

The impact of limb autotomy on mate competition in blue crabs *Callinectes sapidus* Rathbun

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Summary. This study is the first to demonstrate experimentally that autotomy (self-amputation of a body part) adversely affects competition for mates. Experiments were conducted using blue crabs *Callinectes sapidus* Rathbun to examine the consequences of limb loss and pairing precedence on mate acquisition by males. Two adult males of equivalent size were introduced sequentially into pools containing a sexually-receptive female and observed after 24 h and 48 h. One male in each pair was left intact, while the other experienced: (1) no autotomy, (2) autotomy of one cheliped, or (3) autotomy of both chelipeds, one walking leg, and one swimming leg. In the absence of a competitor (first 24 h), both intact and injured males established precopulatory embraces with females. Intact males were highly successful (84–95%) in defending females from intact or injured intruders in the second 24 h period. Both autotomy treatments, however, significantly reduced the ability of males to defend females from intact intruders. Females in experiments suffered greater frequency of limb loss than did males. In the field, paired blue crabs showed significantly higher incidence of limb loss than unpaired crabs. Limb loss frequency increases with body size, and field observations indicated that larger males may be more successful than smaller males in obtaining females. Both experimental manipulations and field studies provide strong evidence for mate competition in this ecologically and commercially important portunid species.

Key words: Autotomy – Blue crabs – Mate competition – Pairing precedence – Body size

Convergent evolution of an autotomy response (self-amputation of a body part) in molluscs (Fishelson and Kidron 1968; Lewin 1970), annelids (Kennedy and Kryvi

1980), arthropods (McVean 1982; Eisner and Camazine 1983; Smith 1990a; Robinson et al. 1991a; Smith and Hines 1991a), echinoderms (Bowmer and Keegan 1983), and chordates (Maiorana 1977; Vitt et al. 1977; Willis et al. 1982) suggests universal fitness benefits (e.g., predator escape) from the behavior. While important for immediate survival (Robinson et al. 1970; Dial and Fitzpatrick 1984; Smith 1990b), autotomy is not without cost. Appendage loss can slow growth (Kuris and Mager 1975; Smith 1990a) and limit foraging rate (Slater and Lawrence 1980; Smith and Hines 1991b), locomotory efficiency (Spirito 1972; Smith 1990b; Robinson et al. 1991b), escape success (Vitt et al. 1977; Dial and Fitzpatrick 1984; Smith 1990b), and agonistic ability (Conover and Miller 1978; Berzins and Caldwell 1983). Autotomy could be detrimental both to individuals and to populations (e.g., Harris 1989), if it significantly impairs reproductive success. Appendage loss might decrease an individual's ability to attract mates, lower competitive performance for partners, physically hinder copulation, or reduce fecundity. Of these potential costs, only the effect of autotomy on fecundity has been examined in any detail (e.g., Dial and Fitzpatrick 1981). Studies of salamanders and lizards indicate decreased reproductive effort following autotomy because either energetic reserves are lost or metabolic resources are diverted from egg production to regeneration (Smyth 1974; Maiorana 1977; Vitt et al. 1977; Dial and Fitzpatrick 1981; Vitt and Cooper 1986). The impact of autotomy on mate choice, mate competition (Sekkelsten 1988), or the mechanics of pairing has received surprisingly little attention. The present study examines the importance of limb autotomy to mate competition in blue crabs *Callinectes sapidus* Rathbun, an ecologically and commercially important decapod crustacean species occurring in near-shore waters of the western Atlantic Ocean (Millikin and Williams 1984).

A four year study of autotomy in *Callinectes sapidus* populations in the Chesapeake Bay and along the southeastern United States coast and Gulf of Mexico revealed

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high frequencies of limb loss and regeneration (18–39%; Smith and Hines 1991a). These estimates exclude individuals that might have been injured during capture. Single cheliped loss was the most common injury at all sites. Chelipeds are used in blue crab courtship displays (Gleeson 1980) and in agonistic interactions (Jachowski 1974); their loss could reduce male ability to attract, capture, or defend females. Approximately 8% of adult blue crabs captured in the Rhode River, Maryland from 1986–1989 were missing one or both chelipeds (Smith and Hines 1991a; 1991b), but it is not known whether this segment of the population experienced disproportionately fewer matings.

Reduction in reproductive success due to autotomy will depend on the functional importance of the appendage to mating behavior and on the intensity of sexual selection in the population. In mating associations in which intrasexual competition is important (e.g., polygyny, Emlen and Oring 1977), injured individuals may lose mating opportunities because they are unable to defend mates or breeding territory from undamaged competitors. When one sex becomes limiting, either temporally or spatially, competition for mates should intensify (Emlen and Oring 1977; Ims 1988). Under such circumstances, theory predicts individuals of the more common sex will search for and guard members of the limiting sex (Parker 1974; Grafen and Ridley 1983). In both cancrid (e.g., *Cancer magister*) and portunid (e.g., *Callinectes sapidus*) crab mating systems, females can copulate only during a brief timespan immediately following their molt (Gleeson 1980; Christy 1987). The problem is magnified for portunids, because females appear to mate only once, at the terminal, maturity molt (Milikin and Williams 1984; but see Gleeson 1991). This limited window for copulation coupled with high mobility makes sexually-receptive (i.e., prepubertal) females an unpredictable resource for males (Christy 1987). Blue crab males exhibit both pre- and postcopulatory guarding of females and leave sperm plugs in the female's genital openings following mating, presumably to prevent insemination by other males (Wenner 1989; Diesel 1991). Wenner (1989) observed almost 100% insemination of mature *C. sapidus* females sampled in South Carolina waters, which suggests that sexually-receptive females are the limiting resource. With the breeding population sex ratio skewed towards males, strong male-male competition for mating opportunities can be expected (Emlen and Oring 1977), and the cost of autotomy could be high. Other factors such as body size (Ridley and Thompson 1979; Berrill and Arsenault 1982; Sekkelsten 1988) and male pairing precedence (i.e., the advantage guarding males may have over intruders) may play critical roles in mate competition; however, neither have been examined in blue crabs. The study reported here is the first to test experimentally for the effects of autotomy and pairing precedence on male competitive ability for mates. In addition, field comparisons of injury levels and body sizes of paired and unpaired blue crabs assess whether either factor correlates with mate acquisition.

Materials and methods

Mate competition experiments: Pool design. Experiments to test the effects of limb loss and pairing precedence on male competitive success for females were conducted in circular plastic pools (100 cm diam. × 20 cm depth) at the Smithsonian Environmental Research Center, Edgewater, Maryland between 31 July and 24 September 1989. Each of ten pools was filled with 6 cm of muddy sand sediment and 10 cm of estuarine water. A 40 cm tall strip of hardware cloth (1.27 cm mesh) was positioned around the inside perimeter of each pool to prevent crab escape. A plywood sheet (1.5 m length × 1.5 m width × 0.01 m height) was anchored on top of the hardware cloth barriers to shade the pools. Pool salinity matched that of the Rhode River (5–10‰). Water temperature in all pools (20–25°C) was 2–5°C lower than in the Rhode River; however, temperature was consistent ($\pm 1^\circ\text{C}$) among pools within each experiment. All pools were drained after each experiment, and new water added 6 h before the start of the next experiment. To discourage cannibalism during experiments, two soft-shell clams (*Mya arenaria*) were placed in each pool. Adult, intermolt male and late-premolt (i.e., pink or red-sign; Ary et al. 1985), prepubertal female blue crabs were collected for experiments in baited crab pots in the Rhode River and at fish impoundments outside the Rhode River. Male crabs found in copulatory or postcopulatory embraces were not used. Experimental animals were held separately for short periods (≤ 3 d) in floating cages anchored in shallow water. Crabs were fed 1–2 fish (*Brevoortia tyrannus*) daily.

Experimental design. In each of eighteen replicate experiments, twenty adult intermolt male crabs were paired by size (± 5 mm carapace width, CW). One male in each pair remained intact while the other experienced: (1) no autotomy, (2) autotomy of the right cheliped, or (3) autotomy of both chelipeds, the right first walking leg, and left swimming leg. Crabs were induced to autotomize limbs 24 h before the start of an experiment. The experimental design consisted of five competitive pairings based on each male's autotomy status and order of introduction into pools (Table 1); these treatment pairings were duplicated and run concurrently in an experiment (= 10 pools). Initially, one male (= first) was placed in each pool with a single, intact, late-premolt prepubertal female. During the first 2 h, physical contact between males and females was prevented by a plastic divider. After the equilibration period, the divider was raised and males and females were allowed to interact undisturbed for 24 h. At the end of 24 h, the presence of a precopulatory, copulatory, or postcopulatory embrace was noted. The second male in each size-matched pair was then introduced into the pool. At the end of the second 24 h, pairings were examined and any instance of displacement of the first by the second male was recorded. A new set of 30 crabs was used in each experiment.

Field survey. To determine whether limb loss or body size correlated with mate acquisition, single and paired male and female blue crabs were examined in the upper-mid Chesapeake Bay. Between 16 July and 30 October 1989, *Callinectes sapidus* individuals were collected by dip net from the sides of commercial pound nets located in the

Table 1. Summary of autotomy treatments and sequence of introduction of size-matched males into pools

Male Priority	Autotomy treatment pairings				
	1	2	3	4	5
First	0	0	0	-1	-4
Second	0	-1	-4	0	0

The first male was given 24 h to establish a precopulatory embrace with the female before the second male was introduced. 0 = intact, -1 = missing one cheliped, -4 = missing both chelipeds, right first walking and left swimming legs

Chesapeake Bay 1 km east of the Rhode River subestuary, Maryland (38°51'N, 76°32'W). Water temperature ranged from 20–30°C during the sampling period, and salinity varied between 5–10‰. The following data were collected for each crab: (a) pairing status (paired, unpaired); (b) type of embrace (precopulatory, copulatory, postcopulatory); (c) carapace width, (distance between lateral spine tips); (d) sex; (e) sexual maturity [juvenile, prepubertal (females only), adult]; (f) molt stage (postmolt, intermolt, early or late premolt); and (g) type and side of any missing or regenerating limbs. Sexual maturity in female blue crabs was determined by examining abdominal allometry and color (Van Engel, 1958). For males, sexual maturity was indicated by the ease with which the abdomen could be pulled away from the ventral surface of the cephalothorax (Van Engel 1958; 1990). Molt stages were determined by assessing carapace hardness and by examining the propodus of the fifth pereopod for evidence of epidermal retraction (Van Engel 1958; Johnson 1980). A limb stump that was either scarred or possessed a papilla or limb bud was classified as a missing limb. A regenerating limb was considered to be a functional appendage that had undergone at least one molt since autotomy, but was shorter than the intact, contralateral limb. Crabs that possessed an unscarred stump wound, indicating possible injury caused during collection, were not measured.

Statistical Analyses

Mate competition experiments. The effects of limb loss and pairing precedence on mate acquisition were compared on pooled experiments using a replicated goodness of fit test (Sokal and Rohlf 1981; p. 722) with treatment pairings substituted for replicates. If pairing success among treatments revealed significant heterogeneity, then linear contrasts were used to make comparisons. Pairing success of first and second males within treatments and pooled over all treatments was tested against an expected 1:1 ratio. The relative effect of male and female body size on pairing success was compared among pooled treatments using analysis of covariance after data were \log_e -transformed [covariate = $\log_e(\text{female CW})$; Sokal and Rohlf 1981]. Variances and slopes of regression lines were tested to assure homogeneity.

Field survey: Because of the significant size increase at the females' maturation molt, pre- and postcopulatory females were treated as separate groups in all analyses. Both sexes were divided into two size classes with the breakpoint occurring at the median value of their respective size-frequency distribution: for mature males, carapace width (CW) \leq or $>$ 130 mm; for prepubertal females CW \leq or $>$ 110 mm; for mature females CW \leq or $>$ 160 mm. Frequencies of paired and unpaired individuals of a given sex were compared to determine whether pairing status was independent of body size, injury, or their interaction (logistic regression, Cox and Snell 1989; PROC CATMOD with maximum likelihood estimation, SAS Institute, 1985). The relationships of injury and season (mid-July through August versus September through early October) to pairing status were also examined. Comparison of injury frequencies was made between paired males and females using two-way contingency tables (G -test, Sokal and Rohlf 1981). T -tests were used to compare mean carapace widths between: (a) paired and unpaired individuals of the same sex; and (b) paired individuals of the opposite sex.

Results

Mate competition experiments. Mating behavior in pools was consistent with patterns described in previous blue crab studies (e.g., Gleeson 1980). In the presence of a prepubertal female, the male would rise up on his walking legs, extend his chelipeds laterally, and vigorously wave both swimming legs above his carapace while ad-

vancing. If the female was receptive, the male would grasp and turn her with his chelipeds, holding her upright underneath him with his first pair of walking legs. Males were capable of fending off advances of other males while carrying the female in a precopulatory embrace. After the female molted, the male would turn her over so that their ventral surfaces were in contact and the pair would copulate. Subsequent to copulation, the female would be righted and carried in a postcopulatory embrace. Both paired and unpaired crabs were frequently found buried in the sediment.

In experimental pools, male pairing success was significantly affected by limb autotomy (treatment heterogeneity, $G_H = 16.5$, 4 df, $P < 0.005$) and pairing precedence (pooled effect for first and second males, $G_P = 25.4$, 1 df, $P < 0.001$; Fig. 1). When an intact male established a precopulatory embrace with the prepubertal female during the first 24 h (i.e., prior to introduction of the second male), he successfully maintained that

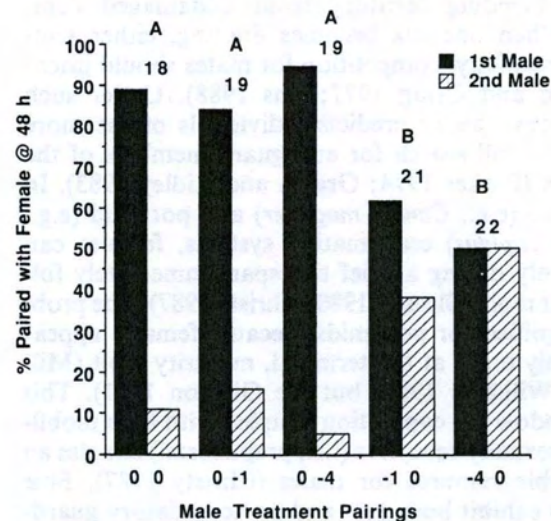


Fig. 1. Comparison of male pairing success with females at the end of 48 h in instances where the first male had established a precopulatory embrace before the second male was introduced. Bars represent the first and second males and their respective autotomy treatments. 0 = intact, -1 = missing one cheliped, -4 = missing both chelipeds, one walking and one swimming leg. Sample size for each treatment pairing (e.g., 0 0 vs. 0 -1) is given. Treatment pairings with the same letter were not significantly different (G -tests, 1 df, $P > 0.05$)

Table 2. Pairing success of first versus second males for each treatment pairing tested against an expected 1:1 ratio

Treatments	df	G	P-value
0 vs 0	1	12.4	<0.001
0 vs -1	1	9.8	<0.005
0 vs -4	1	18.5	<0.001
-1 vs 0	1	1.2	>0.50
-4 vs 0	1	0.0	>0.99
Total	5	41.9	

0 = intact, -1 = missing one cheliped, -4 = missing both chelipeds, right first walking and left swimming legs

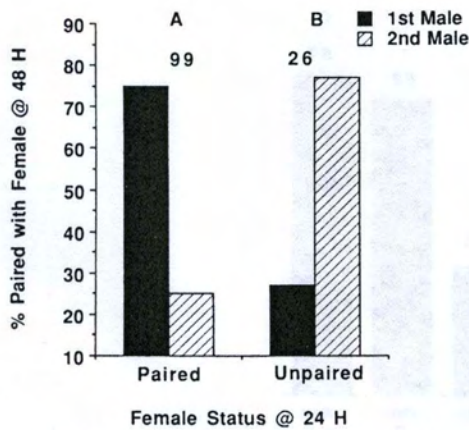


Fig. 2. Comparison of male pairing success at the end of 48 h in instances where the female: 1) was in a precopulatory embrace at 24 h (paired), or 2) was not in a precopulatory embrace at 24 h (unpaired) prior to the second male being introduced. Autotomy treatment pairings are pooled for first and second males. Sample size for each pairing status is given. Pairing success of first and second males at 48 h differed significantly depending on whether pairing had occurred at 24 h (G -test, 1 df, $P < 0.001$)

embrace subsequent to introduction of the second male in 84–95% of the trials (Table 2; Fig. 1). In contrast, first males missing one or four limbs were significantly less capable of maintaining a precopulatory embrace when an intact male was introduced (Table 2; Fig. 1). Males missing one cheliped were displaced by the second male in 38% of the trials; whereas, males missing both chelipeds, one walking leg and one swimming leg surrendered the female 50% of the time to an intact male. If the first male failed to establish a precopulatory embrace during the first 24 h, the female paired with the second male in 73% of the trials in which pairing occurred ($G = 20.0$, 1 df, $P < 0.001$; Fig. 2). Sample sizes were too small to distinguish treatment differences in these cases ($n = 26$); hence, the data were pooled.

On twelve occasions, females molted during the first day and were in copula. These instances were distributed evenly among treatments. In three cases (two '4-0' and one '0-1' treatment pairing), the second male was found copulating with the female at the end of 48 h, although it was not determined whether the first male had deposited sperm. Of the remaining nine, two females died while seven were found in postcopulatory embrace with the first male.

In 23 of 175 trials (13%), females failed to pair with either male by the end of 48 h. In several of these instances, females were observed fending off advances by males with their chelipeds. For combined treatments, the back-transformed, least-square mean carapace width of unpaired males (132.3 mm) was smaller than that of paired males (137.1 mm) when adjusted for female body size (ANCOVA, $F = 3.8$; 1, 147 df; $P = 0.05$). Twenty-seven (15%) crabs died during the experiment; of those, twelve (7%) showed no evidence of physical injury, and fifteen (8%) had been cannibalized. Mortality was distributed evenly among experimental treatments but was significantly higher in females (14% of 175 crabs) than males (0.9% of 350 crabs) ($G = 38.4$, 1 df, $P < 0.001$).

Mean male body size in pools where females experienced mortality (back-transformed $CW = 143.3$ mm) was significantly larger than that of males (137.1 mm) in pools where successful pairing was observed (ANCOVA, $F = 6.3$; 1, 147 df; $P < 0.01$).

Limb loss during the experiment was disproportionately higher in surviving females (9.9% of 151 crabs) than in surviving males (0.9% of 347 crabs) ($G = 22.7$, 1 df, $P < 0.001$). Autotomy of a single limb was observed in ten of fifteen females (67%) and multiple autotomy (2 to 3 limbs) in the remaining five. For females, limb loss was distributed evenly among chelipeds, walking legs, and swimming legs. On two occasions, swimming legs were autotomized during ecdysis and remained in the shed exoskeleton. Although males were observed grasping each other's chelipeds during agonistic encounters, these limbs were never autotomized in the experiments. Among males, only walking legs were lost.

Field Survey. Paired *Callinectes sapidus* individuals ($n = 374$) were missing limbs significantly more often (16%) than unpaired individuals (10%, $n = 266$) at pound nets outside the Rhode River ($G = 4.7$, 1 df, $P < 0.05$; Fig. 3). Larger crabs ($CW \geq 120$ mm) were missing limbs significantly more often (16.2% of 376 crabs) than smaller crabs ($CW < 120$ mm; 9.8% of 264 crabs) ($G = 5.5$, 1 df, $P = 0.02$). When mature males, prepubertal females, and mature females were analysed separately, however, the frequency of missing limbs did not differ significantly between paired and unpaired members of any group, regardless of body size (logistic regressions, 4 df, $P > 0.05$; Fig. 3). Paired and unpaired males and females also did not differ significantly in the frequency of regenerating limbs or total limb loss (i.e., missing or regenerating limbs). Paired prepubertal females showed a tendency toward higher frequency of total limb loss than did unpaired prepubertal females ($G = 3.3$, 1 df, $P = 0.07$). Paired and unpaired individuals did not differ significantly in the relative types (i.e., chelipeds, walking legs, swimming legs) or numbers (1, 2, ≥ 3) of limbs lost

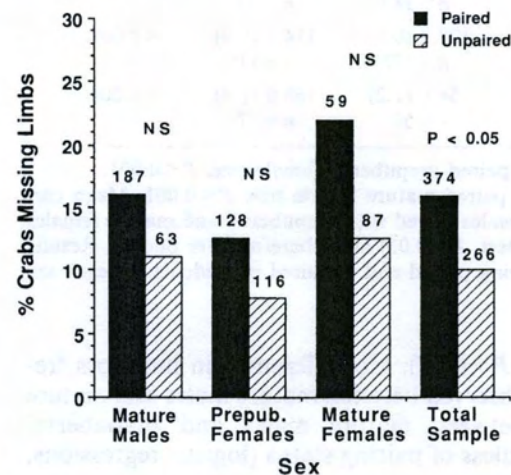


Fig. 3. Percentages of unpaired and paired mature males, prepubertal females, mature females, and total sample missing one or more limbs outside the Rhode River, Maryland in 1989. NS, not significant, $P > 0.05$

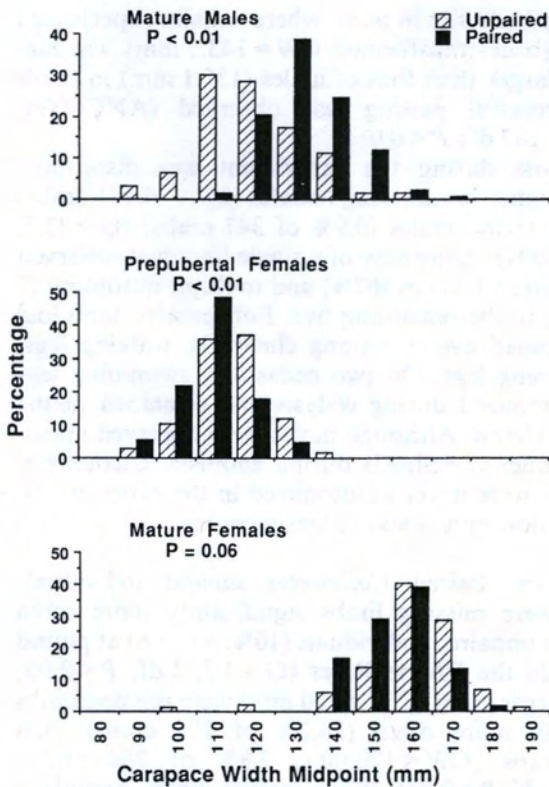


Fig. 4. Size-frequency histograms of unpaired and paired mature males, prepubertal females, and mature females captured outside the Rhode River, Maryland in 1989. *P*-values from comparisons of paired and unpaired size-frequency distributions within sex for mature males, prepubertal and mature females are given (Kolmogorov-Smirnov two-sample test)

Table 3. Summary of mean carapace widths (mm) (± 1 SE) of paired and unpaired mature males, prepubertal females, and mature females collected from pound nets outside the Rhode River

Sex	Pound Net		<i>P</i> -value
	Paired	Unpaired	
Male (mature)	132.6 (0.8) <i>n</i> = 187	118.7 (1.8) <i>n</i> = 63	<0.001
Female ^a (prepub)	108.8 (0.8) <i>n</i> = 128	114.1 (0.9) <i>n</i> = 116	<0.001
Female ^b (mature)	154.6 (1.2) <i>n</i> = 59	160.0 (1.4) <i>n</i> = 87	<0.004

^a Paired male vs paired prepubertal female size, *P* < 0.001.

^b Paired male vs paired mature female size, *P* < 0.001. Mean carapace widths of males paired with prepubertal and mature females did not differ (*t*-test, *P* > 0.05) and, therefore, are pooled. Results of *t*-tests comparing paired and unpaired individuals for each sex are presented

(*G*-tests, 2 df, *P* > 0.05). No differences in limb loss frequency were observed between mature males and mature females or between mature males and prepubertal females, regardless of pairing status (logistic regressions, 4 df, *P* > 0.05).

Size distributions of paired and unpaired individuals differed significantly within sex for mature males and prepubertal females (Kolmogorov-Smirnov two-sample

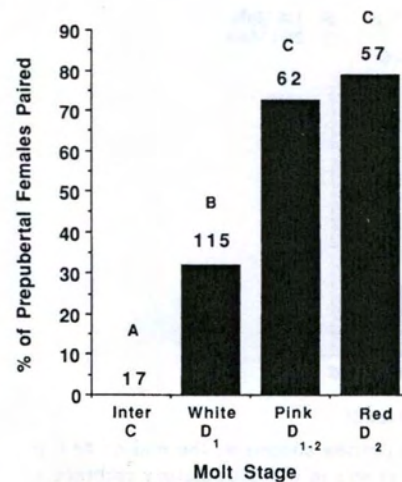


Fig. 5. Percentage paired of prepubertal females in a given molt stage. Molt stages: intermolt (C); premolt whitesign (D_1), pink-sign (D_{1-2}), and red-sign (D_2). Sample size for each molt stage is presented. Pairing frequencies with the same letter above bar were not significantly different (*G*-test, 3 df, *P* > 0.05)

Table 4. Percentage of paired individuals collected from late July through August and September through early October outside the Rhode River

Sex	% Paired		Significance
	Jul.-Aug.	Sept.-Oct.	
Male	34% (273)	56% (167)	<i>P</i> < 0.001
Female (prepub.)	37% (182)	73% (82)	<i>P</i> < 0.001
Female (mature)	30% (83)	48% (71)	<i>P</i> = 0.06

Sample sizes (paired and unpaired individuals) and significance levels of logistic regressions comparing frequencies of paired and unpaired individuals between time intervals for a given sex

tests, *P* < 0.01; Fig. 4). Pairing success was dependent on body size for both males and females, but in opposite ways (logistic regressions, 4 df, *P* < 0.001; also Table 3). Mean carapace width of paired adult males was significantly greater than that of unpaired males (Table 3). In contrast, paired prepubertal and mature females were slightly smaller than their unpaired counterparts (Table 3).

The frequency of pair formation varied temporally. The relative percentages of prepubertal females that were paired increased as these females neared their pubertal molt ($G = 68.4$, 3 df, *P* < 0.001; Fig. 5). A significantly higher percentage of blue crabs were paired in September and early October than in late July and August (logistic regression, 4 df, *P* < 0.05; Table 4). These seasonal effects were consistent across body sizes.

Discussion

This study is the first to demonstrate experimentally that autotomy has a negative impact on male competitive

ability for mates. In staged encounters between size-matched *Callinectes sapidus* males, individuals missing one or four limbs were at a significant disadvantage when guarding females against intact competitors. Field surveys of the same species, however, indicate that paired individuals overall had higher incidence of injury than unpaired crabs and that larger males were more likely to pair than smaller males. Together, these pool experiments and field surveys provide strong evidence that *Callinectes sapidus* males compete aggressively for females.

Autotomy does not physically prevent mating in blue crabs. In the absence of competitors, male crabs missing up to four limbs readily established a precopulatory embrace with females and, in several instances, copulated. Similarly, tail loss in male plethodontid salamanders had no significant effect on courtship ability or insemination success (Houck 1982). Less than 2.5% of blue crabs in the Rhode River and elsewhere were missing or regenerating four or more limbs (Smith and Hines 1991a); consequently, the majority of injured adult male blue crabs were probably competent to mate. In pool experiments, injured males, instead, lost mating opportunities because they were displaced by other males. The loss of one or both chelipeds coupled with long intermolt periods (ca. 40 d; Tagatz 1968; Smith 1990a) in adult male blue crabs could potentially reduce mating opportunities for much of the mating season in the Chesapeake Bay. Studies involving other crustaceans provide indirect evidence that limb loss could lower mating success by reducing a resident's ability to defend a burrow from intact conspecifics (e.g., snapping shrimp, Conover and Miller 1978; lobsters, O'Neill and Cobb 1979; and mantis shrimp, Berzins and Caldwell 1983). If species defend burrows for breeding purposes (e.g., *H. americanus*, Atema, 1986; Karnofsky and Price 1989; Cowan and Atema 1990), such displacement could decrease reproductive fitness.

The higher overall frequency of limb loss observed in paired than unpaired blue crabs (i.e., combined male and female samples) in the Rhode River may be a consequence of: (a) accumulated injuries in larger, competitively superior males; (b) damage received by females from courting males; or (c) greater susceptibility of paired individuals to attack. The present field survey as well as experimental work (Smith unpubl. data) indicate that larger males dominate smaller males when mating. Larger blue crabs also exhibit higher frequencies of limb loss than smaller crabs (Smith and Hines 1991a). Advantages of increased body size in intrasexual mate competition have been noted for other crustaceans (Ridley and Thompson 1979; Berrill and Arsenaault 1982; Diesel 1988) and for arachnids (Zeh 1987), insects (Borgia 1980; Hieber and Cohen 1983; Flecker et al. 1988), amphibians (Shine 1979), and mammals (Ralls 1977). Repair rates, however, slow with increased body size in most crustaceans (Hartnoll 1982; Smith 1990a), and cease altogether for female blue crabs when sexual maturity is reached (Millikin and Williams 1984).

Models of female guarding have examined the benefits (e.g., ensured mating and parentage) and costs (e.g., lost

opportunity to mate with others) of this strategy in terms of male time investment (Parker 1974; Grafen and Ridley 1983), while ignoring possible benefits and costs to females being guarded (Christy 1987). Mate competition experiments demonstrated that females are particularly susceptible to injury and mortality during the reproductive stage. In addition to the hazards normally associated with molting (e.g., increased risk of predation, physiological stress; Shirley et al. 1991), females face the added risk of receiving damage during male-male agonistic encounters. To avoid injury during reproductive bouts, females should seek large males for protection and cease pheromonal advertisement once such a mate has been found.

Paired crabs might have higher levels of autotomy, regardless of size or sex, if the act of guarding makes them prone to attack. If so, the principal injury-causing agents are probably predators rather than competitors. Limb loss was surprisingly low (< 1%) among male crabs in experimental pools. Autotomy in males was infrequent whether competitors were of similar size (this experiment) or of different size (Smith, unpubl. data). As with many brachyuran species studied, intraspecific competitive interactions between blue crabs appeared ritualized and did not result in severe injury (Schone 1968; Hazlett 1972; Jachowski 1974; Hyatt and Salmon 1978).

Differences in pairing success between injured male crabs in pool experiments (negative effect) and the field survey (no effect) may reflect: (a) greater opportunity for handicapped guarding males to escape in the field; (b) confounding effects of male body size during mate competition; and (c) the relatively low incidence of autotomy in the Rhode River area. Prolonged periods of precopulatory mate guarding (e.g., up to 5–7 d for females paired in early premolt stage; Fig. 5) and pheromonal advertisement by females (Christofferson 1978; Gleason 1980) make competitive encounters between males highly likely. Takeovers, however, may be less frequent in the field than in pools, if injured guarding males flee with their mates. In addition, limb loss may become a determining factor in competitive bouts only when the size difference between opponents is small. Unless larger male blue crabs are severely handicapped, it is likely they will displace smaller competitors (Fig. 4, Table 5). Competitive inequalities resulting from autotomy will be difficult to detect statistically, unless sample sizes are very large or the frequency of claw damage is high (e.g., 33% in Patuxent River, Maryland; Smith and Hines 1991a). Autotomy was comparatively low in the present survey;

Table 5. Probable outcomes of male competitive encounters

<i>Different Size Males</i>		
Large, Intact	>	Small, Intact
Large, Intact	>	Small, Injured
Large, Injured	>	Small, Injured
Large, Injured	< >	Small, Intact
<i>Similar Size Males</i>		
Intact	>	Injured

Winner > loser. < > denotes uncertain outcome

only 9% of 250 mature males collected at pound nets were missing or regenerating one or both chelipeds. The lack of significant difference in injury between paired and unpaired individuals was consistent across size-classes and sex. In contrast, Sekkelsten (1988) observed proportionately fewer handicapped male shore crabs (*Carcinus maenas*) of certain size classes in precopula or copula than intact crabs.

Theoretical models suggest that nonlethal injury could regulate population abundances if injury rates were density-dependent and significantly reduced long-term survival or reproduction (Harris 1989). Studies of lizard, salamander, and insect populations have shown that autotomy frequency is often density-dependent (Robinson et al. 1991a; Van Buskirk and Smith 1991) and that injury can lower individual fecundity and delay breeding (Smyth 1974; Maiorana 1977; Dial and Fitzpatrick 1981). The present study is significant in showing that autotomy has the potential to affect male-male competition in a polygynous mating system. Empirical field evidence is needed to demonstrate that these various reproductive costs are indeed sufficient to alter population abundance. Injury frequency in blue crabs correlated positively with abundance in the Rhode River, Maryland between 1986–1989 (Smith and Hines 1991a), but the most commonly observed pattern of limb loss (i.e., loss of a single cheliped) had minimal impact on processes important to long-term survival (e.g., growth rate, predator avoidance, foraging ability; Smith 1990a; 1990b; Smith and Hines 1991a; 1991b). Despite its potential cost to courting males, cheliped autotomy was probably too infrequent to affect the blue crab population in the Rhode River. In populations with significantly higher injury levels (e.g., lower-mid Chesapeake Bay, South Carolina, Florida, and Alabama; Smith and Hines 1991a), autotomy might reduce male reproductive fitness. Population abundances could also be affected significantly if females lost mating opportunities, experienced higher mortality, or reduced fecundity as a result of autotomy.

Future studies should test experimentally for the effects of body size and the interaction of body size and limb autotomy on the outcome of mate competition. Experimental work is also needed to determine whether a threshold size difference is necessary for pair formation, and whether female choice is indeed operating in portunid mating associations. Sex ratio undoubtedly influences the intensity of mate competition, but field and experimental data are lacking for most decapod crustaceans groups. Portunid crabs, such as *Callinectes sapidus*, provide model systems for increasing our understanding of invertebrate mating systems. Morphological cues give clear signals as to the reproductive status of both sexes, making them ideal subjects to test theories of sexual selection.

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