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# ALTERNATIVE MATING STRATEGIES IN MALE MORPHOTYPES OF THE FRESHWATER PRAWN *MACROBRACHIUM ROSENBERGII* (DE MAN)

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## ABSTRACT

Males in a mature, single-age, pond population of the freshwater prawn *Macrobrachium rosenbergii,* can be divided into three distinct morphological types, representing three phases in the male developmental pathway (Brody *et al.,* 1980). Behavioral and physical characteristics of all three morphotypes were examined with regard to mating behavior and reproductive probabilities.

Two alternative mating strategies are described. The largest, dominant males actively court and protect the females prior to mating. Males of the intermediate category demonstrate a reduced rate of reproductive activities in the presence of dominant males. The smallest males practice a form of sneak mating consistent with their small size and high mobility. A cost-benefit balance for each particular strategy is offered, based on qualitative features such as morphology and behavioral observations, as well as on quantitative data, including growth rates, relative proportion of each morphotype in the male population, and the respective frequencies of social encounters with females, which result in successful matings, or, in fatal injuries.

## INTRODUCTION

A social organization with obvious size dependent hierarchical characteristics and aggressive tendencies at both the alimentary and breeding levels is known to exist in a number of species of insects (Alcock *et al.,* 1977; Ward, 1983) and in aquatic organisms (Collins *et al.,* 1967; Gandolfi, 1971; Constantz, 1975; Dominey, 1980). When male reproductive success depends on male-male competition and aggression, as is usually the case in polygamous species, individuals which are at a competitive disadvantage sometimes adopt an entirely different constellation of reproductive behaviors. In most cases, individuals practice only a single reproduction option throughout their lifetime. However, when such alternative mating patterns are practiced as part of a developmental sequence, they can be considered parts of a single lifetime reproductive strategy (Dominey, 1980).

The reproduction behavior of the freshwater prawn *Macrobrachium rosenbergii* falls into the latter category. A single age population is characterized by a sex-associated size distribution in which the weights of females are quite homogeneous, while the males, at nearly 1:1 ratio with the females, yield individual weights to form a wide, positively skewed distribution, with half the population being considerably larger than the females, and half being quite small (Smith *et al.,* 1978; Ra'anan and Cohen, 1985). A close examination of the males reveals three distinct morphotypes based upon size

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ranking, claw color, and the ratio of claw length to body length (relative claw length). The three male categories include (a) small (SM) males, represented in the peak of the male distribution, characterized by clear chelae with a relative length of 0.5–0.7; (b) orange claw (OC) males, larger than SM males, characterized by the orange color of their chelae and by a relative claw length of 1.0–1.5; and (c) blue claw (BC) males, the largest individuals of the male population, characterized by thick dark blue chelae with a relative claw length of 1.5–2.0. Whereas the weight of small males is mainly restricted to the range between 1–10 g, the weight and size of OC and BC males vary widely with cultural procedures. Nevertheless, the relative proportions of the three male morphotypes, SM, OC, and BC, remain nearly constant at 5:4:1, respectively, under a wide range of environmental conditions (Brody *et al.,* 1980; Cohen *et al.,* 1981). These ratios are maintained at a dynamic state, in which individual males are capable of undergoing a transformation from one morphotype to another, following an irreversible order: from SM to OC to BC. Such transformations would occur whenever large individuals either die or are selectively removed (Ra'anan and Cohen, 1985).

Aquarium and field observations on the three male morphotypes suggested the existence of a reproductive-dominance hierarchy in which the BC males are the climax of the male development pathway. A BC male is dominant, territorial, and sexually active, usually in association with eight to ten females (Raman, 1967). Whenever a female becomes receptive to fertilization, the BC male displays a characteristic courtship behavior which is followed by mating. OC males are sub-dominant, non-territorial, and were never observed courting and protecting a receptive female, although occasional fertilizations by OC males have been recorded (Ra'anan and Cohen, 1985). Small males are not territorial, they are submissive to all other males and are highly mobile (Peebles, 1980; Harpaz, 1980). SM males were observed to be strongly attracted to receptive females, and in several events, females were successfully fertilized when only SM males were present, indicating the SM males are sexually competent (Sagi, 1984).

The present study evaluates the relative reproductive potential of each of the morphotypes while examining their mating strategy by means of aquarium observations. We have also tried to arrive at a qualitative cost-benefit evaluation of each of these morphotypes (representing three different developmental stages) according to each type's specific physical characteristics, typical behavior, and probability of achieving successful fertilization.

## MATERIALS AND METHODS

### *Source of animals*

Prawns for this study were obtained from a commercial fish pond stocked with a single age juvenile population, so that all individuals were of the same hatching batch and were reared under the same environmental conditions.

The selection of males was performed according to the morphologically distinctive characteristics of the three male categories, and the selection of females was based on their state of sexual maturation as determined by gonad development (Sagi and Ra'anan, 1985).

### *Experimental groups*

Mating probability of SM and OC males was examined in aquaria by stocking each of these morphotypes either alone with females or together with a dominant BC male. In addition, the dominant BC male, in one experimental group, was operated on so that it was unable to release its own spermatophores. This was performed by sealing the gonopores with a drop of quick-set adhesive cyanoacrilate (commercial name: Super Glue). We have previously shown that such treatment does not interfere with the male's display of courting behavior (Sagi and Ra'anan, 1985). The rate of female fertilization by the subordinate SM and OC males in the presence of a 'blocked' BC male indicates the actual probability of SM and OC males to achieve a successful copulation in a situation more similar to that prevailing in nature where BC males are guarding and protecting receptive females.

The number of males distributed to the aquaria was chosen to simulate the morphotypes' relative frequency within the male population in nature (Cohen *et al.*, 1981), and was limited by the size of the aquarium. The following stocking combinations were set up:

(a) 6 SM males (5–10 g each)
(b) 3 OC males (30–40 g each)
(c) 3 BC males (40–50 g each)
(d) 1 BC male and 5 SM males
(e) 1 BC male and 2 OC males
(f) 1 blocked BC male and 5 SM males
(g) 1 blocked BC male and 2 OC males

Three aquaria were set up for each stocking combination. Whenever a male went through a morphotypic transformation, died, or suffered a physical injury (such as lost claws while molting or fighting), it was replaced by another male of a similar morphotype. Altogether, all males in each aquarium were replaced 5–6 times within the entire observation period of 5 months.

In addition to the males, a female with ripe gonads was present at any given time in each aquarium. Whenever a female became berried, it was replaced by an equivalent female, and was transferred into a separate aquarium for a 15 day follow-up of embryonic development. When a receptive female in an observation aquarium either did not become berried, or lost all eggs within 48 hours from the pre-mating molt, it was replaced by another female and a failure of fertilization was recorded. Altogether, 16–45 females were examined for each of the male stocking combinations.

### *Experimental conditions*

Observations were carried out in 130 l glass aquaria (100 × 37 × 39 cm), equipped with built-in biofilters and temperature control devices which kept a constant temperature of 25–27°C. Each aquarium contained substrates in the form of six or seven plastic pipes, 10 cm in diameter and 20–25 cm long, which provided shelters for newly molted individuals.

All animals were fed daily with minced fish fillet and live *Daphnia,* occasionally supplemented with commercial fish pellets (25% protein). Uneaten food and other accumulated particulate matter were removed from each aquaria by siphoning once a week.

Aquaria were checked daily for molts, male morphotypic transformations, and berried females.

Berried females were kept isolated in 8 l aquaria (20 × 20 × 40 cm), also equipped with biofilters and kept under the same temperature.

### *Observations and measurements*

Behavioral observations were carried out for a few hours at a time during daytime only, especially when a pre-mating female was observed. Special attention was given to the relative position of each individual in the aquarium, to the typical male-male interactions (agonistic behavior) and to the male-female interactions (protecting and mating).

Whenever a female was removed, some 48 hours after a pre-mating molt, its physical state was recorded, *i.e.,* lost appendages, broken antennae, and other signs of physical injury. Embryonic development was determined two weeks later by a microscopical examination of eggs sampled from the female's abdomen and served as the ultimate proof of successful fertilization.

The percentages of successful fertilizations, failures to fertilize, female mortalities due to physical injuries inflicted by males soon after pre-mating molt, and other female mortalities unrelated to interactions with males, were calculated. Differences in the relative proportions of each of these categories among the various male stocking combinations were tested by a $\chi^2$ contingency table.

## RESULTS

### *Behavioral characteristics of the three male morphotypes*

A qualitative comparison of the mating strategies of the three male morphotypes is presented in Table I. This table shows the main characteristic features of each morphotype and the typical behavior observed when a receptive female is present.

A major behavioral difference is apparent between BC and SM males. BC males spend most of the time resting and grooming themselves, or else they are actively courting and protecting the receptive female while displaying agonistic behavior toward all other approaching individuals, males and females.

SM males are highly mobile. They are the first to react to the introduction of food and are strongly attracted to receptive females. They usually avoid physical contact with superior males, both BC and OC males, by retreating into the water column whenever closely threatened. However, there are always a few SM males continuously hovering around a female, whether the female is alone or protected by a BC male. Occasionally, an SM male would attempt to sneak under the female and to attach its spermatophore to the female's abdomen. This mating strategy may be referred to as 'sneak copulation.' Being quick and small enough, SM males were observed sneaking in between the BC male and the female as is shown in Figure 1. In the absence of a

TABLE I

*Qualitative comparison of the main characteristics, physical and behavioral, of the three male morphotypes*

| Category | BC | OC | SM |
|---|---|---|---|
| a) Body size | Large | Large | Small |
| b) Relative claw length | 1.5–2.0 | 1.0–1.5 | 0.5–0.7 |
| c) Claw color | Dark blue | Orange | Clear or pink |
| d) Mobility | Mainly resting and self-grooming | Mainly resting and self-grooming | Mainly exploring |
| e) Agonistic competition | Aggressive and dominant | Aggressive but subdominant | Submissive |
| f) Courtship | Protecting and grooming | Never observed courting | Never observed courting |
| g) Copulatory attempts | Must turn over | Must turn over | Sneaking while turning itself underneath |

FIGURE 1. Small males (sm) in a sneaking attempt between a dominant blue claw (bc) male and a female (f).

BC male, a female would occasionally be injured by the continuing attempts of several SM males to approach her at the same time.

OC males are almost as immobile as the territorial BC males. Although they were attracted to receptive females, they were easily chased away by the dominant BC male when present, and in many instances after one or two agonistic encounters they would ignore the mating couple. In the absence of a BC male, a series of agonistic encounters among the OC males would result in one of them (usually the largest) trying to capture the female prior to mating. While receptive females were observed actively seeking the protection of BC males, they tried to avoid both SM and OC males. Whereas a SM male can steal under the female for copulation, the large OC and BC males must turn the female over, and actual copulation may occur only when the female's abdomen is exposed to an upright position. OC males were never observed protecting or grooming a female prior to mating (as is the normal courting behavior of BC males), and, indeed, in many instances a female would be badly, sometimes fatally, hurt by an OC male.

### *Reproductive potential of the three male morphotypes when separated*

A comparison between the relative frequencies of successful fertilizations by the three male morphotypes (Table II, treatments 1, 2, 3) clearly shows the reproductive advantage of BC males over SM and OC males. While 93.3% of the females were successfully fertilized in the presence of a BC male and only 3.3% failed to become berried, in the cases of SM and OC males, successful fertilization occurred in 33.3% and 37.5% of the females, respectively, while infertility was recorded for 42.2% and 43.6% of the females, respectively. The reproductive success of the BC male was significantly higher than that of the two other morphotypes ($P < 0.05$) which did not differ significantly between themselves.

In addition to the high probability of achieving a successful fertilization, BC proved to be better guards of receptive newly molted females than SM and OC males. Only BC males were observed to protect the females during courtship activity. Moreover, only one female (2.2%) died as a consequence of male aggression whenever BC males were present, whereas females stocked with SM and OC males, had a mortality rate of 22.2% and 18.7%, respectively.

TABLE II

*Reproduction potential of the three male morphotypes when held separately and in combinations* with a female*

| Treatment # | Stocking combination | Successful fertilization** | Failure to fertilize | Mortality due to inflicted injuries | Natural mortality |
|---|---|---|---|---|---|
| 1 | 3 BC | 93.3% (a)<br>(28) | 3.3% (a)<br>(1) | 0 (a) | 3.3%<br>(1) |
| 2 | 3 OC | 37.5% (b)<br>(6) | 43.6% (b)<br>(7) | 18.7% (b)<br>(3) | 0 |
| 3 | 6 SM | 33.3% (b)<br>(15) | 42.2% (b)<br>(19) | 22.2% (b)<br>(10) | 2.2%<br>(1) |
| 4 | 1 blocked BC + 2 OC | 16.6% (c)<br>(3) | 77.7% (c)<br>(14) | 0 (a) | 5.5%<br>(1) |
| 5 | 1 BC + 2 OC | 100.0% (a)<br>(19) | 0 (a) | 0 (a) | 0 |
| 6 | 1 blocked BC + 5 SM | 33.3% (b)<br>(15) | 51.1% (d)<br>(23) | 2.2% (a)<br>(1) | 13.3%<br>(6) |
| 7 | 1 BC + 5 SM | 84.4% (a)<br>(38) | 4.4% (a)<br>(2) | 0 (a) | 11.2%<br>(5) |

* Index letters indicate statistical significance of differences between stocking combinations within each column. The values bearing the same index letter within each column do not show a significant difference at the level of $\alpha = 0.05$ ($\chi^2$ contingency table).

** Numbers in parentheses indicate # of individuals.

### *Reproductive potential of SM and OC males in the presence of a dominant BC male*

Stocking of OC males with a blocked BC male (Table II, treatment 4) ensures that berried females were fertilized exclusively by OC males. The frequency of successful fertilizations by OC males differed significantly, 37.5% *versus* 16.6% ($P < 0.05$), when held by themselves or in the presence of a blocked BC male, respectively. Failures of OC males to fertilize were recorded in 77.7% of the cases when a BC male was present, as compared with 43.6% when OC males were kept alone. In short, BC males reduced the chances of fertilization by OC males.

The reproduction potential of SM males, in contrast to that of OC males, was not affected by the presence of a blocked BC male. Thirty-three percent of the females were fertilized whether SM males were held separately or were kept with a BC male, indicating that the chances for a successful mating of SM males, applying the 'sneak copulation' strategy, are independent of the presence of dominant BC males.

Although blocked BC males could not achieve fertilization, they could still pursue their normal courting and protecting behavior, as indicated by the negligible percentage of females which died of physical injuries in their presence (0 and 2.2% in treatments 4 and 6, respectively).

In the control treatments, where SM or OC males were kept together with untreated, normal BC males (Table II, treatments 5 and 7), 84.4% and 100% of the females were successfully fertilized, indicating that females may readily become berried, under these experimental conditions, depending only on the ability of the male morphotypes present, to complete successful matings.

## DISCUSSION

Blue claw (BC) males and small (SM) males may represent two alternative ways of mating while the orange claw (OC) males may be considered an intermediate developmental stage between the two, with a relatively low mating probability as such, in the presence of a BC male. This notion is supported by the fact that both SM and BC males hardly increase in body size while OC males are characterized by a rapid growth rate (Smith *et al.,* 1979; Ra'anan and Cohen, 1985), thus, investing relatively little energy, if any, in reproduction during this stage of development. The BC mating strategy may rely on superiority in threatening display towards the other males, while investing a great deal of energy in developing its weaponry (large, massive claws), defending a territory, and protecting the females. The SM male strategy, designated as 'sneak copulation,' takes advantage of the male's small body size and high mobility. This form is inferior in physical encounters, but wastes little energy in generating fighting devices.

Table III summarizes most of the apparent costs and benefits for the two extreme male developmental stages. The information gathered in this table is based on the present study (Table I, II), personal qualitative observations, and literature sources. In general, BC males seem to enjoy most of the benefits which contribute to male reproduction success, namely, high attractiveness for females, advantage in agonistic encounters with other males, and high survival probability of fertilized females following mating. These benefits are expressed in the high fertilization rate observed whenever a normally functioning BC male was present (85–100%). The main costs associated with BC mating strategy involve energy expenditure in defending a territory, reduced flexibility to readjust to changing environmental conditions, and the reduced ability to molt and thereby regenerate lost limbs, resulting in a relatively short life span. SM males, on the other hand, are less attractive to females. However, their ability to readjust quickly to changing conditions, together with the ever-present option to shift to the OC rapid growing phase, and its associated chance of becoming a BC male, may balance the lower probability of fertilizing females while being a SM male (only 33% under the present experimental conditions).

Polymorphism among sexually mature males is known for some insect species (Wilson, 1971; Alcock *et al.,* 1977; Ward, 1983) and mainly for vertebrates (Keenleyside, 1972; Constantz, 1975; Brown, 1975). In some cases, the alternative solutions for mating were assumed to be genetically based. A mechanism which would continually act toward an equalization of selective advantages of two alternatives and would therefore lead to a persistent dimorphism was offered by Gadgil (1972). Also relevant in this regard, a sex-linked gene in the platy fish, *Xiphophorus maculatus* (Kallman *et al.,* 1973), has been shown to control the age and thereby the size at which maturation of the gonadotrophic zone occurs. For other similar situations, in which large territorial males and small 'sneak' males coexist in a population (the megachilid bee *Antidium manicatum* L., and the anthophorid bee *Centis pallida,* Alcock *et al.,* 1977), it was suggested that the male polymorphism is maintained by means of parental manipulation, *e.g.,* the way in which a female divides her time and energy among her male progeny.

In the case of *M. rosenbergii,* neither genetic differences nor parental manipulation can account directly for male polymorphism. The former possibility is unlikely since we have proven that a SM male is capable of transforming into an OC male and eventually becoming a dominant BC male when the number of BC males in the population is reduced (Cohen *et al.,* 1981). It is possible, however, that some differences in genes which direct the individual relative growth rate, determine the preliminary size hierarchy observed already in early juvenile stages (Ra'anan and Cohen, 1984a, b). From that stage on, the order in which male transformation occurs might be dictated by size ranking. The second possibility of parental manipulation does not apply to

TABLE III

*Costs and benefits of contrasting mating strategies of the two extreme developmental stages (SM and BC) in* M. rosenbergii *male developmental pathway*

| | Dominant BC males | | Submissive SM | |
|---|---|---|---|---|
| Categories | Cost | Benefit | Cost | Benefit |
| a) Body size | Reduced sexual activity during OC phase | Higher competitive ability | Lower competitive ability | Less time to sexual maturity, small enough to sneak |
| b) Claw length and color | High investment in weaponry; easier predator target | Increased threatening effect on males: increased attractiveness to females | Disadvantage in agonistic encounters | Little energy invested in fighting devices; less conspicuous to predators |
| c) Mobility | Reduced ability to adapt to changing environmental conditions (personal field observations; Peebles, 1979) | Little energy expenditure | Energy investment in high mobility | Quick enough for sneak copulation; able to move to better areas when local conditions worsen (Peebles, 1979) |
| d) Courtship and copulatory attempts | Time and energy consuming | Increased probability of female survival after mating | Inflicting physical injuries to females, risking female mortality; high energy investment in hovering and sneaking | |
| e) Somatic growth and molting frequency | Reduced ability to regenerate lost limbs; physical deterioration due to lack of molting (Smith *et al.*, 1979; Peebles, 1979); low longevity (Ra'anan and Cohen, 1985) | No energy invested in growing or molting | | Quick regeneration of lost limbs; high longevity |
| f) Male morphotypic transformation | Irreversible (Ra'anan, 1982) | Top status | Lowest status | Capable of becoming OC and eventually BC males (Ra'anan, 1982; Ra'anan & Cohen, 1985) |

*M. rosenbergii* since there is no parental care after the eggs hatch, and the size distribution of the eggs is normal (Ra'anan, 1982).

We suggest that the male's mating strategy in *M. rosenbergii* is dependent primarily on the individual's size ranking within the population. A direct relationship between relative size and mating behavior was also described in the cases of the dung flies *Sepsis cynipsea* (Ward, 1983), and *Scatophaga stercoraria* (Borgia, 1981). In both cases most of the size variation was attributed to environmental causes. Constantz (1975) suggested that a highly competitive environment, in which there is a high frequency of large males, may favor small, sneaking males, since territorial males primarily will be occupied with agonistic behavior that consumes a significant fraction of their time and energy. By contrast, if the frequency of large males is low, their relative reproduction advantage over the small males should increase. At an evolutionary stable strategy, the relative proportions of the two male types in the population should be at an equilibrium in which the fitness of both is equal (Maynard Smith and Price, 1973). This hypothesis is consistent with the existing observations of a constant frequency distribution of the three male morphotypes of *M. rosenbergii* over a wide range of population densities and ecological conditions in the ponds (Cohen *et al.,* 1981). The signals by which any individual determines its relative position within the size hierarchy, and the mechanisms by which these signals are translated to mating behavior and to the regulation of growth rate are presently unknown.

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