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SEMIDOME BUILDING AS SEXUAL SIGNALING IN THE FIDDLER CRAB *UCA LACTEA* (BRACHYURA: OCYPODIDAE)

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ABSTRACT

During the mating season, males of the fiddler crab *Uca lactea* build semidomes of mud at the entrances of their burrows to which they attract females for mating in the upper intertidal zone. Related species build similar structures which either reduce aggression between neighboring males or attract sexually receptive females. Male *U. lactea* did not build disproportionately more semidomes as density increased, suggesting that these structures do not modulate aggression. Larger males built higher and wider semidomes as would be expected if the semidomes are a courtship signal. When the high tides were too low to cover their habitat and the sediment dried, males were unable to build new or repair existing semidomes. Towards the end of the mating season more small males built semidomes perhaps because large males prevented them from courting earlier when most females mated. We made two experimental enclosures, added males to one and males and females to the other, and monitored semidome building. Males built significantly more semidomes in the enclosure with females. Overall, our observations support the hypothesis that the semidomes of *U. lactea* are a sexual signal.

Many species of intertidal brachyuran crabs build mud or sand structures on the surface of the sediment near or at their burrow entrances, such as hoods (Zucker, 1981; Clayton, 1988), pyramids (Linsenmair, 1967), mounds (Wada *et al.*, 1994), chimneys (Wada and Murata, 2000), and mudballs (Oliveira *et al.*, 1998). In many species, only reproductively active males build structures, which have been shown to reduce aggression between neighboring males (Zucker, 1974; 1981; Clayton, 1988; Wada *et al.*, 1994) or to attract females to males' burrows for mating (Crane, 1975; Christy 1988a, b, 1995; Oliveira *et al.*, 1998; Christy *et al.*, 2001, 2002).

During the June to August mating season, males of the fiddler crab *Uca lactea* construct low semidomes at the entrances to their burrows in the upper intertidal zone (Fig. 1). Reproductively active males of 17 species of fiddler crabs (approx. 100 species) are known to build similar structures variously called hoods, pillars, domes, and semidomes, depending on their size and shape (Christy, 1988a; Christy *et al.*, 2001). Semidome building by *U. lactea* in Japan was first reported as "shelter building" (Yamaguchi, 1971). Recently, Kim and Choe (2003) and Kim *et al.* (2004) considered semidomes to be indicators of courtship activity, although neither the function of these structures nor their physical characteristics were described in detail. Here we describe the semidomes of *U. lactea* and aspects of semidome building behavior in relation to the possible function of these structures for reducing aggression or attracting females.

Some other fiddler crabs usually build their structures in the mid intertidal zone, where they are destroyed daily by tides (e.g., pillars in *Uca beebei*, see Backwell *et al.*, 1995; hoods in *Uca musica*, see Christy *et al.*, 2001). In contrast, the semidomes of *U. lactea* are built in the upper intertidal zone in the Korean intertidal mudflat above the reach of the tide for several days during the neap tides. We tested whether sediment moisture content affects structure building by destroying semidomes on days that the habitat was, and on days it was not, covered by the tide. We evaluated whether semidomes reduce aggression by monitoring semidome building over the natural range in male density. If males build semidomes in response to declining nearest-neighbor distances, then their numbers should increase disproportionately with density (Zucker, 1981). For example, given a random dispersion of burrows, the mean nearest-neighbor distance $= 1/2\sqrt{\text{density}}$

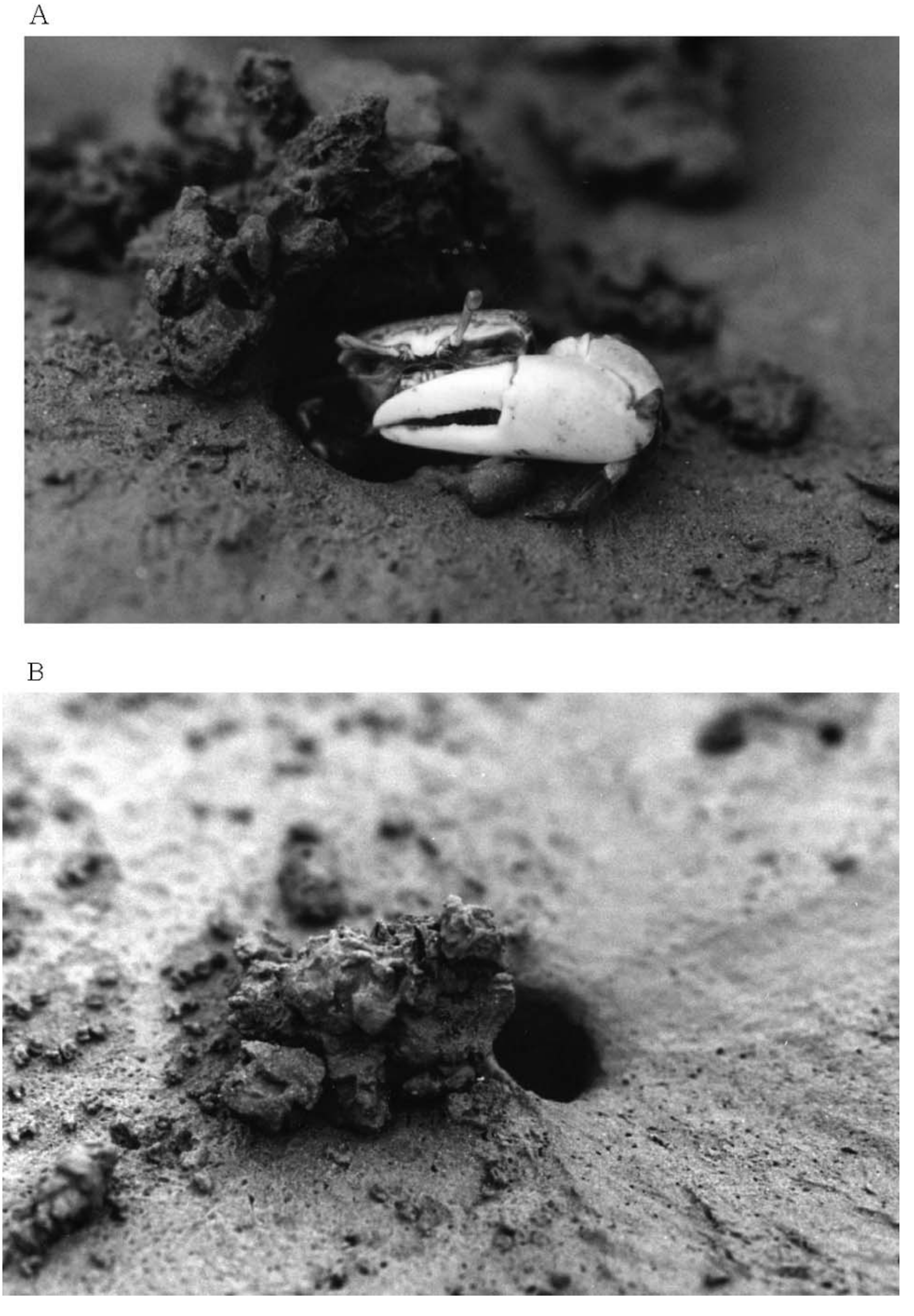

Fig. 1. (A) Male *Uca lactea* with a semidome, (B) lateral view of a semidome.

(Clark and Evans, 1954). If semidomes are a sexual signal to females, then males should build them more often when females are present than when they are absent. We tested this by manipulating male and female density in enclosures and monitoring hood building.

Materials and Methods

Study Species

Uca lactea live in the upper intertidal zone on mudflats in the temperate, tropical and subtropical Indo-Pacific (Kim, 1973; Crane, 1975). In South Korea, during the cold months from November to April, this species remains underground in burrows. On the warmer days in early May, as the tide recedes and exposes their habitat, they emerge and feed almost continuously on organic matter on the sediment surface. When the tide covers their habitat, at night, and during heavy rains, crabs remain in their burrows which they plug with mud. Except when mating, crabs occupy burrows alone.

At the beginning of the breeding season in early June, males dig their burrows, which have one entrance, to a depth of about 40 to 50 cm. During 3- to 5-day periods of intense courtship twice each lunar month, many males construct semidomes out of mud at the entrance to their burrow. Males court passing females by waving claws toward them and females respond by approaching and briefly entering males' burrows. Females sequentially visit several males before they choose a mate by staying in a male's burrow. In some cases, about 15 to 30 minutes later, the male emerges and walks away leaving the burrow to the female, which she then plugs with mud from below. In other cases, the male may plug the burrow and stay with the female for a day or more before leaving. Finally, males sometimes approach neighboring females, follow them to their burrows, and then tap for several minutes on the edge of the burrow opening with their walking legs while the female is below. If the female emerges, the crabs mate on the surface, after which the male returns to his burrow.

Study Site

The study was conducted at the "Choji" intertidal mudflat in Kilsang-myon, Kanghwa Island (37°35′N, 126°32′E) from June to August in 2000–2001. This period included the monsoon season in South Korea. The study site is along the intracoastal waterway, downstream of the Han River, about 1 km from Daemyong Port in the Kimpo Area. The sediment was primarily silt (sand: 6.9–17.2%; silt: 72.9–82.8%; clay: 5.9–10.3%; mean grain diameter: 4.4 phi) and contained 0.5% total organic carbon. Maximum tidal height ranged from 10 to 930 cm. *Uca lactea* lives in a 400–500 m^2 area on the upper intertidal mudflat at from 700 to 850 cm elevation. This area is not flooded by the tides and dries out for 5–6 days each semilunar cycle.

Semidome Building Behavior

In an area with high male density from July 1–August 3, 2000, we delimited a 2 × 2 m plot with nylon strapping supported by four 50-cm-long stakes of PVC tubing. Each male's burrow inside the plot was marked with a small numbered flag. We sat in a chair near the plot and observed crabs directly or through binoculars. For the three days when most males courted during each semilunar period, we made notes on each crab's behavior and recorded the number of semidomes on the surface every hour.

The Relationship Between Male Size and Burrow Size

We determined the relationship between male size and the diameter of the burrow entrance by measuring the entrance diameter of males' burrows with vernier calipers (0.1 mm precision). We then captured the males at these burrows by placing the chisel-shaped end of a 1.2 m bamboo stick next to the burrow opening. When the male emerged and walked about 20 cm away, we quickly blocked the burrow entrance with the stick and enclosed the male with a 10 cm high plastic ring. Using the vernier calipers we measured the carapace width and the propodus length of the large claw of each male.

Seasonal Variation in the Sizes of Semidome Builders

To determine whether the size of semidome builders shows seasonal variation, we randomly chose burrows with semidomes and measured the entrance diameter and the height and width of the semidome using vernier calipers. We made these measurements on June 11 ($n = 11$), June 18 ($n = 18$), July 5 ($n = 13$), July 26 ($n = 20$), and August 7 ($n = 19$), 2000. In addition, we captured active males separately and measured the carapace width of active crabs on June 4 ($n = 6$), June 18 ($n = 30$), July 5 ($n = 23$), July 17 ($n = 6$), July 29 ($n = 37$), and August 1 ($n = 19$) to see whether the size of active crabs changes with the season.

Semidome Rebuilding

To determine whether sediment moisture content affects the ability of males to build semidomes, we destroyed 36 randomly selected semidomes during low tide, shortly after they were built, on days when the previous tide had covered the habitat. We also did this on days that the habitat had not been inundated and the sediment was relatively dry. Thirty minutes after we destroyed these semidomes we recorded how many were rebuilt.

Social Context and Semidome Building

If males build semidomes to reduce the frequency with which they interact aggressively with other males, then they should build them whether females are present or not. In contrast, if males build semidomes to attract females, they should build them only when females are present. We tested these predictions by putting males in two enclosures in the field, one with males only and the other with both sexes, and we recorded the frequency of semidome building. The enclosures were 1 × 1 m^2 with walls of stainless steel mesh (< 0.5 mm mesh width) 30 cm tall buried to 15 cm in the mud. The corners were fastened with wire and the top edge was capped with split plastic pipe (3 cm diameter) and elbow fittings forming a barrier that the crabs could not climb. We selected the area where crabs are relatively rare, and then set up the enclosures. We removed all burrow-holding crabs from inside the enclosures by capturing them using the method described above. This process was done for 10 days before the experiment started. We measured each male's carapace width and length and the length of the propodus and individually marked each with paint and adhesive labels. We made burrows for males inside the enclosures by forcing bamboo sticks (1 cm diameter) into the mud in an evenly spaced array. We added 20 males to each plot and 10 adult females to one plot only. Male size did not differ between plots (Mann-Whitney U-test, carapace width: $U = 163.5$, $Z = 0.987$, $P = 0.32$; carapace length, $U = 162.5$, $Z = -1.01$, $P = 0.31$; major claw length: $U = 159$, $Z = -1.10$, $P = 0.27$).

From June 1 to 30, 2001, a period spanning two semilunar cycles, we observed the enclosures daily from 3 h before to 3 h after low tide. On June 7, males began semidome building. We observed the crabs from about 1 m away while sitting on a chair. We recorded the number of males active on the surface, the number of semidome builders, the times that semidomes were built, and the number of semidomes. We excluded from the analysis observations on days that few crabs were active either because low tide occurred at dusk (June 15–18) or because it rained heavily (June 24, 29–30). On June 11–14 and 27–28, the high tide did not reach the enclosures, and the sediment became too dry for crabs to build semidomes. On those days, we destroyed any semidomes remaining from the previous day, and we poured 10 L of seawater into each enclosure to

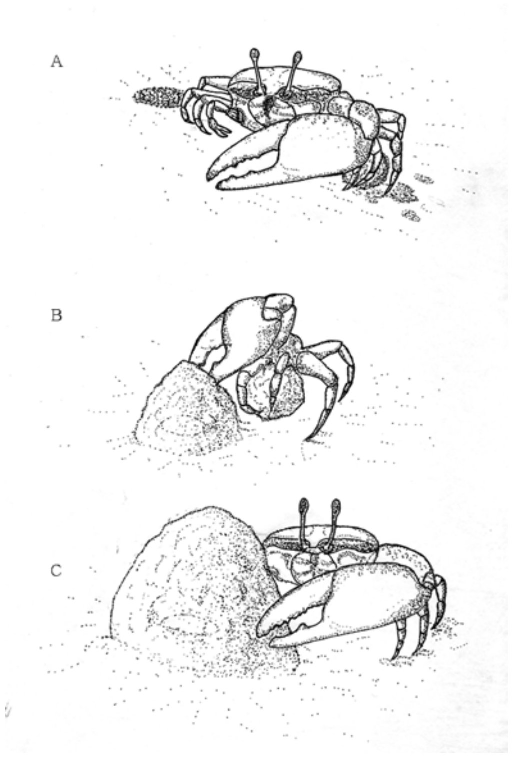

Fig. 2. Semidome building: (A) dragging mud, (B) stacking mud, and (C) modifying the structure.

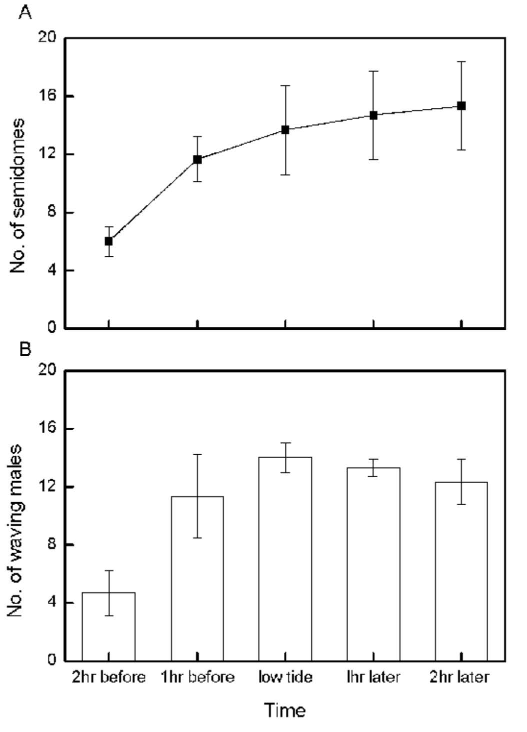

Fig. 3. Mean (± SD) numbers of (A) semidomes built and (B) waving males on the surface of the 2 × 2 m plot in relation to the time of low tide.

extend the days possible for semidome building. We did this because we wanted to know the exact number of semidome builders on each day regardless of sediment condition and the number of semidomes built previously.

RESULTS

Semidome Building Behavior

Males began building semidomes in early June at the start of the breeding season. They built semidomes by scraping up bits of sediment from the surface with their four walking legs on the side with the major claw, and stacking the material at the edge of their burrow entrance (Fig. 2). Males did not finish their semidomes at once but rather added material to them in repeated trips over many minutes. Over 80 percent of males completed their semidomes by the time of low tide (Fig. 3A) when the number of waving males peaked (Fig. 3B).

The Relationship Between Male and Semidome Size

Semidomes averaged 17.6 ± 5.0 mm ($n = 38$) high and 26.7 ± 5.6 mm ($n = 37$) wide. Burrow entrance diameter was significantly correlated with male carapace width ($r = 0.729$, $n = 34$, $P < 0.0001$) and major claw length ($r = 0.705$, $n = 33$, $P < 0.0001$). Males with larger diameter burrows (larger males) built higher and wider semidomes (height = 5.699 + 1.161 × entrance diameter, $r = 0.344$, $F_{1,36} = 4.839$, $P = 0.03$; width = 6.359 + 1.999 × entrance diameter, $r = 0.529$, $F_{1,35} = 13.57$, $P < 0.001$; Fig. 4a). Semidome height and width were correlated significantly ($r = 0.383$, $n = 37$, $P < 0.0001$, Fig. 4b; width = 2.678 + 0.56 × height; $F_{1,35} = 13.0$, $P < 0.0001$).

Seasonal Variation in Body Size of Semidome Builders

There was significant variation in the burrow entrance diameter of semidome builders across the season (One-way ANOVA, $F = 4.86$, *d.f.* = 4, 76, $P < 0.002$; Fig. 5). Pair-wise comparisons of dates (Fisher's PLSD) showed significant differences in entrance diameter between June 18 and July 26 ($P = 0.039$), June 18 and August 7 ($P = 0.0003$), and July 5 and August 7 ($P < 0.001$). The sizes of semidome builders

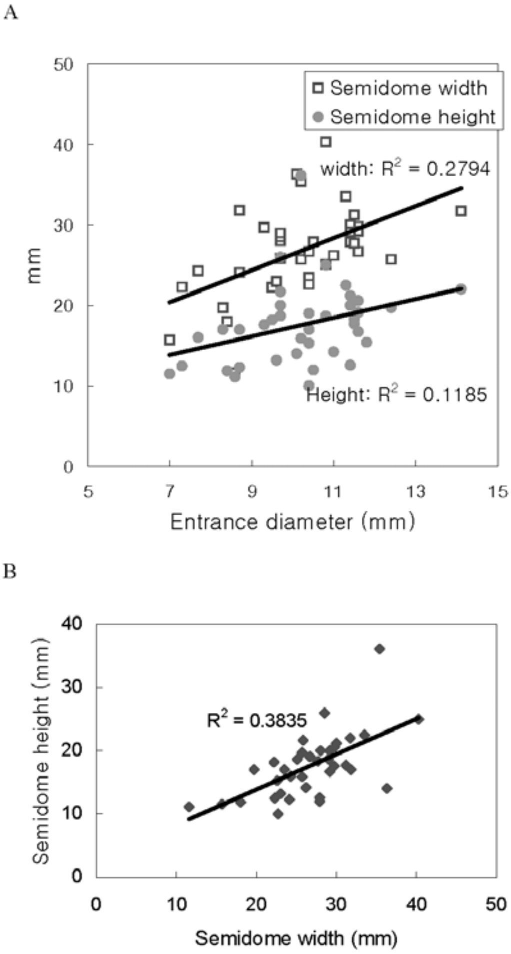

Fig. 4. (A) Semidome width (open squares) and height (filled circles) in relation to burrow entrance diameter. (B) Semidome width in relation to height. The lines are from least squares regression.

decreased toward the end of the breeding season. However, the carapace width of active males did not differ between any sampling dates (mean range: 14.03–15.03 mm; ANOVA, $F_{5,115} = 0.590$, $P = 0.70$).

The Density of Waving Males and Semidome Building

The number of semidomes did not increase disproportionately with the number of waving males as expected if a density-dependent mechanism affects the proportion of dome builders. Semidomes increased linearly with waving-male density from 1 to 25 males/4m^2 ($r = 0.939$, $n = 16$, $P < 0.0001$; Fig. 6).

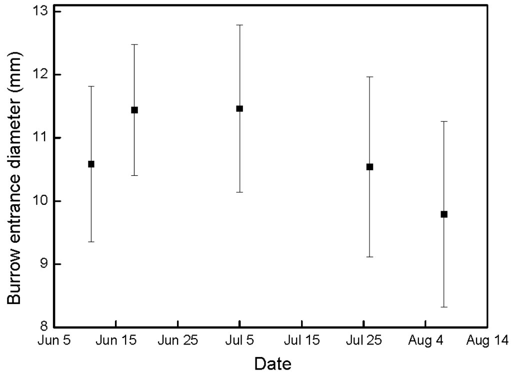

Fig. 5. Seasonal changes in burrow entrance diameter (mean ± SD) of semidome builders. See Materials and Methods for sample sizes.

Semidome Rebuilding

On the days when the habitat was covered by the previous tide, 84.0% ($n = 137$ of 163) of the courting males built semidomes. On these days, 17 of 36 males (47.2%) rebuilt semidomes within 30 min after we destroyed them at low tide. On the days when the tides did not flood the habitat, 82.1% ($n = 55$ of 67) of the wavers had semidomes at their burrow entrance. None of the 36 males rebuilt their semidomes from the dry mud after we destroyed them.

Social Context

In the enclosure with females, each male built more semidomes than did the males that had no contact with females ($t = 2.933$, $n = 19, 20$, $P = 0.0057$), whereas there was no significant

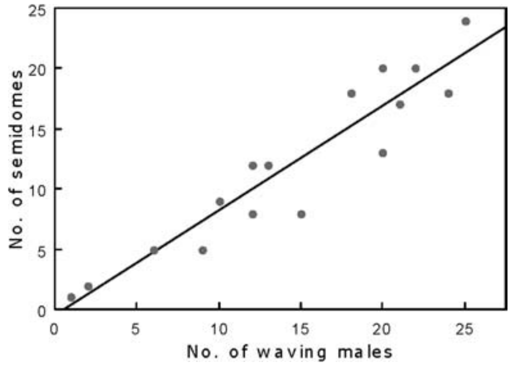

Fig. 6. The relationship between the numbers of waving males and semidomes in a 2 × 2 m plot. Observations were made on 16 clear days. The line is from least squares regression (Y = –0.531 + 0.872 X; $r^2_{adj} = 0.874$, $P < 0.0001$).

difference in the number of days each male was active in the two enclosures ($t = -1.377$, $n = 19$, 20, $P = 0.17$).

Discussion

The results of this study suggest that the primary function of semidomes in *Uca lactea* is related to courtship signaling but not to aggression between males. During the breeding season in June through August, males built semidomes on the days of each semilunar cycle that they courted females with claw waving. The number of semidomes increased linearly with the number of waving males, which would not be expected if males built semidomes in response to the nonlinear decrease in interburrow distance with density. Finally, males built significantly more semidomes when females were present in the experimental enclosure than they did when they had only male neighbors. Because we added females to only one enclosure, the densities in the two enclosures were not equal, and this density difference could have affected our results. However, usually only two to three females were active each day in the female-added enclosure, and we doubt this relatively small difference in density is sufficient to explain the highly significant difference in semidome building between the two enclosures.

Zucker (1981) suggested that male *U. musica* build hoods to reduce territorial overlap and rates of aggression with neighbors, giving each male more time to court during limited mating periods. Christy (1988a) tested this idea in *Uca beebei* and found that the pillars males of this species build do not affect space use or aggression between neighbors. Instead, Christy (1988b) found that males with pillars were more attractive to females perhaps because they elicit landmark orientation, a behavior that reduces the risk of predation on crabs that move away from the immediate safety of a burrow, as do mate-sampling females (Christy, 1995). This idea subsequently received strong support from an experimental study of the function of hoods in *Uca musica* (Christy *et al.*, 2001, 2002, 2003a, b).

The semidome destruction test showed that almost half of the semidome builders would rebuild them but not when the previous neap high tide was too low to have covered the habitat. Semidome building probably is limited by the water content of the sediment. Alternatively, it is possible that the tendency for males to attempt to rebuild is lower during the neap tides. However, this does not seem to be the case because nearly the same proportion of active males built semidomes during each period. When we poured water on the dry sediment during the neap tides, males were stimulated to build semidomes. The general level of semidome building was the same because of the almost same proportion of semidomes built by courting males irrespective of tidal periods. If female *U. lactea* orient to structures when they move between males as they search for a mate as do female *U. musica* and *U. beebei*, then males that have their semidomes destroyed during neap tides will be less attractive to females.

The entrance diameter of burrows with semidomes, and hence, the sizes of semidome builders, decreased towards the end of the mating season. Zucker (1984) found that smaller courting males from a low-density population failed to court when they were placed in a high-density population with larger males. She suggested that smaller males delay courtship in response to competition from larger males. In *U. annulipes*, females tended to visit smaller males more often later in the semilunar cycle, suggesting that the benefits of investing in structure building vary with male size and the timing of the investment (Jennions and Backwell, 1998). It is unclear whether competitive inhibition of structure building by smaller males or variation in the allocation of time to this behavior according to potential benefits explains why smaller *U. lactea* built more structures later in the season.

In a separate study, Kim and Choe (2003) found that food availability influenced not only the intensity of semidome building but also the onset of courtship behavior. This suggests that semidome building may signal male condition as affected by food availability. In most *Uca* species in which males build structures, females visit several males before they choose a mate, and the presence of a structure has been shown to increase male attractiveness. This should create directional selection for more frequent structure building (Christy *et al.*, 2001) and perhaps for building large structures that might be seen at greater distances. We showed that larger males built wider and higher semidomes, as expected if they are a signal under directional selection, but we do not know whether male attractiveness increases with semidome size. Indeed, there currently is no strong evidence that female fiddler crabs prefer large males, males with relatively large claws, or males with other large signals.

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