

Adaptive Significance of Reproductive Cycles in the Fiddler Crab *Uca pugilator*: A Hypothesis

Abstract. *Semimonthly peaks in courtship behavior of male crabs coincide with peaks in the temporal distribution of receptive females. Females mate once each month, 4 to 5 days before one of the semimonthly spring tides. The relation of the time of reproduction to tide cycles may be an adaptation to increase to a maximum the probability that the final stage of the planktonic larvae will be transported by tidal currents to substrates suitable for adults.*

Fiddler crabs of the genus *Uca* are found on estuarine shores in tropical, subtropical, and warm temperate regions throughout the world. Males of most Neotropical and North American species court from and defend burrows dug into intertidal or supratidal substrates (1). Sexually receptive female *Uca pugilator* approach and follow courting males down their burrows (2). Mating occurs in the burrow; females emerge several days later and release their planktonic larvae into the estuarine waters. In contrast, nonbreeding male and female *Uca pugilator* inhabit temporary burrows during high tide. During low tide these crabs emerge and form aggregations which move over intertidal substrates and feed (1).

Reproductive activity in males of several *Uca* species is known to cycle twice each month. Within each species males show synchronized peaks of sexual display just before or during the semimonthly spring tides (3-6). Although little is known about reproductive cycles in individual females, studies by von Hagen and Feest (4, 5) suggest that there are two peaks of mating each month followed several days later by peaks in larval release. The adaptive significance of reproductive cycles in *Uca* has received little attention.

Here I report reproductive cycles in individually marked male and female *Uca pugilator*. Females mate at most once each lunar month, 4 to 5 days before one of the semimonthly spring tides. Within a local population there are two groups of females, each group mating before alternate spring tides. Larval release occurs about 13 days after mating, 7 days before each spring tide. Cycles of reproductive activity in males are coincident with and probably evolved in response to semimonthly cycles of receptivity in females. I report data suggesting that the phase relationship between female reproductive cycles and the semilunar cycle of tidal amplitude and current velocity is an adaptation to maximize the probability that the final larval stage will settle on substrates suitable for adults.

The study was made on a small sandy beach on the southwest shore of Cayo

Pelau, a mangrove island in Charlotte Harbor on the west coast of Florida. The animals were held in an enclosure (3 by 6.5 m) with its long axis perpendicular to the water's edge. The enclosure was built of galvanized hardware cloth and aluminum flashing and was designed to prevent crabs from entering or leaving (Fig. 1). Between 29 June and 13 July 1976, 300 females and 209 males were captured from inside the enclosure, marked, and returned (7). From 15 July to 21 August these crabs were watched for an average of 5 hours each day. I recorded the behavior and identity of reproductively active individuals and, during low tide, the identity of each marked crab in the feeding aggregation. The date of onset of a period of reproductive activity for each male was judged by observation of either repeated aggressive encounters with other courting males or courtship of females and burrow defense. Reproductive activity was considered to end on the day the male was next observed in the feeding aggregation. Since mating males remain underground for 1 to 3 days (mean = 1.8 ± 0.17 ,

$N = 18$) any male not seen for up to three consecutive days was considered to be reproductively active during that period, provided that he was seen courting or fighting on the days preceding and following the absence (8). I used the duration of absences from the feeding aggregation to determine reproductive activity for females not otherwise known to have reproduced. I have found that females remain in the terminal chamber of the burrows in which they mate while they incubate their clutch. They usually remain underground until the night on which hatching occurs, whereupon they emerge, walk to the water's edge, and release their larvae. The mean length of absence from the feeding aggregation for females known to have mated was 14.5 ± 0.64 days; range, 11 to 17 days ($N = 30$). Therefore, I assume that any female not seen feeding for 11 to 17 days reproduced in that period (9).

Thirty-six records that were complete enough for an analysis of reproductive cycles indicate that males cycled through bouts of reproductive activity, separated by bouts of feeding, with peaks of reproductive activity on 22 July and on 4 and 5 August (Fig. 2, A and B).

Direct observations of reproductive behavior and the temporal pattern of the presence and absence of individual females in the feeding aggregation permit estimation of the temporal distribution of both the number of receptive females and the number of females releasing larvae. None of the females for which the records of activity were of sufficient

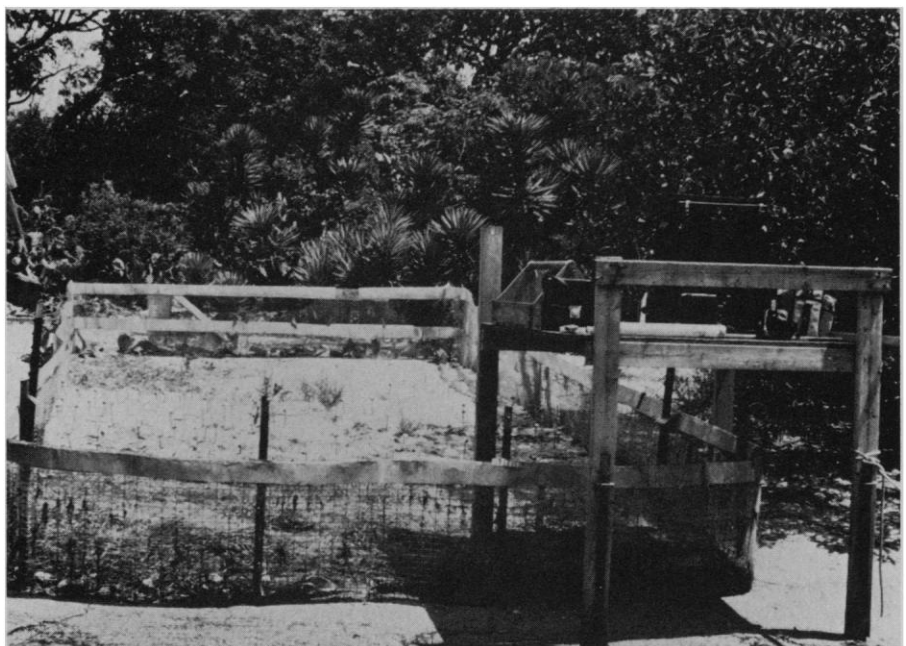


Fig. 1. The enclosure. View up the beach at low tide. At high tide, water covers approximately the lower third of the sand inside the enclosure. The platform at front right was used for making observations.

length for analysis reproduced more than once between 14 July and 9 August (10). The distribution of the number of females closing in the burrows of courting males per day (Fig. 2C) shows two peaks, each about 5 days before one of the spring tides. Sixty percent of the females mated before the new moon spring tides and 40 percent before the full moon spring tides. Twelve days after each peak in mating, there was a peak in the number of females who released their larvae; these peaks occurred at the neap

tides about 7 days before the next spring tides (Fig. 2D).

Comparison of the variances of the distribution of closures for females mating between 15 and 28 July and the distribution of larval release for these females (29 July to 10 August) shows that hatching occurs over a significantly shorter period (F test of the equality of variances, one-tailed, $P < .025$). This suggests a mechanism that permits precise timing of larval release.

One possibility is that, after closing

with a male in his burrow, females either delay or hasten copulation or oviposition depending on when in the cycle they close. A positive correlation between the length of time a male was closed and the date of closure would support this hypothesis since a male does not open the burrow until after the female has laid her eggs. Such a correlation was found in a sample for which the exact time of closure and emergence were known ($r = .64$, $N = 13$, $P < .05$). In addition, I found significant correlations between the length of time from closure to hatching and the date of closure for females closing during both the first ($r = .57$, $N = 93$) and second ($r = .49$, $N = 59$) periods of mating, thus suggesting that females closing early in the cycle delayed the initial stages of reproduction. As a result, larval release occurred during a relatively brief period.

Both synchrony in sexual receptivity and the ability of females to adjust the timing of the initial stages of reproduction, resulting in narrow peaks of larval release, may reflect selection for accurate timing of larval release relative to the semimonthly tide cycle. As suggested by von Hagen (4), reproductive cycles in males may simply be viewed as an adaptive response to the semimonthly variation in the number of receptive females. Here I argue that the timing of larval release may be a behavioral adaptation related to the dispersal ecology of *Uca* larvae.

The adults of nearly all *Uca* species are found on substrates characteristic of estuaries (1). Since the net depth-averaged current flow is seaward in estuaries (11), *Uca* larvae are in danger of being transported out of the estuary, leaving the final stage (the megalopa) to settle on exposed substrates unsuitable for adults. Vertical migration by developing *Uca* larvae may be an adaptation to increase retention of larvae in estuarine waters (12-14). The pattern of seaward nontidal drift near the surface and landward drift near the bottom is characteristic of most estuaries (11). Sandifer (14) found that early larval stages were abundant near the surface and later stages abundant near the bottom; he suggested that by remaining near the bottom the later stages were transported up the estuary and returned to substrates suitable for adults. In a homogeneously mixed estuary that lacks nontidal drifts, DeCoursey (13) found that stage one *Uca* larvae remain near the bottom during ebb tide, where tidal current velocities are least, and rise in the water column during flood tide. Thus, vertical migration both within and

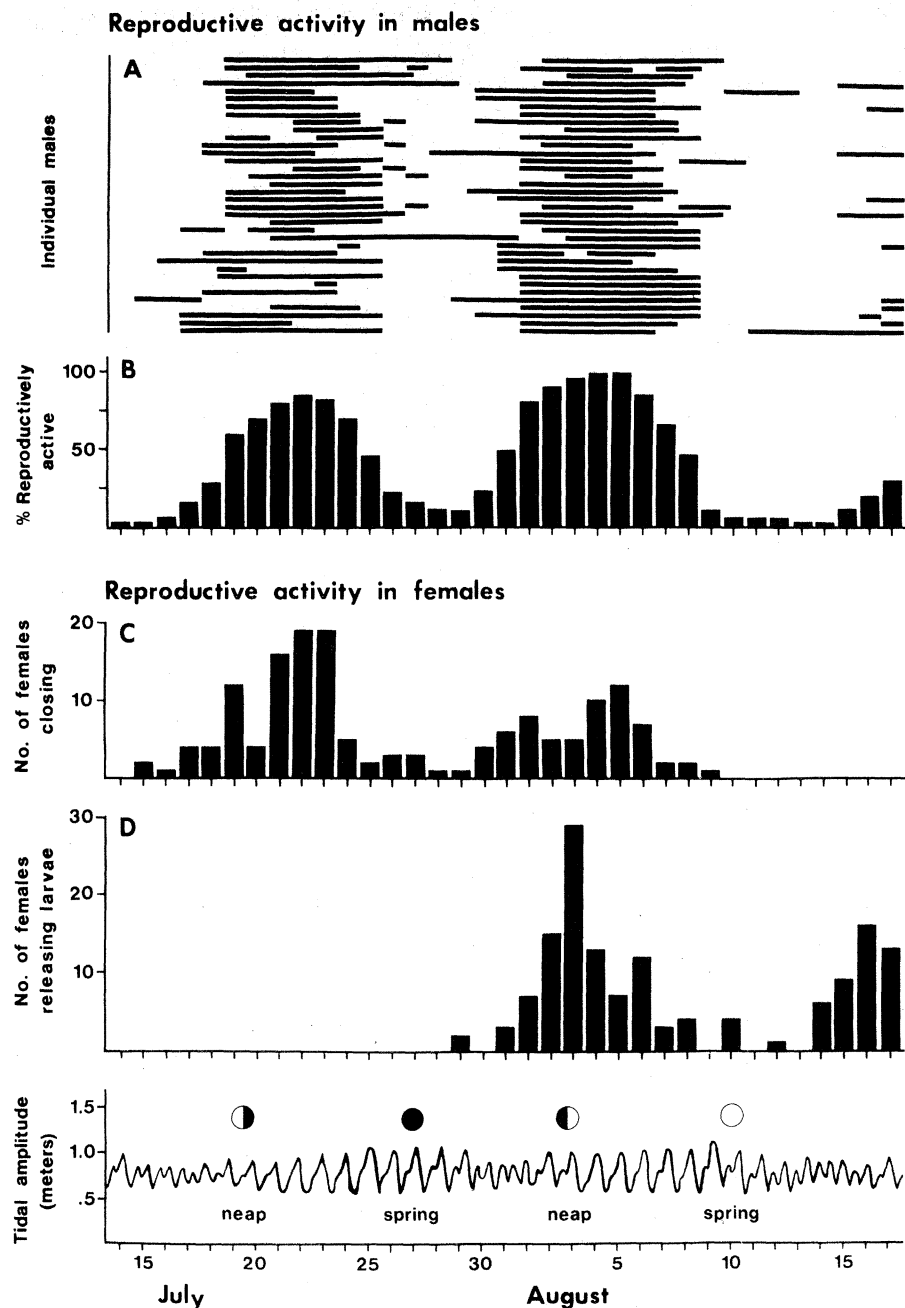


Fig. 2. Reproductive activity of male and female *Uca pugilator* in relation to tide cycles. (A) Horizontal bars indicate the days on which reproductive activity was observed or presumed to occur in individual males. (B) Temporal distribution of the percentage of reproductively active males. (C) Temporal distribution of the number of females seen or presumed to have closed to mate in a male's burrow. (D) Temporal distribution of the number of females releasing their larvae. Tide height was recorded with a gauge adjacent to the study beach. ●, ○, ○, ○: new moon, first quarter, full moon, last quarter, respectively.

between larval stages may reduce the rate of seaward transport.

Although the rate of transport out of the estuary depends on the pattern of vertical migration of developing larvae and on the variance and magnitude of residual drift and tidal currents, many larvae are probably displaced seaward during development, each stage moving further toward the mouth of the estuary (14). Any behavior that would increase the magnitude of the up-estuary transport of the megalopae when they are ready to settle would be strongly favored. Female *Uca pugnator* are releasing their larvae at a time in the semi-monthly cycle of tidal amplitude and current velocity such that the megalopae experience maximum up-estuary transport when they are ready to colonize adult habitats.

Laboratory-reared *Uca pugnator* take about 18 days at 28° to 30°C to reach the megalops stage, and molt to the first crab after spending 3 to 15 days as megalopae (15). On the assumption that the megalopae will first be ready to settle after about 4 days, megalopae from clutches released 7 days before a spring tide would be ready to settle about 22 days later, during the next spring tides. If megalopae show the same patterns of vertical migration relative to the tide currents as stage one *Uca* larvae, then these megalopae would experience maximum up-estuary transport. Megalopae released near or during the spring tides would be ready to settle at the time of the neap tides. They would have a decreased probability of being carried to suitable substrates because of the smaller magnitude of their horizontal displacement by the neap tide currents.

This hypothesized behavioral adaptation of adults, which may be a general characteristic of the genus, should be viewed as complementary to behavioral adaptations of larvae that reduce transport out of the estuary. Both should increase the probability that larvae will reach substrates suitable for settlement.

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References and Notes

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7. The crabs were marked by gluing a small piece of Scotch brand plastic tape onto their carapace with Duro Super Glue 3. The tags were num-

- bered with a Sanford's black ink Sharpie Marker. During the first week of observation, counts of marked and unmarked animals revealed that about 80 percent of the females and 90 percent of the males in the enclosure were marked. I do not know whether the sex ratio inside the enclosure was an unbiased estimate of the true sex ratio of the adult population.
8. For absences where a male was last seen courting and next feeding, or feeding and then courting, I was unable to determine on which days of the absence he was and was not reproductively active. I have eliminated from this analysis all activity records with blanks of more than 2 days.
 9. To estimate the dates of onset and termination of reproduction for cases where one or both were not observed, I added 1 day to the date on which a female was last seen feeding and subtracted 1 day from the date she was next seen feeding. The average lag between when a female was last seen feeding and when she closed with a male was 1.3 ± 0.28 days ($N = 23$). Six females who were seen to emerge with a ripe clutch and were allowed to naturally release their larvae were seen feeding on the day after larval release.
 10. I was not able to judge whether females who disappeared after 9 August were reproducing since systematic observation ended on 17 August and

the mean length of absence when reproduction occurs is 14.5 days.

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Particles in the Eruption Cloud from St. Augustine Volcano

A recent report by Hobbs *et al.* (1) describes airborne measurements of the effluents from St. Augustine volcano in Cook Inlet, Alaska. A series of eruptions began on 23 January 1976, and explosive activity continued intermittently until

about 18 February. The largest eruptions occurred during the period 23 through 26 January.

The measurements of Hobbs *et al.* were made during the period 8 through 18 February. They examined and ana-

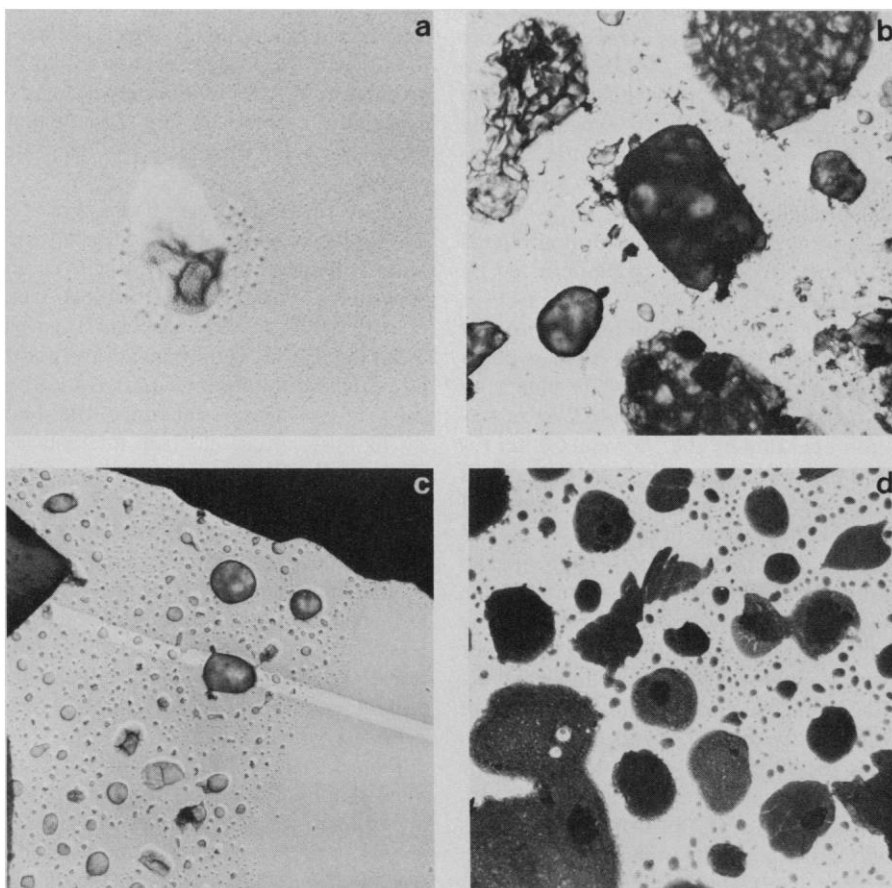


Fig. 1. Transmission electron micrographs of fume particles from the St. Augustine eruption. Distances across individual micrographs: (a) 1.9 μ m; (b) 4.1 μ m; (c) 13 μ m; and (d) 13 μ m. The area in (d) had been allowed to evaporate in the electron beam. The other samples were gold-shadowed before being examined with the electron microscope.