Precopulatory Mate Guarding, Mating System and Pairing Parental Care in *Hyale rubra* (Peracarida; Amphipoda; Gammaridae)

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**ABSTRACT:** Mating behaviour of the gammarid amphipod, *Hyale rubra*, was observed. *H. rubra* displayed precopulatory mate guarding: males clasped females with their gnathopods during copulation, forming a pair. Males also participated in embryo care during the incubation period. The population was small, and the sex ratio was almost equal. Energy allocation for mating effort and parental effort in the two sexes appear to be almost equal. The mating system was sequentially polygamous (or promiscuous) and there was conspicuous sexual dimorphism in the size of the gnathopod, which was used for mate guarding. However, there appears to be relatively weak sexual competition for mating opportunities despite conspicuous sexual dimorphism. *H. rubra* did not display territorial competition or external fertilization. Nevertheless, the male provided paternal care. Since *H. rubra* inhabit tide pools and live on algae, the polygamous mating system of the species can be explained by the polygyny threshold model. The evolution of mate guarding and parental care may have been favored by the species’ low population density and harsh environments, an interpretation consistent with the optimality model.

**Key words:** Mate guarding, Mating system, Parental care

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**INTRODUCTION**

Gammarids are common amphipods living in the bottom of the ocean or intertidal areas (Ruppert and Barnes 1991). *Hyale rubra* inhabits tide pools with algae around intertidal areas. Gammarid amphipods are known to perform precopulatory mate guarding, which is thought to lead to more successful fertilization. In some gammarids, the female is clasped by the male's gnathopods during copulation so the two individuals form a pair. To copulate, the male of most gammarid amphipods twists his abdomen so that his uropods touch the female’s marsupium near the ventilating current of the female. Then the pair separates and eggs are released into the brood chamber, where fertilization takes place (Ruppert and Barnes 1991, Borowsky 1991).

After copulation, most gammarid amphipods display female care for their broods (Dick et al. 1998, Thiel 1999). Preemergence care, first identified in *Crangonyx pseudogracilis*, involves brood ventilation, egg cycling, and ejection of nonviable eggs (Dick et al. 1998). Such preemergence brood care activities are related to environmental conditions; maternal care is a characteristic of amphipods in harsh environments (Dick et al. 1998).

Littoral rock pools are harsh environments for amphipods at ebb tide (Ganning 1971, Trucot and Duhamel-Jouve 1980, Morris and Taylor 1983). Amphipods living in rock tide pools have been reported to provide maternal care for the embryos during the incubation period to promote brood survival in the harsh environments (Dick et al. 1998, Dick et al. 2002). Dick et al. (1998) described patterns of brood care in response to internal and external cues for *C. pseudogracilis* and then investigated components of putative active brood care in *Apherusa jurinei* with respect to developmental and environmental cues. The objective of the current study is to describe the pattern of precopulatory mate guarding behavior and parental care and to analyze the factors affecting male parental behavior in *Hyale rubra*.

**MATERIALS AND METHODS**

*H. rubra* were collected with a dipnet (1 mm mesh size) during ebb tide in algae-filled tide pools on Dongback island, South Korea (35° 10' N, 129° 03' E). Some samples were fixed in a 5% formaldehyde solution and preserved in 70% alcohol, while other live amphipods were carried to the laboratory. The live amphipods were maintained in aerated jars (15 × 15 cm) at 12°C, dissolved oxygen (5mg/L) and 32~33 psu salinity, the conditions under which the specimens were caught. The mating behavior of each pair was constantly observed from the time of capture. Parental care was photographed and recorded using a camcorder throughout the incubation
period of the female. The population abundance, pattern of sexual dimorphism, sex ratio, and reproductive characters were analyzed. Sexual dimorphism in color, total length, and size of gnathopod (propodus and dactylus length) was determined. Sex was determined by the presence (female) and absence (male) of oostegite and embryos. The number of eggs produced by each female was counted, and egg size was measured under the microscope. Egg development was classified into three different stages: immature, intermediate, and mature.

Two experiments were conducted to examine mate guarding behavior and parental care. The experiments were divided into 5 treatments to observe how each sex selects a partner for mating and to determine whether they change partners during mating. Unmated individuals were put together in 500 mL glass jars as follows: one female with one male, two females with two males, several females with several males, partner exchange (female and male that had formed a pair were artificially separated and then the male was replaced with a different male), and one female only.

Juveniles produced in each experimental treatment' one female with one male, two females with two males, several females with several males, a male replacement treatment, and one female only, were also collected in jars. Additional experiments were repeated under different sets of conditions to determine how variation in environmental factors such as dissolved oxygen concentration affects embryo development and hatchability.

RESULTS

Abundance and Sex Ratio

*H. rubra* was distributed in tide pools with plentiful macroalgae. The populations were small in size and the sex ratio was almost equal during the sampling period from February to June (Figs. 1 and 2).

Sexual Dimorphism

Sexual dimorphism in size and color was substantial. Males were larger than females in length (mean male length: 11.49 mm, mean female length: 8.92 mm) and were mostly green in color, while females were brown. Male gnathopods were much larger and stronger than those of females (Fig. 3).

Precopulatory Mate Guarding and Mating System

Precopulatory mate guarding behavior was observed in *H. rubra*, and it occurred prior to pair formation, the third stage of mating in amphipods. Males usually searched for females and contacted females to check whether females were ready for copulation. When a male recognized a fertile female, it started to guard the female utilizing