The influence of male–male competition and female choice in mating associations in the blue crab, *Callinectes sapidus* (Rathbun)

Matthew S. Kendall[a],*, Thomas G. Wolcott[b]

[a]*NOAA/NOS, Strategic Environmental Assessments Division, 1305 East-West Highway SSMC-4, Silver Spring, MD 20910, USA*
[b]*Dept. of Marine, Earth, and Atmospheric Sciences, North Carolina State University, P.O. Box 8208, Raleigh, NC 27695-8208, USA*

Abstract

Male *Callinectes sapidus* allowed complete recovery of sperm resources and then mated a single time had significantly lower *vas deferens* weight than males allowed complete recovery of sperm resources but prevented from mating. In laboratory experiments, when a recently mated male (having low sperm volume) competed with a male that had not recently mated (having high sperm volume) for a single pubertal female, the female was just as likely to initiate pairing with the recently mated male as with a male that had not recently mated, despite possible reduction in her fertilization potential. At the end of trials in which stable pair formation occurred, recently mated males were paired significantly more often than males that had not recently mated. The combined effects of the lack of mate choice by females and high mating frequency of some males may result in many females in the population receiving low quantities of sperm. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Sexual selection theory suggests that males are limited with respect to the number of ejaculates they can deliver because of the time required to restore depleted sperm reserves (Dewsbury, 1982). Once a male has become depleted, there is little selective

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*Corresponding author. Tel.: 301-713-3000, ext: 194; fax: 301-713-4384.
E-mail address: matt.kendall@noaa.gov (M.S. Kendall)

advantage for him to continue mating, but perhaps more importantly, there is little selective pressure preventing him from doing so (Trivers, 1972). In contrast, there may be a large cost to females that mate with depleted males. Females should be selective, so as not to mate exclusively with males that have recently ejaculated and thus possess sperm resources too low to provide adequate fertilization (Dewsbury, 1982).

In some mating systems, the probability that a male will mate is often a function of two variables: females' choice of males and male–male competition for females. If possible, females should select large, healthy males that have not recently mated, as these attributes are usually positively correlated with sperm volume. If females mate with males having insufficient sperm resources to fertilize their egg production, they could experience reduced fertilization success as a result of sperm limitation. For example, female *Drosophila melanogaster* and *Hyphessobrycon pulchripinnis* (Pisces: Characidae) do not accept recently mated males with reduced fertility as mates (Markow et al., 1978; Nakatsuru and Kramer, 1982).

In systems with male–male competition, competitive interactions are influenced by male size, health, physiological state, and mating history. Consequently, to maximize reproductive output males should optimize time spent feeding, growing (molting), courting, and mating. However, even small or recently mated males with very low sperm volume obtain a small gain in fitness by monopolizing a given female. Consequently, in some systems, males may be expected to mate whenever possible; in fact, males of many arthropod species do not wait until they can produce a large ejaculate before mating again (Schwartz, 1991; Bissoondath and Wiklund, 1996).

We considered both male and female influences on mating success by examining the effects of males' past mating experience on their future mating success in the blue crab, *Callinectes sapidus*. In this system, males compete for females. Females have a single opportunity to mate during their ~ 2–3 year life span and use stored sperm to fertilize multiple broods (10^6 eggs each). Hence, obtaining a sufficient quantity of sperm, i.e. mating with a fit male, could be critical for maximizing female reproductive success.

An intense fishery aggravates the possibility that a female may be mated by a male with reduced fitness. The fishery's size limit (based on carapace width) results in selective removal of large males from areas in which courtship and mating take place (Casey et al., 1990). Remaining males may become chronically sperm-depleted due to the demands of servicing the still relatively un-fished female population. Furthermore, average male size has been declining over the past thirty years as pressure from the fishery has increased (Abbe and Stagg, 1996). Consequently, females may have difficulty finding a large, fit male capable of transferring a large ejaculate because these males constitute a very small segment of the population.

We tested the null hypothesis that males with high sperm volume (that have not mated recently) pair with the same frequency as males that have mated recently and have low sperm volume. We expected the former group to obtain mates more readily than the latter, for two reasons: (1) Males with high sperm volume have a much greater potential gain in fitness than males with much lower sperm volume and should therefore be more aggressive competitors (i.e. be willing to risk energy expenditure or injury during agonistic competitive interactions with other males). (2) Females should select males with high sperm volume due to the potentially serious reduction in lifetime fitness they might face if their mates had a low sperm volume.

2. Materials and methods

All experiments were conducted during the blue crab mating season (June–Sept.) at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland USA (38°51′N, 76°32′W). SERC is located on the Rhode River, a sub-estuary in northwest Chesapeake Bay.

Large male crabs (140–170 mm carapace width, mean = 148 mm, SEM 1.5 mm) were collected by crab pot in the Rhode River. Only intact (no limbs autotomized), intermolt (molt stage C) crabs were used in these experiments. As males of the correct size, condition, and molt stage became available, groups of them were held in large submerged cages near the SERC dock. Each group was held for 20 days prior to experimentation, a sufficient time for them to recover sperm resources that might have been spent prior to collection (Fig. 1). Crabs were fed a mixed diet of fish and molluscs placed into the cages each day in amounts based on estimated daily feeding rates for crabs of this size (Nye, 1989). At the conclusion of the twenty day recovery period, crabs were removed from the enclosure and assessed for molt stage and general condition. We assume that the enclosures provided suitable habitat for growth and normal crab interactions because mortality was low (M < 0.1 during recovery periods) and most crabs were found in good condition (intact).

Following the recovery period, males were randomly split into two groups; 're-covered' or 'depleted'. Those assigned to the 'depleted' group were allowed to mate
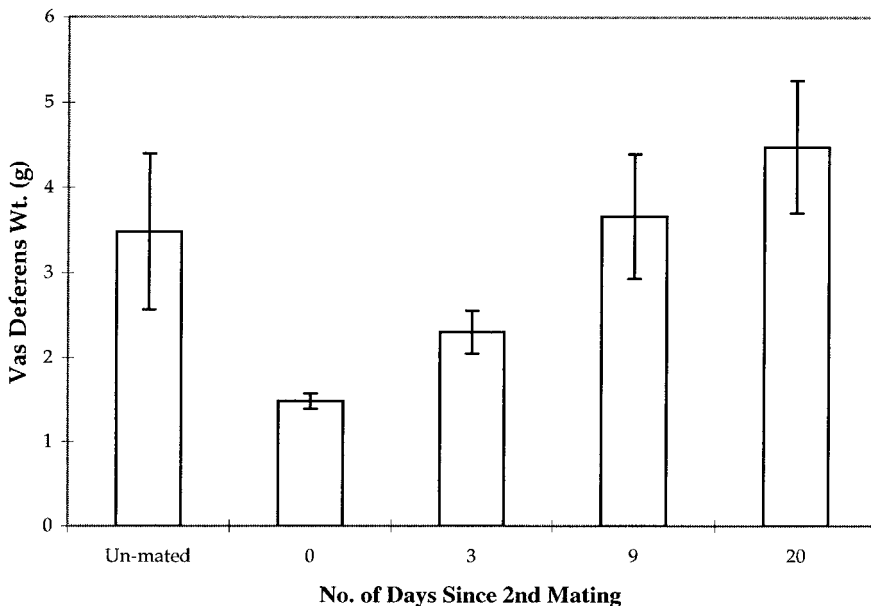

Fig. 1. Recovery rate of *vas deferens* weight following mating. *Vas deferens* weight (g) of males > 140 mm carapace width allowed complete development of sperm stores (un-mated), and those mated twice in close succession then allowed to recover for 0, 3, 9, and 20 days respectively (from Kendall et al., in press). Note: Error bars denote SEM.

twice in close succession, which reduced their stored sperm resources to near zero (Fig. 1). In most cases, males mated twice in 2–4 days if they were offered a D_3 molt stage pubertal female (D_3 females molt within 0–2 days, see Millikin and Williams, 1980) after their first mate was removed. After the second mating was complete (mature female observed in post-copulatory guarding position), the male was removed.

Mate competition experiments were conducted in oval ~ 1 m$^2 \times 20$ cm deep arenas. Arenas contained ~ 5 cm of sandy sediment to allow crabs to bury and were filled with filtered water (5–10 ppt) from the Rhode River. Water was changed daily before trials were conducted. To determine the effect of male mating history on future pairing success, a single 'recovered' male competed with a 'depleted' male of equal size for a single pubertal female in each trial. Males were acclimated to the arena ~ 12 hours prior to trial initiation. A single pubertal female of molt stage D_2 was placed in the arena (but isolated from the males by a wire screen) just prior to the beginning of each experiment (in the field, most females are observed paired by molt stage D_1 or D_2; ~ 5–7 days pre-molt; Jivoff, 1998). Food was provided throughout each trial in the form of a cracked mussel or a piece of fish. Trials were initiated when the screen was removed from the female, allowing the males to interact physically with her. There was no need to physically separate males prior to trial initiation because they did not interact until the screen was removed from the female. Because previous research suggested that in competition experiments of this type, most crab interactions (such as courtship displays, mate stealing, and ultimately stable pair formation) would occur within a few hours of trial initiation (Jivoff, 1995), competition trials were limited to two hours. Each experiment was conducted behind a screen to avoid visual disturbance and video taped for later review of crab interactions and pairing success. Scored behaviors included pairing attempts initiated by females (female with meral spread backs under male) and behaviors from males including courtship displays (male exhibiting meral spread and waving the swimming paddles); mate stealing (a male physically displacing another male in precopula); and pair formation (pre-copulatory embrace). These behaviors were selected because they indicate male interest in mating or competing for mates (Jivoff, 1998). However, stable pair formation was considered the primary indicator of a males' competitive success.

3. Statistical analysis

Pairing success of recovered vs. depleted males, and choice by females' were analyzed using G-tests (null hypothesis 50:50, alpha = 0.05). Williams' correction was used because it provides a better approximation of the chi-square distribution than the unadjusted G statistic, and a more conservative test at low sample sizes (Sokal and Rohlf, 1981).

4. Results

The 22 male–male competition trials yielded 44 hours of videotape, which revealed a

variety of sexual behaviors displayed by both sexes. These included all of the classic elements of blue crab courtship (prepubertal female emits pheromone; male responds by elevating his body, orienting toward the female, and vigorously waving the swimming paddles; female may give a 'rocking' display; crabs move toward each other until the female is seized by the male and placed into the 'cradle carry' position; see Jivoff, 1998 for complete description of sexual behaviors). The presence of a given behavior and its frequency of occurrence was highly variable. In some trials, pairing occurred quickly with very little prior interaction between any of the crabs and relative quiescence thereafter. In others, interactions continued for the duration of the trials; in a few, no stable pair had been formed by the end of the two hours.

Stable pair formation occurred in 16 of 22 trials. Both males and females were observed to initiate pair formation. Females approached or backed under 'recovered' and 'depleted' males with the same frequency (8:9, not significantly different from 50:50). Courtship displays by one or both males occurred in 18% of the trials. 'Recovered' and 'depleted' males were observed performing courtship displays in 3 and 2 trials respectively. Backing under a male by females and courtship displays by males are signs of willingness to pair; however, these activities do not always result in pair formation nor are they required for pair formation to occur. Mate stealing occurred in few trials as well (9%). 'Depleted' males attempted mate stealing on two occasions, and both attempts were successful. One 'recovered' male made a single unsuccessful takeover attempt. Courtship displays and mate stealing are considered indicators of male interest; however these activities occurred with such low frequency that statistical evaluation was not possible. On the other hand, stable pair formation, the primary indicator of competitive dominance, occurred with sufficient frequency to allow a G-test. 'Depleted' males were observed paired significantly more often than 'recovered' males (12:4) at the end of trials in which stable pair formation occurred (null hypothesis 50:50; $G = 4.06 > \chi^2_{(0.05,1)}$).

5. Discussion

Competition between males for mates should evolve when receptive females are a rare and unpredictable resource in space and time (Christy, 1987). Choice of mates by females should evolve whenever males differ in ability to fertilize eggs (Trivers, 1972). All of these traits characterize the blue crab mating system: females are mobile, mate infrequently, and fertilize multiple broods from sperm obtained at a single mating; males differ widely in volume of sperm they possess (Fig. 2). Consequently, we expected to observe both competition between males for receptive females, and choice of mates by females.

We hypothesized that males with high sperm volume would be better competitors for mates than males with much lower sperm volume. In the field, this would be evidenced by a slightly reduced sperm volume for all males; however, extremely low sperm volume would not occur for any individual because males would become progressively less able to obtain mates as their sperm became depleted. To the contrary, our results indicate that recently-mated males (with low sperm volume) out-compete those that have
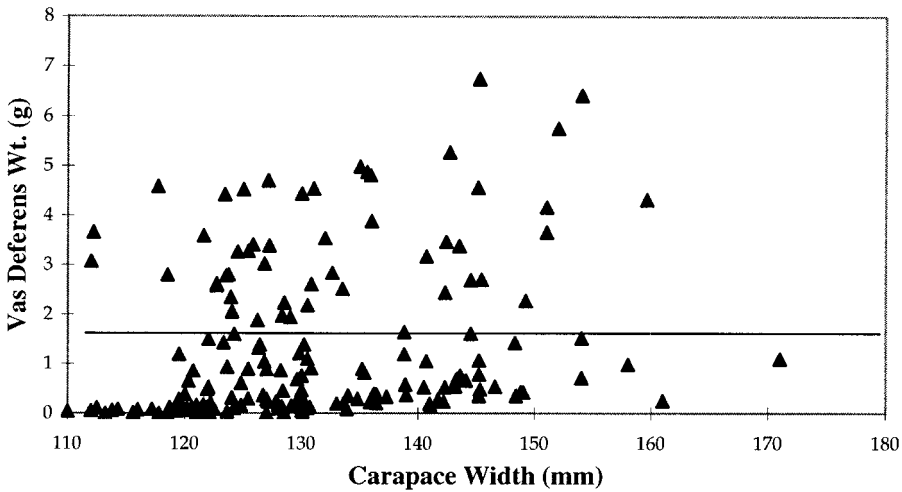
Fig. 2. *Vas deferens* weight of males caught in the field. Scatter plot of *vas deferens* weight. (g) vs. carapace width (mm) for crabs collected in the Rhode River during the 1996 reproductive season. The horizontal line denotes *vas deferens* weight of a crab allowed full recovery of sperm resources than mated a single time (from Kendall et al., in press).

not recently mated and possess much larger volume of sperm. Although the reasons for this competitive dominance are unclear, it helps account for the large proportion of males in the field population that have very low sperm volume (Fig. 2).

Although theory would predict that females should choose males capable of transferring an ample amount of sperm, in our experiments females did not preferentially initiate pairing with 'recovered' males. In nature, the combined effects of the competitive success by 'depleted' males and a lack of mate preference by females apparently allows many males to mate so frequently that their sperm stores reach extremely low levels (Fig. 2).

There are several potential explanations for the apparent lack of mate selection by females. It is possible that females are not selecting specific males because they would suffer no loss in fertilization success by mating with a depleted male; however, this would suggest that even a very small quantity of sperm is sufficient to fertilize their lifetime egg production ($\sim 3 - 10 \times 10^{6}$ eggs). It is also possible that females are not selective of specific mates because it may be more beneficial to be paired with and defended by a depleted male that can fertilize at least a portion of their eggs than to risk predation or remaining completely unfertilized. Females, rather than actively rejecting or accepting ('choosing') individual males, may have evolved to insure that they will be paired with a large, aggressive male by simply advertising their receptivity in a system where males compete for mates (Christy, 1987), or by otherwise inciting males to compete for them (Cox and LeBoeuf, 1977). It is also possible that females simply can't tell the reproductive condition of males. This could be attributable to males having evolved the ability to conceal their depleted reproductive status despite the probability that continued mating would yield only a small gain in their fitness. More probably, over

evolutionary time it has been unnecessary for females to have evolved the tools to identify a male's reproductive fitness (e.g. mating history) because in natural, un-fished populations because the abundance of large males capable of delivering larger ejaculates (Jivoff, 1995) was ample.

Under natural conditions, the combined times of pre- and post-copulatory mate guarding behavior exhibited by this species may be sufficient to allow males to fully recover sperm resources between successive matings. According to field observations and experiments conducted in 1 m^2 pools, post-copulatory guarding lasts from 2 to 5 days. Its duration depends primarily on sex ratio; males of all sizes guard females longer when other males or potential cannibals are present. Pre-copulatory guarding time is estimated to be 5–7 days based on molt stage of pubertal females observed in the field (Jivoff, 1995). This suggests that even frequently-mating males could use this seven to twelve days of total guarding time to recover sperm levels between consecutive matings since large males require < 9 days to recover *vas deferens* weight following mating (Fig. 1). Additional research is needed to determine if guarding times estimated in the lab reflect actual guarding times in the field. We also must determine the periodicity of mating during the reproductive season. There is little potential for individual males to monopolize multiple females if females in the population become receptive synchronously; by the time a given male could locate a first female, court, and mate, most of the other females would already have been inseminated (Emlen and Oring, 1977; Christy, 1987).

On the other hand, the possibility that mate guarding intervals offer sufficient time for males to recover sperm volume is inconsistent with our observation that large numbers of males in the field have sperm volume even lower than the value predicted had they mated just a single time following complete recovery of sperm resources (Fig. 2). As suggested by the results of our male–male competition experiments, the strategy for males may be to mate as frequently as possible, even if there is insufficient time for complete recovery of sperm resources between consecutive matings. Males, by continuing to mate, would not only effectively exclude other males from obtaining a female's reproductive potential (since female blue crabs rarely mate more than once), but would also receive an additional small gain in fitness because even frequently-mating males would transfer some sperm and fertilizing at least a portion of each mate's eggs (Trivers, 1972). Furthermore, our results indicate that male interest in obtaining additional mates seems to be augmented by prior mating experience. Thus, high fishing pressure on males may have a two-fold impact; not only are there few large males remaining in the population but a subset of those remaining males may be doing a disproportionate share of the mating.

While laboratory studies such as ours provide a good basis for forming hypotheses regarding behaviors that occur in nature, we still must examine the competitive interactions between males on the scales at which they occur in the field. Caution should be used in drawing broad conclusions based solely on experiments conducted in areas that offer no opportunity for escape of uninterested mates and that offer more limited mate variety than is likely to be found in the organisms' natural mating system (Cox and LeBoeuf, 1977).

Factors that influence the competitive dominance of recently mated males have not yet

been identified. For example, behavior is influenced by conditioning experience in many animals. It is also probable that hormones influence courtship and mating behavior. Once a male's interest in mating has been initiated, it may require some change in his physiology such as the approach of his next molt (which would make continued mating an impossibility) to reduce that interest. A chemical cue from pubertal females initiates male interest (Gleason, 1980); perhaps a similar cue from mature females in post-copulatory mate guarding terminates male interest. By allowing males to carry out post-copulatory guarding and to release mature females naturally (rather than being forced to separate as in our experiments), we can determine if this behavior somehow reduces male interest.

6. Conclusion

Mating systems theory suggests that both sexes share the goal of maximizing reproductive output despite conflicting behaviors that may arise (e.g. female avoidance of a pursuing male that is sperm-depleted but seeks to mate as frequently as possible). However, our observations are consistent with the notion that in most mating systems, members of one sex compete more intensely for mates than members of the other sex.

Our results have important implications for fishery management as well, if intensive exploitation of males is leading to sperm limitation and reduced reproductive output by females in the population. Unfortunately, there are currently no direct data to support or refute the occurrence of sperm limitation in the blue crab system. However, there is a growing pool of circumstantial evidence (Abbe and Stagg, 1996; Jivoff, 1995; Kendall et al., in press), including the results of this study, leading workers on blue crabs and other heavily fished crab populations (Powell et al., 1973; Smith and Jamieson, 1991; Paul and Paul, 1992; Hankin et al., 1997) to suspect this possibility. The potential consequences of overlooking such a phenomenon are serious, suggesting that the research community should seek to understand how anthropogenic alterations of population structure effect the species' biology, especially the dynamics of mate selection and competition.

Because the fishery began altering population structure by intensively exploiting males only recently (~ 50 years) on evolutionary time scales, female blue crabs may not yet have acquired the ability to judge a male's mating history. Males that have already mated show greater interest (than un-mated males) in additional mating. The combined influence of this lack of mate choice by females and the propensity of males to mate more frequently than the recovery time of their sperm resources suggests that many females in the field may be receiving very low quantities of sperm. Prudent management will require that we determine if sperm limitation is leading to reduced fertilization success in heavily fished populations like those in Chesapeake Bay.

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