

## Alternate mating strategies of polymorphic males of *Libinia emarginata* appear to depend on methyl farnesoate

HANS LAUFER<sup>1</sup>, AMIR SAGI<sup>2</sup> and JONNA S.B. AHL<sup>3</sup>

<sup>1</sup>*Department of Molecular and Cell Biology, University of Connecticut, Storrs, CT 06268; Marine Biological Laboratory, Woods Hole, MA 02543, USA*

<sup>2</sup>*Department of Life Sciences, Ben Gurion University of the Negev, Beer Sheva 84105, Israel*

<sup>3</sup>*New Mexico Highlands University, Las Vegas, NM 87701, USA*

Received 22 March 1993; Accepted 9 December, 1993

### Summary

The spider crab *Libinia emarginata* has six male morphotypes that differ with respect to their appearance and reproductive readiness. Large abraded males compete actively for females and have the largest claws and reproductive system indices and highest methyl farnesoate (MF) blood levels. Smaller abraded males with short claws attempt mating in the absence of large abraded males but employ the alternative tactics of sneak mating and female mimicry when large aggressive males are present. Unabraded morphs of any size do not attempt to mate, either in competition or in isolation with receptive females. Their MF levels are lower (usually one-half that of abraded males) indicating that they are in a state of reproductive diapause. Incompletely abraded males have intermediate levels of MF and are moderately active in reproduction. These data suggest that MF may be involved in directing the reproductive behavior of different male morphotypes.

---

### MINI-REVIEW

Alternate mating strategies are commonly found in polygamous populations with polymorphic males that have variable mating success (Gadgil, 1972). These strategies have been explained mostly from an ethological perspective based upon the physical differences of the morphotypes and less from the standpoint of their physiology. An exception to this

is seen in insects where differences in mating behavior and polymorphism have been attributed to hormone levels in the blood (DeWilde, 1983; Denlinger, 1985; Hardie and Lees, 1985).

The development of the reproductive system in insects and mating behavior is controlled by juvenile hormone (JH). This substance is actively synthesized

and released from the corpus allatum in reproductive animals (DeWilde, 1983). In some species the adults live long enough to participate in several breeding seasons. During the non-breeding season, their JH titers decrease concomitant with gonadal regression and cessation of mating behavior and enter a state of reproductive diapause.

In Crustacea male morphotypes exhibiting different patterns of mating behavior have been described for several decapod species 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 the spider crab *Libinia emarginata* (Laufer et al., 1992). Of these species, hormone levels of male morphotypes have been described only in *L. emarginata* (Homola et al., 1991; Laufer et al., 1992).

Crustaceans produce a compound that is similar in structure to the insect JH. This compound, methyl farnesoate (MF), is synthesized by the mandibular organs (MO) and appears to have a similar role in reproduction (Laufer et al., 1986, 1987). For example, it is found in *L. emarginata* males that have the largest reproductive systems (Homola et al., 1991; Laufer et al., 1992) and in females that are vitellogenic (Laufer et al., 1986, 1987). That the MO affects reproduction in a causal relationship was suggested by Hinsch (1986), who transplanted active MOs into juvenile females which resulted in growth and maturation of the ovaries. In this paper we report that MF levels in the blood vary according to the reproductive state as portrayed by behavior in male *L. emarginata*.

Male spider crabs (Majidae) exhibit marked polymorphism regarding claw (propodus) length (PL) relative to carapace length (CL) (Hartnoll, 1963; Aldrich, 1974; Homola et al., 1991). In the common east coast spider crab *L. emarginata*, several morphotypes have been described which consider the condition of the exoskeleton as well (Sagi et al., 1991): large-bodied (60–80 mm CL) males with large claws (longer than the CL) have either pubescent (unabraded), bare (abraded), or incompletely abraded exoskeletons; large-bodied unabraded males with small claws (less than the CL); and small-bodied (<60 mm CL), both abraded and unabraded, males with small claws. The abrasion process, which appears to take about 1 year, is the wearing away of the epicuticle covering the exoskeleton. The large-

claw males with either exoskeletal condition are presumed to have undergone a terminal molt and are anecdytic (Hinsch, 1972; Homola et al., 1991). The other morphs have at least one more molt (such as the small-claw male with the large carapace) or several more if they have small carapaces. All of the morphotypes  $\geq 19$  mm CL have sperm in their vas deferens (Homola et al., 1991) and, therefore, may be considered to be sexually mature (Hinsch, 1969).

The morphotypes of *L. emarginata* that actively mate, whether in competition with other males or in isolation with a receptive female, are either abraded or are in the process of becoming abraded. The large abraded males have the largest reproductive indices (Table 1) (reproductive system wt/body wt  $\times 100$ ) ( $2.39 \pm 0.43$ ) (Homola et al., 1991) and highest MF levels ( $67 \pm 16.6$  ng/ml) (Sagi et al., 1993), and are the primary reproductive animals (Homola et al., 1991). The small abraded males also have high MF levels ( $62.4 \pm 5.9$  ng/ml) (Sagi et al., in press) and large reproductive indices ( $2.86 \pm 0.35$ ), but attempt copulation in the absence of the larger males (unpublished observations) or resort to alternative tactics such as sneak mating and female mimicry (Sagi et al., in press).

Small abraded males are often the same size as the females (30–55 mm CL), and in the presence of large abraded males they are very passive, which is similar to female behavior. Occasionally, in captivity, small males have been observed being carried by large-claw abraded males when a receptive female was present in the tank. During one such observation (unpublished), a small male that was being carried grasped a receptive female, then commenced copulation. Males which resemble females in appearance due to their small size avoid aggressive behavior from the primary reproductives, as evidenced by their being carried like a female, and may be able to increase their mating opportunities by "sneak" mating (Wendelken and Barth, 1985).

The large incompletely abraded males have reproductive indices ( $1.23 \pm 0.21$ ) (Sagi et al., in press) and MF blood levels ( $27.1 \pm 8.1$  ng/ml) (Sagi et al., in press) that are intermediate to those of the large-claw abraded males and are in the process of becoming competitive breeders both physiologically and behaviorally. They are less competitive than the large abraded males but actively pursue females in the absence of dominant reproductives. That the exoskeleton is incompletely abraded suggests to us that these crabs are experiencing their first mating season since undergoing the final molt, which took

Table 1. Size and reproductive system characteristics of male morphotypes of the spider crab *Libinia emarginata* in relation to MF levels

Type	Carapace length (mm)	Propodus length (mm)	Reproductive system index (% body weight)	MF blood level (ng/ml)
Large-claw abraded	60–80	70–100	2.39 ± 0.43 <sup>a</sup>	67.0 ± 16.6 <sup>b</sup>
Large-claw incompletely abraded	60–80	70–100	0.58 ± 0.22 <sup>a</sup>	29.0 ± 7.1 <sup>b</sup>
Large-claw unabraded	60–80	70–100	1.23 ± 0.21 <sup>c</sup>	27.0 ± 8.1 <sup>c</sup>
Large carapace with small claw unabraded	50–60	25–60	0.27 ± 0.32 <sup>a</sup>	9.9 ± 5.6 <sup>a</sup>
Small-claw abraded	36–45	15–25	2.86 ± 0.35 <sup>c</sup>	62.4 ± 16.3 <sup>c</sup>
Small-claw unabraded	36–45	15–25	0.27 ± 0.09 <sup>a</sup>	10.7 ± 6.0 <sup>b</sup>

<sup>a</sup>Homola et al., 1991; <sup>b</sup>Sagi et al., 1993; <sup>c</sup>Sagi et al., in press.

place some time during the previous autumn. This also suggests that perhaps prior experience contributes to the mating success of the completely abraded males, which are most likely at least to be in their second mating season.

The lack of mating behavior of the unabraded males, together with their small gonad indices (0.27–0.58) and low MF hemolymph levels (9.9–29 ng/ml) can be regarded as their being in a state of reproductive diapause according to comparable information derived from insects. Although it could be argued that the small unabraded males are reproductively inactive because they are immature, it is important to emphasize that they have sperm present in their reproductive tracts, which indicates sexual maturity of one sort. However, these crabs have not yet undergone their terminal molt, so in essence they are still growing. If in spider crabs mating is delayed so that energy can be invested in growth, resulting in a larger body and claw size that ultimately enhances mating success (Sagi et al., 1988), then it is logical that mating is not attempted by small unabraded males even though sperm have been produced. The large unabraded males, on the other hand, have reached their maximal size externally; but their internal organs, especially those in the reproductive system, are probably about the same size they were prior to the terminal molt. So, once again, energy is used for growth at this stage to build up the reproductive system prior to the commencement of the energetically expensive effort of competing for females and mating.

Methyl farnesoate, similar to JH, may be responsible for the type of reproductive behavior displayed by male morphotypes in the spider crab. The large-

claw abraded males with high levels of MF are the primary reproductives. The small-claw abraded males, also exhibiting high MF levels, are secondary reproductives, while the recently molted unabraded males with lower MF levels do not mate and appear to be in reproductive diapause. However, the exact mechanism by which MF works requires further elucidation.

#### Acknowledgements

We would like to thank David Dodge and the staff of the New England Utilities Environmental Laboratory at Millstone Power Plant for the collection of *Libinia emarginata*. We also thank Dr. F. Maury of the University of Connecticut Biotechnology Center for technical advice and for use of the center's HPLC facilities.

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

#### References

- Aldrich, J.C., Allometric studies on energy relationships in the spider crab *Libinia emarginata* (Leach). *Biol. Bull.*, 147 (1974) 257–273.
- Borowsky, B., Differences in reproductive behavior between two male morphs of the amphipod crustacean *Jassa falcata* Montagu. *Physiol. Zool.*, 58 (1985) 497–502.

- Conan, G.Y. and Comeau, M., Functional maturity and terminal molt of the male Snow crab, *Chionoecetes opilio*. Can. J. Aquat. Sci., 43 (1986) 1710-1719.
- Denlinger, D.L., Hormonal control of diapause. In: G.A. Kerkut and L.I. Gilbert (eds.), Comparative Insect Physiology, Biochemistry, and Pharmacology, Vol. 8, Endocrinology II. Pergamon Press, New York, 1985, pp. 353-412.
- DeWilde, J., Endocrine aspects of diapause in the adult stage. In: R.G.H. Downer and H. Laufer (eds.), Invertebrate Endocrinology, Vol. 1, Endocrinology of Insects. Liss, New York, 1983, pp. 357-368.
- Donaldson, W.E. and Adams, A.E., Ethogram of behavior with emphasis on mating for the Tanner crab *Chionoecetes bairdi* Rathbun. J. Crust. Biol., 9 (1989) 37-53.
- Gadgil, M., Male dimorphism as a consequence of sexual selection. Amer. Natur., 106 (1972) 574-580.
- Hardie, J. and Lees, A.D., Endocrine control of polymorphism and polyphenism. In: G.A. Kerkut and L.I. Gilbert (eds.), Comparative Insect Physiology, Biochemistry, and Pharmacology, Vol. 8, Endocrinology II. Pergamon Press, New York, 1985, pp. 441-490.
- Hartnoll, R.G., The biology of the Manx spider crabs. Proc. Zool. Soc. London, 141 (1963) 432-496.
- Hinsch, G.W., Microtubules in the sperm of the spider crab, *Libinia emarginata* L. J. Ultrastruct. Res., 29 (1969) 525-534.
- Hinsch, G.W., Some factors controlling reproduction in the spider crab *Libinia emarginata*. Biol. Bull., 143 (1972) 358-366.
- Hinsch, G.W., Effect of mandibular organ implants upon the spider crab ovary. Trans. Am. Micros. Soc., 99 (1986) 317-322.
- Homola, E., Sagi, A. and Laufer, H., Relationship of claw form and exoskeleton condition to reproductive system size and methyl farnesoate in the male spider crab, *Libinia emarginata*. Invert. Reprod. Develop., 20 (1991) 219-225.
- Laufer, H., Borst, D., Baker, F.C., Carrasco, C., Sinkus, M., Reuter, C.C., Tsai, L.W. and Schooley, D.S., Identification of a juvenile hormone-like compound in a crustacean. Science, 235 (1987) 202-205.
- Laufer, H., Landau, M., Borst, D. and Homola, E., The synthesis and regulation of methyl farnesoate, a new juvenile hormone for crustacean reproduction. In: M. Porchet, J.C. Andries and A. Dhainaut (eds.), Advances in Invertebrate Reproduction, Vol. 4. Elsevier Science, Amsterdam, 1986, pp. 135-143.
- Laufer, H., Sagi, A. and Ahl, J.S.B., Juvenile hormone-like compounds in Crustacea and their implications for reproductive behavior. In: B. Bennettova, I. Gelbic and T. Soldan (eds.), Advances in Regulation of Insect Reproduction, Institute of Entomology, Czech Academy of Science, 1992, pp. 153-155.
- Ra'anana, Z. and Sagi, A., Alternative mating strategies in male morphotypes of the freshwater prawn *Macrobrachium rosenbergii* (deMan). Biol. Bull., 196 (1985) 592-601.
- Sagi, A., Ahl, J., Danaee, H. and Laufer, H., Methyl farnesoate and reproductive behavior in male morphotypes of the spider crab *Libinia emarginata*. Am. Zool., 31 (1991) 87A.
- Sagi, A., Ahl, J.S.B., Danaee, H. and Laufer, H., Methyl farnesoate levels in male spider crabs exhibiting active reproductive behavior. Horm. Behav., in press.
- Sagi, A., Homola, E. and Laufer, H., Distinctive reproductive types of male spider crabs *Libinia emarginata* differ in circulating and synthesizing methyl farnesoate. Biol. Bull., 185 (1993) 168-173.
- Sagi, A., Milner, Y. and Cohen, D., Spermatogenesis and sperm storage in the testes of the behaviorally distinctive male morphotypes of *Macrobrachium rosenbergii* (Decapoda, Palaemonidae). Biol. Bull., 174 (1988) 330-336.
- Shuster, S.M., Alternative reproductive behaviors: three discrete male morphs in *Paracerceis sculpta*, an intertidal isopod from the northern Gulf of California. J. Crust. Biol., 7 (1987) 318-327.
- Wendelken, P.W. and Barth, R.H. Jr., On the significance of pseudofemale behavior in the neotropical cockroach genera of *Blaberus*, *Archimandrita*, and *Byrsotria*. Psyche, 92 (1985) 493-504.