The influence of sexual selection and predation on the mating and postcopulatory guarding behavior of stone crabs (Xanthidae, *Menippe*)

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Summary. Postcopulatory mate guarding in crustaceans traditionally has been viewed as a behavioral mechanism that prevents predation on the soft post-molt female. This study tests the effects of sexual selection and predation on the postcopulatory guarding durations of male stone crabs, *Menippe mercenaria*, *M. adina*, and their hybrid. Male stone crabs were held with a pre-molt female, and either another adult male stone crab, an intermolt female, or a male blue crab, which corresponded to intermale competition, control, and predation treatments, respectively. The mating behavior of the heterosexual pair was recorded with a time lapse video system and the durations of copulation and postcopulatory guarding were measured. Males guarded longer in the intermale competition treatment than either the control or predation treatments. In the competition treatment, agonistic encounters occurred between the males at the den containing the female and several mate takeovers occurred. Females survived the predation treatment in trials in which the guarding durations were the longest, whereas females were eaten by the blue crab in trials with the shortest guarding durations. Sexual selection appears to be important in maintaining postcopulatory mate guarding in stone crabs.

Introduction

Postcopulatory mate guarding commonly occurs in insects (reviewed in Thornhill and Alcock 1983) and those crustacean species that mate only when the female's exoskeleton is soft (Hartnoll 1969). Benefits of guarding have been more throughly ex-

amined in insects. In this taxon, postcopulatory guarding is a behavioral mechanism that prevents sperm competition (Parker 1970a; Waage 1979), i.e., by guarding, a male prevents other males from inseminating his mate(s) before oviposition occurs. In many insects, sperm precedence from multiple matings results in the last male to mate fertilizing the greatest proportion of the eggs (Gwynne 1984). Alternatively, males may benefit from postcopulatory guarding through reduced predation on their mates prior to oviposition.

In contrast, the postcopulatory mate guarding of crustaceans is largely presumed to deter predators from consuming the soft, and therefore, vulnerable female (Van Engel 1958; Hartnoll 1969; Nelson and Hedgecock 1977; Hazlett 1975; Wittenberger 1981). Males presumably benefit from guarding by ensuring their mates survive to use their sperm in the fertilization of future clutches of eggs. The predation hypothesis is indirectly supported by the fact that only soft (post-molt) crustacean females are guarded. A sexual selection hypothesis, i.e., postcopulatory guarding prevents sperm competition, has also been suggested as an alternative function of postcopulatory guarding in crustaceans (Ghiselin 1974; Salmon 1983; Elner et al. 1985). Sexual selection is commonly associated with precopulatory guarding in amphipods (Birkhead and Clarkson 1980) and isopods (Ridley and Thompson 1979; Manning 1980) in which inter-male competition for mates stimulates males to guard pre-molt females. The female's brief predictable period of post-molt sexual receptivity lowers the cost:benefit ratio of precopulatory guarding for males (Ridley 1983), as is presumably the case for postcopulatory guarding as well. Empirical tests of the predation and sexual selection hypotheses concerning postcopulatory guarding in

crustaceans have not been conducted. I examined these hypotheses by comparing the relative effects of predation and sexual selection on the duration of postcopulatory guarding by males in the stone crab complex (*Menippe mercenaria, M. adina,* and their hybrids). Stone crabs recently were recognized as two species that hybridize along the northeastern Gulf of Mexico (Williams and Felder 1986) where mating within habitats occurs randomly with respect to taxonomic form (Wilber 1987, in press).

Stone crab mating behavior

Male stone crabs typically begin guarding a female a few days before she molts and continue guarding for several days thereafter. The time a female remains receptive after she molts is unknown, therefore, males that share burrows with post-molt females (Savage 1971), may be waiting to copulate or may be engaged in postcopulatory guarding. Female stone crabs store sperm in paired spermathecae and can retain sperm through a molt (Cheung 1968; Wilber 1988) although the amount of sperm retained is very low. Because mating occurs primarily in the fall (Cheung 1969) and spawning occurs in the summer (Noe 1967; Sullivan 1979), most sperm are stored approximately six months prior to fertilization. Stone crab spermathecae are connected to the paired genital openings by genital ducts, thus forming a cul-de-sac morphology (sensu Austad 1984). Sperm enter and exit each spermathecae via a single conduit, suggesting that in the absence of sperm mixing the last sperm deposited are closest to the exit and the first used in fertilization. Under this scenario, sperm from the last male to mate would have priority in fertilization.

Materials and methods

Male and pre-molt female stone crabs were held in heterosexual pairs in one of four 2000 liter recirculating circular tanks, 1.8 m diameter, with a third crab representing one of three treatment conditions. The treatment crab was either an adult male stone crab, an intermolt female stone crab, or a male blue crab *Callinectes sapidus*, representing intermale competition, control, and predation treatments, respectively. The sexual selection hypothesis predicts males guard longer in the presence of other males (intermale competition treatment) than in the absence of potential threats to their sperm investment. The intermolt female treatment served as a control providing a background estimate of postcopulatory guarding durations in the absence of other males, receptive females, and potential predators while maintaining a constant crab density among treatments. Blue crabs were used to test the effect that a potential predator of soft post-molt females had on male postcopulatory guarding

durations. Blue crabs are opportunistic scavengers that eat post-molt stone crabs, but not hard-shelled crabs.

Because stone crabs mate randomly with respect to species in the *Menippe*-complex in the field (Wilber, in press) and *Menippe* species did not affect precopulatory mate guarding behavior (Wilber 1987), stone crab species were paired randomly in this experiment. Most males are larger than the females they guard (Wilber, in press), therefore, at least one male in each trial was larger than the pre-molt female. In the predation treatment, male blue crabs initially were added to the tanks along with the heterosexual pairs. In three trials, however, the blue crab ate the female soon after she molted and before copulation had occurred. Although these trials provide evidence that blue crabs are indeed effective predators on post-molt females, the hypothesis being tested concerned postcopulatory guarding tenacity, thus copulation must occur before the trial could be counted. These trials, therefore, were not included in the experiment and in the remaining trials, blue crabs were added to the tanks while the stone crabs were copulating.

Nocturnal behavior of the crabs was recorded via a time-lapse video system and infra-red light source (described in Wilber and Herrnkind 1986) that continually scanned the tanks, viewing each for five minutes before rotating to the next tank. Video tapes were analyzed at 18 times normal speed on a television monitor. Behaviors recorded for the guarding males include walking, feeding, den maintenance, guarding, cohabitation, copulation, and agonistic encounters. Trials were terminated three days after the guarding males last shared a den with their mates for more than half of the night. This criterion was based on the observation that guarding males typically ceased cohabitation abruptly, i.e., rarely returning to the female's den after leaving for more than half the night.

Female molt condition was estimated by the presence and size of limb buds. Large limb buds are indicative of crabs that are in advanced stages of limb regeneration and close to ecdysis (Bliss 1960). Field surveys show that approximately 40% of the females have at least one limb bud, thus females used in the experiment were not atypical. If the intermolt females were not missing legs, there was no phyical clue as to their molt status, therefore they were held in the laboratory for one month following the termination of their trial to insure they were not pre-molts. No females molted during this holding period. Three brick dens were provided in each tank, and crabs fed *ad libitum* on the mussel *Modiolus squamosa*. Water temperature in the tanks was maintained at 25° C and a 12 h L : 12 h D light cycle was maintained by an automatic dimmer that provided dawn and dusk crepuscular periods.

Several trials of the intermale competition and control treatments were manipulated to determine whether females were sexually receptive after the males had stopped guarding. In four control trials, guarding males were removed from the tanks within 24 h after guarding stopped (107.7 ± 15.0 h past the females' molts; all values given refer to the mean ± SD) and another adult male was added to the tank. A mating between the new male and post-molt female would indicate guarding had ceased even though the female was still sexually receptive. In five competition trials, guarding males were similarly removed (162 ± 34 h past the females molts) and replaced by intermolt females. Copulation between the non-guarding male and post-molt female would, likewise, indicate the female was still sexually receptive.

After 25 of the 36 trials, the anterior vas deferens were dissected from the males and stored sperm were counted (see Wilber 1987 for the sperm quantification technique). Sperm stored in the spermathecae of the post-molt females were also counted in these trials. Sperm quantification in mating pairs was used to ascertain the relative gametic investment (% of

sperm transferred) by males in the three treatments. All sperm data were log transformed and the percentages of sperm transferred were arcsin square root transformed to better fit the assumption of normality prior to statistical analyses. All analyses were ANOVA unless stated otherwise.

Because the number of tanks and molting females were limited, females estimated to be closest to molting were used first when setting up trials. When trials began, therefore, males were exposed to females at different stages in the females' molt cycles, resulting in some males engaging in precopulatory mate guarding longer than others. Because the duration of precopulatory guarding may have been artificially shortened, correlations between pre- and postcopulatory guarding durations were not conducted.

Results

Stone crab mating behavior

Stone crabs readily inhabited the brick dens, most commonly with one crab in each den and were active from the evening to the dawn crepuscular periods. Blue crabs buried in the sand near the middle of the tanks and were intermittently active throughout the day and night. Stone crab pair formation typically resulted from a male encountering a pre-molt female in the tank, rising on the tips of his pereopods with his chelae spread, and either standing over the female or walking above her as she moved. Females remained active until several hours before molting. In one trial, the pair occupied the den previously occupied by the male, in 13 trials the pair's den was previously occupied by the female, and in 22 trials no clear residency pattern was established prior to pair formation. Males guarded females in the dens during the female's molt and, in contrast to cancrid crabs (Edwards 1966) did not help the female withdraw from her exoskeleton. After the females molted, males carried the exoskeletons to the opposite side of the

tanks and then returned directly to the post-molt females. Precopulatory guarding lasted an average of 34.8 ± 19.8 h before copulation (Table 1) and neither differed between treatments ($F = 0.03$, $P > 0.75$), nor was correlated with female size ($r = 0.18$, $P > 0.2$).

A male typically began copulation by positioning a female by simultaneously rotating and turning her with his walking legs. Females extended their abdomens around the male's postero-dorsal carapace. The duration of copulation did not differ between treatments (Table 1, $F = 1.17$, $P > 0.25$), lasting 8 to 26 h, and averaged 13 h. Copulating males deterred both intermolt females and other males from approaching their den by quickly extending their chelae. Copulation was interrupted in five of the competition trials due to agonistic encounters between the male stone crabs. Blue crabs were never observed to approach a mating pair. Multiple copulations by the guarding male occurred in 6 of the 15 competition trials, 1 of 13 control trials and 0 of 8 predation trials ($X^2 = 9.2$, $P < 0.05$, Yate's correction for continuity; Table 1). The intervening time between copulations in the competition treatment averaged 40 hours. The duration of single matings in this treatment (10.6 ± 4.1 h) was less than the combined durations of double matings (19.5 ± 4.5 h; $T = 3.85$, $P < 0.005$). There was no difference in the duration of copulation between first (10.3 ± 5.5 h) and second (9.2 ± 3.0 h) matings in cases where double copulations occurred ($T = 0.85$, $P > 0.10$).

Stone crab postcopulatory guarding behavior

After copulating, males stood on the tips of their walking legs over their mates and kept the females positioned beneath them. This form of postcopula-

Table 1. Mating behavior and sperm transfer data (mean $\pm$ SD). Number of agonistic encounters include only those encounters observed during each tank's video taping (the total time each tank is viewed is one quarter of the night). Numbers in parentheses indicate the number of trials

	Treatment		
	Intermale competition ($n = 15$)	Control ($n = 13$)	Predation ($n = 8$)
Time from molt to copulation (h)	33.1 ± 11.9	35.2 ± 30.4	33.9 ± 14.3
Duration of copulation (h)	14.2 ± 6.1	11.3 ± 5.2	12.2 ± 1.2
No. of agonistic encounters with the guarding male	10.3 ± 2.1	1.6 ± 0.8	–
No. of sperm stored in vas deferens (log transformed)	7.8 ± 0.1	7.8 ± 0.3	8.0 ± 0.2
Female sperm storage (% of male's sperm no.)	12.2 ± 0.1	9.3 ± 5.4	5.6 ± 3.0

tory guarding is analogous to contact guarding in insects and generally was followed by a form of non-contact guarding in which the females were sequestered in the dens while the males remained at the entrance and chased away intruders. The video system did not have enough resolution to compare contact and non-contact guarding durations, however, contact guarding appeared to last about one to two days, based on direct observations during the day. While engaged in non-contact guarding, males carried mussel clumps to the entrances of their dens where they fed and performed den maintenance. Generally, on nights when postcopulatory guarding stopped, males occupied vacant dens during the dawn crepuscular period where they remained for the day. On subsequent nights, males rarely returned to dens occupied by their mates.

Guarding durations under the three experimental treatments were measured in two ways: (1) hours past the female's molt (post-molt), and (2) hours past the end of the last copulation (postcopulatory). A comparison of the variances in these measures potentially could indicate the relevant feature of the female being guarded. For example, termination of guarding a consistent number of hours after her molt may signify that the exoskeleton had hardened sufficiently to prevent copulation or reduce predation. Guarding terminated a consistent number of hours after copulation may indicate the sperm investment is no longer at risk of either displacement (Waage 1979), mixing (Woodhead 1985), or pre-emption (Parker 1970b) by other males.

Both post-molt ($F = 5.92$, $P < 0.01$) and postcopulatory ($F = 5.44$, $P < 0.01$) guarding durations differed between the treatments, with males in the competition treatment guarding the longest (Fig. 1). The mean duration of guarding past the female's molt in the competition treatment was 125.9 h compared to 84.5 and 83.5 h in the control and predation treatments, respectively. Mean postcopulatory guarding was 80.1 hours in the competition treatment, 47.5 h in the control treatment, and 37.3 h in the predation treatment. Variances in post-molt and postcopulatory guarding measures were similar (Fig. 1), as were the relative differences between the measures across treatments. Post-molt guarding durations and female size were not correlated in any treatment (all P-values > 0.4).

In the four predation trials with the longest post-molt guarding durations (109.2 ± 28.0 h), females were not eaten by the blue crabs, whereas, in the four trials where post-molt guarding was
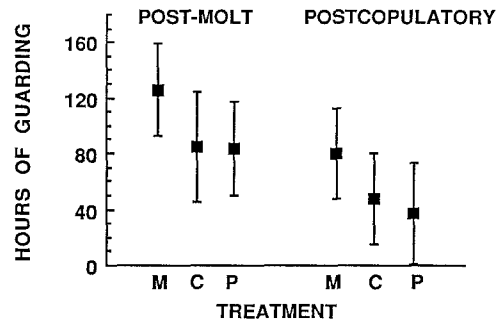

Fig. 1. Means and standard deviations of the duration of guarding by males measured as hours past the females molt (post-molt) and hours past the end of copulation (postcopulatory) for the inter-male competition (M; $n = 15$), control (C; $n = 13$), and predation (P; $n = 8$) treatments

the shortest (57.8 ± 10.9 h), three of the females were eaten by blue crabs and the remaining female's major chela was eaten. Blue crabs always retreated from encounters with male stone crabs.

Agonistic behavior and mate takeover

Agonistic encounters involving the guarding male were more frequent in the competition than the control treatment (Table 1). The average size difference between males in the competition treatment was 8.5 ± 5.1 mm carapace width (CW). In 14 of the 15 competition trials, the largest male in the tank guarded and copulated with the female. Most (68%) agonistic encounters occurred when the non-guarding male approached the den occupied by the mating pair. Guarding males typically responded by rapidly extending their chelae, and frequently chasing the intruding male up to 0.75 m away from the den. In two trials not included in the previous results, the non-guarding male evicted the guarding male, copulated with the female, and successfully assumed a postcopulatory guarding role despite repeated approaches by the original mate. Evictions occurred 72 and 75 h after the females molted and copulation with the second male began 40 and 5 h, respectively, after the takeovers. In both cases, copulation involving the second male lasted less than two hours. In a third mate take-over attempt, the non-guarding male (103 mm CW) approached the female 120 h after her molt while the female's mate (95 mm CW) was at a nearby mussel clump. The second male turned the female with his walking legs, but did not appear to copulate with her. After 90 min, the second male was chased away by the original male, who immediately began his third copulation with her.

In one of the four control trials where the guarding male was replaced by another male after guarding stopped, a second copulation occurred. Copulation by a non-guarding male did not occur in any of the five intermale competition trials in which the guarding male was removed after guarding stopped.

Sperm transfer

Male size and sperm number in the vas deferens were positively correlated ($r = 0.47$, $P < 0.02$). The amount of sperm in guarding males in the predation treatment was marginally higher than that of males in the other treatments (ANCOVA using male size as the covariate, $F = 2.65$, $P > 0.09$; Table 1). The amount of sperm stored by females calculated as a percentage of the total number of their mates' sperm was marginally higher in the competition treatment than the control or predation treatments (Table 1, $F = 3.02$, $P < 0.10$). The duration of copulation (the sum of multiple copulations where appropriate) was unrelated to both the percentage of sperm transferred ($r = 0.24$, $P > 0.2$) and the number of sperm stored by females ($r = 0.28$; $P > 0.1$). The percentage of sperm transferred from multiple copulations ($14.4 \pm 5.0\%$) exceeded that of single copulations ($8.1 \pm 4.6\%$; $T = 13.7$, $P < 0.0005$).

Discussion

The influence of sexual selection on postcopulatory guarding in male stone crabs was demonstrated both by longer guarding durations and the high number of agonistic encounters in the intermale competition treatment. Males held with another male stone crab guarded their mates nearly two days longer than those in the control and predation treatments and agonistic encounters between males were common. Although there was no control treatment in which the number of agonistic encounters between males not held with a receptive female could be compared, a previous study of stone crab locomotory activity (Wilber and Herrn-kind 1986) using paired adult males in the same tanks recorded few agonistic encounters. The prevalence of agonistic encounters at the den containing the female and the occurrence of mate takeovers supports the contention that males were fighting over access to the female and not some other resource. Fights rarely occurred at dens that did not contain a molting female. In addition, the occurrence of a male copulating with his mate immediately after chasing another male away from

her is similar to observations of multiple matings in insects, e.g., water bugs (Smith 1980), that result from sexual selection.

Because both female sexual receptivity and vulnerablility to predation are probably a function of exoskeletal hardening, most of the discussion of guarding durations refers to hours past the female's molt. Males in the competition treatment guarded their mates an average of 126 hours past the female's molt, which may not be the upper limit of the duration of female sexual receptivity (matings were observed as late as 144 and 156 h past the females' molts). Matings did not occur, however, between the non-guarding male and post-molt female in any trial in which the guarding male was removed after guarding stopped. The average postcopulatory guarding duration for male *Cancer pagurus* is five days past their mates' ecdysis, which is at least one day less than the period of female receptivity (Edwards 1966). On three occasions (trials not included in this study) I have observed non-guarding males copulate after a postcopulatory guarding male was removed from the tank, providing additional evidence that male stone crabs will copulate with a recently mated, unguarded post-molt female.

Copulation in stone crabs started no earlier than 10 h after the females' molt and considerably later in most trials, averaging 34 h. Presumably, females are receptive during this initial post-molt period, however, it is possible that damage to the genital ducts and genital pores could result if copulation occurs too soon, although mating occurs within a few hours of the female's molt in *Cancer pagurus* (Edwards 1966). Calcification of the exoskeleton may be associated with crab size, which may affect the timing of both copulation and guarding. Female size was not correlated with either the number of hours past the female's molt of copulation or the duration of post-molt guarding in this experiment.

The occurrence of the largest male in the competition treatment becoming the female's mate is consistent with both field (Wilber 1986, 1987) and laboratory (Wilber 1987) evidence that large males are more successful in acquiring mates. Size was an important factor in establishing dominance among *Menippe mercenaria* males (Sinclair 1977) in a laboratory study of agonistic behavior. The species of males in the *Menippe*-complex did not affect the dominance relationship between males.

The incidence of multiple copulations in the competition treatment and resulting longer copulatory durations and percentage of sperm transferred is consistent with behavioral responses to sexual

competition by insects (Smith 1980; Sillen-Tull-berg 1981; Dickinson 1986). Longer copulatory durations result in the transfer of more sperm in milkweed leaf beetles (Dickinson 1986) and is a form of guarding in which gametes are no longer transferred, but female lygaeid bugs are protected (Sillen-Tullberg 1981). Separation of mating pairs at various time intervals to establish the timing of sperm transfer was not performed on stone crabs, however, copulatory durations and the percentage or number of sperm stored by females were not correlated, suggesting sperm transfer does not occur throughout the entire copulatory period. Greater percentages of sperm transferred resulted from multiple copulations and were not directly related to the duration of copulation.

The predation treatment demonstrated both that blue crabs can readily prey on soft post-molt stone crabs and that males do not respond to this predation threat by guarding until their mates are no longer vulnerable. Blue crabs and stone crabs occur sympatrically in both intertidal and subtidal habitats on the northeastern Gulf of Mexico. Blue crabs, however, do not occupy the burrows and dens inhabited by stone crabs, and therefore, may encounter post-molt females infrequently. *Octopus vulgarus* preys upon both hard and soft-shelled stone crabs and also occupys the same dens and crevices. Octopods may elicit different behavioral responses in guarding male stone crabs and should be tested analagously before the predation hypothesis is discounted. Female survival in the predation treatment exclusively in those trials with the longest guarding durations suggests the females' exoskeletons had hardened sufficiently in these trials to prevent predation. The female guarded the longest before being eaten was 73 h past her molt, whereas a female 80 h past her molt when guarding stopped survived the trial. Blue crabs foraged among the mussel clumps, so post-molt females were not the only available food source.

Lengthened guarding by males in the competition treatment indicates sexual selection affects postcopulatory mate guarding in stone crabs and suggests sperm competition occurs. The absence of a response in the predation treatment, in spite of the blue crabs' effectiveness as a predator on females, does not eliminate the predation hypothesis because male stone crabs may respond to other predators differently. More importantly, the two functions are not mutually exclusive. While postcopulatory guarding in a particular instance may be stimulated by interactions with other males, it concomitantly may reduce predation on females. Likewise, the current utility served by the behavior does not necessarily reflect the historical selective regime that influenced its evolution. This study does not reject the predation hypothesis, but demonstrates that the sexual selection hypothesis is a viable explanation of the function of postcopulatory mate guarding in crustaceans.

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