monogamy. *Partnerships in Birds: The Study of Monogamy: The Study of Monogamy*, 21.
- Harmon, L., Weir, J., Brock, C., Glor, R., Challenger, W., & Hunt, G. (2009). GEIGER: analysis of evolutionary diversification. *R package version*, 1(1).
- Hernández, CE, Rodríguez-Serrano, E, Avaria-Llautureo, J, Inostroza-Michael, O, Morales-Pallero, B, Boric-Bargetto, D, Meade, A (2013). Using phylogenetic information and the comparative method to evaluate hypotheses in macroecology. *Methods in Ecology and Evolution*.
- Huey RB and ER Pianka (1981). Ecological consequences of foraging mode. *Ecology* 62: 991 – 999.

- Hughes, C. (1998). Integrating molecular techniques with field methods in studies of social behavior: a revolution results. *Ecology*, 79(2), 383-399.
- Huelsenbeck, J. P. (1997). Is the Felsenstein zone a fly trap?. *Systematic Biology*, 46(1), 69-74.
- Janetos AC (1982). Active Foragers vs. Sit-and-Wait Predators: A Simple model. *Journal of Theoretical Biology*. 95: 381.
- Jutte, P. A. (1997). *The ecology, behavior, and visual systems of Pullosquilla litoralis and P. thomassini, two monogamous species of stomatopod crustacean* (Doctoral dissertation, University of California, Berkeley).
- Kocataş, A. (1981). Two new stomatopod species for the Turkish fauna: Nannosquilloides occultus (Giesbrecht) and Meiosquilla desmaresti (Risso). *Crustaceana*, 40(2), 213-215.
- Lack, D. (1968). Ecological adaptations for breeding in birds. Methuen, London. P. 409.
- Li G, Ma J, Zhang L (2010) Greedy Selection of Species for Ancestral State Reconstruction on Phylogenies: Elimination Is Better than Insertion. PLoS ONE 5(2): e8985. doi:10.1371/journal.pone.0008985
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68(4), 619-640.
- Lindstrom, K. S. (2003). *Aspects of the Behavior, Population Genetics, and Phylogeny of Stomatopod Crustaceans* (Doctoral dissertation, University of California, Berkeley).
- Litsios, G., & Salamin, N. (2012). Effects of phylogenetic signal on ancestral state reconstruction. *Systematic biology*, 61(3), 533-538.
- Losos, J. B. (2011). Seeing the forest for the trees: the limitations of phylogenies in comparative biology. *The American Naturalist*, 177(6), 709-727.
- Maddison, W. P. and D.R. Maddison. (2011). Mesquite: a modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org>
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6(6), 183-186.
- Manning, R. B. (1966). Notes on some Australian and New Zealand stomatopod Crustacea, with an account of the species collected by the Fisheries Investigation Ship Endeavour. *Records of the Australian Museum*, 27(4), 79-137.
- Manning, R. B. (1968). A revision of the family Squillidae (Crustacea, Stomatopoda), with the description of eight new genera. *Bulletin of Marine Science*, 18(1), 105-142.
- Manning, R. B. (1977). A monograph of the West African stomatopod Crustacea. < i>Atlantide</i> Report. *Scientific Results of the Danish Expedition to the Coasts of Tropical West Africa 1945-1946*, 12.

- Manning, R. B. (1978). *New and rare stomatopod Crustacea from the Indo-West-Pacific region*. Smithsonian Institution Press.
- Manning, R. B., & Lewinsohn, C. (1986). *Notes on some stomatopod crustacea from the Sinai Peninsula, Red Sea*. Smithsonian Institution Press.
- Mathews, L. M. (2002a). Territorial cooperation and social monogamy: factors affecting intersexual behaviours in pair-living snapping shrimp. *Animal Behaviour*, 63(4), 767-777.
- Mathews, L. M. (2002b). Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)?. *Behavioral Ecology and Sociobiology*, 51(5), 426-432.
- Monaco, P., & Giannetti, A. (2002). Three-dimensional burrow systems and taphofacies in shallowing-upward parasequences, lower Jurassic carbonate platform (Calcarei Grigi, Southern Alps, Italy). *Facies*, 47(1), 57-82.
- Moosa, KM (2000). Marine Biodiversity of the South China Sea: A Checklist of Stomatopod Crustacea. *The Raffles Bulletin of Zoology*. 8: 405-457.
- Pagel, M. (1994). Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 255(1342), 37-45.
- Pagel, M. (1999). The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic biology*, 48(3), 612-622.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20(2), 289-290.
- Porter, M. L., Zhang, Y., Desai, S., Caldwell, R. L., & Cronin, T. W. (2010). Evolution of anatomical and physiological specialization in the compound eyes of stomatopod crustaceans. *The Journal of Experimental Biology*, 213(20), 3473-3486.
- R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reaka, M. L., & Manning, R. B. (1981). The behavior of stomatopod Crustacea, and its relationship to rates of evolution. *Journal of Crustacean Biology*, 309-327.
- Reaka, M. L. (1985). Interactions between fishes and motile benthic invertebrates on reefs: the significance of motility vs. defensive adaptations. In *Proc 5th Int Coral Reef Congr, Tahiti* (Vol. 5, pp. 439-444).
- Schram, F. R. (1969). *Some middle Pennsylvanian Hoplocarida (Crustacea) and their phylogenetic significance*. Field Museum of Natural History.
- Schram, F.R. and Müller, H.-G. (2004). Catalog and bibliography of the fossil and recent Stomatopoda. Backhuys Publishers: Leiden, The Netherlands.

- Schuster SM, Wade MJ (2003). Mating systems and strategies. Princeton (NJ): Princeton University Press.
- Steger, R. (1987). Effects of refuges and recruitment on gonodactylid stomatopods, a guild of mobile prey. *Ecology*, 1520-1533.
- Swofford, D. L. (2002). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Trivers, R.L. (1972). Parental investment and sexual selection. In B. Campbell, ed. *Sexual Selection and the Descent of Man 1871 – 1971*. pp. 139-179. Aldine, Chicago.
- Watling, L., Hof, C. H., & Schram, F. R. (2000). The place of the Hoplocarida in the malacostracan pantheon. *Journal of Crustacean Biology*, 1-11.
- Wickler W and Seibt U (1981). Monogamy in crustacea and man. *Zeitschrift fur Tierpsychologie*. 57: 215 – 234.
- Wittenberger JF, Tilson RL. (1980). The evolution of monogamy; hypotheses and evidence. *Annual Review of Ecological Systems*. 11: 197-232.

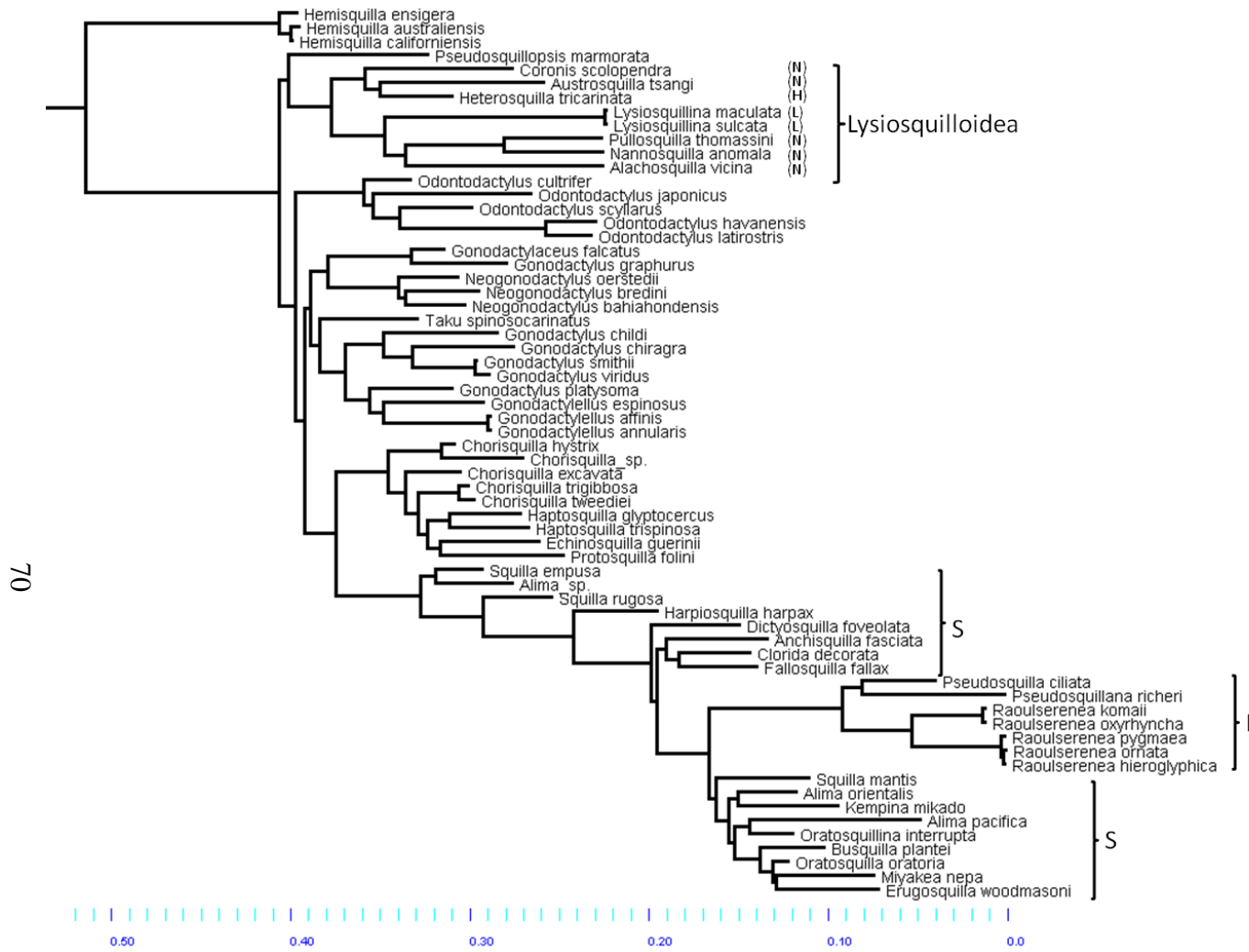


Figure 1. A maximum likelihood tree of 66 stomatopod crustaceans that was constructed from a concatenated matrix of 2589 genetic characters (12S, 16S, 18S, CO1) with the GTR+G+I model using Paup4.0b in *Geneious* (lnL = 189799.6.). Branch lengths represent nucleotide substitutions per site. The family affiliations of the Lysiosquilloids are indicated on the tree: Nannosquillidae (N), Lysiosquillidae (L), and Heterosquillidae (H). The Squilloidea (S) and Pseudosquillidae (P) are also indicated.

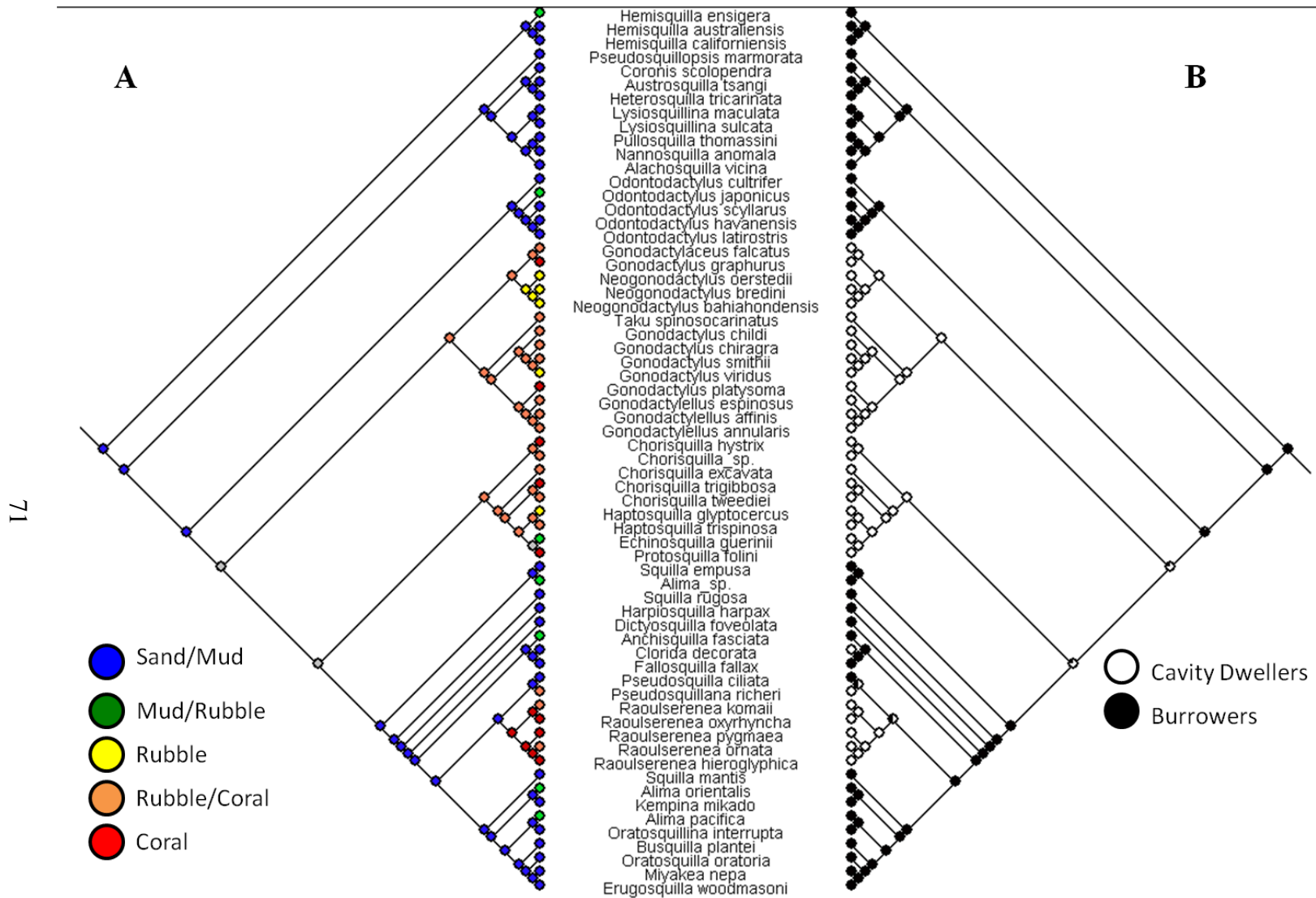


Figure 2. Ancestral reconstructions of A) habitat (Maximum Parsimony) and B) Burrowing/Cavity Dwelling (Maximum Likelihood, Mk1 model) on a tree of 48 stomatopod crustaceans in *Mesquite 2.75*.

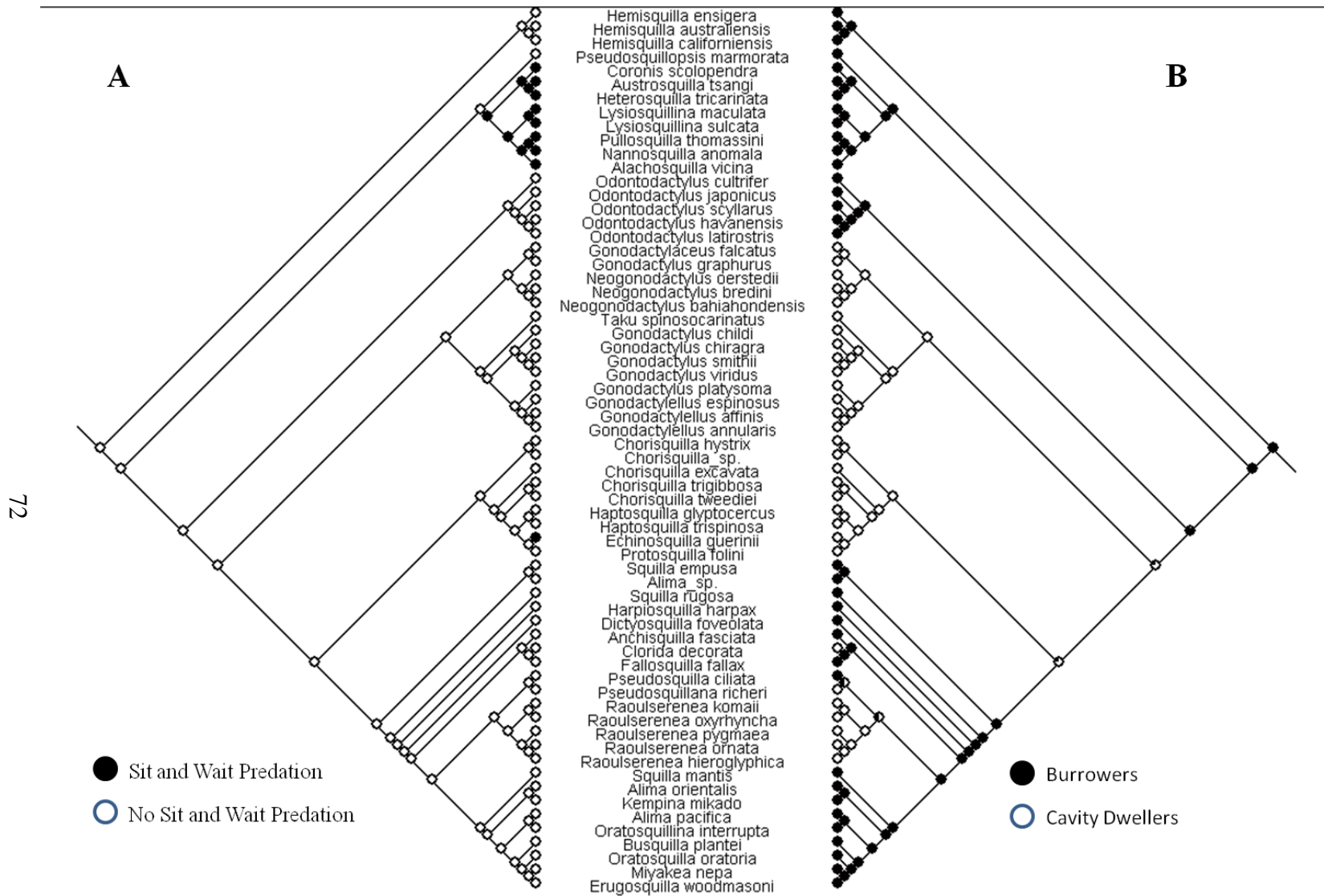


Figure 3. Ancestral reconstructions of A) Sit-and-wait Predation and B) Burrowing/Cavity Dwelling using Maximum Likelihood (Mk1 model) on a tree of 66 stomatopod crustaceans in *Mesquite 2.75*.

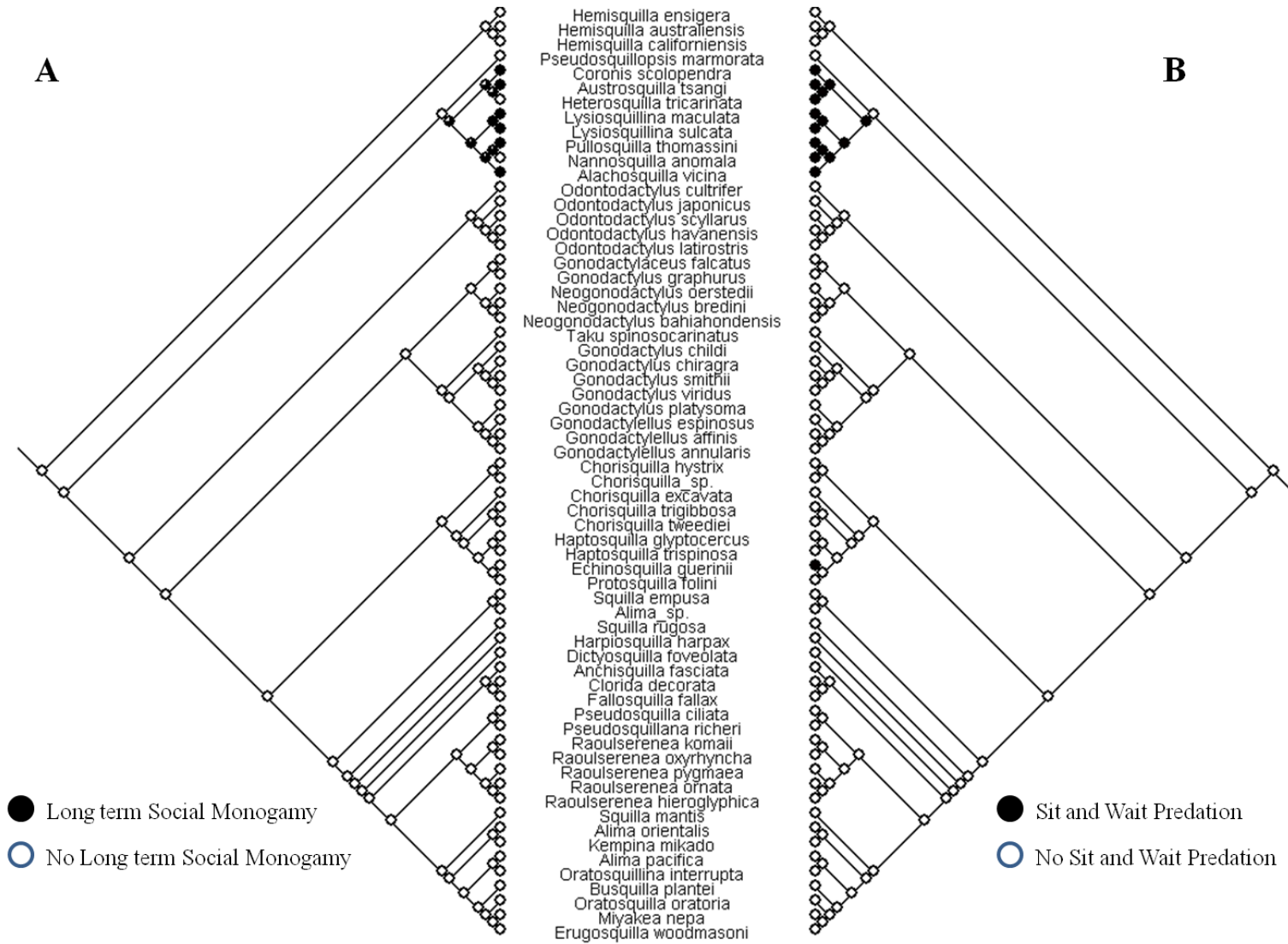


Figure 4. Ancestral reconstructions of A) Long-term Social Monogamy and B) Sit-and-wait Predation using Maximum Likelihood (Mk1 model) on a tree of 66 stomatopod crustaceans in *Mesquite 2.75*.

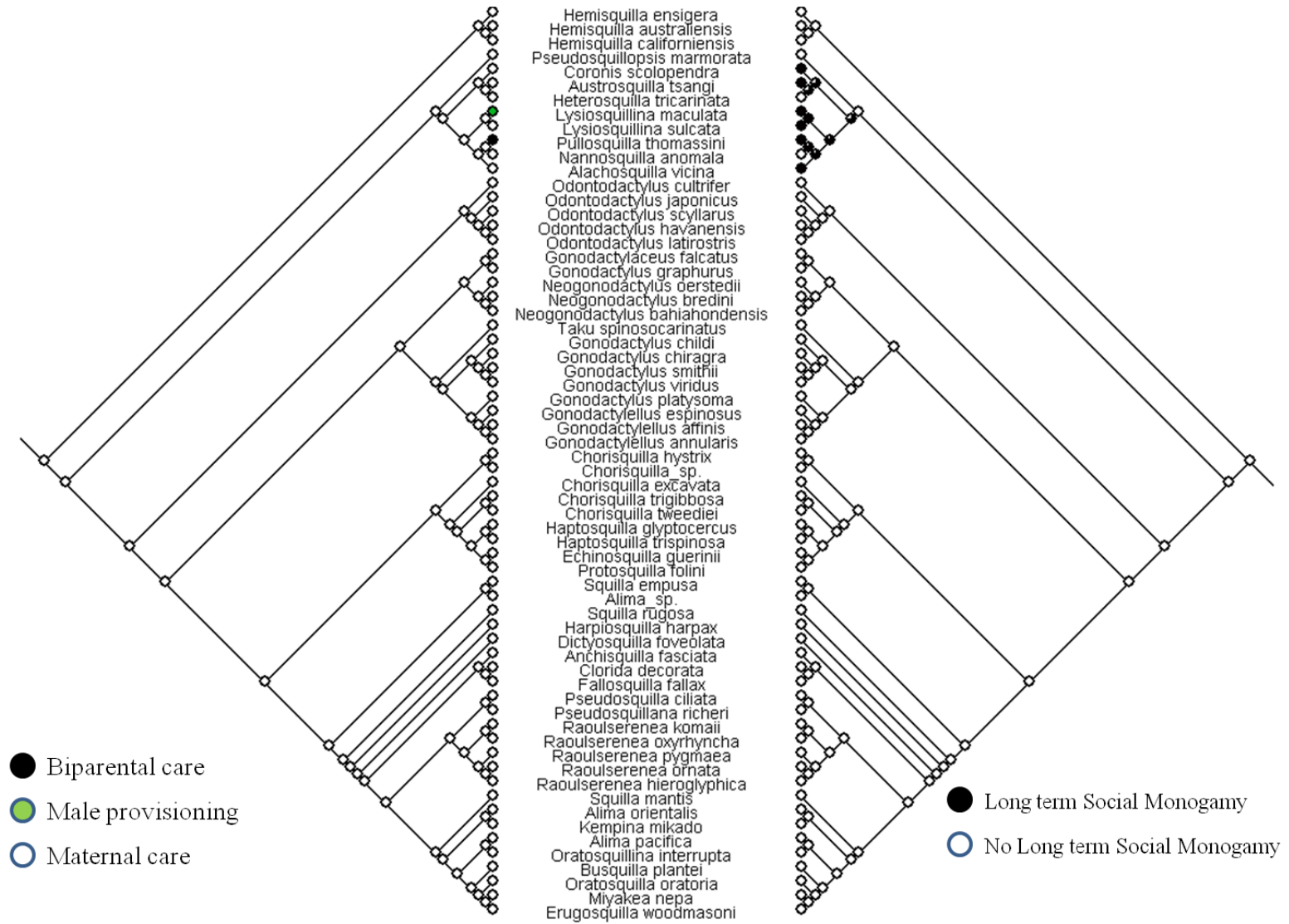


Figure 5. Ancestral reconstructions of A) parental care (Maximum Parsimony) and B) Long-term Social Monogamy (Maximum Likelihood, Mk1 model) on a tree of 66 stomatopod crustaceans in *Mesquite* 2.75.

Table 1. *Genbank* accession numbers of all taxa used to construct the ML phylogeny.

Species	12S	16S	18S	CO1
<i>Alachosquilla vicina</i>	AF107601	AF107608	HM138856	
<i>Alima orientalis</i>		HM138813	HM138857	HM138773
<i>Alima pacifica</i>		HM138814	HM138858	HM138774
<i>Alima sp.</i>	AF107604			
<i>Anchisquilla fasciata</i>		FJ224251		FJ229760
<i>Austrolsquilla tsangi</i>		FJ871139		
<i>Busquilla plantei</i>		HM138815	HM138859	HM138775
<i>Chorisquilla excavata</i>		HM138816	HM138860	HM138776
<i>Chorisquilla hystrix</i>		HM138817	HM138861	HM138777
<i>Chorisquilla trigibbosa</i>	AF107598	AF107609		
<i>Chorisquilla tweediei</i>		HM138818	HM138862	HM138778
<i>Clorida decorata</i>		FJ224254		FJ229763
<i>Coronis scolopendra</i>		HM138819	HM138863	HM138779
<i>Dictyosquilla foveolata</i>		FJ224256		FJ229765
<i>Echinosquilla guerinii</i>		HM138820	HM138864	HM138780
<i>Erugosquilla woodmasoni</i>		FJ224262		FJ229769
<i>Fallosquilla fallax</i>		HM138821	HM138865	HM138781
<i>Gonodactylaceus falcatus</i>		HM138827	HM138871	HM138786
<i>Gonodactylaceus graphurus</i>		AF133678		
<i>Gonodactylellus affinis</i>		HM138823	HM138867	
<i>Gonodactylellus annularis</i>		HM138824	HM138868	HM138783
<i>Gonodactylellus espinosus</i>		HM138822	HM138866	HM138782
<i>Gonodactylus childi</i>		HM138825	HM138869	HM138784
<i>Gonodactylus chiragra</i>	AF107594	AF107614	HM138870	HM138785
<i>Gonodactylus platysoma</i>		HM138828	HM138872	HM138787
<i>Gonodactylus smithii</i>	AF107595	AF107615	HM138873	HM138788
<i>Gonodactylus viridis</i>			AY743947	
<i>Haptosquilla glyptocercus</i>	AF107599	AF107610	HM138874	HM138789
<i>Haptosquilla trispinosa</i>		HM138831	HM138875	HM138790
<i>Harpiosquilla harpax</i>		FJ871137		FJ229772
<i>Hemisquilla australiensis</i>		FJ871141		
<i>Hemisquilla californiensis</i>		HM138832	HM138876	HM138791
<i>Hemisquilla ensigera</i>	AF107597	AF107616		
<i>Heterosquilla tricarinata</i>		FJ871140		
<i>Kempina mikado</i>		FJ871138	AF370802	HM138792
<i>Lysiosquillina maculata</i>	AF107603	AF107618	HM138878	HM138793
<i>Lysiosquillina sulcata</i>			HM138879	
<i>Miyakea nepa</i>		FJ224270		FJ229781

Table 1 continued. *Genbank* accession numbers of all taxa used to construct the ML phylogeny.

Species	12S	16S	18S	CO1
<i>Neogonodactylus bahiahondensis</i>		HM138836	HM138880	HM138794
<i>Neogonodactylus bredini</i>		HM138837	HM138881	HM138795
<i>Neogonodactylus oerstedii</i>	AF107596	AF107612	HM138882	HM138796
<i>Odonodactylus cultrifer</i>		HM138839	HM138883	
<i>Odonodactylus havanensis</i>		HM138840	HM138884	
<i>Odonodactylus japonicus</i>		FJ224282		FJ229798
<i>Odonodactylus latirostris</i>		HM138841	HM138885	HM138797
<i>Odonodactylus scyllarus</i>		HM138842	HM138886	HM138798
<i>Oratosquilla oratoria</i>	NC_014342	FJ224273		
<i>Oratosquillina interrupta</i>		FJ224281		FJ229796
<i>Protosquilla folini</i>		HM138843	HM138887	HM138799
<i>Pseudosquilla ciliata</i>	AY_947836	FJ871142	HM138888	HM138800
<i>Pseudosquillana richeri</i>		HM138846	HM138890	HM138802
<i>Pseudosquillopsis marmorata</i>		HM138845	HM138889	HM138801
<i>Pullosquilla thomassini</i>	AF107602	AF107611	HM138891	HM138803
<i>Raoulserenea hieroglyphica</i>		HM138848	HM138892	HM138805
<i>Raoulserenea komaii</i>		HM138849	HM138893	HM138804
<i>Raoulserenea ornata</i>		HM138850	HM138894	HM138806
<i>Raoulserenea oxyrhyncha</i>		HM138851	HM138895	HM138807
<i>Raoulserenea pygmaea</i>		HM138852	HM138896	HM138808
<i>Squilla empusa</i>	AF107605	AF107617	L81946	HM138809
<i>Squilla mantis</i>	AY639936	GQ328956	GQ328958	
<i>Squilla rugosa</i>		HM138854	HM138898	HM138810
<i>Taku spinosocarinatus</i>	AF107600	AF107613	HM138899	HM138811