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# Effect of female molt stage and sex ratio on courtship behavior of the blue crab *Callinectes sapidus*

**Abstract** In many species, males and females actively participate in courtship, and the outcome of pre-mating interactions influences the mating success of both sexes. Female blue crabs, *Callinectes sapidus*, mate soon after their final molt to maturity; thus female molt stage dictates the timing of mating. In a field experiment, we manipulated female molt stage and sex ratio to test their effects on the courtship behavior of both sexes, if female behavior influences the behavior and pairing success of males, and if male courtship influences male pairing-success. Early-molt-stage females avoided males during courtship, whereas late-molt-stage females sought out males. As a result, males had to pursue and capture early-molt-stage females whereas males displayed to late-molt-stage females and more easily physically controlled them. Males sometimes abandoned late-molt-stage females, but this occurred more often when females were abundant. The rate at which females avoided males was positively correlated with that of males abandoning females, and males that were unsuccessful at pairing met with higher rates of female resistance than successful males, suggesting that female behavior influences male pairing-success. Unlike unsuccessful males, successful males more often made the transition between display and maintaining physical control of the female. At high male sex ratios, males initiated courtship more readily; thus both sexual competition and female behavior influence male courtship in this species.

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## Introduction

An important concept that has influenced the evolution of many male and female pre-mating behaviors is that of intersexual conflict, when interests in mating differ between the sexes (Trivers 1972; West-Eberhard et al. 1987). The extent to which male and female interests influence mating depends on the level of control that each sex can exert on mating (Borgia 1979). In many species, females control when mating occurs because they are receptive for only a short period of time (Ridley 1983; Thornhill and Alcock 1983); thus their abundance and spatial distribution relative to that of males influences the ability of males to control how mating occurs (Emlen and Oring 1977). A male may control his limited opportunity to inseminate the female by temporarily pairing with her prior to mating, also known as precopulatory mate-guarding or precopula, and male courtship influences his ability to establish that pair bond (Parker 1974; Grafen and Ridley 1983). To determine the role of male courtship in the outcome of intersexual conflict and to understand how these behaviors evolved, it is important to identify the behaviors males use during courtship, the factors that control variation in courtship behavior among males, and how male courtship influences male mating-success.

In species that exhibit pre-copulatory mate-guarding, male mating-success is influenced by the ability of males to obtain a female and the amount of time males spend with each mate (Parker 1974). In many species, males mate more frequently by obtaining females that require short mate-guarding times (Manning 1975; Shuster 1981; Diesel 1988). Large males have advantages in aggressive interactions with other males for females, and in struggles with females to capture or physically control them (Berrill and Arsenault 1984; Atema 1986; Donaldson and Adams 1989). As a result, the mating behavior of males may vary based on their size, the array of competitors they face, and the availability of potential mates (Davies and Halliday 1979; Borgia 1980; Shuster

1989). In theory, variation in the ability of males to interact aggressively for females, male courtship behavior, and sex ratio produces the following: (1) at all sex ratios, large males spend less time guarding each female than small males, and (2) as females become rare, males search less, court more persistently, and guard longer because females that require longer guarding times are more numerous (Parker 1974; Grafen and Ridley 1983). However, this may create a conflict of interest between the sexes, if extended periods of guarding are costly to females (Christy 1987). As a result, females requiring longer guarding times may resist male guarding attempts, and males may alter their behavior from courtship to forced capture (Borgia 1980; Henmi et al. 1993).

In a variety of species, females exhibit some control over mating during pre-mating interactions with males (Thornhill 1979; West-Eberhard et al. 1987). Females may dictate how mating occurs to minimize the costs associated with mating (Walker 1980; Rowe et al. 1994; Weigensberg and Fairbairn 1994). In mate-guarding species, females may incur costs during guarding, including increased risk of injury during takeover attempts (Borgia 1980; Smith 1992) or pre-mating struggles (Donaldson and Adams 1989), increased vulnerability to predation (Strong 1973; Verrell 1985; Arnqvist 1989a), and decreased access to alternative mates or to food because the male feeds less during guarding (Robinson and Doyle 1985) and may determine the female's access to food. Therefore, females may prevent mate-guarding altogether (McCauley and Wade 1978; Berrill and Arsenault 1984; Arnqvist 1989b), or influence when and/or which males are successful at mate-guarding (Verrell 1983; Ward 1983b; Jormalainen and Merilaita 1993) by physically resisting males during pre-mating interactions. Females may selectively resist mate-guarding attempts by certain males in order to mate with others (Shuster 1981). Many of the costs to females of mate-guarding increase with the duration of guarding; therefore females that require short periods of guarding may resist less and court males (Strong 1973).

The blue crab *Callinectes sapidus* offers the opportunity to test if female behavior influences male courtship-behavior, which in turn may influence male pairing-success. Male and female courtship behavior in the blue crab has been described; however the behaviors that lead to pair formation, the factors that regulate courtship differences among males, and the relative control of each sex in determining mating success are unknown (Teytaud 1971). Female blue crabs typically mate once, immediately after their final (pubertal) molt to maturity (Van Engel 1958), when their exoskeleton is soft and they are vulnerable to predation (Shirley et al. 1990). Males court and pair with pre-pubertal females, and after copulation guard them from both predators and competitors (Van Engel 1958; Jivoff 1997). Females that are early in the final molt cycle may avoid prolonged guarding so as not to lose feeding opportunities that provide the necessary energy for the final molt. Alternatively, females that are late in the final molt cycle may

seek out males to avoid the risk of being unpaired during their soft, vulnerable phase.

Differences in female behavior related to female molt stage (Jivoff and Hines, 1998) suggest that, in contrast to male behavior towards late pre-pubertal females, male courtship towards early pre-pubertal females will consist of pursuit and attempts at forced capture rather than display behaviors, and that physically controlling them will be more difficult. Theory predicts that, as the sex ratio becomes more male-biased, males will court more diligently, for example by increasing their interactions with females, and display more vigorously (suggesting a role for female mate choice), or forgo display and try to forcibly capture females (suggesting that male–male competition is important) (Parker 1974).

This study (1) recorded the behaviors performed by males and females during pre-mating interactions; (2) tested the effect of female behavior on male courtship by comparing the behavior of males trying to pair with females of different molt stage; (3) tested how the availability of potential mates influences male courtship by comparing the behavior of males among different sex ratios, and (4) examined the influence of male courtship on pairing success by comparing the behavior of paired and unpaired males.

## Materials and methods

The research was carried out at the Smithsonian Environmental Research Center (SERC) on the Rhode River, a sub-estuary of Chesapeake Bay, in Maryland (38°51′N; 76°32′W) from mid-June through late September 1991 to 1994. All *Callinectes sapidus* used in experiments were collected in the field. Seines and trawls were sometimes used, but most specimens were taken with a dip net, two to three times per week, from the sides of 150 to 200 m-long commercial pound nets stretched between vertical posts near the mouth of the Rhode River. Crabs were transported to SERC, measured, separated by sex, and maintained in floating field cages in the Rhode River until used in experiments; they were fed fish daily. Subjects were never held in field cages for more than one week.

Field experiment

The effects of female molt stage and operational sex ratio were tested using field enclosures. Five circular (4.2 m diam × 1 m high), enclosures were deployed in shallow water (1 to 2 m deep) along the shoreline at SERC. The enclosures consisted of a plastic pipe (PVC) frame entirely covered with Vexar plastic mesh attached to the frame with plastic cable-ties. The top of each enclosure had two doors for adding, removing, and feeding crabs. Each enclosure was held in position by four wooden poles. During behavioral observations, the enclosures were lifted from the substrate and hung from the poles. Enough water (50 cm) remained in the enclosures to enable crabs to swim freely while allowing easy observation of all crabs in the murky estuarine water. An observer stood near an enclosure and recorded all interactions among all crabs on data sheets. The behavior of crabs in the enclosure was not influenced by crabs from adjacent enclosures. When observations were not being made, the enclosures were lowered to the substrate.

The experiment was a 2 × 5 design with two levels of female molt stage (early and late) and five levels of operational sex ratio (number of males: number of pre-pubertal females) as follows: 5:1, 4:2, 3:3, 2:4 and 1:5. The female molt stages used in the experiment fell within the range of molt stages of females found paired in the

field (Jivoff and Hines 1998), and female molt stage did not significantly influence whether a male performed courtship toward females ($\chi^2 = 2.39$, $df = 1$, $P = 0.122$), suggesting that females from both treatments equally elicited male courtship-behavior. Early-molt-stage females were 8 to 10 d pre-molt, and late-molt-stage females were no more than 4 d pre-molt. Each enclosure contained six crabs producing densities (0.5 crabs per $m^2$) consistent with summer peak densities in the Rhode River (Hines et al. 1987). Each replicate ($n = 8$) contained all ten combinations of female molt stage and sex ratio; however only five combinations could be run simultaneously. Therefore, early-molt-stage females were tested separately from late-molt-stage females. We alternated the order in which the levels of female molt stage occurred in each replicate to prevent observation biases among replicates. Each level of female molt stage lasted for two days. On the first day, each enclosure was randomly assigned a sex ratio and crabs were randomly assigned to the enclosures. Crabs were added to one enclosure at a time and each enclosure was then observed for 15 to 60 min (average observation time was $53.2 \pm 13.6$ SD min). Observation time did not influence the rates of male courtship ($n = 147$, $P = 0.520$), male persistence ($n = 147$, $P = 0.625$) or female resistance ($n = 164$, $P = 0.829$). On the second day, each enclosure was observed for 30 min, after which all crabs were removed from each enclosure. No crabs were reused between the levels of female molt stage or among replicates. Crabs were uniquely marked on the dorsal carapace with paint to distinguish them during observations.

In the enclosures, crabs typically encountered individuals in sequence rather than aggregations of crabs; hence the behavioral data reflect what occurred between each pair of crabs. Males often began courting females within several minutes of being introduced to the enclosure, and typically there was a period (5 to 30 min) of increased activity during which pairing occurred. We considered a male and female to be paired when they formed the pre-copulatory embrace for at least 1 min. The observation time on the first day was sufficient to observe the majority of interactions that lead to pairing. We tried to minimize the effect of confinement on the behavioral interactions between crabs, but we were not always successful. In some cases, the enclosures may have prevented resistant females from successfully avoiding male guarding-attempts or made it easier for unpaired males to capture resistant females and/or displace guarding males from females.

Data analysis

Behaviors were categorized as either: courtship, resistance or male persistence behaviors. Courtship behaviors were elicited in the presence of an opposite-sex crab and appeared to increase the courting crab's chances of pairing. Resistance behaviors prevented one crab from remaining close to another crab. Male-persistence behaviors occurred when females resisted male guarding-attempts, and appeared to enhance a male's chances of guarding the resistant female. Behavioral acts occurred in two different contexts: (1) specific actions were performed by one crab toward a second crab in the absence of any specific behaviors by the second crab, and (2) specific actions were responses by one crab to the behaviors performed by another individual. In each enclosure, each male may have come into contact with each female. However, a behavioral interaction, or one containing pre-mating behaviors, did not occur in all cases; thus, no courtship behaviors were performed (31% of males and 43% of females) or responses occurred (36% of males, 22% of females) between these dyads. We excluded those dyads from the behavioral analysis because they provided no data on the effect of female molt stage and sex ratio on intersexual behaviors that lead to pairing. Female molt stage did not significantly influence whether a female responded to the behavior of males ($\chi^2 = 2.44$, $df = 1$, $P = 0.118$), but late pre-molt females initiated behavioral interactions with males more often than early pre-molt females (Jivoff and Hines 1998). Sex ratios were not adjusted for crabs that had no intersexual interactions, since the presence of these crabs may have influenced the behavior of others during intrasexual interactions.

For each male, the frequency of each pair of behaviors that was performed in sequence (i.e. "behavioral sequence") towards each female was tallied. Observation times, the amount of time females remained unpaired, and the number of females that males had access to varied among the enclosures. Therefore, we standardized male behavior among enclosures by calculating the rate (number of each behavioral sequence per time the females remained unpaired per number of opposite-sex crabs in the enclosure) of each behavioral sequence that occurred between each intersexual dyad. In each enclosure, we summed the rates of each behavioral sequence that each male performed towards each female, because female size had no effect on the total rate of male courtship ($n = 203$, $P = 0.464$) nor on male persistence-behavior ($n = 203$, $P = 0.328$). Finally, we averaged the total rate of each behavioral sequence among males in each enclosure. A three-way non-parametric ANOVA ($H$) was used to test the effect of female molt stage (early or late), sex ratio (1:5, 2:4, 3:3, 4:2, 5:1), and male pairing-status (successful or unsuccessful), as well as the interactions between each pair of independent variables, on the mean rates of male behavioral sequences (Sokal and Rohlf 1981). Spearman rank correlation coefficients ($\rho_s$) were calculated between the mean rates of male behavioral sequences and that of female responses, and were tested for significance ($P < 0.05$) using the Student's $t$ distribution (Steel and Torrie 1980). The frequencies of behavioral sequences were also converted into discrete behavioral data (1: frequency $> 0$; 0: frequency $= 0$), and log-linear models were used to test if the percentage of males that performed each behavioral sequence was associated with female molt stage and male pairing-success (SYSTAT 1992).

## Results

There was considerable variation in the mean rates and sequence of behaviors that were influenced by both female molt stage and male pairing success in *Callinectes sapidus* (Fig. 1). The majority of intersexual behavioral interactions (male behaviors = 87%, male responses = 79%, female behaviors = 75%, female responses = 85%) including guarding, occurred on the first day; therefore, all data presented are from the first day of observation only.

Description of behaviors

*Courtship behaviors*

*Approach.* A male or female is elevated on the tips of the walking legs and moves towards another crab. Approach is often combined with chelae spread and paddling.

*Chelae spread.* A male or female lifts and fully extends the chelae laterally, with the dactyls closed. This is often combined with approach and paddling.

*Paddling.* The male or female's swimming paddles are held above the dorsal carapace and waved in a circular motion. The rate of waving varies, but often increases as the displaying crab moves closer to the other crab. Paddling is typically combined with approach and chelae spread.

*Paddle up.* The male or female swimming paddles are held above the carapace, however they are not waved in a circular motion.

**Fig. 1** *Callinectes sapidus.* Mean rates of behavioral sequences by successful (**a**), and unsuccessful (**b**) males towards early pre-molt females, and by successful (**c**), and unsuccessful (**d**) males towards late pre-molt females (see "Results – Description of behaviors") (*Width of each continuous line and size of its arrow* are proportional to mean rate of behavioral sequence they represent; *dashed lines* sequences performed at low rates by no more than two different males)

a Successful Male, Early Pre-molt Female

b Unsuccessful Male, Early Pre-molt Female

c Successful Male, Late Pre-molt Female

d Unsuccessful Male, Late Pre-molt Female
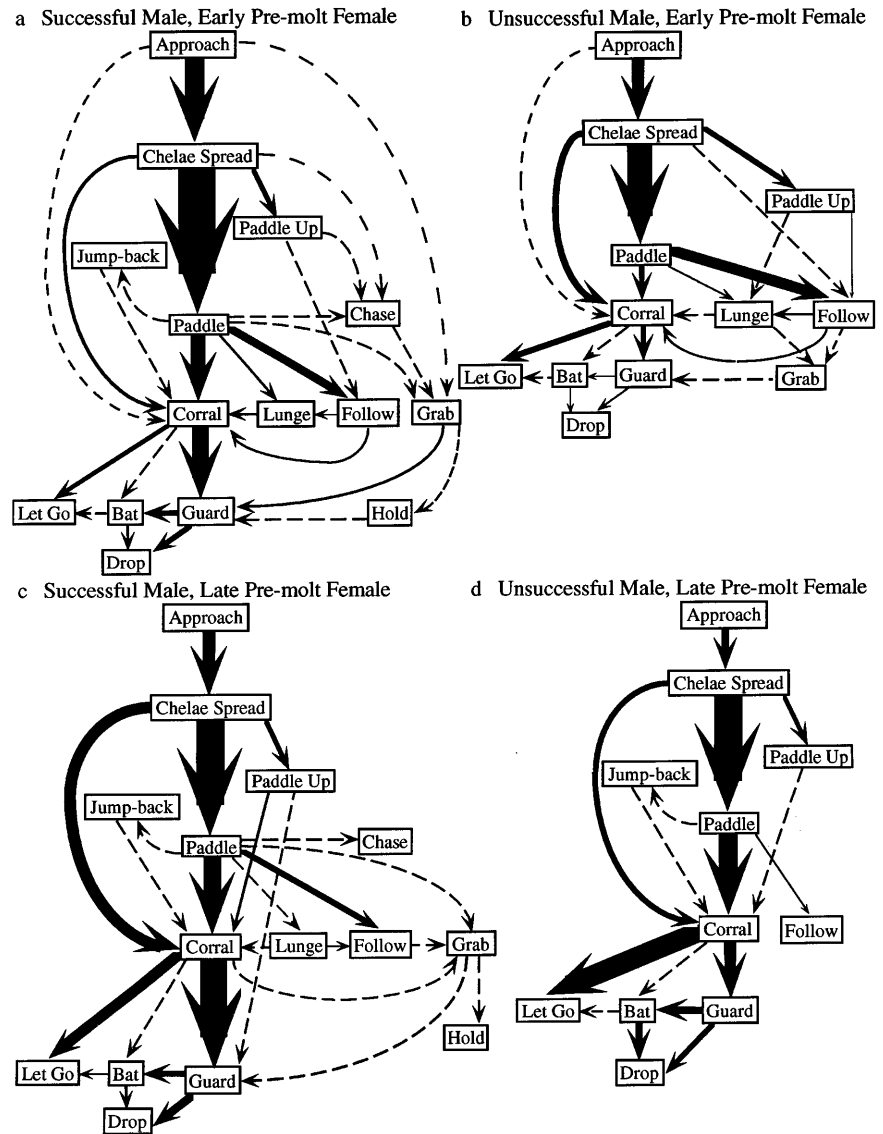
*Jump-back.* During paddling, the male lifts the anterior portion of his body, and then thrusts his body backwards with an extremely vigorous paddling motion.

*Corral.* A male (I have never seen a female corral another crab) moves his chelae inward from a laterally extended position to physically enclose a female between them and position the female beneath him such that both crabs face in the same direction.

*Let go.* The male simply lets a female go after corraling her (before a pre-copulatory embrace is established). This may occur for no apparent reason, during a takeover attempt, or due to female resistance.

*Pre-copulatory embrace.* Once the male is on top of the female, he wraps his first pair of walking legs under the female and carries her with his sternum against her dorsal carapace until immediately before copulation.

*Copulatory embrace.* Once the female has finished molting, the male flips her onto her dorsal carapace with his chelae such that his abdomen rests on hers, his walking legs cradle her, and they face in the same direction. Copulation begins once the female lifts her abdomen and the male inserts his pleopods into the exposed vulvae.

*Drop.* The male simply lets a female go from a pre-copulatory embrace. This may occur for no apparent reason, during a takeover attempt, or due to female resistance.

*Persistence behaviors*

*Follow/chase.* A male or female pursues another crab, while both are walking. A chase develops when both crabs are rapidly swimming. Unpaired males chase fe-

males to capture them and guarding males during takeover attempts.

*Lunge.* The male makes a large, forward movement towards the female, typically with his chelae extended to capture her.

*Grab/hold.* The male captures the female by grasping her with one or both of his chelae. Grabbing often occurs after following or chasing, but males also grab females without courtship and place them in the pre-copulatory embrace.

*Bat.* After the pre-copulatory embrace is formed, the female often lifts her chelae and waves them (see following subsection). A male responds to female chelae waving by hitting the female's chelae with his own.

### Resistance behaviors

*Wave.* After the pre-copulatory embrace is formed, the female may lift her chelae above her carapace and move them back and forth in front of her.

*Threat.* A male or female lifts and laterally spreads its chelae, usually with the dactyls open.

*Move away.* A male or female walks away from another crab, often combined with threatening.

*Flee.* A male or female swims rapidly away from another crab.

*Block.* A male or female lifts one chelae and presents it as a barrier to another crab.

*Push.* A male or female presses one chelae against another crab and moves the other crab.

*Poke.* A male or female lifts one chelae with the fingers closed and thrusts it at a second crab.

### Effect of female molt stage on male courtship-behavior

Female molt stage significantly influenced the mean rate of behavioral sequences that males performed during courtship. Males performed higher mean rates of behavioral sequences involving persistence behaviors such as paddle–follow ($H = 12.16$, $n = 122$, $P < 0.001$), follow–corral ($H = 4.86$, $n = 122$, $P < 0.05$) and grab–guard ($H = 4.33$, $n = 122$, $P < 0.05$) towards early pre-molt females than towards late pre-molt females (Fig. 2). Alternatively, males performed higher mean rates of behavioral sequences involving display (paddle–corral; $H = 4.06$, $n = 122$, $P < 0.050$), and of establishing physical control over the female (corral–guard; $H = 7.37$, $n = 122$, $P < 0.010$), but also of abandoning
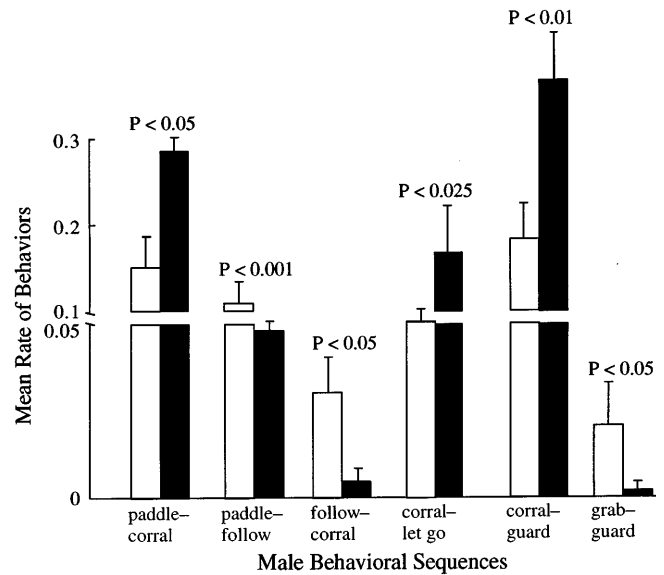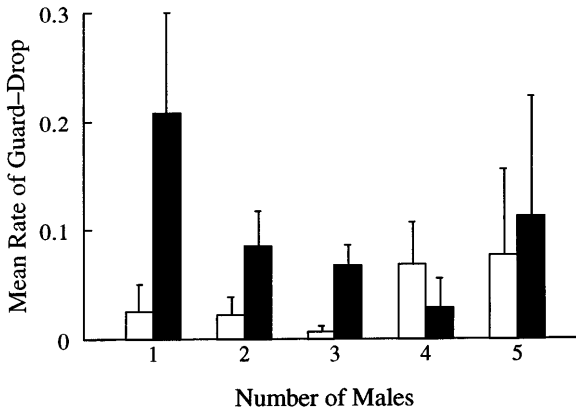


**Fig. 2** *Callinectes sapidus.* Mean rates of male behavioral sequences performed towards early (*open bars*) and late (*black bars*) pre-molt females in experimental field enclosures (*Vertical lines* + SE)

(corral–let go; $H = 5.58$, $n = 122$, $P < 0.025$), towards late pre-molt females than towards early pre-molt females (Fig. 2).

Late pre-molt females elicited higher mean rates of chelae spread–corral than early pre-molt females ($H = 4.34$, $n = 122$, $P < 0.05$), and there was a significant interaction between female molt stage and male pairing-success ($H = 5.82$, $n = 122$, $P < 0.025$), such that successful males more easily physically controlled late pre-molt females than unsuccessful males (Fig. 3). Males abandoned late pre-molt females more often than
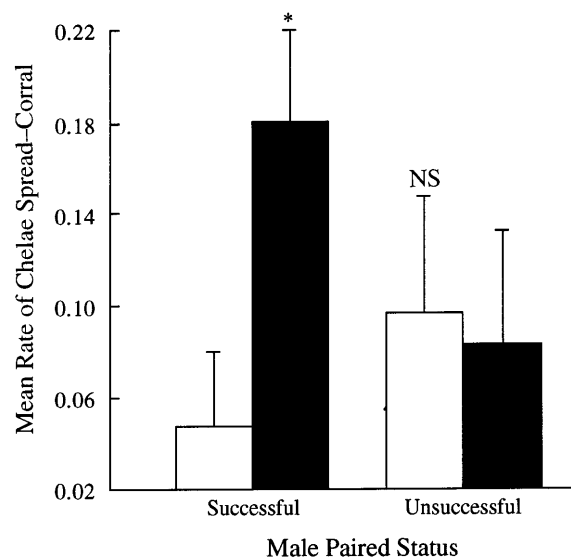


**Fig. 3** *Callinectes sapidus.* Mean rate of chelae spread–corral behavior by successful and unsuccessful males towards early (*open bars*) and late (*black bars*) pre-molt females in experimental field enclosures (*Vertical lines* + SE; * $P < 0.05$)

**Fig. 4** *Callinectes sapidus.* Mean rates of guard–drop performed by males towards early (*open bars*) and late (*black bars*) pre-molt females among five sex ratio levels in experimental field enclosures (*Vertical lines* +SE)

early pre-molt females by performing higher mean rates of guard-drop ($H = 5.99$, $n = 122$, $P < 0.025$); however, a significant interaction was found between female molt stage and sex ratio ($H = 11.31$, $n = 122$, $P < 0.025$), such that males more often abandoned late pre-molt females when females were abundant (Fig. 4). Overall, these results indicate that male courtship towards early pre-molt females involves more persistence than display, and that it is more difficult to establish physical control over them. Alternatively, male court-ship-display leads to establishing physical control over late pre-molt females, although they may be abandoned if other females are available.

### Effect of male courtship-behavior on male pairing-success

Male pairing-success was influenced by the ability of males to establish and maintain physical control of females. Males that successfully paired performed higher mean rates of corral–guard ($H = 15.18$, $n=122$, $P < 0.001$) but lower mean rates of corral–let go ($H = 5.57$, $n = 122$, $P < 0.025$) than unsuccessful males (Fig. 5). Furthermore, compared with unsuccessful males, a larger proportion of successful males made the transition from display to physically controlling late pre-molt females by performing chelae spread–corral ($\chi^2 = 9.03$, $df = 1$, $P = 0.003$) (Fig. 6).

### Effect of female resistance on male courtship and pairing success

Female resistance both before and after males had established physical control of females influenced male behavior and the ability of males to maintain physical control of females. As the total mean rate of early pre-molt female resistance increased, both successful males ($\rho_s = 0.58$, Student's $t = 3.89$, $df = 30$, $P < 0.001$) and
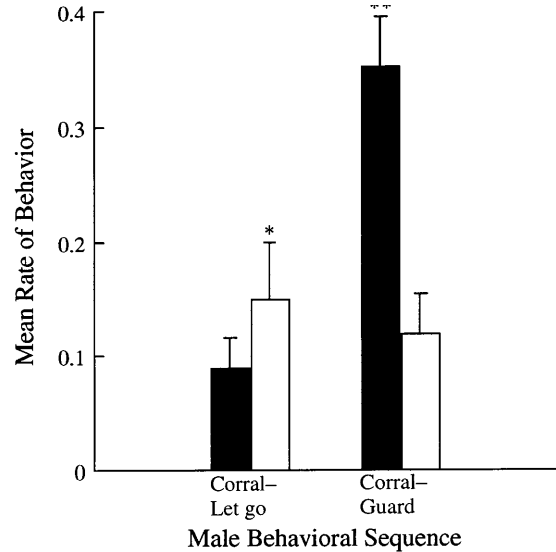


**Fig. 5** *Callinectes sapidus.* Mean rate of male behavioral sequences performed by successful (*black bars*) and unsuccessful (*open bars*) males in experimental field enclosures (*Vertical lines* +SE; *$P < 0.025$; ** $P < 0.001$)

unsuccessful males ($\rho_s = 0.89$, $t = 9.57$, $df = 24$, $P < 0.001$) increased the total mean rate of abandoning behaviors such as, corral–let go, bat–drop and guard–drop. However, successful males also attempted to overcome high mean rates of early pre-molt female resistance by increasing their mean rate of corral–bat ($\rho_s = 0.60$, $t = 3.23$, $df = 30$, $P < 0.01$). As the total mean rate of late pre-molt female resistance increased, both successful males ($\rho_s = 0.51$, $t = 3.69$, $df = 39$, $P < 0.01$) and unsuccessful males ($\rho_s = 0.65$, $t = 3.74$, $df = 19$, $P < 0.01$) increased the total mean rate of abandoning behaviors. Although both successful and
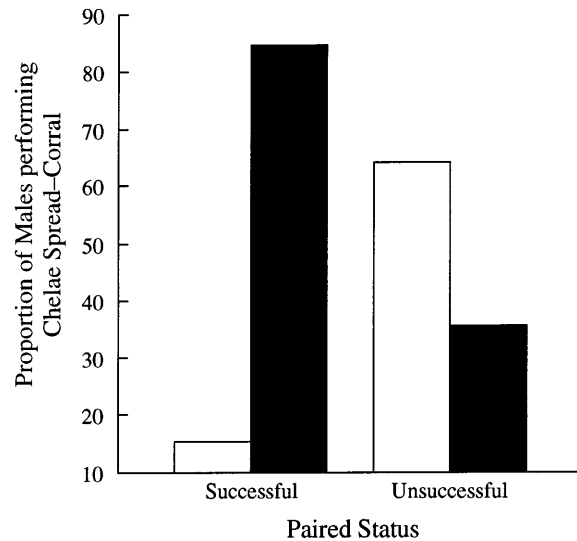


**Fig. 6** *Callinectes sapidus.* Proportion of successful and unsuccessful males performing chelae spread–corral towards early (*open bars*) and late (*black bars*) pre-molt females in experimental field enclosures
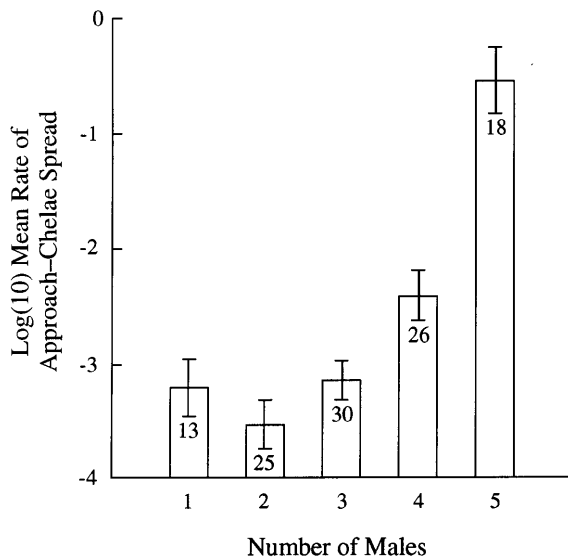
unsuccessful males more often abandoned highly resistant females, unsuccessful males met with a higher total mean rate of female resistance from both early (Mann-Whitney U-test = 528, $n = 58$, $P = 0.017$) and late pre-molt females (Mann-Whitney U-test = 594, $n = 62$, $P = 0.004$) than successful males, suggesting that lower levels of female resistance led to male pairing-success.

### Effect of male size on male courtship and pairing success

Males that successfully paired with early pre-molt females were not significantly larger than males paired with late pre-molt females (Students's $t = 1.16$, $df = 72$, $P = 0.249$). No significant difference was found between the size of successful and unsuccessful males ($t = 0.089$, $df = 120$, $P = 0.93$), however, as the size of males that successfully paired with late pre-molt females increased, they physically controlled females more often by performing higher mean rates of paddle–corral ($\rho_s = 0.37$, $t = 2.50$, $df = 40$, $P = 0.02$) and corral–guard ($\rho_s = 0.34$, $t = 2.31$, $df = 40$, $P < 0.05$).

### Effect of sex ratio on male courtship

Sex ratio had a significant effect on the mean rate of the behavioral sequence that is used to initiate a courtship display. Males performed the highest mean rate of approach–chelae spread at the highest male sex ratio ($F_{4,107} = 25.21$, $P < 0.001$) (Fig. 7). No significant differences were found in either the size of successful males ($F_{4,69} = 0.562$, $P = 0.691$), or that of unsuccessful males ($F_{4,43} = 1.01$, $P = 0.415$) among the sex ratios.

## Discussion

The courtship behavior of male blue crabs *Callinectes sapidus* is consistent with that of other portunids (Ryan 1966; Fielder and Eales 1972; Berrill and Arsenault 1982; Campbell 1982), and is similar to a variety of other crustaceans. For example, male blue crabs use their chelae to display to the female, and to control and/or manipulate the female prior to copulation. This behavior is widespread in crustaceans (crabs: Edwards 1964; Bigford 1979; Elner et al. 1987; Donaldson and Adams 1989; Perez and Bellwood 1989; Claxton et al. 1994; shrimps: Seibt and Wickler 1979; Nakashima 1995; lobsters: Lipcius et al. 1983; Atema 1986; Waddy and Aiken 1991; crayfish: Mason 1970; Ingle and Thomas 1974; Stein 1976; Snedden 1990). Female blue crabs actively participate in courtship and, as in many other crustacean species, female behavior towards males influences male pairing-success (amphipods: Strong 1973; Dick and Elwood 1989; Wen 1993; isopods: Shuster 1981; Jormalainen and Merilaita 1993; copepods: Durbaum 1995; anostracods: Forbes et al. 1992; crabs: Adams 1982; Henmi et al. 1993; crayfish: Berrill and Arsenault 1984). A unique aspect of courtship behavior in the blue crab compared with that of other non-swimming crabs, is the use of the specialized fifth set of appendages (swimming legs or paddles) as a courtship display. Paddling may be important as a visual display, but a strong current is also generated by the movement of the paddles and is directed towards the female due to the position of the male's body and the lateral extension of the chelae (Jivoff personal observation). Thus, paddling may also contain tactile and/or chemical information (Atema 1986; Cowan 1991; Gleeson 1991) carried in the strong directional currents thus produced.

The present results show that males use different courtship behavior towards females of different molt stage partly because female molt stage influences female behavior towards males. Early pre-molt females resist male mate-guarding attempts, while late pre-molt females initiate pre-copulatory mate-guarding with males (Jivoff and Hines 1998). Early pre-molt females typically resist by moving away from a displaying male, thus prevents the male from capturing her. The behavioral sequences performed at high rates towards early pre-molt females, such as paddle–follow and follow–corral, reflect high levels of female resistance to being guarded, whereas those performed towards late pre-molt females, such as chelae spread¯corral, and paddle–corral are consistent with increased female receptivity. Late pre-molt females show some resistance by waving their chelae or leaning away from the male, typically only after they have been corraled or embraced by the male. As a result, males, especially males that are unsuccessful at pairing, may abandon (e.g. let go or drop) late



**Fig. 7** *Callinectes sapidus*. Mean rate (log 10) of approach–chelae spread performed by males among five sex-ratio levels in experimental field enclosures. Pairwise comparisons between sex ratios are as follows: 5 > 4 ($P = 0.002$), 5 > 3 ($P < 0.001$), 5 > 2 ($P < 0.001$), 5 > 1 ($P = 0.004$) and 4 > 2 ($P = 0.002$) (*Numbers inside bars* sample sizes; *vertical lines* ±SE)

pre-molt females. This result suggests either, that female behavior influences how and when males can physically control females, or that unsuccessful males are somehow inferior to successful males. However, no size differences were found between successful and unsuccessful males. Alternatively, males that abandoned late pre-molt females did so more often when receptive females were abundant, suggesting that males may abandon one female in favor of another.

In other species, females make choices among potential mates by influencing which males physically control them (McCauley and Wade 1978; Shuster 1981; Snedden 1990). A female may make it more difficult for a male to control her to insure that she mates with a large male (Shuster 1981). In blue crabs and many other species, a male's size influences his ability to, (1) guard and/or protect the female during takeover attempts (Ridley and Thompson 1979; Berrill and Arsenault 1982; Ward 1983a; Berrill and Arsenault 1984; Jivoff and Hines 1998), which might result in damage to her (Borgia 1981; Smith 1992); (2) physically carry the female (Adams and Greenwood 1987; Crespi 1989) or copulate with her (Beninger et al. 1991); and/or (3) provide her with a large quantity of sperm (Wilber 1987; Sainte-Marie 1993; Jivoff 1995). Therefore, female resistance may represent a strategy for mating differentially with large males. Large males that successfully paired with late pre-molt females performed higher rates of paddle–corral and corral–guard than smaller males, suggesting an increased ability to make the transition from courtship display to establishing physical control of the female. In the field, large male blue crabs are over-represented in mate-guarding pairs (Jivoff 1995). However, in the enclosures no significant differences were found between the sizes of paired and unpaired males or between the sizes of males paired to females of different molt stage, suggesting that female resistance did not result in an increase in the size of paired males.

The results indicate that female molt stage not only influences the courtship behavior of males but, through its effect on female behavior, also influences male pairing-success. There are three pieces of evidence suggesting that female behavior towards males influences male pairing-success: (1) unsuccessful males met with higher rates of female resistance than successful males; (2) significant correlations between the rates of female resistance and that of males abandoning females; (3) differences between the behavior of successful and unsuccessful males that in some cases were modified by female molt stage. Compared with unsuccessful males, successful males performed higher rates of corral–guard but lower rates of corral–let go; thus, the ability to establish and maintain physical control of females is critical to male pairing-success. Similarly, as the rate of early pre-molt female resistance increased, only successful males responded with increased rates of persistence behaviors such as corral–bat, suggesting that actively subduing female resistance is also important for male pairing-success.

In a variety of species, males alter their mating behavior under more intense levels of sexual competition (Verrell 1983; Kodric-Brown 1988; McWilliams 1992; Grant et al. 1995). In the presence of competitors, male blue crabs try harder to capture females (Jivoff and Hines 1998), mate-guard for longer durations, and pass larger ejaculates (Jivoff 1997). Our results here show that all males present higher rates of approach–chelae spread at high male sex-ratios, suggesting that males initiate courtship more readily to compete for a limited supply of receptive females. Thus, when faced with greater levels of sexual competition, male blue crabs increase their investment in behavioral interactions with females, in the duration of mate-guarding, and in the amount of ejaculate passed to females. These aspects of increased male investment support the hypothesis that male–male competition regulates male behavior and reproductive success in the blue crab (Smith 1992; Jivoff 1995). The results here suggest that the behavior of females, as influenced by female molt stage, also plays a role in shaping the behavior of males that leads to male pairing-success.

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