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Male Mating Tactics in the Shrimp *Palaemonetes pugio* (Decapoda, Caridea): Precopulatory Mate Guarding vs. Pure Searching

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Bauer, R. T. & Abdalla, J. H. 2001: Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology* **107**, 185–199.

Abstract

The guarding of females approaching a limited period of sexual receptivity is a common mating tactic of males. In many decapod crustaceans, such as the shrimp *Palaemonetes pugio*, females can only copulate during a short period after a reproductive molt. It has been predicted that mate guarding by males (pre-copula) evolves in such species if sex ratios are not highly female-biased and if males can detect the molt stage of the female. The mating tactics of males were investigated in *P. pugio*. Time-lapse video observations were made on interactions among two males, a pre-molt female, and an inter-molt female (20 replicates). There was no evidence that males recognized a pre-molt female until 24 h before its molt. Significant numbers of male contacts with pre-molt females occurred 1 h before and after the female molt. Copulation took place within 1–3 min of the molt. No behavior commonly associated with mate guarding in decapods was observed – no clasping, agonistic behavior, or close association. It is concluded that the male's mating tactic is pure searching, wherein males haphazardly contact many females in order to find a receptive one. The high encounter rate in nature of these very mobile, aggregated shrimps is proposed as the factor responsible for the evolution of pure searching. It is hypothesized that pure searching is the male tactic of the many species of decapod shrimps with small males, sexually monomorphic cheliped weapons, and aggregated populations.

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Introduction

Several theoretical papers and reviews have addressed ecological, demographic, and reproductive characteristics that have influenced the evolution of mating systems in crustaceans (Wickler & Seibt 1981; Grafen & Ridley 1983; Ridley 1983; Jormalainen 1998). Particular attention has been focused on crustacean species in which mating and insemination is confined to a brief period after the female molt (Ridley 1983; Jormalainen 1998). This reproductive trait limits the number of females with which males can mate at any given time. Grafen & Ridley (1983) and Ridley (1983) proposed a model demonstrating that pre-copulatory mate guarding should evolve in species in which females can only be fertilized during a short, predictable time period. In mate guarding, a male assures his insemination of a female by associating with and defending her until her reproductive molt, after which copulation takes place. A male maximizes the number of females inseminated by guarding a female for a limited but variable time, abandoning her after copulation in order to seek another female to guard until her reproductive molt. A key assumption in this model is that males can detect the molt stage of the female; that is, how close she is to molting after which she will be receptive to copulation. Important variables in the model are sex ratio and the rate at which males and females encounter each other. When female receptivity is short and predictable, permanent mate guarding (monogamy) should evolve unless sex ratios are female-biased, in which case temporary mate guarding is predicted. Pre-copulas would not be adaptive when receptive females are numerous and encounter rates are extremely high. Ridley (1983) tested the model using information from the literature on crustaceans and other groups with time-restricted mating, such as some insects, mites, spiders, and frogs.

Wickler & Seibt (1981) proposed another model on male mating tactics for crustacean species, in which mating occurs within a brief interval after female molting. In this model, it is not assumed that males can detect the stage of a female's molting and spawning cycle. The encounter rate of males with females and the inter-spawn interval are the most important variables. Pre-copulatory mate guarding is predicted when the female inter-spawn interval is greater than 3–4 d, as it is for most crustaceans, and when the male meets on average up to two females per day (Fig. 1 in Wickler & Seibt 1981). At higher encounter rates, however, a pure searching strategy is predicted. In pure searching, highly mobile males constantly seek out females in the population. If a contacted female is receptive, mating is attempted; if the female is not receptive, the male immediately moves on and continues searching. When females are rarely encountered, a permanent mate guarding (monogamy, partner fidelity) should be selected for.

In many decapod crustaceans (shrimps, lobsters, crabs), copulation is restricted to a brief period after the female molt. In such species, mate guarding is predicted as the male mating strategy (Ridley 1983). Typical mate-guarding behavior in male decapods includes close physical association with, clasping or carrying, and defense of females (Ridley 1983; Atema 1986; Wilber 1989; Gleeson 1991). In decapod species in which pre-copulatory mate guarding occurs, males

exhibit characteristics that aid them in sequestering and guarding females, such as increased body size (as large or larger than females), relatively enlarged cheliped weapons used in agonistic encounters, and conspicuous aggressive behavior towards conspecifics (Kitteredge et al. 1971; Ridley 1983; Atema 1986; Christy 1987; Wilber 1989; Gleeson 1991; Jivoff & Hines 1998). Jormalainen's (1998) review revealed similar adaptations for mate guarding in amphipod species.

In caridean shrimps and in many species of penaeoidean shrimps, mating is limited to a brief period after the molt (Bauer 1976, 1989, 1991, 1996; Bauer & Holt 1998). Mate guarding has not been reported in penaeoidean shrimps (Bauer 1996). However, as predicted by the Grafen & Ridley (1983) and Ridley (1983) model, both permanent and temporary mate guarding has been shown in a variety of caridean species. Examples include many alpheid, such as *Alpheus* spp. (Knowlton 1980; Salmon 1983) and *Betaeus* spp. (Hart 1964; pers. obs. by RTB on *B. harfordi* and *B. macginitiae*), *Hymenocera picta* (Seibt & Wickler 1979), pontonines (Hipeau-Jacquotte 1973; Bruce 1976), and palaemonids such as *Macrobrachium australiense* (Lee & Fielder 1982) and *M. rosenbergii* (Ra'anana & Sagi 1985). Males of these caridean species exhibit some or all of the morphological and behavioral traits associated with mate guarding in decapod crustaceans.

However, Ridley (1983) pointed out that the literature on several species of caridean and penaeoidean shrimps indicated a lack of obvious pre-copulatory guarding. Ridley believed that this was due to two circumstances. First, the studies that he cited (e.g. Needler 1931; Kamiguchi 1972; Bauer 1976) dealt with the mechanics of copulation, but observations on pre-copulatory behavior were absent or incomplete. Secondly, mate guarding might not be as obvious in the species cited as it is in decapods, in which mate guarding has been previously observed. Ridley felt that if careful observations were made on caridean and penaeoidean shrimps, a less obvious form of pre-copulatory mate guarding would be observed, such as close proximity of a male to the female which he guards.

Taking Ridley's observations and comments into account, it occurred to us that in most penaeoidean shrimps and a great number of caridean species, males do not appear particularly well-adapted for guarding females (Bauer 1996). Adult males of such species are smaller on average than breeding females, are not conspicuously aggressive towards conspecifics, and are 'weakly armed' – the major chelipeds are not proportionately larger than those of females. A socio-ecological correlate of many such species is that individuals are highly aggregated, occurring at locally high abundances: many hippolytids (littoral *Heptacarpus* spp.: Bauer 1976, 1979; pers. obs.; various seagrass species: Bauer 1985; coastal species: Allen 1966); many palaemonids (especially *Palaemon* and *Palaemonetes* spp.: Höglund 1943; Allen 1966; Anderson 1985); and crangonid, pandalid, and penaeoid shrimps important in commercial trawl fisheries (Butler 1980; Boddeke 1989; Iversen et al. 1993; Dall et al. 1990). It is species with these characteristics that figure in the examples given by Ridley (1983) of shrimps in which pre-copulatory guarding of females by males should occur but which had not yet been described.

The major objective of this study was to test Ridley's (1983) prediction that some form of pre-copulatory mate guarding of females by males would be found

in shrimp species if careful pre-mating observations were made. The shrimp *Palaemonetes pugio* was used as a test organism because it is typical of those caridean species for which mating behavior has been described but in which mate guarding has not been reported (Welsh 1975; Alon & Stancyk 1982; Berg & Sandifer 1984). Experiments were conducted in order to determine: (i) whether males can distinguish between inter-molt and pre-molt (pre-spawning) females; and (ii) whether males guard pre-spawning females prior to their reproductive molt and subsequent copulation. A pure searching tactic was considered as an alternative to mate guarding. Observations on factors important to an understanding of the mating system of *P. pugio* – the relationship between molting, mating and spawning; population structure; and the form of sexual dimorphism in body size and in cheliped weapons – were made and are reported.

Methods

Collections of *Palaemonetes pugio* were made with a long-handled dipnet of 1 mm mesh along the marsh shoreline at Cypremort Point State Park (Vermilion Bay, Louisiana) on Sep. 12, Nov. 9, 1995, and Jan. 11, Mar. 22, Apr. 17, May 10, June 20, July 22, and Aug. 8, 1996. Approximately 200 specimens were collected for observations on population structure and breeding condition. These specimens were anesthetized by chilling after collection, preserved in 10% seawater formalin, and later stored in 70% ethanol. Additional live specimens were taken as needed for observations on reproductive biology and behavior. In caridean shrimps, females can be inseminated and are receptive to males only during the period between a pre-spawning molt and spawning (Bauer 1976, 1989). In order to establish the duration of this period in *P. pugio*, daily observations on the occurrence of molting and spawning were made on females isolated in individual containers on re-circulating water tables. Live specimens for these observations and for those on mating behavior were maintained under conditions of salinity (3–6 ppt), temperature (27–29 °C), and photo-period (14 h light:10 h dark), consistent with late spring and summer breeding conditions (Wood 1967; Alon & Stancyk 1982). They were fed a tropical fish food (shrimp pellets).

Observations on interactions among reproductive males and females were recorded with time-lapse video in order to test the hypotheses predicted by the mate guarding model (Grafen & Ridley 1983; Ridley 1983) that: (i) males distinguish between inter-molt and pre-molt (pre-spawning) females; and (ii) males guard pre-molt females for a period greater than 24 h. The experiments also allowed testing of the corollary hypothesis that relative male size is a factor in male success in associating with pre-molt females and in obtaining copulations with them after the molt. In each replicate recorded ($n = 20$), two males were maintained with two females in different reproductive states. The pre-molt (molting) female had mature ovaries (visibly full of vitellogenic oocytes), indicating the approach of a molt, after which the female is attractive and receptive to males (Berg & Sandifer 1984). The other inter-molt (non-molting) female had immature ovaries and incubated embryos at an early stage of development, indicating that

their molting would not occur during the observation period. Two males were chosen haphazardly from a laboratory population. Individuals were marked with randomly assigned 1–2 pairs of small pieces of reflective tape using cyanoacrylate glue (Bauer 1996) to facilitate their identification in the videotapes. The four individuals were maintained together and videotaped in a space 20 cm long \times 12 cm wide and 20 cm high in a 38-l aquarium partitioned by porous dividers. Shrimps were allowed to acclimate in the viewing chambers for 24 h prior to videotaping. Activities were recorded with an infrared-sensitive surveillance video camera using an 8 mm or 12 mm lens, connected to a time-lapse video recorder. Recordings were made up to the molt of the pre-molt female, a period that varied from 2 to several days, and then were continued for 1 d after her molt. Day illumination was provided by overhead fluorescent lights and night illumination by infrared lamps (880 nm). Videotapes were recorded at 24-h speed (5 frames/s). Water temperatures, photo-period, salinity, and feeding were the same as those described earlier for laboratory populations. At the end of a replicate, all individuals were chilled and preserved so that male size and other observations could be made.

Observations from videotapes taken 48 h prior to and 24 h after molting of the pre-molt female were recorded and analyzed. For each of these 72 h, a 10-min segment was chosen at random and the number of contacts of males with females was recorded. Contact was defined as any activity involving obvious physical touching of individuals with any part of the body or thoracic appendages, usually the third maxillipeds, chelipeds, or antennal flagella. Since many of these hourly observations contained no contacts (values of zero), the 10-min hourly periods were pooled into 12-h time blocks from 48 h before to 24 h after a female molt. Activity increased shortly before and after the female molt, and therefore all male–female contacts were recorded for each 5-min period from 115 min before the female molt and thereafter until it spawned (1.5–3 h). Total contacts for each 5-min interval are reported and compared from 115 min before until 105 min after the molt.

For the 12-h and 5-min time intervals used in statistical analyses, contacts were classified into one of four variables: number of contacts by both males (1) with the pre-molt female that had molted during the observations (molting female) and (2) with the non-molting female; number of contacts with the molting female by (3) the larger and (4) the smaller of the two males, haphazardly chosen for each replicate. The number of copulations by each male with the molted, pre-spawning female was recorded, as well the time at which subsequent spawning occurred. Every effort was made to observe and to record obvious or overt agonistic behavior.

To test the null hypothesis of no difference in the number of contacts by males with the molting female and non-molting female, a Wilcoxon signed-ranks test for paired values was performed on each of the statistically independent 12-h and 5-min intervals for which contacts were recorded. The same procedure was used to test the hypothesis of no difference in the number of contacts with the molting female by the larger male and smaller male. Males used in the replicates ranged in size from 5.3 to 8.4 mm carapace length. The size difference between the larger male and smaller male used in individual replicates ranged from 0.1 mm to 2.0 mm

carapace length, with a median of 0.7 mm carapace length (95% cl, 0.4 mm, 0.9 mm; $n = 20$).

Observations taken on preserved specimens from monthly collections included carapace length (a standard measure of body size, Bauer & VanHoy 1996), sex (appendix masculina present on second pleopods in sexually mature males, absent in females; Bauer 1976; Berg & Sandifer 1984), and presence or absence of incubated embryos in females. Sex ratio, defined here, as in Grafen & Ridley (1983), as the ratio of mature males to mature females, was calculated for the months in which reproductive (embryo-carrying) females were found. Females were considered mature or capable of reproductive activity if they were as large or larger than the smallest female (3.7 mm carapace length) with embryos from all samples (following Alon & Stancyk 1982). All males sampled had appendices masculinae on the second pleopods, a character showing sexual maturity in caridean males (Bauer 1976; Bauer & Holt 1998).

The second chelipeds are the larger (major) pair of chelipeds used in palaemonid shrimp as weapons in prey capture, defense, and agonistic interactions. To test for possible sexual dimorphism in cheliped weapons, measurements were made on the arm and chela of the second chelipeds: arm length (sum of lengths of ischial, meral, and carpal segments) and length and height of the chela propodus. These measures were made on 120 males and 120 females, 30 of each sex selected at random from each of four population samples from reproductive months (Sep. 1995, Mar., May, June 1996). Regressions of various cheliped characters on body size (carapace length) were calculated using log-transformed measures. The model used was the allometric growth equation of the form $\log y = \beta \log x + \log \alpha$, where y is a cheliped measure, x is carapace length, β is the slope of the transformed equation, and α is the y -intercept, the size of y when $x = 1$ (Kuris et al. 1987).

Results

Male Mating Tactics

The video observations on males and females showed that the period during which copulations were physiologically possible, from the molting female molt to spawning, ranged in duration from 92 to 176 min, with a median period of 119 min (95% confidence limits, 113 min, 140 min, $n = 20$). However, copulations with the molting female by males occurred only in the minutes immediately after her molt. Of 36 copulations observed in 20 replicates, 27 took place within 0–1 min, seven within 1–2 min and two within 2–3 min of the female molt. The number of copulations ranged from one to five, with a median of one (95% cl = 1,2, $n = 20$).

With the exception of the act of copulation, males did not show any obvious interaction with the molting female, such as clasping, stroking with antennal flagella or chelipeds, or standing alongside. Interactions among males and females appeared to occur as haphazard contacts, which involved an approach by one or both, followed by a brief touch of anterior thoracic appendages and/or antennal flagella, after which one or both either continued onwards or reversed path. Furthermore, no overt agonistic behavior, such as obvious threat displays, attacks

with the second chelipeds or other appendages, or defense of one individual by another, were observed.

There was no difference in the number of male contacts with the molting female and the non-molting female in the intervals 48–36 h before the molt ($p = 0.067$), 36–24 h before ($p = 0.455$), 0–12 h after ($p = 0.147$), and 12–24 h after ($p = 0.125$) (Wilcoxon signed ranks tests, $n = 20$ per interval) (Fig. 1a). However, there were significantly more male contacts with the molting female in the intervals 24–12 h ($p = 0.047$) and 12–0 h ($p = 0.014$) before the molt.

Male activity increased dramatically within a short time period before and after the female's molt (Fig. 2a). There was a significantly greater number of contacts by males with the molting female than with the non-molting female in all 5-min intervals extending from 40 min before until 35 min after the female molt (Wilcoxon signed ranks test, $p \leq 0.05$, $n = 20$ per interval).

There was no difference between the smaller male and larger male in their number of contacts with the molting female in any of the 12-h intervals before and after the molt (Wilcoxon signed ranks test, $p > 0.05$, $n = 20$ per interval; Fig. 1b). In the 5-min intervals before and after the molt (Fig. 2b), there was no difference between the smaller male and larger male in 39 of the 44 intervals (Wilcoxon signed ranks test; $p < 0.05$, $n = 20$ per interval). In five intervals, all at least 25 min before or after the molt, there was a significant difference ($p < 0.05$), with a greater number of contacts made by the larger male in three intervals and by the smaller male in two intervals (Fig. 2b).

The number of copulations by the larger male and smaller male was compared in each of the 20 replicates. In four replicates, the difference in number of copulations between larger male and smaller male was zero, reducing the sample size to 16 replicates (Tate & Clelland 1957). Although in 11 of the remaining 16 replicates the smaller male either had the only copulation or had more copulations than the larger male, this trend was not significant ($p = 0.20$).

Observations on Breeding, Sex Ratio, and Sexual Dimorphism

Females incubating embryos were found in monthly samples taken in Sep. 1995 and Mar.–Aug. 1996 but not in the Nov. and Jan. 1996 samples, as expected from previous studies showing a spring and summer breeding season for *Palaemonetes pugio* (Wood 1967; Alon & Stancyk 1982). The percentage of females of reproductive size carrying embryos ranged from 12.7% in Mar. to 59.4% in Apr. (Fig. 3). Observations on females collected during these months and maintained in the laboratory without contact with males showed that the maximum period between molting and spawning, the only period in which copulation in caridean shrimps can occur, is short. Of the 64 females observed, 95.3% spawned within 1 d and 4.7% within 2 d after the molt.

Sex ratios in the monthly samples were male-biased (1.41–2.91), except for Mar. (0.50; Fig. 3). The sex ratio was significantly different from 1 : 1 in all months (χ^2 -test, $p < 0.025$) except in the Sep. 1995 sample ($0.10 > p > 0.05$).

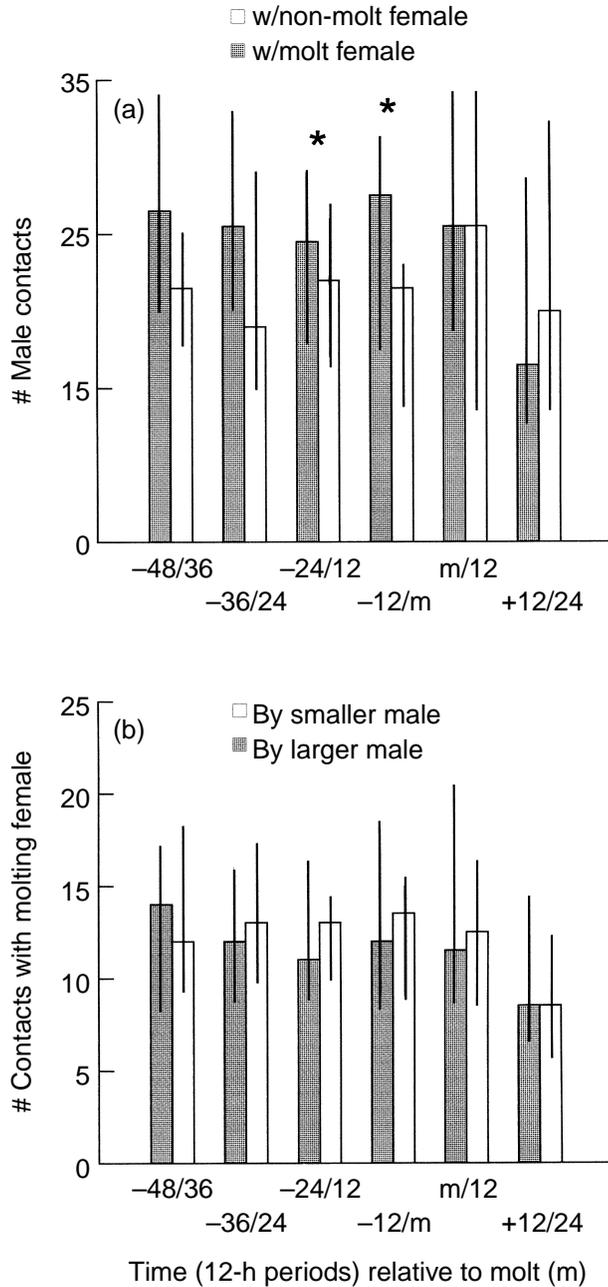


Fig. 1. Male contacts with females from 2 d before to 1 d after the molting female's molt. Number of contacts are from randomly selected 10-min observation periods each hour, summed over 12-h intervals before and after the molt. Observations were taken from time-lapse video replicates ($n = 20$). Medians and 95% confidence intervals are illustrated. Asterisks indicate time intervals in which the null hypothesis of 'no difference in contacts' is rejected (Wilcoxon signed-rank tests; $p \leq 0.05$). (a) Comparison of contacts by both males with the molting female and non-molting female relative to the molt. (b) Comparison of contacts by the larger male and smaller male with the molting female relative to the molt

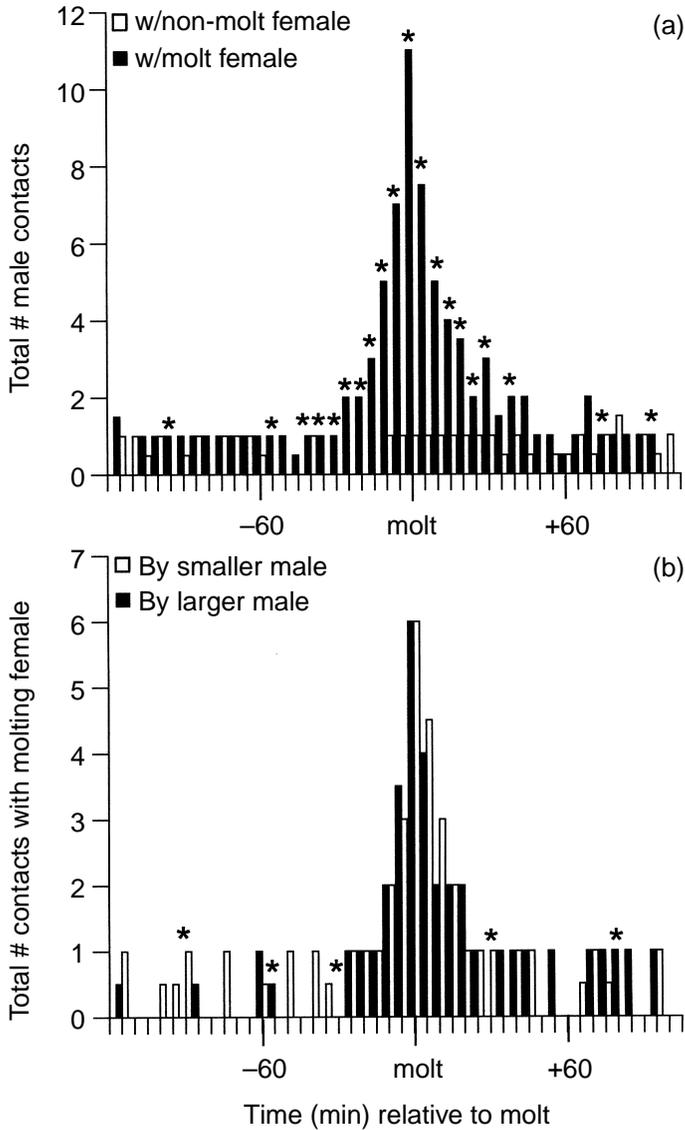


Fig. 2: Total number of male contacts with females per 5-min period from 115 min before to 105 min after the molting female molt. Observations were taken from time-lapse video replicates (n = 20). Median values are illustrated. Asterisks indicate time intervals in which the null hypothesis of 'no difference in contacts' is rejected (Wilcoxon signed-rank tests; $p \leq 0.05$). (a) Comparison of contacts by both males with the molting female and non-molting female relative to the molt. (b) Comparison of contacts by the larger male and smaller male with the molting female relative to the molt

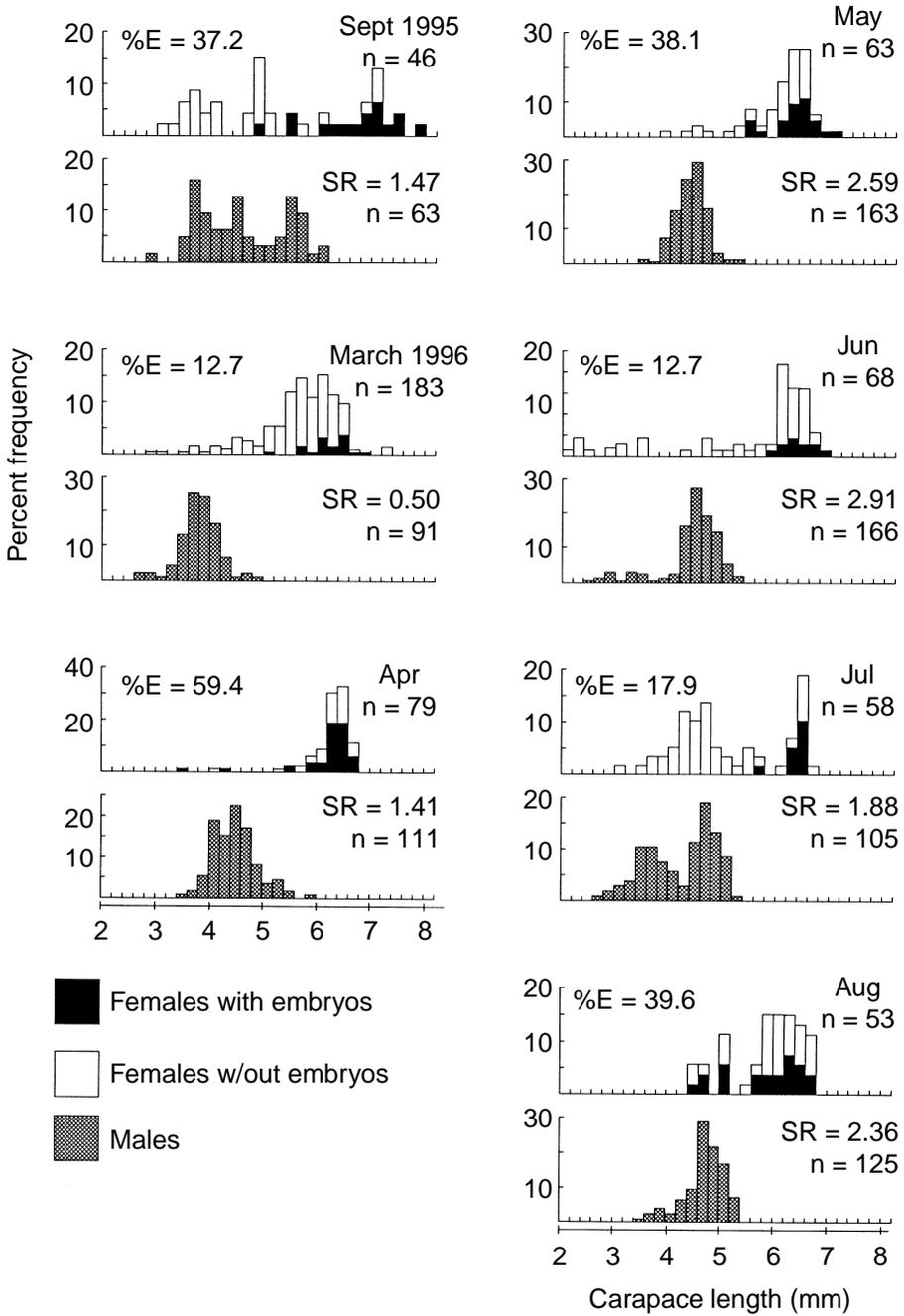


Fig. 3. Size-frequency diagrams of males and females from population samples taken during reproductive months, with figures on percentage mature females incubating embryos (%E) and sex ratio (SR), the ratio of mature males to mature females

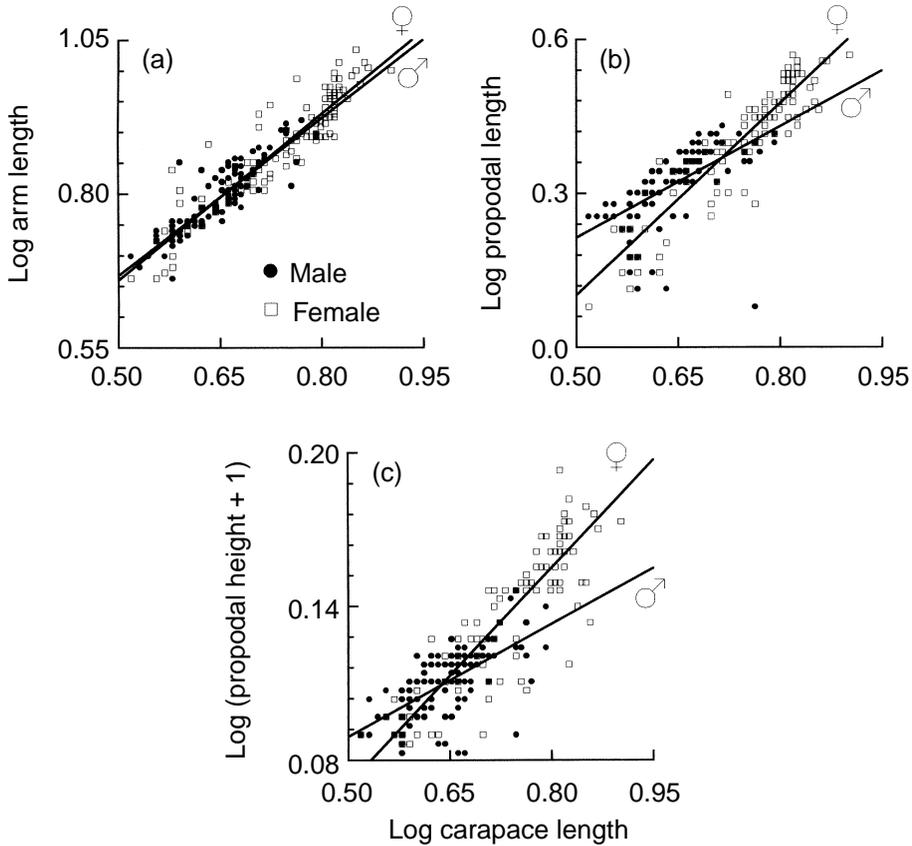


Fig. 4: Comparison between males and females of different measures of the second cheliped weapons. Regression lines and equations follow the form $\log y = \beta \log x + \log \alpha$ where y is a measure of cheliped size in mm; x is carapace length, a measure of body size, in mm; β is slope, α is the y -intercept; R^2 is the square of correlation between $\log x$ and $\log y$. For all regressions, $n = 120$, and p ($\beta = 0$) < 0.001 . (a) Arm length; males, $\beta = 0.893$, $\alpha = 1.64$, $R^2 = 0.821$; females, $\beta = 0.900$, $\alpha = 1.62$, $R^2 = 0.921$ (plotted regression lines for males and females overlap); (b) Propodus length; males, $\beta = 0.802$, $\alpha = 0.63$, $R^2 = 0.672$; females, $\beta = 1.289$, $\alpha = 0.28$, $R^2 = 0.911$; (c) Propodus height + 1; males, $\beta = 0.163$, $\alpha = 1.01$, $R^2 = 0.697$; females, $\beta = 0.283$, $\alpha = 0.85$, $R^2 = 0.876$

The considerable sexual dimorphism in body size in *Palaemonetes pugio* is shown by the male and female size–frequency distributions from months in which reproductive females were collected (Fig. 4). Males were, on average, smaller than reproductive females, with the size classes of larger males showing no, little, or only moderate overlap with size classes containing reproductive females.

Possible sexual dimorphism in cheliped weapons was examined (Fig. 4a–c). The regression lines of cheliped arm length on carapace length for males and females overlap almost completely (Fig. 4a). The slopes of these lines are not significantly different ($p = 0.889$). The y -intercepts (elevation) of these lines, adjusted for differences in male and female size by ANCOVA, are not significantly

different ($p = 0.925$). The slope of the regression for propodus length on carapace length (Fig. 4b) is significantly higher in females ($\beta = 1.289$) than in males ($\beta = 0.802$; $p < 0.001$). In contrast, the y-intercept for males ($\alpha = 0.63 \pm 0.08$) is higher than that of females ($\alpha = 0.28 \pm 0.03$). However, the hypothesis of no difference between these y-intercepts cannot be tested by ANCOVA because the prerequisite of homogeneity (equality) of slopes is not met. The result of the higher female slope and higher male y-intercept is that small males have slightly longer propodi than females of the same size. With increasing male size, the difference decreases until, at larger male sizes, the regression lines cross and female propodus length at a given size is greater (Fig. 4b). A similar situation occurs in propodus height, except that the crossing of regression lines takes place at a smaller male size (Fig. 4c). For propodus height on carapace length (Fig. 4c), the slope of the line for females ($\beta = 0.283$) is higher than that for males ($\beta = 0.163$) (p of no difference in $\beta < 0.001$). The y-intercept for propodus height is greater in males ($\alpha = 1.01 \pm 0.02$) than for females ($\alpha = 0.85 \pm 0.02$).

Discussion

Our observations on the breeding biology of *Palaemonetes pugio* show that this caridean shrimp species is appropriate for testing the Grafen & Ridley (1983) and Ridley (1983) model about mate guarding. Female receptivity and copulation were restricted to a short time period after a predictable event, the female molt. The possibility of copulation and insemination is terminated by spawning in carideans (Bauer 1976, 1989), which occurred in *P. pugio* within 2–3 h after the molt, when females were mated and within 1 d when females were isolated from male contact. In our video observations, copulations occurred within only a few minutes after the female molt.

Sex ratios observed in this study suggested that, according to the model tested, guarding of females by males should take place. In six out of the seven months in the breeding season, sex ratios, defined as in Grafen & Ridley (1983) as the ratio of mature males to females, were highly male-biased. The male bias in sex ratio may be even higher than that reported here. The operational sex ratio, the ratio of fertilizable females to sexually active males (Emlen & Oring 1977), is more indicative of the intensity of intra-sexual competition among males than the sex ratio which we report. The number of such fertilizable (recently molted) females, as well as the number of pre-molt reproductive females that males might benefit from guarding, could not be reliably estimated from the population samples. However, that number is surely much less than the simple number of mature females in each monthly sample. The operational sex ratio is thus even more strongly male-biased than the reported sex ratios indicate. Based on this characteristic of the population, selection for mate guarding by males of *P. pugio* would seem to be quite strong.

However, our results do not support Ridley's (1983) prediction that mate guarding would be found in shrimps if careful observations were made on male–female interactions prior to the female's spawning molt. Males did not exhibit any

behavior indicative of mate guarding in crustaceans. Males did not grasp females prior to copulation, did not remain close by them, nor defend them from other males. In *P. pugio*, the only interactions between the highly active, mobile males and females appeared to be brief haphazard encounters involving momentary contacts with antennal flagella or thoracic appendages.

A high number of brief contacts by a male with a female in the day before her spawning molt might constitute a subtle form of mate guarding. In our video observations, males contacted both the molting female and the non-molting female with equally low frequency in the penultimate day before the molt. In the day before the molt, there was a small but statistically significant increase in the number of male contacts with the molting female, perhaps indicating recognition. There was an obvious increase in male contacts with the molting female in the hour before the molt and copulation. However, this time period is much too short to be considered mate guarding. Ridley (1983) reasonably defined mate guarding as a pre-mating association with a duration of more than 1 d. Our interpretation of the above results is that males can recognize a pre-spawning female but only shortly before her molt. They contact her more frequently during this period to determine whether she has molted and is receptive to copulation.

We found no male adaptations for mate guarding in *Palaemonetes pugio*. Males tend to be smaller than mature females, rather than similar or larger in body size, as in males of crustaceans species with pre-copulas (Bauer 1996; Jormalainen 1998). In our video replicates, in which the two males differed in size, the larger male neither contacted pre-molt females more frequently nor had greater success in obtaining copulations than the smaller one. Enlarged cheliped weapons in males were not shown by morphometric analysis of chelipeds.

Our results agree better with a male mating tactic of pure searching (Wickler & Seibt 1981) than mate guarding. We suggest that the key factor accounting for this is a high rate of encounter of males with females in *Palaemonetes pugio*. Given the interspawn interval in *P. pugio* of 2–4 wks (Bauer & Abdalla, pers. obs.), pure searching is predicted if males can contact two or more females per day (Fig. 1 in Wickler & Seibt 1981). Although it was not measured in this study, an encounter rate of ≥ 2 per day is quite likely in *P. pugio*, a highly active and mobile shrimp occurring in characteristically high population abundances (Welsh 1975; Alon & Stancyk 1982; Anderson 1985; Bauer & Abdalla, pers. obs.).

Pure searching has also been shown as the mating tactic of males in the penaeoidean shrimp *Sicyonia dorsalis* (Bauer 1996), a species with sexual dimorphism and population biology similar to *P. pugio*. We predict, contrary to Ridley (1983), that careful study will reveal pure searching in other such shrimp species with small male size, sexually monomorphic weaponry, and aggregated population dispersion.

Acknowledgements

We wish to thank NOAA Louisiana Sea Grant Program (grant No. NA46RG0096-R/ZM-4) and the Neptune Trust for financial support. We thank D.L. Felder, P.L. Klerks, and R.G. Jaeger for their

comments on the study. We are grateful to the editor and reviewers for their useful comments and suggestions. This is Contribution no. 73 of the UL Lafayette Laboratory for Crustacean Research.

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Received: February 2, 2000

Initial acceptance: May 19, 2000

Final acceptance: July 31, 2000 (J. Brockmann)