

Female behaviour, sexual competition and mate guarding in the blue crab, *Callinectes sapidus*

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Abstract. Blue crabs mate immediately after the female's final moult. We tested the influence of female moult stage, sex ratio and male size on the pre-mating behaviour of both sexes, and the ability of males to pair with females and aggressively compete for access to females. We observed crabs in field enclosures and surveyed pre-copulatory mate-guarding patterns in the field. Female behaviour changed as they progressed through the final moult cycle, such that early moult-stage females avoided males, but late moult-stage females initiated pair formation. The changes in female behaviour influenced both the behaviour and pairing capability of males. Males courted and paired with late moult-stage females on their first attempt, but pursued early moult-stage females because their first attempts to pair often failed. In the field, early moult-stage females were paired less often than late moult-stage females. The pre-mating behaviour of both sexes also varied with sex ratio; when males were abundant, males traded courtship for forced capture and females courted less. Large males were more successful at take-overs, but did not pair more often with late moult-stage females, suggesting that large males do not consistently guard for less time than small males. The changes in female behaviour are consistent with the female's need to avoid the costs of guarding and suggest that females influence how pre-copulatory mate guarding occurs in this species.

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Intersexual conflict, when interests in mating differ between the sexes, has influenced the evolution of many male and female sexual behaviours (Trivers 1972; West-Eberhard et al. 1987). The extent to which male and female interests influence mating will depend 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 time (Ridley 1983; Thornhill & Alcock 1983). A male may control his limited opportunity to inseminate the female by temporarily pairing with her prior to mating, also known as pre-copulatory mate guarding or precopula (Parker 1974; Grafen & Ridley 1983).

Males control their mating success in a variety of ways. In species with pre-copulatory mate guarding, males mate more frequently by obtaining females that require short mate-guarding times (e.g. Manning 1975; Diesel 1988). Males also enhance their reproductive success by mating with larger, more fecund females (Ridley & Thompson 1985; Ward 1988). In many species, large males have advantages in aggressive interactions with other males for access to females and in struggles with females to capture or physically control them (e.g. Berrill & Arsenault 1982, 1984; Atema 1986; Donaldson & Adams 1989). As a result, males often have different mating strategies based on their size and the array of their competitors (e.g. Davies & Halliday 1979; Borgia 1980; Shuster 1989). A mathematical model for predicting the evolutionarily stable duration of precopula based on the differences in aggressive ability between males of different size produced two male mating strategies: (1) as females become rare, males search less and guard longer, because

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females that require longer guarding times are more numerous; (2) at all sex ratios, large males spend less time guarding each female than do small males (Grafen & Ridley 1983).

The Grafen & Ridley (1983) model has been criticized for ignoring the costs of guarding to females (Christy 1987). These costs may dictate female behaviour towards males, which gives females varying levels of control over mating (Ahnesjö et al. 1992). By resisting males during pre-mating interactions, females prevent mate guarding altogether (e.g. McCauley & Wade 1978; Berrill & Arsenault 1984; Arnqvist 1989a), determine which males are successful at mate guarding (Adams 1982; Ward 1983; Krupa et al. 1990; Jormalainen & Merilaita 1993) or selectively avoid certain males to mate with others (Shuster 1981; Snedden 1990). In some species, the costs of guarding to females change with the number of available mates; therefore, female behaviour towards males varies with sex ratio (Moore 1989; Rowe et al. 1994). In many crustaceans, females mate immediately after moulting, when their carapace is soft and they are vulnerable to predators (Hartnoll 1969), and males guard for some time prior to the female's moult and protect them during moulting. Therefore, as females approach the time of moulting, they resist less and court males more often (Strong 1973).

In the blue crab, *Callinectes sapidus*, females influence the way that mating occurs in several ways. Females typically mate once, immediately after their final (pubertal) moult to maturity (Van Engel 1958), when they are vulnerable to predators (Shirley et al. 1990). Pre-pubertal females attract males with a urinary-born pheromone that is released for several days before mating, and they actively participate in courtship behaviour with males (Teytaud 1971; Gleeson 1980). Thus, female behaviour may influence how and when pre-copulatory mate guarding begins. Pre-copulatory mate guarding can last 5–7 days (Jivoff 1995), but females in the early stages of the final moult cycle may avoid prolonged guarding. In blue crabs (Smith 1992) and other species (Borgia 1980), prolonged guarding increases the female's risk of injury during take-over attempts or pre-mating struggles (Donaldson & Adams 1989; Perez & Bellwood 1989) and the number of lost opportunities to feed, because males feed less during guarding (Robinson & Doyle 1985) and determine the female's access to food. Feeding

opportunities early in the final moult cycle provide the necessary energy for the final moult, because females discontinue feeding later in the moult cycle (Van Engel 1958); hence, early pre-moult females may avoid male guarding attempts. Alternatively, females that remain unpaired for too long risk predation during their vulnerable phase (Sivinski 1983), harassment from males (Arnqvist 1992) and missing their limited opportunity to mate.

In this study, we examined the relative control that each sex has over pair formation and how intersexual conflict over pre-copulatory mate guarding is resolved in blue crabs. We experimentally manipulated operational sex ratio and female moult stage, variables that influence the cost of guarding to females and the ability of males to pair with females, and examined their influence on the pre-mating behaviour of both sexes and the outcome of intersexual interactions.

Predictions

If the behaviour of female blue crabs allows them to control how mating occurs, then female behaviour will vary with their progress through to the final moult cycle, such that early pre-moult females will avoid the potential costs of prolonged guarding (for example, injury during take-overs, reduced feeding rate), but late pre-moult females will avoid the potential costs of being unpaired (such as predation and lost mating opportunities). Female behaviour will also vary with operational sex ratio, because males are expected to make repeated guarding attempts for females (i.e. persist; Parker 1974) and guard longer (Grafen & Ridley 1983) when females are in short supply. At male-biased operational sex ratios, the threat of extended guarding for early pre-moult females increases, but that of being unpaired for late pre-moult females decreases. Thus, early pre-moult females will avoid male attempts to guard, increasing avoidance with the number of males, but late pre-moult females will seek out males, decreasing the search as the sex ratio becomes male-biased.

If early pre-moult females resist male guarding attempts, then they will be more difficult to obtain. In other species, large males are more advantageous at obtaining resistant females (e.g. Berrill & Arsenault 1984; Donaldson & Adams 1989; Krupa & Sih 1993); hence, males guarding

early pre-moult females may be larger than males guarding late pre-moult females. Alternatively, large males are more advantageous at take-overs, so they may have greater access to late pre-moult females (Grafen & Ridley 1983). In a field experiment, we manipulated female moult stage, operational sex ratio and male size to test their effects on the pre-mating behaviour of both sexes and male pairing success, as a way of examining intersexual conflict in the blue crab.

METHODS

We conducted this research at the Smithsonian Environmental Research Center (SERC) on the Rhode River, a sub-estuary of Chesapeake Bay, in Maryland, U.S.A. (38°51'N, 76°32'W) from mid-June to late September 1991–1994. All crabs used were collected in the field. We sometimes used seines and trawls, but most specimens were taken with a dip net, two to three times/week, from the sides of commercial pound nets, 150–200 m long, stretched between vertical posts near the mouth of the Rhode River. We transported crabs to SERC where they were measured, separated by sex, and maintained in floating field cages in the Rhode River and fed fish daily until used in experiments. Subjects were never held in field cages for more than 1 week.

Data collected from field captured crabs included sex, paired status (pre-copulatory, post-copulatory, copulating or unpaired), moult stage (see below), sexual maturity (juvenile, pre-pubertal or pre-moult, mature), carapace width (distance, in mm, between the tips of the lateral spines) and the number and identity of autotomized limbs. We determined moult stage by examining the propodus on the fifth appendage for evidence of epidermal retraction and colour variation (Van Engel 1958). Pre-moult females were designated: early/D₀ (9–10 days pre-moult); early-mid/D₁ (7–8 days pre-moult); mid/D₂ (5–6 days pre-moult); mid-late/D₃ (3–4 days pre-moult) and late/D₄ (1–2 days pre-moult; Drach 1939). Pre-moult females have a triangular, darkened abdomen; adults have a semi-circular abdomen. We designated males sexually mature if the second pleopods lay within the first pleopods (intromittent organs), if the penes were inserted into the second pleopods and if the abdomen easily pulled away from the sternum (Van Engel 1990). We

used only mature, intermoult males that had both chelae and that were missing not more than one walking leg, which does not affect mating behaviour and/or mating success (Smith 1992).

Statistical Procedures

We analysed the field and experimental data using SYSTAT (SYSTAT 1992). In all instances, we tested data for normality using the Kolmogorov–Smirnov test and for homogeneous variances using the Bartlett's test (Sokal & Rohlf 1981). When transformed data failed to meet the assumptions of parametric tests, we used the appropriate non-parametric test. Procedures include linear regression, one-way ANOVA, non-parametric two-way ANOVA with unplanned comparisons to detect differences between treatments, the *t*-test, the combined probabilities test (Sokal & Rohlf 1981) and the *G*-test with Williams' correction. The Williams' correction was used because it improves the *G*'s approximation of the chi-square, especially when sample sizes are low (Sokal & Rohlf 1981). Means are presented with their standard error.

Quantifying the Behavioural Repertoire

We used descriptions of courtship (Teytaud 1971) and preliminary observations in the experimental enclosures to define the repertoire of behaviours and to identify the behaviours of each sex that influence pair formation. The behaviours fell into three categories, which we defined as courtship, resistance and male persistence behaviours (Table I). Courtship behaviours were elicited in the presence of an opposite sex crab and appeared to increase the courting crab's chances of pairing. Resistance behaviours prevented one crab from remaining close to another crab. Male persistence behaviours occurred when females avoided male guarding attempts and appeared to enhance a male's chances of guarding the resistant female. We describe only the behaviours that typically occur during male–female interactions (see also Jivoff 1995).

Field Experiment

We tested the effects of operational sex ratio, female moult stage and male size using field enclosures. Five circular (4.2 m diameter × 1 m

Table I. Description of behaviours by category based on preliminary observation in enclosures

Category/Behaviour	Performer	Description
Courtship		
Approach	Both sexes	Crab elevated on walking legs, moves towards another crab. Often combined with chelae spread and paddle.
Chelae spread*	Both sexes	Crab lifts and fully extends chelae laterally with fingers closed. Often combined with approach and paddle.
Paddle*	Both sexes	Crab's paddles (swimming legs) held above dorsal carapace and waved in circular motion. Rate of waving varies but often increases as the displayer moves closer to the other crab. Often combined with approach and chelae spread.
Corral	Male	Male moves chelae inward from a laterally extended position to physically enclose female between them and positions the female beneath him so both crabs face in same direction.
Pre-copulatory embrace*	Male	Once male is on top of female, he wraps his first pair of walking legs under her and carries her with his sternum against her dorsal carapace until just before copulation.
Copulatory embrace*	Male	Once female is done moulting, male flips her onto her dorsal carapace with his chelae so that his abdomen rests on hers, his walking legs cradle her and they face in the same direction. Copulation begins once female lifts her abdomen and male inserts his pleopods into her exposed vulvae.
Backing	Female	Female turns away from the male and moves beneath him into the pre-copulatory position.
Persistence		
Follow/chase	Both sexes	Crab pursues another crab while both are walking. A chase develops when both crabs are rapidly swimming. Unpaired males chase both females to capture them and guarding males during take-over attempts.
Resistance		
Threat*	Both sexes	Crab lifts and laterally spreads chelae towards another crab, usually with the fingers open.
Move away	Both sexes	Crab walks in the opposite direction of another crab, often combined with threat.

*Indicates behaviours previously described by Teytaud (1971).

high), enclosures were deployed in shallow water (1–2 m) 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 behavioural observations, the enclosures were lifted from the substrate and hung from the poles. Enough water (50 cm) remained in the enclosures so that crabs could swim freely while allowing easy observation of all crabs in murky estuarine water. An observer stood near the focal enclosure and recorded all interactions among all crabs on data sheets. The behaviour of crabs in the focal enclosure was not influenced by crabs from adjacent enclosures. When observations were not

being made, we lowered the enclosures to the substrate.

The experiment was a 2×5 design with two levels of female moult stage (early and late) and five levels of operational sex ratio (number of males: number of pre-moult females): 5:1, 4:2, 3:3, 2:4 and 1:5. Early moult-stage females were 8–10 days pre-moult, and late moult-stage females were no more than 4 days pre-moult. Each enclosure contained six crabs producing densities (0.5 crabs/m²) that were consistent with summer peak densities in the Rhode River (Hines et al. 1987). Each replicate ($N=8$) contained all 10 combinations of female moult stage and sex ratio, but only five combinations could be run simultaneously. Therefore, early moult-stage females were run separately from late moult-stage females. We alternated the order in which the levels of

female moult stage occurred in each replicate to prevent observation biases among replicates. Each level of female moult stage lasted 2 days. On the first day, we randomly assigned each enclosure a sex ratio and crabs were randomly assigned to the enclosures. We added crabs to one enclosure at a time, and each enclosure was then observed for 15–60 min (average \pm SD observation time = 53.2 ± 13.6 min). On the second day, we observed each enclosure for 30 min, after which all crabs were removed from each enclosure. No crabs were re-used between the levels of female moult stage or among replicates. We uniquely marked crabs on the dorsal carapace with paint to distinguish them during observations.

In the enclosures, crabs typically encountered individuals in sequence rather than in aggregations; hence, the behavioural 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 (5–30 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 behavioural 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

Behavioural acts occurred in two contexts: (1) specific actions were performed by one crab towards a second crab in the absence of specific behaviours by the second crab, and (2) specific actions were responses by one crab to the behaviours performed by another individual. In each enclosure, each male did not interact with each female, so sometimes no behaviours were performed (31% of males and 43% of females) and no responses (36% of males, 22% of females) occurred between these dyads. We excluded those dyads from the behavioural analysis because they provided no data on the effect of female moult stage and sex ratio on intersexual

behaviours that lead to pairing. Female moult stage did not significantly influence whether a female responded to the behaviour of males ($\chi^2_1 = 2.44$, $P = 0.118$) but did influence which females initiated behavioural interactions with males (see Results). Sex ratios were not adjusted for crabs that had no intersexual interactions, because the presence of those crabs may have influenced the behaviour of others during intrasexual interactions.

Observation times and the time that females remained unpaired varied among the enclosures. Therefore, we calculated rates (number of each behaviour per time the females remained unpaired per number of opposite-sex crabs in the enclosure) and proportions (number of each behaviour in the total of recorded behaviours) of each behaviour that occurred between each intersexual dyad. In each enclosure, we averaged the rates as well as the proportions of each male's behaviour towards different sized females, because male behaviour did not vary significantly with female size (Table II). We did the same for each female's behaviour towards different sized males, because male size did not significantly influence the behaviours females performed or the responses of females towards males (Table II). Neither male nor female behaviour rates changed significantly with observation time (Table II). The continuous behaviours that were performed by few individuals, at low rates (less than one per hour) and that were uncommon (less than 2% of total behaviours) were not included in the analyses, because they had little influence on the outcome of interactions between crabs.

We tested the effect of female moult stage and operational sex ratio on the individual behaviours within each category (courtship, persistence, resistance) using non-parametric two-way ANOVA. The individual behaviours within each category were not completely independent events, so we adjusted alphas for statistical comparisons involving the individual behaviours as follows: $a' = 1 - (1 - 0.05)^{1/b}$, where b is the number of behaviours in the category (Sokal & Rohlf 1981). The adjusted values were as follows: male and female courtship behaviours (0.013), resistance behaviours (0.025) and male persistence behaviours (0.025). We tested the effect of female moult stage and operational sex ratio on each behavioural category with the combined probabilities test ($CP\chi^2$) using the significance values

Table II. *P*-values for several linear regression comparisons

Comparison	<i>N</i>	Rates			Proportions		
		Courtship	Persistence	Resistance	Courtship	Persistence	Resistance
Male behaviour versus female size	203	0.464	0.328	—	0.932	0.354	—
Female performance versus male size							
Early	20	0.479	—	0.479	0.285	—	0.123
Late	111	0.281	—	0.171	0.989	—	0.989
Female response versus male size							
Early	127	0.137	—	0.378	0.666	—	0.571
Late	99	0.166	—	0.071	0.859	—	0.937
Male behaviour versus observation time	147	0.520	0.625	—	—	—	—
Female behaviour versus observation time							
Performance	90	0.497	—	0.843	—	—	—
Response	164	0.644	—	0.829	—	—	—

from the tests of the individual behaviours within each category (Sokal & Rohlf 1981).

We considered each bout of courtship and/or persistence behaviour that a male directed towards a female an attempt to pair with her. We examined the effect of female moult stage (early versus late) and male pairing success (paired versus unpaired) on the number of attempts males made to pair with females with a *t*-test. We used a *G*-test to test whether female moult stage was associated with both the female's response towards a male's first attempt and a male's success at pairing on his first attempt. We compared the average proportion of early and late pre-moult females that were paired with one-way ANOVA for crabs both in the field and in the enclosures.

RESULTS

In some cases, females initiated intersexual interactions, and late pre-moult females did so more often than did early pre-moult females ($\chi^2_1 = 51.42$, $P < 0.0001$). The majority of intersexual interactions (male behaviours = 87%, male responses = 79%, female behaviours = 75%, female responses = 85%), including pairing, occurred on the first day; therefore, all of the data presented are from the first day of observation only.

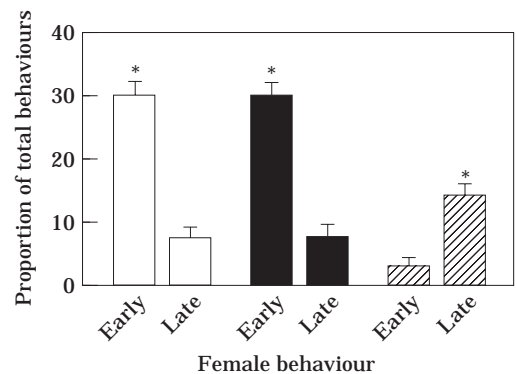


Figure 1. Proportion \pm SE of threats (□), moving away (■) and backs (▨) performed by early and late pre-moult females in response to males in experimental enclosures. * $P < 0.001$.

Do Early Pre-moult Females Avoid Male Guarding Attempts?

Early pre-moult females performed a greater proportion of resistance behaviours in response to males than did late pre-moult females ($CP\chi^2_4 = 43.28$, $P < 0.001$); that is, early pre-moult females performed greater proportions of moving away ($H = 16.18$, $N = 67$, $P < 0.001$) and threats ($H = 19.25$, $N = 67$, $P < 0.001$) in response to males than did late pre-moult females (Fig. 1). The

interaction between female moult stage and sex ratio for the proportions of moving away ($H=1.04$, $N=67$, $P=0.903$) and threats ($H=2.01$, $N=67$, $P=0.735$) was not significant. Early pre-moult females also responded to males with greater rates of resistance behaviours than did late pre-moult females ($CP\chi^2_4=44.66$, $P<0.001$); that is, early pre-moult females moved away from ($H=16.32$, $N=68$, $P<0.001$) and threatened ($H=19.43$, $N=68$, $P<0.001$) males at greater rates than did late pre-moult females. The interaction between female moult stage and sex ratio for the rates of moving away ($H=2.11$, $N=68$, $P=0.717$) and threats ($H=3.06$, $N=68$, $P=0.552$) was not significant.

Late pre-moult females responded to male behaviours with a greater proportion ($CP\chi^2_4=20.46$, $P<0.001$) and rate ($CP\chi^2_4=14.84$, $P<0.005$) of courtship behaviours than did early pre-moult females; that is, late pre-moult females responded to males with a larger proportion ($H=12.87$, $N=67$, $P<0.001$; Fig. 1) and higher rate ($H=9.78$, $N=68$, $P=0.002$) of backing than early pre-moult females. The interaction between female moult stage and sex ratio for the proportion ($H=1.08$, $N=67$, $P=0.897$) and rate ($H=1.07$, $N=68$, $P=0.898$) of backing was not significant. No significant relationship was found between female size and the rate of early ($N=84$, $P=0.450$) or late ($N=80$, $P=0.236$) pre-moult female resistance or between female size and the rate of early ($N=84$, $P=0.291$) or late ($N=80$, $P=0.595$) pre-moult female courtship.

Does Female Behaviour Change Across Sex Ratios?

Operational sex ratio had a significant effect on the rate of late pre-moult female courtship behaviour ($CP\chi^2_8=19.43$, $P=0.014$) but not on the rate of early pre-moult female courtship ($CP\chi^2_8=7.69$, $P=0.477$); that is, sex ratio had a significant effect on the rates of approaches ($H=11.75$, $N=32$, $P=0.021$) and chelae spreads ($H=9.48$, $N=32$, $P=0.050$) performed by late pre-moult females. Late pre-moult females performed the greatest rates of both approaches and chelae spreads when they had access to only one male. A significant linear decrease occurred in the rates of late pre-moult female approaches ($Y=0.428X-0.084$, $N=32$, $P=0.012$) and chelae

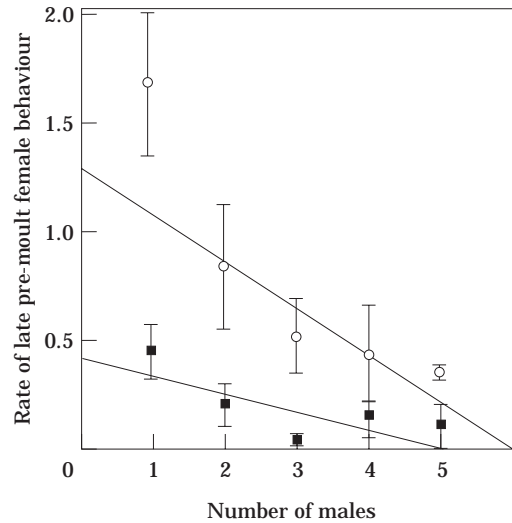


Figure 2. Rate \pm SE of approaches (○) and chelae spreads (■) performed by late pre-moult females towards males according to the number of males in the experimental enclosures. Unplanned comparison results are as follows: approaches 1>2,3,4,5 ($P<0.05$); chelae spreads 1>2,3,4,5 and 2>5.

spreads ($Y=1.73X-0.332$, $N=32$, $P<0.001$) as the number of males increased (Fig. 2).

Do Males Make Repeated Attempts to Guard Early Pre-moult Females?

Males performed a higher rate ($CP\chi^2_4=19.62$, $P<0.001$) and proportion of ($CP\chi^2_4=20.72$, $P<0.001$) persistence behaviours towards early pre-moult females than towards late pre-moult females; that is, males performed a greater proportion ($H=13.66$, $N=68$, $P<0.001$; Fig. 3) and rate ($H=12.61$, $N=68$, $P<0.001$) of follows towards early pre-moult females than late pre-moult females. The interaction between female moult stage and sex ratio for the rate ($H=1.42$, $N=68$, $P=0.837$) and proportion ($H=2.98$, $N=68$, $P=0.566$) of follows was not significant.

Males performed a greater proportion of courtship behaviours towards late pre-moult females than early pre-moult females ($CP\chi^2_8=31.20$, $P<0.001$); that is males performed a greater proportion ($H=19.98$, $N=68$, $P<0.001$; Fig. 3) and a greater rate ($H=10.59$, $N=68$, $P=0.002$) of corrals towards late pre-moult females than early pre-moult females. The interaction between female moult stage and sex ratio for the proportion



Figure 3. Proportion \pm SE of follows (\square) and corrals (\blacksquare) performed by males towards early and late pre-moult females in the experimental enclosures. * $P < 0.001$.

($H = 0.153$, $N = 68$, $P > 0.995$) and rate ($H = 2.12$, $N = 68$, $P = 0.715$) of corrals was not significant.

Does Male Behaviour Change Across Sex Ratios?

Operational sex ratio had a significant effect on the rate of courtship behaviour that males performed towards both early ($CP\chi^2_8 = 16.13$, $P = 0.042$) and late ($CP\chi^2_8 = 24.98$, $P = 0.002$) pre-moult females; that is, sex ratio had a significant effect on the rate of approaches that males performed towards both early ($H = 16.93$, $N = 33$, $P = 0.003$) and late ($H = 12.83$, $N = 35$, $P = 0.013$) pre-moult females, as well as the rate of chelae spreads that males performed towards late pre-moult females ($H = 13.73$, $N = 35$, $P = 0.009$). Males performed the lowest rates of approaches towards both early and late pre-moult females, and low rates of chelae spreads towards late pre-moult females when the number of females was twice that of males (Fig. 4). There was a significant linear increase in the rates of approaches ($Y = 0.081X + 0.157$, $N = 35$, $P = 0.028$) and chelae spreads ($Y = -0.042X + 0.242$, $N = 35$, $P = 0.015$) that males performed towards late pre-moult females as the number of males increased.

Operational sex ratio also had a significant effect on the proportion of courtship behaviour that males performed towards early pre-moult females ($CP\chi^2_8 = 24.17$, $P = 0.003$). Specifically, sex ratio had an effect on the proportion of approaches ($H = 11.88$, $N = 33$, $P = 0.019$), chelae spreads ($H = 11.41$, $N = 33$, $P = 0.023$) and paddles ($H = 9.58$, $N = 33$, $P = 0.048$) that males performed

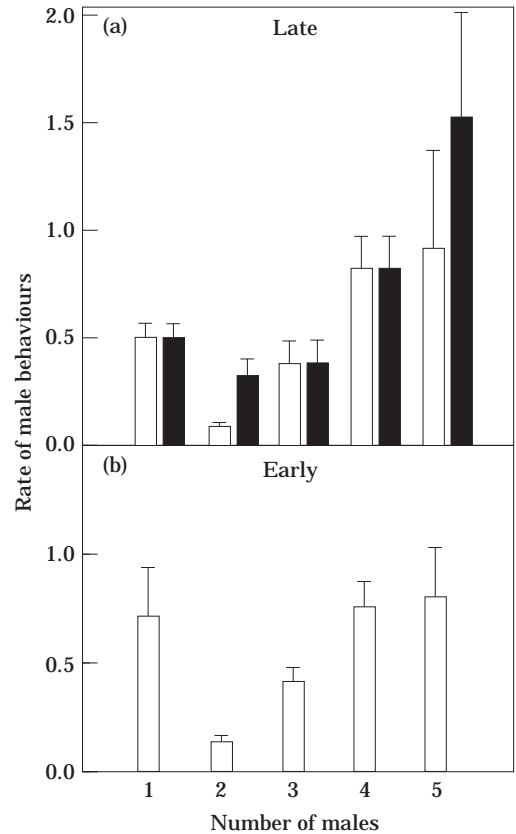


Figure 4. Rate \pm SE of approaches (\square) and chelae spreads (\blacksquare) that males performed towards (a) late and (b) early pre-moult females according to the number of males in the experimental enclosures. Unplanned comparison results are, for male approaches towards both early pre-moult females, 1,3,4,5 > 2 and 5 > 3 ($P < 0.05$), and late pre-moult females 1 > 2, 3 > 2, 4 > 1, 2, 3 ($P < 0.05$) and for male chelae spreads towards late pre-moult females 4 > 1, 2, 3, and 5 > 1, 3 ($P < 0.05$).

towards early pre-moult females. Males performed the smallest proportion of approaches towards early pre-moult females when the number of females was twice that of males, but performed small proportions of chelae spreads and paddles when males outnumbered females (Fig. 5). There was a significant linear decrease in the proportions of chelae spreads ($Y = 0.385X - 0.040$, $N = 33$, $P = 0.012$) and paddles ($Y = 0.233X - 0.034$, $N = 33$, $P = 0.003$) that males performed towards early pre-moult females as the sex ratio became male-biased.

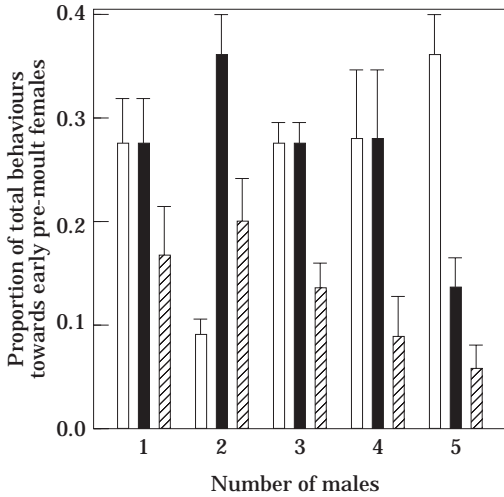


Figure 5. Proportion \pm SE of approaches (\square), chelae spreads (\blacksquare), and paddles (\hbar) that males performed towards early pre-moult females according to the number of males in the experimental enclosures. Unplanned comparison results for approaches are 1,3,4,5>2 ($P<0.05$), for chelae spreads: 1,2,3,4>5 ($P<0.05$) and for paddles: 1,2,3>5 ($P<0.05$).

Are Early Pre-moult Females More Difficult to Guard?

In the enclosures, female moult stage did not influence the proportion of pairs that formed ($H=1.80$, $N=69$, $P=0.261$). The majority (86.5%) of paired males obtained their female on the first attempt and the proportion of unsuccessful first attempts was greater in interactions with early pre-moult females than late pre-moult females ($G_1=42.04$, $P<0.001$). Early pre-moult females resisted the first attempts of males while late pre-moult females courted males more often ($G_1=83.9$, $P<0.001$). Males that successfully paired with early ($t_{81}=3.4$, $P=0.001$) and late ($t_{65}=5.5$, $P<0.001$) pre-moult females made fewer guarding attempts than males that remained unpaired. In the field, the proportion of females that were paired increased as females approached the time of moulting and, for mid to late pre-moult females, increased as the mating season progressed in 1991, 1992 and 1993 (Fig. 6). The proportion of late pre-moult females that were paired was larger than that of early pre-moult females ($t_6=8.16$, $P<0.001$).

Does Female Moult Stage Influence the Pairing Success of Different Sized Males?

In the enclosures, paired males were larger than unpaired males ($F_{1,144}=5.32$, $P=0.022$). Female moult stage did not significantly influence the pairing success of different sized males. Males that paired with early pre-moult females ($\bar{X} \pm \text{SE} = 143.43 + 1.94$, $N=35$) were not significantly larger than males that paired with late pre-moult females ($141.20 + 1.43$, $N=59$; $t_{92}=0.936$, $P=0.352$). In the field, female moult stage may have influenced the pairing success of different sized males but in an inconsistent pattern. In 1992, males that paired with late pre-moult females were larger than males that paired with early pre-moult females ($t_{123}=2.24$, $P=0.027$); in 1993, the reverse occurred ($t_{148}=2.80$, $P=0.006$).

Does Sex Ratio Influence the Pairing Success of Different Sized Males?

In the enclosures, operational sex ratio did not influence the pairing success of males based on their size. There were no differences in paired male size among the five sex ratios in the early ($H_4=0.696$, $P=0.952$) or late ($H_4=6.84$, $P=0.145$) pre-moult female treatments. No significant relationship was found between male size and the rate of male courtship behaviour ($N=145$, $P=0.634$) or between male size and the rate of male persistence behaviour ($N=145$, $P=0.480$). In the field, sex ratio (of crabs captured at the pound nets) may have influenced the size differences between males paired to pre-moult females of different moult stage. Each month during 1992 (when larger males were paired with late rather than early pre-moult females) had male-biased sex ratios, but 3 of 4 months during 1993 (when larger males were paired with early rather than late pre-moult females) had female-biased sex ratios. August was the only month in 1993 when males that paired with early pre-moult females were larger than males paired with late pre-moult females ($t_{95}=2.11$, $P=0.038$), and this was the most female-biased month in all years (number of males/number of females=0.55).

In the enclosures, operational sex ratio had a significant effect on the proportion of pairs that formed ($H=16.10$, $N=69$, $P=0.003$) with the lowest proportion occurring under the equal sex ratio as compared to either the female-biased or male-biased sex ratios (Fig. 7). There was a significant

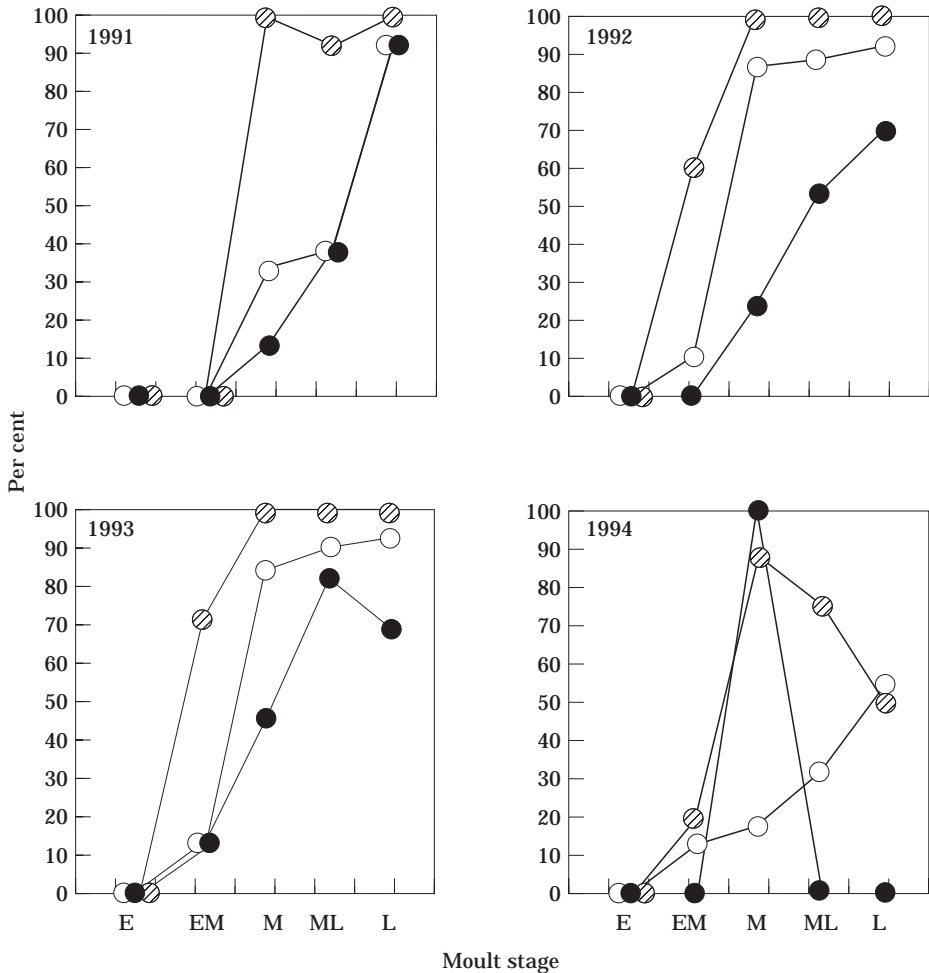


Figure 6. Per cent of paired pre-moult females from each moult stage (E=early, EM=early-mid, M=mid, ML=mid-late and L=late) in the field during the first (●), second (○) and third (⊗) portions of each mating season. The proportion of paired females increased significantly with moult stage ($P < 0.001$) in each year: $G = 177.02$ (1991), $G = 174.71$ (1992), $G = 592.31$ (1993), $G = 89.66$ (1994). In 1991, females were placed into fewer moult stage categories than other years. Crab abundance was low in 1994.

quadratic relationship between the proportion of pairs that formed and the number of males ($Y = 1.283X - 0.449 + 0.076$, $N = 69$, $P = 0.005$).

Does Male Size Influence Take-over Success?

The size difference between paired and unpaired males in the enclosures may have been the result of male-male competition for females. Males successful at displacing guarding males from females were larger than the ousted males (paired $t_{17} = 2.62$, $P = 0.018$) and guarding males successful

at preventing displacement were larger than their aggressors (paired $t_{12} = 3.12$, $P = 0.009$; Fig. 8). Successful take-overs occurred in 10.4% of the incidences of guarding and were not significantly associated with female moult stage ($G_1 = 0.095$, $P > 0.05$) or sex ratio ($G_3 = 0.055$, $P > 0.05$).

DISCUSSION

Our results indicate that the behaviour of female blue crabs towards males changes as females

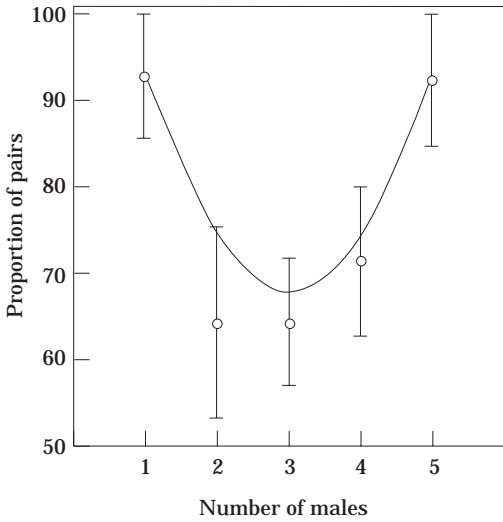


Figure 7. Proportion \pm SE of pairs that formed according to the number of males in the experimental enclosures. Unplanned comparison results are as follows: 1>2 ($P=0.021$), 1>3 ($P=0.009$), 1>4 ($P=0.024$), 5>2 ($P=0.028$), 5>3 ($P=0.001$) and 5>4 ($P=0.031$).

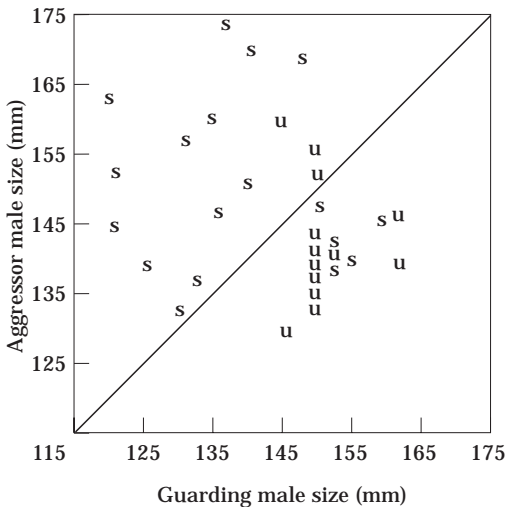


Figure 8. Distribution of successful (s) and unsuccessful (u) take-overs according to the sizes of the guarding male and the unpaired aggressor occurring in experimental enclosures. Successful take-overs resulted in the displacement of the guarding male; unsuccessful attempts did not.

progress through their final moult cycle. Early pre-moult females resisted male guarding attempts by threatening and moving away from males, but

late pre-moult females initiated mate guarding with males by backing under them. As the sex ratio became male-biased, late pre-moult females reduced their rate of courtship towards males. Behavioural differences among pre-moult females influenced both male behaviour and how easily males paired with females. Males more often failed on their first attempt to pair with early pre-moult females and thus pursued them but easily corralled late pre-moult females into the pre-copulatory embrace. Obtaining females efficiently is important for male pairing success, since the majority (86.5%) of males that successfully paired did so on their first attempt. In the field, there was a sharp increase in the proportion of females that were paired once they passed the early stages of the final moult cycle. Female moult stage did not significantly affect the pairing success of males based on their size, but large males had advantages in displacing smaller males from females and in preventing their own displacement.

The results suggest that female blue crabs have some behavioural control over how pre-copulatory mate guarding occurs. Females are expected to exert control over mating to balance the costs and benefits of mating (Thornhill & Alcock 1983; Rowe et al. 1994). In other species, the costs and benefits of guarding to females are influenced by the level of sexual competition among males (Borgia 1980; Arnqvist 1992) and the threat of predation (e.g. Gwynne 1989; Sih et al. 1990; Magnhagen 1991). Crustaceans are unique in that mating is often coupled with female moulting (e.g. Hartnoll 1969; Lipcius 1985; Ridley & Thompson 1985), when females are especially vulnerable to predation and physically incapable of exerting control over mating. Additionally, male mating success is often dictated by the competition for access to females prior to their moult (Stein 1976; Christy 1987; Christy & Salmon 1991) when females are able to exert control over mating. Thus, the changes we observed in the behaviour of pre-moult females towards males with their proximity to moulting and the level of sexual competition suggest that females are responding to the potential costs and benefits of guarding.

The way that pre-moult female behaviour varies with their progress through the final moult cycle is consistent with the female's need to avoid the potential costs of mate guarding. Early

pre-moult females resisted male guarding attempts, suggesting that prolonged mate guarding is costly to females. Prolonged guarding increases the probability of aggressive encounters with unpaired males (Parker 1974), which can result in female injury (Donaldson & Adams 1989; Smith 1992) and reduces feeding opportunities needed for the final moult. Late pre-moult females initiated mate guarding with males, suggesting that these females pay a high cost when they are not paired. This is especially true in blue crabs, because females have a single mating opportunity during their final soft phase; hence, unpaired females risk both predation and forgoing mating.

The variation in female behaviour with the level of sexual competition among males also reflects changes in the potential costs of guarding to females. As males became abundant, late pre-moult female courtship decreased, suggesting a lesser need to attract males when finding a mate is likely, especially if females risk injury when courted by multiple males (Borgia 1981; Howard & Kluge 1985). Male-biased sex ratios also provide females with increased opportunities to choose particular males. As in other species, we might expect female blue crabs to choose large males because of their increased ability to successfully carry (Adams & Greenwood 1983, 1987) and/or protect the vulnerable female (Atema 1986) or because of their increased encounter rates with large males (Forbes *et al.* 1992). Early pre-moult females did not selectively resist small males, however, nor did late pre-moult females preferentially initiate mate guarding with large males, suggesting that the behavioural changes in females are not a mate choice strategy for large males.

The effect of female behaviour on that of males and male pairing capability suggests that females have some behavioural control over when pre-copulatory mate guarding begins. Males had to follow early pre-moult females to pair with them and more often failed on their first attempt to obtain early pre-moult females, suggesting that it is easier to pair with late pre-moult females. Furthermore, when early pre-moult females were in short supply, males performed fewer courtship displays (paddling and chelae spreads) but initiated more interactions with females suggesting that males altered their strategy for obtaining resistant females from courtship to forced capture. In the field, females in the earlier part of the final moult cycle are more abundant than those in the

later portion, because the duration of the later stages is much shorter. However, late pre-moult females were more often paired than early pre-moult females, suggesting that early pre-moult females avoid being guarded while late pre-moult females seek out males. In other species, females can influence when mating occurs by controlling their progress through the moult cycle (Cowan & Atema 1990), the frequency of interactions with males by controlling the release of an attractive pheromone (Christofferson 1978), or the duration of pre-copulatory mate guarding by resisting males during guarding (Jormalainen & Merilaita 1995). Female behaviour prior to pairing with males may influence the duration of pre-copulatory mate guarding by determining when guarding begins.

Interactions between males rather than between males and females of different moult stage may influence the size of males that successfully pair. Large males more often displaced guarding males and prevented displacement during encounters for females, suggesting that large males are more advantageous in aggressive interactions for access to females. In a variety of species, large males are more advantageous in direct competition for females (e.g. Shuster 1981; Salmon 1983; Ridley & Thompson 1985). As in other species, large male blue crabs have proportionately longer chelae (P. Jivoff, unpublished data), which provide an advantage during aggressive interactions for females (e.g. Stein 1976; Berrill & Arsenault 1984; Claxton *et al.* 1994) as well as in physically controlling females (e.g. Arnqvist 1989b; Snedden 1990; Lee 1995). In the enclosures, however, we found no difference between the size of males that paired with females of different moult stage, and in the field there was no consistent pattern between the size of paired males and their mate's moult stage. These results suggest that males do not differ in their ability to physically control females of different moult stage and that pre-copulatory mate guarding durations do not differ among males.

In contrast to theoretical expectations (Grafen & Ridley 1983), our results suggest that male blue crabs do not change their strategy for obtaining females as they become larger. For large male blue crabs to spend consistently less time guarding, they must specialize on late pre-moult females. Large males were not consistently over-represented in pairs with late pre-moult females,

however, suggesting that males may be unable to specialize on them. Unpaired late pre-moult females are relatively rare, because they are easily controlled and seek out males. As a result, longer periods of searching and take-overs are essential for specializing on late pre-moult females as predicted by theory (Grafen & Ridley 1983). In the enclosures, however, the frequency of take-overs was only 10.4%, even though the opportunities for take-overs may have been increased due to elevated encounter rates. Furthermore, males in the enclosures tried harder to pair with early pre-moult females as they became rare, and in the field, as the mating season progressed, males paired with females of earlier moult stages. Both results suggest that males are willing to guard longer as mating opportunities become rare. Thus, for male blue crabs, longer periods of mate guarding offer a higher probability of mating for a given investment of time than increased searching for females that require short periods of guarding.

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