

## COMPARISON OF MATING BEHAVIOR AND COPULATION IN MALE MORPHOTYPES OF THE SPIDER CRAB *LIBINIA SPINOSA* (BRACHYURA: MAJOIDEA: EPIALTIIDAE)

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### ABSTRACT

The mating behavior of the spider crab *Libinia spinosa* Milne Edwards 1834 was studied in the laboratory. Two male morphotypes as morphometrically immature (MI) with small chelae and morphometrically mature (MM) with large chelae were used in non competitive and competitive mating trials. The liberation of putative hormones by receptive females to attract males was studied. We examined whether male body or cheliped size influence mate acquisition and copulation. The liberation of putative hormones by receptive females could not be demonstrated because males did not behave differently among four treatments exposed to water from 1) ovigerous females, 2) non ovigerous females, 3) males, and 4) a control of water unexposed to crabs. Under non competitive and competitive scenarios, copulation occurred immediately after physical contact between partners, thus a contact pheromone could be involved. The copulatory behavior and the time of copulation were similar between both male morphotypes. In non-competitive mating trials, MI males copulated successfully with females, and immediately after the mating pairs decoupled. By contrast, MM males displayed a post-copulatory guarding behavior that consisted of holding the female with the major cheliped and carrying her around the aquarium. In a competitive scenario, MM males guarded females for several hours by either caging them within the legs, or holding them out of the water when MI males approached. MI males of larger sizes than MM males did not gain mates and avoided agonistic interactions with MM males; thus, large chelae size is a more decisive trait than large body size for mate acquisition.

KEY WORDS: Epialtidae, guarding, *Libinia*, mating behavior, morphotypes, spider crabs

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### INTRODUCTION

Brachyuran crabs exhibit complex mating strategies and differ widely in terms of the mode of male competition for receptive females. For a number of crab species with indeterminate growth, such as portunids and Cancrids, mating is linked to molting, when males defend mates just prior to ecdysis (Hartnoll, 1969); copulation is only possible for a limited time before the female's shell hardens (Salmon, 1983). Other species, such as varunids and multiparous majoids, intermolt hard-shelled mating occurs where the reproductive activity is not tied to the female's molt cycle (Hartnoll, 1969).

Spider crabs (Majoidea, sensu Ng et al., 2008) exhibit determinate growth where females reach a pubertal molt, and the morphological changes necessary for mating are produced with no subsequent molts occurring (Jones and Hartnoll, 1997). Consequently, only one mating event occurs for female majoids during the 'soft-shelled stage' and any subsequent mating occurs during the 'hard-shelled stage'. Studies on the reproductive behavior of majoids indicate that some species, *Inachus dorsettensis* (Pennant, 1777), *Libinia emarginata* Leach, 1815, *Libinia spinosa* Milne Edwards, 1834, and hymenosomatid crabs copulate predominately during the hard-shelled stage (Sagi et al., 1994; Jones

and Hartnoll, 1997; González-Gurriarán et al., 1998; van den Brink and McLay, 2009; Sal Moyano et al., 2010a). Other majoid species, *Chionoecetes opilio* (Fabricius, 1788), *Chionoecetes bairdi* Rathbun, 1893 and *Maja squinado* (Herbst, 1788), copulate in both hard and soft-shelled stages (Baal, 1953; Carlisle, 1957; Adams and Paul, 1983; Paul, 1984).

Pre- and post-copulatory mate guarding behaviors are generally non-compulsory, highly flexible, and influenced by socio-sexual factors (Rondeau and Sainte-Marie, 2001; Sainte-Marie et al., 2008). Such behaviors are particularly common in crustaceans; they enable males to secure females prior to and during the female's period of receptivity (Parker, 1974; Grafen and Ridley, 1983). Chemical signals are important in mate recognition and elicit mate guarding behaviors (Breithaupt and Thiel, 2011). In aquatic species, this type of courtship involves the release of pheromones by receptive females in combination with sensorial information (Gleeson et al., 1984; Dunham, 1988). The pheromones emitted by females (presumably from the ovaries) promote mate searching, courtship display, and pre-copulatory behavior in males (Hinsch, 1968; McCleese et al., 1977; Hooper, 1986; Cowan, 1991); and they exclude inseminated or ovigerous females from the mating advances of males.

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Male-male agonistic competition typically facilitates paternal success in brachyurans. Size differentiation in the chelipeds of male crabs is often related to morphological maturity, and their enlargement is a secondary sexual characteristic that likely facilitates mate embracing and mate guarding behaviors. Males that have undergone a pubertal molt are considered 'morphologically mature' (MM) and thus, are capable of breeding (Sampedro et al., 1999; Mura et al., 2005). For instance, Wirtz and Diesel (1983) demonstrate that larger male brachyurans generally out-compete smaller ones for mates. However, in several majoid species, 'morphologically immature' (MI) males that have not undergone a pubertal molt occasionally contain fully-formed spermatophores in the vas deferens (Beninger et al., 1988), and they are often successful in copulating with females (Moriyasu and Conan, 1988; Sagi et al., 1994; Sainte-Marie et al., 1997). Moreover, male crabs also compete by means of sperm competition when multiple mating occurs in females and sperm from numerous males vie for unfertilized eggs (Parker, 1970). Diesel (1991) divided the female brachyuran seminal receptacle into two morphological types: dorsal and ventral receptacles. Accordingly, the first or the last male to inseminate the female is believed to have an advantage in fertilizing the oocytes. Additional studies examining male sperm precedence (Urbani et al., 1998; van den Brink and McLay, 2009) also support the conclusions of Diesel (1991). Consequently, differing reproductive behaviors are displayed by males to facilitate paternity and to discourage other males from copulating with the female until fertilization occurs.

*Libinia spinosa* is a common spider crab in the southwestern Atlantic from Espirito Santo State, Brazil to Chubut Province, Argentina (Melo, 1996; Boschi, 2000). This species bears a ventral type seminal receptacle, and experimental studies indicate that female *L. spinosa* will mate with multiple males during a single reproductive period (Sal Moyano et al., 2010a). Physiological maturity in male

*L. spinosa* is indicated by the ability to produce spermatophores and it is acquired prior to morphometrical maturity (Sal Moyano et al., 2010b). Hence, physiological mature males could be considered MM when they possess enlarged chelae and MI males those bearing relatively small chelae (Fig. 1).

The purpose of the present study is to examine the mating behavior of *L. spinosa* under various experimental scenarios. Here we test if putative hormones released by females influence male mating behavior, we describe the mating behavior of both MI and MM male morphotypes under competitive and non competitive conditions, and we determine if body or cheliped size in males correspond with mate acquisition and copulation.

## MATERIALS AND METHODS

### Collection of Crabs and Basic Experimental Set-Up

A total of 154 *L. spinosa* were collected along the coast of Mar del Plata, Argentina (38°S, 57°33'W) in October 2007 (N = 43) and January 2009 (N = 111) by trawl nets towed by commercial fishermen at a depth of 5-20 m. Live crabs were immediately transported to the J. J. Nágera Coastal Station at the National University of Mar del Plata. Sexes were kept isolated in aerated communal seawater tanks (4 m<sup>3</sup>), under natural daylight conditions, during two weeks of acclimation. Crabs were fed squid twice a week and the water was changed weekly. Non-agonistic interactions were observed in the communal tanks and recorded. Individuals were measured with a caliper to determine morphological maturity and categorized as MM or MI following Sal Moyano et al. (2010b). Physiologically mature individuals were recognized by the development of mature ovaries or the presence of spermatophores (Sal Moyano et al., 2010b). Only physiologically mature females (CW > 40.2 mm) and males (CW > 33.6 mm) with an abraded hard-shell

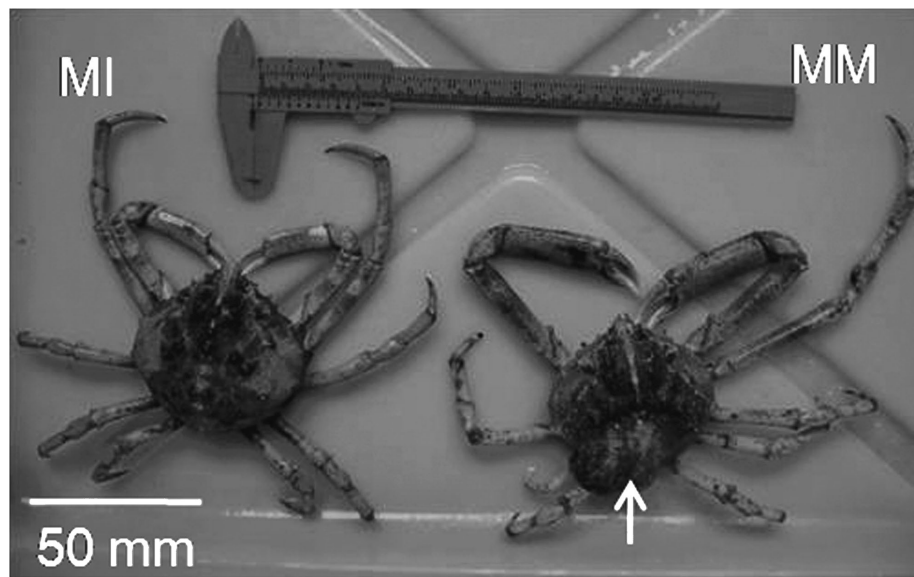


Fig. 1. Two different male morphotypes of *Libinia spinosa* exhibiting similar sizes of carapace width. The 'morphometrically immature' (MI) male has relatively small chelipeds and the 'morphometrically mature' (MM) male has enlarged chelipeds. Note that MM male has an anemone attached to its left-carapace side (arrow).

condition were used for the experiments. Experiments were conducted during the reproductive season from October 2007 to February 2008 and from January 2009 to March 2009, in aerated seawater plastic aquaria ( $0.4 \times 0.5 \times 0.2$  m). Behaviors were recorded with a Sony Cyber-shot camera. Three sets of experiments were conducted. Data were tested for normality for all three experiments and, as homogeneity of variances was not met; non-parametric tests were used in all cases (see below for each experiment).

#### Experiment 1: Male Behavioral Responses

Single “test” males were placed in different aquaria using filtered seawater that was previously exposed to a “treatment” crab under 4 treatments: 1) ovigerous females, 2) either mature, non-ovigerous or post-ovigerous females (with few or unfertilized eggs attached to the pleopods), 3) other males, and 4) a control sample of water unexposed to crabs. Following Jones and Hartnoll (1997), treatment crabs were individually placed in experimental aquaria for two or 24 hours, allowing for the buildup of pheromones presumed to be released in the urine. Afterwards, all treatment crabs were removed and a test male crab was randomly selected (MI or MM) and placed in each aquarium. It was acclimated for two minutes before behavioral observations were recorded. The bottom surface of each aquarium was divided into six equal-sized sections and the number of sections crossed by a test male was registered in order to quantify any response to potential chemical stimuli associated with treatment crabs-exposed water. Following Bouchard et al. (1996) behavior observations were recorded every 15 minutes. A minimum of 15 observations were carried out for each treatment, considering the number of sections crossed by each male as the dependant variable. A Kruskal-Wallis test was conducted in order to demonstrate that differences in time spent by the treatment crabs (two or 24 hours) among treatments 1-3 did not lead to greater concentrations of chemical signals and greater responses by the test crab. A posterior Kruskal-Wallis test was performed to analyze differences between the numbers of sections crossed within the four treatments for each male morphotype. A Mann-Whitney test was conducted to analyze the differences between the intensity of the activity of the two male morphs.

#### Experiment 2: Non Competitive Mating Trials

Untreated filtered seawater was used in this experiment. Thirteen MI (41-56.3 mm CW, mean = 48.6, SD  $\pm 4.6$ ) and 13 MM (64.7-80.9 mm CW, mean = 70.8, SD  $\pm 5.4$ ) males were individually placed in an experimental aquarium and then a randomly mature receptive female (ranging from 40 to 53.9 mm CW, mean = 46.7, SD  $\pm 3.9$ , for trials with MI males; and from 49.7 to 55.6 mm CW, mean = 52.9, SD  $\pm 1.8$ , for trials with MM males) was added. The mating behaviors were continuously monitored for two hours, described in detail, and the duration of copulation. Successful mating was considered to have occurred when both the female and male pleons were opened and the male gonopods inserted into the female gonopore (Sal Moyano et al., 2010a). The end of copulation was recognized when the mating pair separated. Successful post-copulatory mate guarding was considered to have occurred when the male retained the female with his chelae until the end of

the trial (two hours of observation). Differences between morphotypes in the duration of copulation were assessed by Mann-Whitney test. A Fisher's Exact Test was conducted for analyzing differences in the frequency of successful post-copulatory guarding behaviors displayed by both categories of males once copulation was recorded.

#### Experiment 3: Competitive Mating Trials

Twenty-one trials between MI (51.3-69.6 mm CW, mean = 59.5, SD  $\pm 6.9$ ) and MM (46.2-65.7 mm CW, mean = 55.6, SD  $\pm 7.1$ ) males were run using untreated filtered seawater. Each trial consisted of placing a single male of each morph in the experimental aquarium, using MI males of larger body size than MM males. After an acclimation period of 15 min, a randomly selected mature receptive female (43.5-54.7 mm CW, mean = 49.9, SD  $\pm 4.2$ ) was added. The mating behavior was recorded for two hours. We recorded agonistic interactions between males, the duration of copulations, the identity of the copulating male and the existence of a post-copulatory guarding behavior. A Binomial test was conducted to analyze differences between the proportions of each male morphotype that copulated successfully. A Mann-Whitney test was conducted to analyze differences in the duration of copulation between male morphs.

## RESULTS

#### Experiment 1: Male Behavioral Responses

The time spent by treatments crabs did not differ between treatments 1-3 (Kruskal-Wallis,  $H = 1.06$ ,  $p = 0.588$ ). There were no differences in response to the number of sections crossed by test males during the individual treatment types (1-4) for each morphotype (Kruskal-Wallis, MI males:  $H = 2.25$ ,  $p = 0.521$ ; MM males:  $H = 3.52$ ,  $p = 0.317$ ). Because there was no difference within a morphotype in the response to the four treatments, data corresponding to treatments 1-4 was pooled for each morphotype. There were differences in the number of overall sections crossed by MI and MM males: MI males crossed significantly more sections than MM males (Mann-Whitney,  $U = 147.5$ ,  $p < 0.05$ ; Fig. 2). Differences in behavior displayed by MI and MM males were observed. For instance, MI males were always in an erect, vertical position, with the rostrum facing upwards, chelae spread, and backed against the aquarium wall. The MI males were almost always active and rarely remained still during the experiment. By contrast, MM males stayed in a horizontal position, with the rostrum and chelipeds directed towards the center of the aquarium, exhibiting few movements. Antennae and maxilliped movements were registered in both male morphotypes.

#### Experiment 2: Non Competitive Mating Trials

Mating pairs were formed by both male morphotypes and copulation was recorded in all experimental aquaria. In all cases they showed a brief pre-copulatory behavior which occurred once the male and the female were introduced in the aquaria. Immediately after physical contact occurred between partners, the male grasped the female using his chelipeds, positioned rostrum-to-rostrum and maintained this for  $2.3 \pm 1.7$  min. They then assumed a sternum-to-sternum position and copulation was observed (Fig. 3).

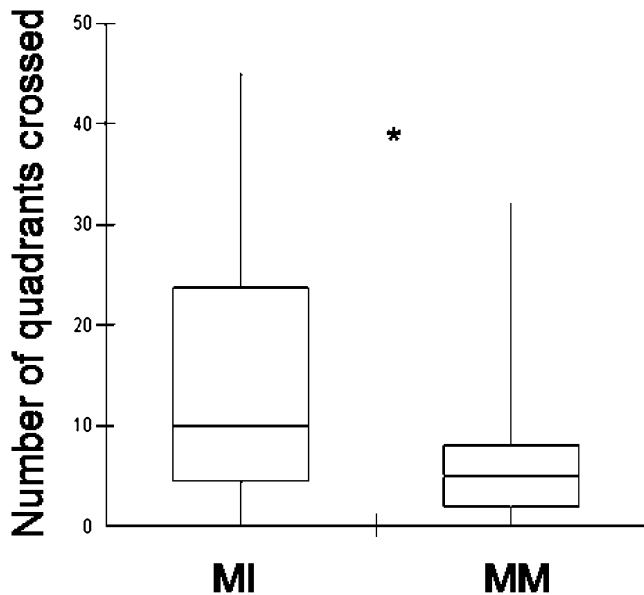


Fig. 2. Activity of different male categories. Number of quadrants crossed by morphometrically immature (MI) and mature (MM) males. Box plots are constructed with the limits of boxes being the 75th and 25th percentiles, lines inside the boxes are medians. \* Significant differences were encountered between the two categories of males (Mann-Whitney  $U = 147.5$ ,  $p < 0.05$ ).

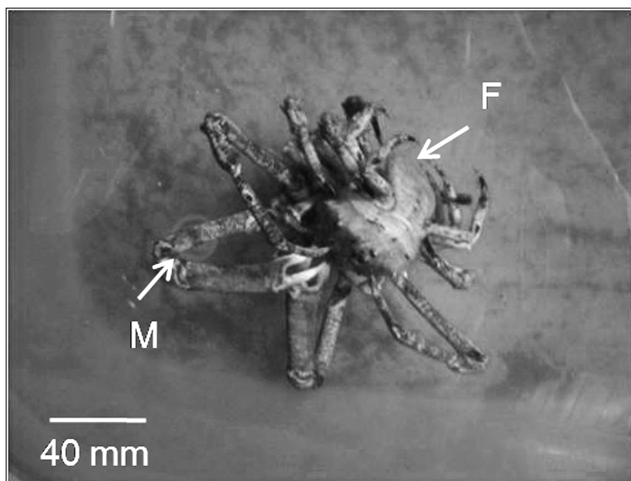


Fig. 3. Individuals during copulation showing the sternum-to-sternum position. The female (F) showing her pleon open (arrow), and the male (M) showing his chelae (arrow).

No significant differences were recorded in the copulating duration between MI ( $8.46 \pm 3.7$  min) and MM ( $6.76 \pm 4.5$  min) males (Mann-Whitney,  $U = 64$ ,  $p = 0.293$ ). When copulation ended, differences were noted in the frequency of post-copulatory guarding behaviors exhibited by MI and MM males (Fisher's Exact Test,  $p < 0.001$ ) (Fig. 4A). The majority of the mating pairs including MI males decoupled immediately after copulation, because either the female was successful in escaping, or males showed no interest in guarding them. By contrast, MM males exhibited post-copulatory mate guarding that consisted of holding the female with one cheliped and carrying her around the

aquarium, sometimes almost lifting her out of the water, and remaining in this position for several hours (Fig. 4B).

### Experiment 3: Competitive Mating Trials

In 5 out of 21 trials the MI male successfully copulated with the female while the MM remained quiescent. During the remaining trials, mating pairs always included MM males that successfully copulated with the introduced female. Thus, differences were observed between the proportions of both male morphs that copulated successfully (Binomial Test,  $Z = -3.39$ ,  $p < 0.001$ ). Encounters between males were only observed when the MI male was the first to approach and contact the female. In those cases, the MM male grasped the female while the MI male let go and no fighting between male morphs occurred. Copulating time between MI males ( $7.38 \pm 3.29$  min) and MM males ( $7.51 \pm 3.86$  min) showed no differences (Mann-Whitney,  $U = 38.5$ ,  $p = 0.901$ ). No post-copulatory guarding behavior was observed in the 5 mating pairs formed by MI males, while MM males showed the same post-copulatory guarding display described above which lasted several hours: MM males guarded females for several hours by caging them within the legs (Fig. 5) or by holding them out of the water when MI males approached.

### DISCUSSION

Several studies conducted on majoid crabs report the presence of polymorphism in males within the same population, relating these variations to differing mating strategies (Laufer and Ahl, 1995; Moriyasu and Comeau, 1996; Sainte-Marie et al., 1997). This study contributes to the general understanding of majoids mating strategies, providing the first descriptions of mating behavior of *L. spinosa* involving two distinct male morphotypes under non competitive and competitive experimental conditions. Additionally, we demonstrate that there are differences between the mating strategies of the male's morphs of *L. spinosa* in relation to their morphological condition (MI or MM chelae size).

A number of studies conducted in crustaceans and insects have indicated the importance of chemical signals during reproductive behavioral interactions (McCleese et al., 1977; Dunham, 1988; Chapman, 1998; Diaz and Thiel, 2004). Females in a number of crab species are recognized by males through the release of chemical pheromones that initiate pre-copulatory behaviors. The recognition of these pheromones by males is visible through an increase in the movements of the antennules and maxillipeds (Bouchard et al., 1996), or by increased locomotion (Jones and Hartnoll, 1997). Kamio et al. (2002) suggest that at least two types of pheromones may be involved in initiating mating behavior: a 'distance pheromone' that induces pre-copulatory guarding, and a 'contact pheromone' that induces copulation. In this study, no direct evidence was encountered indicating that females of *L. spinosa* release a pheromone due to males did not behave differently among treatments of experiment 1, but mating trials of experiments 2 and 3 showed that mate recognition after physical contact occurs between partners. Some authors suggested that instead of a distance pheromone, mating most likely involves a contact pheromone (Herborg et al., 2006). Different studies conducted on crustaceans sug-

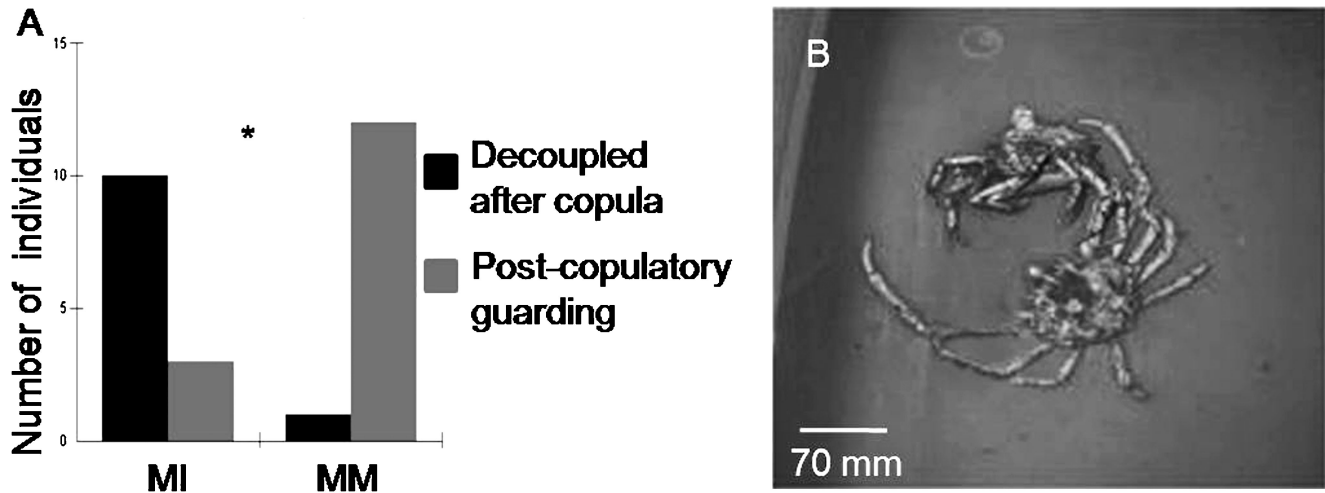


Fig. 4. A) Non-competitive mating trials. Number of morphometrically immature (MI) and mature (MM) males decoupled after copula or exhibiting a post-copulatory guarding behavior. \* Significant differences were encountered between the two categories of males (Fisher's Exact Test,  $p < 0.001$ ). B) Morphometrically mature male exhibiting a post-copulatory mate guarding that consisted of holding the female with one cheliped and carrying her around the aquarium, sometimes almost lifting her out of the water, and remaining in this position for several hours.

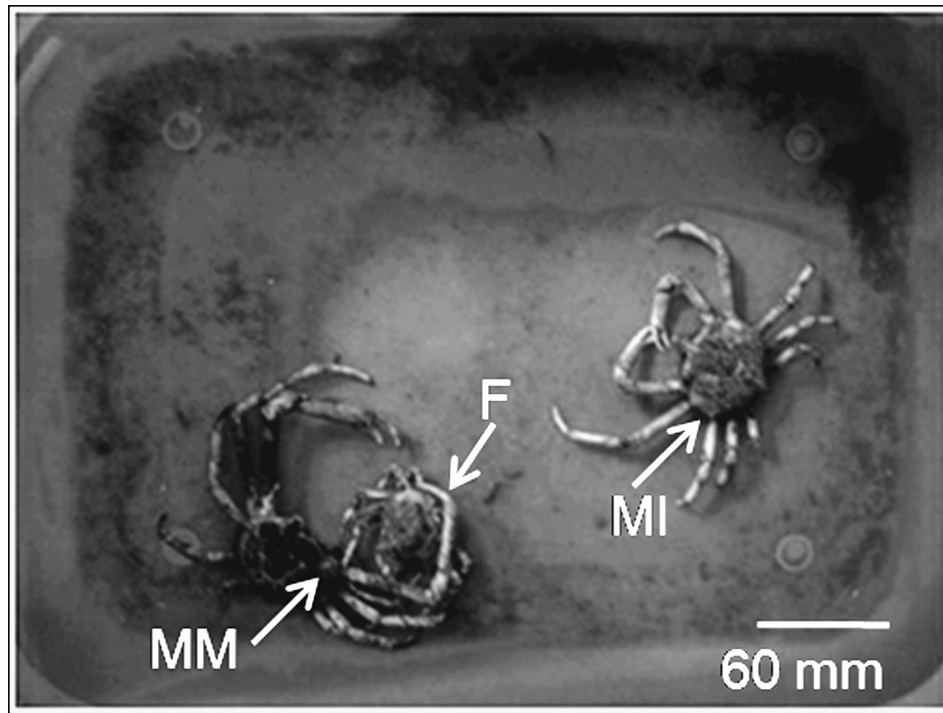


Fig. 5. Competitive mating trials. A morphometrically mature (MM) male showing a post-copulatory mate guarding, caging the female (F) within his legs, while the morphometrically immature (MI) male avoids interaction with the pair.

gested the existence of insoluble substances considered as “contact sex pheromones”, secreted through pore canals distributed all over the female cuticle, which are perceived by males during palpation through chemoreceptors located on their limbs (Borowsky, 1991; Caskey and Bauer, 2005).

The existence of different male morphotypes relative to their claw size in majoid populations has been documented in a number of species such as *L. emarginata* (Sagi et al., 1994; Laufer and Ahl, 1995), *C. opilio* (Elnor and Beninger, 1995), *M. squinado* (Sampedro et al., 1999), and *Anamathia*

*rissoana* (Roux, 1828) (Mura et al., 2005). For *C. opilio*, only large morphometrically mature males are functionally mature, apt to engage in a pre-copulatory embrace, and achieve copulation; while smaller males with undifferentiated chelae are functionally immature, do not demonstrate pre-copulatory sequences, but they bear spermatophores in the vas deferens (Conan and Comeau, 1986). However, studies conducted in other species demonstrated that both morphometrically immature and mature males have the capacity to copulate (Paul and Paul, 1990; Sainte-Marie and Lovrich,

1994), although they display contrasting behaviors (Sainte-Marie et al., 1997). In this study, we observed that *L. spinosa* MI males copulated successfully in both non competitive and competitive trials. In the last case, MI crabs could only mate with the receptive female when the MM male showed no interest in mating. Thus, since functional maturity should be defined as the ability of hard-shelled males to pass sperm and fertilize eggs (Elnor and Beninger, 1989; Sainte-Marie et al., 2008), the MI males of *L. spinosa* are functionally mature and able to copulate with females despite having not undergone a pubertal molt.

In the males of *L. emarginata*, the existence of polymorphism was associated with increased levels of methyl farnesoate in the hemolymph glands and large claws (Sagi et al., 1994; Laufer and Ahl, 1995; Rotllant et al., 2000). In this species, small-clawed males did not mate under competition circumstances, but did so when isolated with receptive females (Sagi et al., 1994). These authors observed small-clawed males, often the same size as females, being carried by large males, and exhibiting the same passive attitude as females (Sagi et al., 1994). These small males that ‘mimic’ females avoid aggressive behavior from the primary MM males and may be able to increase their mating opportunities by “sneak” mating (Laufer and Ahl, 1995). In our study, MI males were more active than MM males, moving continuously around the aquaria and contacting the females faster than adult males. It appears that different male morphotypes are responding differentially to reproductive activities and that increased activity displayed by MI males could represent an active strategy to locate females in the absence of MM males. Yet, while under competitive circumstances, the MI males avoid agonistic interactions and exhibit submissive behavior, suggesting that MI males are ‘mate-and-run’ breeders while MM males are ‘stand-and-defend’ breeders.

Sexual contests among males of different instars, size and body condition are clearly factors in male mating success (Rondeau and Sainte-Marie, 2001). Males exhibit agonistic behaviors when competing for females and, as a result, male size appears to be important for successful mating (Conan and Comeau, 1986; Moriyasu and Conan, 1988). Conan and Comeau (1986) suggest that large body size is a more decisive trait than large chelae size for mate acquisition in *C. opilio*, but Sainte-Marie et al. (1997) report that, in competitive mating situations, *C. opilio* with large chelae confer an advantage in mate acquisition than individuals with smaller chelae. Our results are similar to those of Sainte-Marie et al. (1997) due to MM males of smaller sizes than MI males gained females in competitive mating situations (experiment 3).

The copulatory behavior of *L. spinosa* is similar to other majoids, characterized by an approaching male that clasps the female and positions her in a rostrum to rostrum position. This is followed by a sternum-sternum position in which the pleons of both mating partners open and the male inserts the gonopods into the female’s gonopores (Watson, 1970; Laufer and Ahl, 1995; Bouchard et al., 1996; Jones and Hartnoll, 1997; González-Gurriarán et al., 1998). The post-copulatory guarding behavior exhibited by MM males of *L. spinosa* resembles a pre-copulatory behavior described by Hartnoll (1968) for *Corystes cassivelaunus* (Pennant, 1777).

Post-copulatory mate guarding in majoid crabs serves to ensure that the male has a higher probability of being the sole parent of the brood (Diesel, 1991), and it generally lasts until egg extrusion or until the female is unreceptive. González-Gurriarán et al. (1998) report the absence of any post-copulatory guarding in *M. squinado*, but other majoid species (*L. emarginata*, *I. dorsettensis*, *C. opilio*) engage in post-copulatory behavior (Laufer and Ahl, 1995; Jones and Hartnoll, 1997; Sainte-Marie et al., 1997). Both *L. emarginata* and *I. dorsettensis* exhibit differences in the post-copulatory behavior between MI and MM males. The former avoids it, while the latter always engages in post-copulatory guarding (Claxton et al., 1994). For *C. opilio*, mating behavior can be highly flexible, MM males engage in a pre-copulatory embrace, have long inseminations and show post-copulatory behavior ensuring paternity, while MI males show an abbreviated courting and pre-copulating guarding, brief inseminations and occasional post-copulatory guarding (Sainte-Marie et al., 2008). In *L. spinosa*, regarding the results obtained in non competitive mating trials of experiment 2, the consistent lack of mate guarding of MI males could be related to morphotype or size. Although, according to the similar results obtained in competitive mating trials of experiment 3, we concluded that this may be due to differences between morphotype not caused by size. Thus, under non competitive or competitive mating scenarios, the MI males of *L. spinosa* never showed post-copulatory guarding behavior, while MM males always displayed some. The absence of a post-copulatory behavior of the MI males could be explained by: 1) preference to avoid agonistic interactions with MM males, and/or 2) they cannot retain females for long time because of their small chelae. Sainte-Marie et al. (1997) encountered differences between the duration of copulation of the two types of males and proposed that small chelae males have brief but more frequent inseminations to increase the probability of gaining paternity of a brood. In our study, similar copulation duration between MM and MI males and the absence of multiple mating by a single male were observed, suggesting that paternity of the brood may only depend on the guarding behavior. Because of the presence of a ventral type seminal receptacle in the females of *L. spinosa*, last male sperm precedence by sperm displacement is likely (Sal Moyano et al., 2010a). Although MI males are not likely to gain paternity of female broods, they are encountered inside the population; thus, they are reproducing enough to maintain the polymorphism within the population. It is possible that, because MI males are more active, they encounter and fertilize more females than MM males. But, under competitive circumstances, MM males ensure their paternity through guarding behavior. Therefore it is possible that MI males pass their genes on to the overall population in the absence of MM males, the primary breeders. Their breeding behavior is sufficiently plastic to allow any male bearing spermatophores, independently of morphology and size, to take advantage of the reproductive opportunities (Elnor and Beninger, 1995). The critical size limit for successful mating seems to be flexible depending on the size structure of the male population (Ennis et al., 1990) and the density of large males in the population (Comeau et al., 1991). Thus, reproductive opportunities for each male type

vary according to long-term population cycles influencing inter-male competition levels (Elner and Beninger, 1995).

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