

Methyl Farnesoate Levels in Male Spider Crabs Exhibiting Active Reproductive Behavior

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The concentration of methyl farnesoate (MF) in the hemolymph and its synthesis by the mandibular organs (MOs) were investigated to determine whether this compound is related to the differences in the size of the reproductive system and the mating behavior among male morphotypes of the spider crab, *Libinia emarginata*. Large-claw abraded males displayed mating behavior under competitive conditions. They have the largest reproductive systems, their MOs synthesize large amounts of MF *in vitro*, and the concentration of MF in their hemolymph is high. Small-claw abraded males displayed mating behavior with receptive females only when isolated. These smaller crabs have intermediate-sized reproductive systems, their MOs synthesize the most MF, and they have the highest circulating level of MF relative to their body size. The unabraded males did not display mating behavior; their reproductive systems are smaller; their MO activity is low, as is their circulating level of MF. The strong relationship between MF levels and the intensity of reproductive behavior suggests that MF may be one of the driving forces behind mating behavior in Crustacea. © 1994 Academic Press, Inc.

In vertebrate reproduction, variations in reproductive system size, mating behavior, and sex hormone levels are closely related (Kelley, 1988; Moore, 1991). It has been well established that these hormones play an important role in the regulation of behavior in fish (Cardwell and Liley, 1991), amphibians (Moore, Wood, and Boyd, 1992), mammals (Nyby, Matochik, and Burfield, 1992) and birds (Wingfield, Ball, Dufty, Henger, and Ramenofsky, 1987). Similar relationships have been reported in some invertebrates, such as insects (Breed and Bell, 1983). However, in crustaceans our knowledge concerning the relationship between hormones and sexual behavior is quite limited. This study is concerned with the relationship existing between methyl farnesoate (MF), crustacean reproduction, and reproductive behavior.

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A secretory gland which may influence behavior in crustaceans is the mandibular organ (MO). This organ secretes MF, a compound which is the unepoxidated form of insect juvenile hormone III (Laufer, Sagi, and Ahl, 1987). Juvenile hormones have been most often associated with behavioral changes in adult insects, such as aggression and dominance (Breed and Bell, 1983). However, differences in mating behavior in most insects are also attributed to hemolymph levels of juvenile hormone (DeWilde, 1983; Denlinger, 1985), which controls development and the onset of reproduction. In addition, this hormone is associated with polymorphism in aphids, bees, and termites (Nijhout and Wheeler, 1982; Lees, 1983). In crustaceans, MF has been found in the hemolymph of both males and females in more than 20 species (Laufer *et al.*, 1987). It is not converted to Juvenile hormone by tissues, but is metabolized to farnesoic acid by esterase activity (Laufer and Albrecht, 1990). Thus, MF seems to be inactivated in a manner similar to that seen in insects. It was suggested by Laufer *et al.* (1986, 1987) that MF may be a reproductive hormone, similar to insect JH, because its synthesis is highest in vitellogenic females of the spider crab *Libinia emarginata*.

Variation in male morphology (morphotypes) within a population and the existence of different mating tactics are common in many animal species, particularly in those that are polygamous and in which male mating success varies (Gadgil, 1972). Male morphotypes that exhibit different reproductive behaviors have been described for several crustaceans, such as, the amphipod *Jassa falcata* (Borowsky, 1985), the freshwater prawn *Macrobrachium rosenbergii* (Ra'anani and Sagi, 1985), the isopod *Paracerceis sculpta* (Shuster, 1987), the snow crab *Chionoecetes opilio* (Conan and Comeau, 1986), the Tanner crab *C. bairdi* (Donaldson and Adams, 1989), and recently, the spider crab *L. emarginata* (Homola, Sagi, and Laufer, 1991; Sagi *et al.*, 1991a).

The existence of different mating tactics within crustacean populations has most commonly been explained from an ethological rather than a physiological perspective. This study takes a comparative approach to understanding the endocrinology related to reproductive behavior in male morphotypes of the spider crab *L. emarginata*, by examining whether, as in insects, the levels of the juvenoid MF are related to differences in reproductive behavior.

MATERIALS AND METHODS

Source of Animals

Libinia emarginata were collected off the coast south of Woods Hole, Massachusetts, during June and July. Selected male and female crabs were held indoors in the facilities of the Marine Biological Laboratory, Woods Hole, Massachusetts, in a 4500-liter concrete tank. Fresh seawater,

at ambient temperature (16–18°C), was continuously pumped into the tanks. The animal room was not a controlled light cycle, but was generally illuminated between the hours of 7 AM and 9 PM. The crabs were fed fresh or frozen squid *ad libitum* daily.

Male Types

Male types were identified according to the condition of the epicuticle covering of the exoskeleton, and the size of their claws relative to the length of the carapace. The measurements were made with vernier calipers according to Homola *et al.* (1991).

Behavioral Observations and Behavioral Assays

A population of approximately 100 animals was placed in the holding tank. After 2 weeks of acclimation the population was observed daily for reproductive behavior for an hour in the morning, an hour at midday and an hour in the evening for a period of 3 weeks. Females that were observed mating, being carried by males, or releasing larvae in the tank, were removed for use in the behavioral assay. Since these females attract males, they were termed receptive. Males selected for the assay were categorized into six groups based upon the ratio of the propodus length to the carapace length, and the appearance of their exoskeleton according to Homola *et al.* (1991). Those with worn epicuticle were termed abraded, those with intact epicuticle were termed unabraded. The abraded and unabraded morphs were illustrated previously (Homola *et al.*, 1992; Sagi *et al.*, 1993).

For the behavioral assay, a receptive female was placed in a shallow observation tank (45 cm × 70 cm × 10 cm) supplied with fresh circulating seawater. A male was placed on the table with her, and they were observed for 15 min. The general cascade of mating behavior included the following patterns: male approaching female, male grasping female, ventral to ventral contact between male and female, sperm transfer, male carries female, male abandons female. The time recorded was from the introduction of the male into the tank up to the time in which ventral to ventral contact was observed.

The Reproductive System of Selected Male Types

The body weight and individual tissues (testes, sperm duct and accessory glands) were weighed to the nearest 0.01 g. The reproductive system index was calculated by dividing the sum of the components of the reproductive system by the body weight and multiplying by 100. A sample of semen from the sperm duct of each crab was examined under a light microscope for the presence of spermatophores.

Methyl Farnesoate Synthesis by the Mandibular Organs

Following each behavioral assay, the males were placed on ice to anesthetize them prior to dissection. After 20 min, the paired mandibular

TABLE 1
Comparison of the Male Morphotypes of *Libinia emarginata* with Respect to the Lengths of the Carapace (CL) and the Claw (Propodus) (PL), and Their Ratios (CL/PL)

Type	(N)	Carapace length (mm)	Propodus length (mm)	ratio (CL/PL)
LLA	8	71.1 ± 4.3	77.2 ± 9.5	1.09
LLI	8	69.1 ± 3.8	69.2 ± 9.7	1.00
LLU	8	72.4 ± 7.9	77.4 ± 14.0	1.07
LSU	7	67.3 ± 4.0	49.7 ± 6.5	0.74
SSA	9	41.9 ± 2.4	24.6 ± 2.1	0.59
SSU	8	43.2 ± 1.5	25.1 ± 2.4	0.58

Note. LLA, large-claw abraded; SSA, small-claw abraded; LLI, large-claw incompletely abraded; LLU, large-claw unabraded; LSU, large carapace with small claw unabraded; SSU, small-claw unabraded.

organs from each male were dissected attached to the mandibular tendon as described in Homola *et al.* (1991). They were incubated for 2 hours in culture medium containing [³H]-methyl methionine. Following incubation, isotope incorporation was determined using liquid scintillation spectrometry of a 100- μ l sample of a hexane extract of the glands and medium. DPM were converted to ng MF according to Freifelder (1982).

Methyl Farnesoate Levels in the Hemolymph

Prior to dissection, hemolymph samples (2 ml) were taken from the base of one or more of the walking legs. The samples were transferred to 15-ml glass tubes, containing ice-cold acetonitrile (5 ml) and 4% NaCl (2 ml). An aliquot (35 ng) of *cis-trans* MF, a non-biological isomer, was added to each tube as an internal standard (Sagi *et al.*, 1991). The samples were extracted with 1 ml hexane. Hemolymph titers of MF were determined, using HPLC, according to Homola *et al.* (1991).

RESULTS

Male Morphotypes

Characteristics of the six morphotypes are summarized in Table 1. Abraded animals had bare exoskeletons because the epicuticle had been worn away. Unabraded males appear to be covered with fuzz due to the pubescent nature of the intact epicuticle. The large abraded, large incompletely abraded and large unabraded large-claw crabs are in the same size class (claw length to carapace ratio of 1 or more), but they differ in appearance with respect to the condition of their epicuticles. We estimate that the abrasion of the epicuticle takes anywhere from 9 to 12 months from the last molt. The carapace of the large males with small claws is similar in size to the large-clawed males, but their claws are generally

TABLE 2
Responses of Different Male Types of the Spider Crab, *Libinia emarginata*, to Receptive Females without Competition from Other Males

Type	(N)	Time to mating	Male mating behavior
LLA	8	4.2 ± 2.9	Mates, carries female
SSA	8	8.0 ± 2.6	Mates, abandons female
LLI	8	4.9 ± 2.6	Mates, abandons female
LLU	7		Did not mate
LSU	9		Did not mate
SSU	8		Did not mate

Note. LLA, large-claw abraded; SSA, small-claw abraded; LLI, large-claw incompletely abraded; LLU, large-claw unabraded; LSU, large carapace with small claw unabraded; SSU, small-claw unabraded.

shorter than their carapace length (the claw to carapace ratio is less than 1). The small abraded males are about the same size as the females (carapace length 40–55 mm), and they generally have short claws. The small unabraded males are an unabraded version of the small abraded males. All the male types had sperm in their reproductive systems.

Behavior of Male Morphotypes

The large abraded males with large claws were the only type that were observed mating and carrying females in the holding tank. When a receptive female was present, these abraded males would fight aggressively for possession. A dominant male would then carry the female with his fifth pair of walking legs and vigorously guard her from the grasp of other males with opened claws that were extended in a threatening posture. After mating, he continued to carry the female until she released a new clutch of fertilized eggs into the brood pouch. It is less than 24 hr in *Libinia* from the time that larvae hatch and are released to the time the females deposit another clutch of eggs to be brooded attached to her abdominal pleopods. It took a large abraded male 4.2 ± 2.9 min to approach and initiate mating with a receptive female (Table 2) in a non-competitive test trial.

The large incompletely abraded males and the small abraded males did not mate in the holding tank under conditions of intense competition from large-clawed large abraded males, but did so when isolated with a receptive female within 4.9 ± 2.6 and 8.0 ± 2.6 min, respectively (Table 2). Since small abraded males are often the same size as females and are usually passive, they have been observed being carried by large abraded males when receptive females were present in the tank.

None of the unabraded males, either large or small, attempted mating in the holding tank, nor when isolated with receptive females.

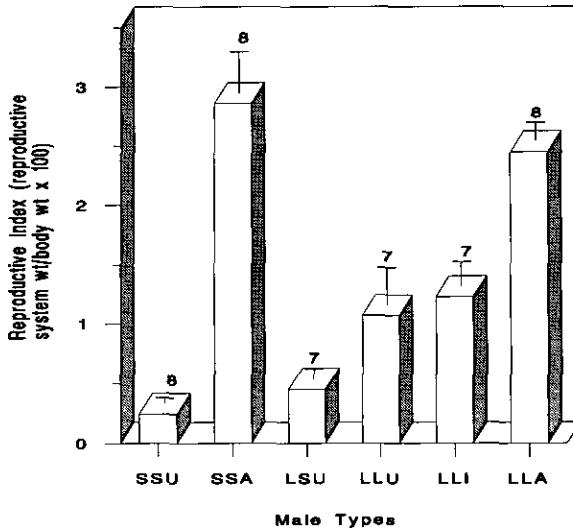


Fig. 1. Reproductive indices (reproductive system wt/body wt \times 100) of male morphotypes of *Libinia emarginata*. SSU, small-claw unabraded; SSA, small-claw abraded; LSU, large-carapace unabraded small-claw; LLU, large-claw unabraded; LLI, large-claw incompletely abraded; LLA, large-claw abraded.

Alternative Mating Tactic of Small Male

On one occasion, we observed and recorded on video tape an alternative mating tactic performed by a small abraded male: A small receptive female was placed in the observation tank containing the following number and types of males: three large-claw abraded, two large-claw unabraded, two incompletely abraded, and a small abraded. The female wandered around the tank for about a minute without stimulating a response from any of the males. After the males "sensed" the presence of a receptive female, as indicated by increased movements of their maxillapeds, they began searching behavior. When any of the males contacted another individual it would immediately grasp and hold it. A small male was grasped by a large-claw abraded male, which then tucked him underneath his body and passed him to the fifth pair of walking legs and proceeded to carry him as though he were a female. This large male then defended the small male that he was carrying, by backing away from a challenging male with his claws held up and extended. The small male was being held in such a way that he could also walk and was facing in the direction that they were both moving. The pair moved in this manner across the tank and stopped near the female. The small abraded male contacted the female, then grasped her. The large male that was holding the small male made no attempt to release the small male, nor did he try to grasp the female. However, the large male continued to defend the small male from other

abraded crabs. The small male then placed the female on her back for mating, while the large abraded male stood on his dactyls, hovering over the couple, and continued to defend them. After the small male had the female in the mating position for sperm transfer, the large male reached underneath, and grabbed the chela of the small male. He then pulled the couple partially out from underneath himself, pried the small male away from the female, and cast him away. The large male continued to hold and hover over the female for a few minutes, then mated with her, and continued to carry her.

Reproductive System Indices in Male Morphotypes

The male morphotypes differed in the relative development of their reproductive systems as revealed by their reproductive indices (Fig. 1). Both the large and the small abraded males have large reproductive indices (2.45 ± 0.16 , and 2.86 ± 0.35 , respectively). The large incompletely abraded males with large-claws, and large-claw unabraded males had intermediate indices (1.23 ± 0.21 , and 1.07 ± 0.32 , respectively). The small-clawed unabraded males with either large or small carapaces have the smallest indices (0.24 ± 0.05 , and 0.45 ± 0.08 , respectively).

MF Synthesis

The mandibular organs (MOs) from the large abraded males synthesized the most MF *in vitro* per hour than any of the other morphotypes ($52.1 \pm 2.1 \times 10^3$ DPM MF/gland/hr) (Fig. 2). The amounts of MF synthesized by the MOs from the large-clawed incompletely-abraded, large-clawed unabraded, large unabraded small-clawed, and small abraded males were intermediate to that of the large-clawed abraded crabs ($19.01 \pm 7.6 \times 10^3$, $29.7 \pm 10.3 \times 10^3$, $29.4 \pm 9.4 \times 10^3$, and $21.2 \pm 7.3 \times 10^3$ DPM/gland/hr, respectively). MOs from the small-clawed unabraded males synthesized the least amount of MF ($7.5 \pm 0.37 \times 10^3$ DPM/gland/hr). Converting MO activity in DPMs to ng of MF synthesized, and normalizing the results to body size (MO activity in ng/hr/g body wt) reveals a different picture (Fig. 2). MOs from the small-clawed abraded males had the highest synthetic activity (3.67 ± 0.08 ng/hr/g body wt); the second most active group, the large-clawed abraded males, is significantly lower ($P \leq 0.01$) (1.48 ± 0.02 ng/hr/g body wt). However, this activity was not significantly different from the small-clawed unabraded males (1.32 ng/hr/g body wt) or the large unabraded small-clawed males (1.08 ng/hr/g body wt). The lowest normalized synthesis was found in the large-clawed unabraded and the large-clawed incompletely-abraded animals (0.74 ± 0.01 and 0.53 ± 0.01 ng/hr/g body wt, respectively).

MF Levels in the Hemolymph

The concentration of MF in the hemolymph was greatest in the small-clawed abraded males (62.4 ± 16.3 ng/ml) and the large-clawed abraded

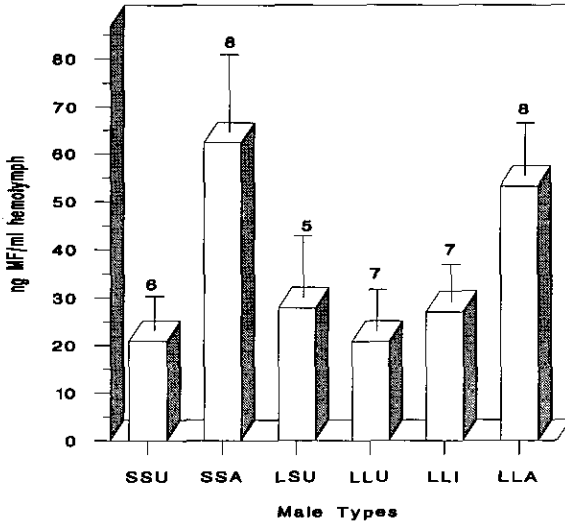


Fig. 2. Methyl farnesoate hemolymph titers (ng/ml) in male morphotypes of *Libinia emarginata*. SSU, small-claw unabraded; SSA, small-claw abraded; LSU, large-carapace unabraded small-claw; LLU, large-claw unabraded; LLI, large-claw incompletely abraded; LLA, large-claw abraded.

males (53.2 ± 11.2 ng/ml), both of which were significantly greater ($P \leq 0.01$) than any of the other morphotypes (Fig. 3) that were unabraded (20.8 ± 8.8 ng/ml– 27.9 ± 12.8 ng/ml) or partially abraded (27.1 ± 7.7 ng/ml).

DISCUSSION

The first account of polymorphism in male spider crabs was presented by Hartnoll (1963), which was based solely on the shape and length of the claw. Homola *et al.* (1991) have described differences in size and weight of the reproductive system, morphological features of the carapace and MF levels between different morphs of the spider crab *L. emarginata*. Our results suggest that there are different types of reproductive behavior, which belong to morphologically distinguishable individuals. These fall into one of three patterns of mating behavior.

The male types that mate are both of the abraded morphs, and the large-clawed incompletely abraded one. The primary reproductives are the large abraded males, with high circulating and synthetic rates of MF. The incompletely abraded males retreat from the more competitive abraded males. However, they successfully display mating behavior, if isolated from the aggressive males. This male type has MF synthetic rates and titers that are significantly smaller than the reproductively dominant large-clawed abraded individuals.

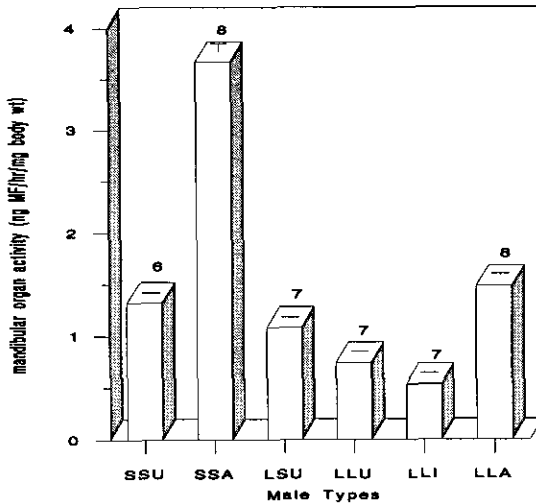


FIG. 3. Methyl farnesoate synthesis normalized to body weight (ng/hr/body wt \times 100) of male morphotypes of *Libinia emarginata*. SSU, small-claw unabraded; SSA, small-claw abraded; LSU, large-carapace unabraded small-claw; LLU, large-claw unabraded; LLI, large-claw incompletely abraded; LLA, large-claw abraded.

The small-clawed abraded morphotype exhibits the same behavior patterns as the large-clawed abraded males when they are competing with similar-sized males, but will not compete with the large dominant ones. Rather, in the presence of the large abraded males, the small abraded type "mimics" females by being passive, which may result in their being carried and guarded by the larger males. Occasionally, these small males may employ an alternative tactic, and mate when the large abraded males are "distracted". This type of behavior has also been described in two other species of crustaceans: the small-claw form of the freshwater prawn *M. rosenbergii* (Ra'anana and Sagi, 1985) and the gamma male of the isopod *P. sculpta* (Shuster, 1987), as well as in many insect species (Alcock and Gwynne, 1991).

Unabraded males appear to be reproductively inactive. This also fits with the fact that the unabraded males are the most recently molted and therefore more likely to be using energy for muscle growth to fill in the new carapace. The low levels of MF in their hemolymph and low synthesis rates by their mandibular organs may suggest that they are in a state of reproductive diapause (Laufer *et al.*, 1992). In insects this condition is due to JH deficiency (Denlinger, 1985). In the unabraded male crabs, the reproductive diapause may be a period of time during which more energy is directed towards growth, either somatic or gonadal, rather than reproduction. This is best illustrated in crustaceans by the fast growing orange-claw form of the freshwater prawn *M. rosenbergii* which almost never

attempts to mate in competition with dominant males, and in which the testes are undergoing active spermatogenesis and enlargement (Sagi *et al.*, 1988).

This study shows a strong relationship between the synthesis rate of MF, its circulating concentration and reproductive behavior. The highest synthetic rates and concentrations in the blood were found in crabs that displayed the most active mating behavior. There are several ways to understand such relationships: MF may affect the level of mating behavior displayed directly, or indirectly through morphotypic differentiation. On the other hand, social interactions between dominant abraded males and subordinate unabraded males may be responsible for the differences found in the levels of MF. The subordinate males may have lower levels of MF due to stress that is induced by exposure to the aggressive behavior displayed by the dominant males. In this case, the MF titers are the outcome of the process and not the cause. However, the female mimicry of small abraded males, as evidenced by their being carried like females, reduces the aggressive behavior towards them by the primary reproductives (Wendelken and Barth, 1985). One possible outcome of this may be the high concentrations of MF found in their blood. A third possibility is that levels of MF and reproductive behavior are parallel processes with no link. Arguing against this latter possibility is the evidence provided by Hinsch (1980) who showed that MO implants into immature female *L. emarginata* stimulated ovarian growth.

The structural similarity of MF and juvenile hormone (JH) suggests a relationship between juvenoids and mating behavior in crustaceans similar to that which is observed in insects. In reproductive insects, JH is actively synthesized and released from the corpus allatum. However, removal of this gland from mature males can result in the cessation of reproductive behavior in some species, such as the desert locust *Schistocerca gregaria* (Pener 1965; Pener, 1967), and the red locust *Nomadacrid septemfasciata* (Pener, 1968). The same effect can be achieved chemically by topical application of precocene II, which interferes with JH synthesis by the corpora allata. This effect can be reversed or prevented by treating the locust with JH (Walker, 1978). Our interpretation of the results of the study presented here is that MF, which has been suggested to be a gonadotropin in Crustacea in several recent studies (Laufer *et al.*, 1987; Homola *et al.*, 1991; Soroka *et al.*, 1993), also appears to affect reproductive behavior. However, only direct experimentation involving mandibular organ replacement or methyl farnesoate administration may establish a cause and effect relationship between methyl farnesoate and reproductive behavior.

ACKNOWLEDGMENTS

We thank Dr. F. Maury of the University of Connecticut Biotechnology Center, and for use of the center's HPLC facilities. We also thank A. Barki for numerous discussions. This

work was supported in part from the Sea Grant College Program, and a Fellowship of the Lady Davis Trust to H.L.; a Fulbright Scholarship, and a Binational Agricultural Research Development Foundation Fellowship to A.S. J.S.B.A. gratefully acknowledges the College of Basic Studies, University of Hartford for research stipends and release time.

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