

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

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 (5 mg/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

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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 macro algae. 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

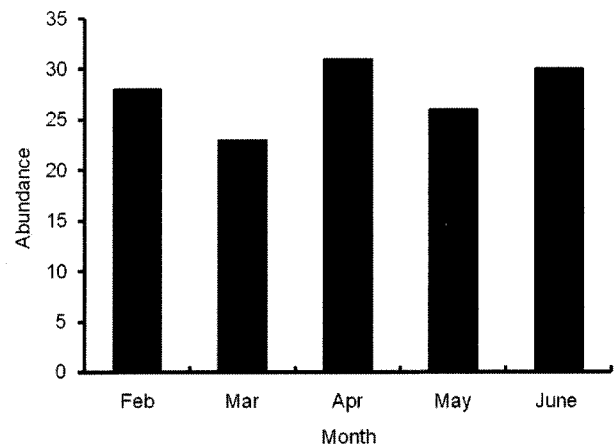


Fig. 1. Abundance of *Hyale rubra*.

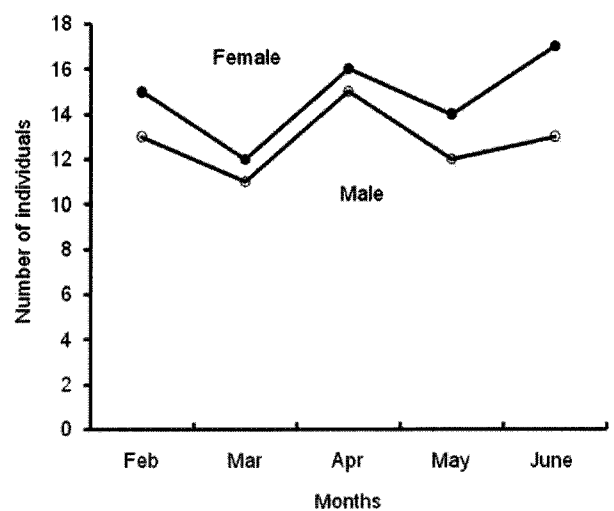


Fig. 2. Sex ratio of *Hyale rubra*.

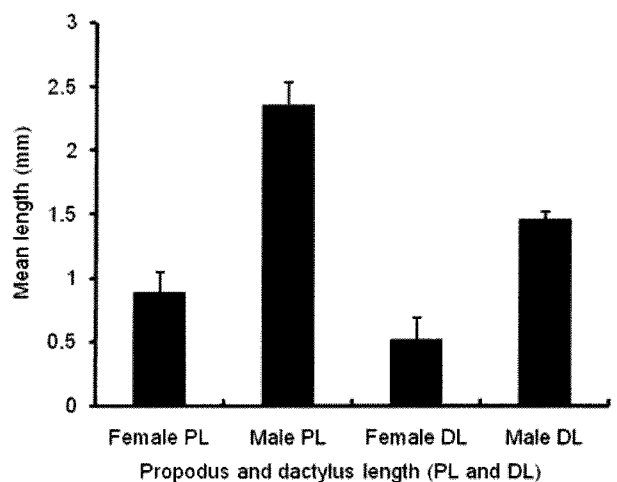


Fig. 3. Sexual dimorphism of propodus and dactylus length of the gnathopod.

its gnathopods, and then attached himself to her to become a pair. After pairing, they occasionally moved around together in a guarding position. The mating system of this species may be sequentially polygamous. Males often formed pair bonds with several different females in turn; each such pair bond only lasted long enough to complete the copulation. In the laboratory experiments, once a pair bond was formed, the females never exchanged males when another male was added to the jar with the pair. However, when the male from a paired couple was separated from the female during the mate guarding stage and a new male was introduced, the female formed a new pair bond with the replacement male.

Parental Care

Females ventilated their broods with their pleopods, a common behavior for gammarid amphipod species with uniparental female care. However, in this species, both sexes were observed participating in brood care while paired (Fig. 4). Before forming a pair, males scanned the females to identify ovigerous females and then made several trials of pairing, finally formed a pair. During the pairing period, males attached themselves to the dorsal side of females with their gnathopods. Pairs occasionally moved together and frequently ventilated their broods together using their pleopods. The position of the pair relative to the brood suggested that the ventilation activity of males could directly affect brood viability. Indeed, in the laboratory experiments, ovigerous females without male help hatched fewer juveniles than females with male help. Therefore, male ventilation of the pleopod and the caring female may enhance the viability of the embryos during the incubation period and increase hatching success. After complete hatching, males and females separated, and then fed on algae, presumably to replenish the energy spent on brood care. Thereafter, the female molted in a day or two.

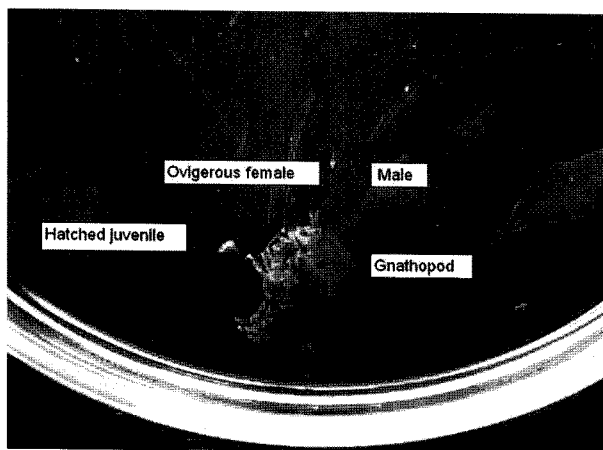


Fig. 4. The behaviour of paternal care for the brood of ovigerous female.

Reproductive Characters

The number of eggs in a brood was 40~55, and the mean embryo size was 0.42 mm in the first developmental stage. Egg size increased significantly as egg development proceeded from stage 1 to stage 3 (Fig. 5) (ANOVA, $P < 0.01$).

Laboratory Experiments

Males participated in precopulatory mate guarding in all experimental conditions, including one female with one male, two females with two males, and several females with several males. All individuals separated after copulation, and the onset of the brood formation by the female apparently induced the male to form a pair with the female, apparently to assist her with brood care. Females accepted new males for brood care following a partner exchange. When males and females formed a pair, they continuously ventilated their broods. Females in jars with a better air supply had greater hatching success.

DISCUSSION

Sex Ratio and Abundance

The operational sex ratio (OSR) in this species was almost even, which is indicative of a lower intensity of intra-sexual competition among males (Emlen and Oring 1977). Emlen and Oring (1977) noted that male mating success and hence mating system evolution may be dependent on the temporal patchiness of receptive females. In theory, if brothers compete for mates, the sex ratio should be female biased (Krebs and Davies 1993). Intense competition is expected in species with limited powers of dispersal. In cases of extreme inbreeding, a mother knows that all her daughters will be fertilized by her sons. The best strategy in this situation is to pro-

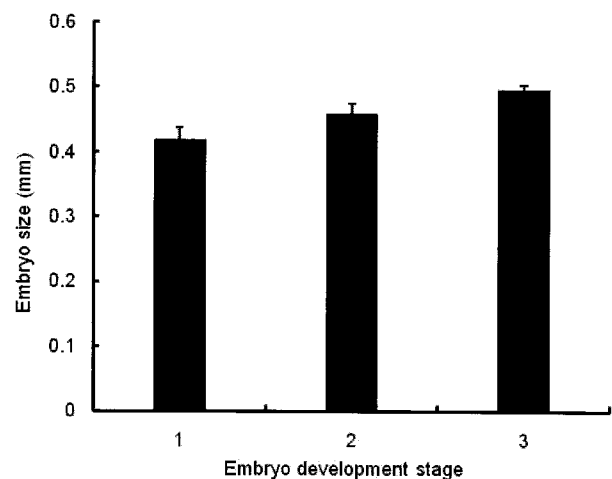


Fig. 5. Embryo size by developmental stage.

duce just enough sons to fertilize the daughters, since any other males will be wasted. Some researchers assert that that sex ratios drive mating systems: polygyny arises when males are in short supply and polyandry occurs when there are not enough females to go around (Pianka 2000). According to this explanation, *H. rubra* should be monogamous because the sex ratio is nearly equal, but they are actually sequentially polygamous or promiscuous.

Sexual Dimorphism and Mating Behaviour

Sexual dimorphism is another factor correlated with mating systems (Bauer 2004). The difference in gnathopod size, length, and color between *H. rubra* females and males was substantial, suggesting that males perform guarding behavior in a monogamous mating system (Bauer 2004). However, the mating system observed was polygamous or promiscuous. The laboratory experiment also showed that previously mated females changed their partners when the original male was artificially detached and a new male was introduced. *H. rubra* showed mating behavior (precopulatory mate guarding) similar to that of *Gammarus palustris* and *Microdeutopus gryllotalpa* (Borowsky 1991).

Mating System, Parental Care, and Reproductive Traits

Wickler and Seibt (1981) succinctly analyzed the essential elements of crustacean mating systems. The dispersion and mating success of females are limited by the distribution of natural resources and predation and also constrained by the benefits and costs of social life. In this case, males are influenced by the dispersion of females (Krebs and Davies 1993). The ratio of sexually receptive females to sexually active males (the operational sex ratio) is affected by species characteristics such as population structure and dispersion, the availability of resources, and female breeding biology (Bauer 2004).

Crook (1965) has suggested that monogamy evolves when food is scarce and care by both parents is necessary to successfully raise the young, whereas polygyny evolves in productive habitats with abundant food where male assistance is less essential. In this study there was abundant food in the natural habitat of the species. According to the polygyny threshold model (Smith 1977), if there is sufficient food, then polygamous mating systems can be favored. *H. rubra* showed male mate guarding, and the population abundance (density) of *H. rubra* was relatively low, favoring a polygamous mating system.

In *H. rubra*, females and males both participate in the brood guarding by ventilating together while joined into a pair. Paternal care is not common in other amphipods. Male care is known to be related to proximate constraints such as fertilization mode and territoriality (Krebs and Davies 1993) that male territoriality and

external fertilization can favor paternal care. However, *H. rubra* is not territorial and does not display external fertilization, yet they showed paternal care. Generally for amphipods, only the female cares for the brood, but in *H. rubra*, males cooperated with females to care for the brood. This behavioral trait may have been favored in small populations due to its positive effect on offspring survival.

The relationship between *H. rubra* reproductive traits (fecundity and egg size) and mating system were considered. The number of eggs produced was small, and egg size (volume) was rather large, which reflects a high investment in each egg relative to mating and parenting effort, although they may be iteroparous. Dick et al. (1998, 1999, 2002) concluded that brood care in amphipods is associated with harsh physical environments such as polluted, disturbed, eutrophic, and marginal habitats. Thus, apparently the population in this study, which was exposed to harsh environmental conditions, has evolved enhanced male participation in brood care and mate as a result of the positive effects of biparental care on embryo development and hatching. Indeed, our laboratory experiments showed that without paternal care, fewer juveniles hatched.

In conclusion, this species showed male care for the brood and the female during the incubation period, which is uncommon in amphipods. Females of this species produce a relatively small number of eggs. However, both females and males invested heavily in mating and parental care. Their mating system is polygamous. Local populations were very small, indicating a high probability of inbreeding. We also found an equal sex ratio. Amphipods generally develop directly (eggs hatching out into juveniles) which leads to a high survival rate from juvenility to adulthood. Thus, a life history strategy involving production of relatively few large eggs (low fecundity), as found in this species, should be favored. This population lived in an area with abundant algae for shelter and food. Given the small population size and harsh environment (tide pool), it is advantageous for both sexes to participate in precopulatory mate guarding and brood care. Therefore, from the evolutionary perspective, precopulatory mate guarding and paternal brood care in this amphipod population inhabiting tide pools is likely to be the outcome of evolution in harsh environments at small population sizes.

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