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## Pillar Function in the Fiddler Crab *Uca beebei* (II): Competitive Courtship Signaling

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*With 2 figures*

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### Abstract

Male *Uca beebei* court and attract females into burrows they defend on muddy sand flats in the intertidal zone on the Pacific coast of the tropical Americas. Mating, oviposition and incubation (breeding) occur underground in males' burrows. Some courting males build mud pillars (2 cm high) at the entrance of their burrow. The purpose of this field study was to assess the role of pillars in competitive courtship signaling among males.

I studied the effect of pillars on female behavior by recording the responses of wandering females to courtship from males resident at burrows with and without pillars. I also caught females, released them individually in a circular arena with an equal number of empty burrows with and without pillars around its circumference, and chased the females with a simulated avian predator. Females moved to burrows of both types more often when they were courted (82 %) than when they were chased (67 %). Receptive females were attracted to the burrows of the males that courted them significantly more often (97 %) when these burrows had pillars than when they lacked pillars (66 %). However, once females entered males' burrows they were equally likely to remain, mate and breed in both types of burrows. Females also more often moved to burrows with pillars (66 %) than to burrows without pillars when they ran from the simulated predator. Both male courtship displays and pillars probably provide cues females use to locate males' burrows. The visual similarity between pillars and a display courting males give immediately before they enter their burrows suggests that pillars are icons of the display. The effect of pillars on female behavior, the timing of pillar building relative to when females choose mates, and contrasts in the behavior of males that do and those that do not build pillars suggest that pillar building has evolved due to competition among males to attract females into their burrows.

### Introduction

Fiddler crabs (genus *Uca*) are perhaps best known for their striking sexual dimorphism. Males are generally more colorful and aggressive than females and one of their two chelipeds is greatly enlarged. It may be used (depending on species) both as a weapon during aggressive interactions, primarily with other males, and as a semaphore during courtship.

Male courtship behavior within the genus (about 80 species) falls into two broad classes depending on which sex wanders and seeks mates and where mating

and breeding occur (CRANE 1975; CHRISTY & SALMON 1984). Males of some Indo-West Pacific species encounter females by wandering through a colony or sallying from a burrow they defend (e. g., SALMON 1984). Males raise and lower their large chela in a simple vertical wave as they move about but only rarely when they approach a female for mating. Mating usually occurs on the surface near burrows females defend and use as feeding and breeding sites. Mating in most American species occurs in burrows males defend and use as courtship sites. Females wander through a colony and descend the burrows of several males before they choose a mate by remaining in a male's burrow. Females of at least some American species oviposit and incubate their eggs in the burrow in which they mate (CHRISTY 1987 a). Male courtship includes wave displays that are more elaborate than those of most Indo-Pacific species. Males may also attempt to herd, chase, startle or capture and carry passing females into their burrows (ALTEVOGT 1969; CRANE 1975; CHRISTY 1980; ZUCKER 1983).

Courting males of at least 14 species that mate in male-defended burrows, build low, massive semidomes or raised rims (6 species) or high, delicate hoods or pillars (8 species) at their burrow entrances (CHRISTY 1988 and references therein). Semidomes and rims are well described but their functions have not been studied. The affects of hoods and pillars on patterns of space use and aggression among neighboring burrow holding males has received more attention. ZUCKER (1974, 1981) presented evidence that the hoods built by courting *U. musica* reduce territorial overlap and the frequency of aggressive interactions among neighboring burrow holders. She argued that this might provide males with more time to court during limited tidal and lunar courtship periods and thereby increase male mating rates. I evaluated this hypothesis as it might apply to the pillars built by courting male *U. beebei* (CHRISTY 1988). These two species are locally sympatric on the Pacific coast of the tropical Americas and are broadly similar in their ecology and mating behavior. However, I found no evidence that the pillars of *U. beebei* function as do the hoods of *U. musica*. This led to a search for an alternative explanation of pillar function.

CRANE (1975, p. 525) noted that females of all species in which males build pillars and hoods, follow males into their burrows for mating. She speculated that these vertical structures may be "releasing or directing mechanisms" that may be better for attracting females to a male's burrow after the male has entered it than an unadorned burrow opening. The purpose of this study was to determine if the pillars of *U. beebei* provide visual cues females might use to find burrows, and to evaluate the role of pillars in courtship.

## Methods

### Study Sites

I studied the reproductive behavior of *U. beebei* from mid-July through September 1985 at two intertidal mud flats, Rodman and Diablo flats, located on the west and east banks respectively of the Panama Canal, about 2.5 km from its entrance to the Pacific Ocean (described in CHRISTY 1988). Densities of courting male *U. beebei* ranged from about 20 to 65/m<sup>2</sup>. Crabs were active on the surface during diurnal low tides for about 3.5 to 4 h.

## Courtship Behavior

I observed crabs directly or through binoculars and made notes on male courtship behavior in order to develop a qualitative description of apparently distinct displays and the courtship sequence. I supplemented these observations with still photography.

### Timing of Wandering by Females and Mating

If pillars provide important visual cues during courtship, males should construct pillars before females choose mates. To determine when females seek mates in the tidal activity period, I counted the number of times wandering females stopped at or entered the burrows of courting males on 10 0.75 by 0.75 m square plots. I observed a single different plot on 4 days and 2 different plots on each of 3 days. Observations began about 1 h before low tide (LT) and continued for 3 to 3.5 h. Counts were totaled at 5-min intervals. The number of courting males and the number of pillars on each plot also were recorded every 5 min. The timing of mate choice was determined from records kept throughout the study of when females entered and remained in the burrows of courting males.

### Male Time Budgets

Some courting male *U. beebei* do not build pillars during a given low tide activity period. I compared the time budgets of males that built pillars and males that did not and found that pillar builders fed less and courted and fought more (CHRISTY 1988). Here I extend the analysis of male time budgets to determine if males that do and those that do not build pillars allocate time to courtship and other behavior differently during the activity period, especially in relation to when receptive females wander and choose mates.

Male time budgets were obtained by recording, at 5-min intervals for 3–3.5 h, the behavior of all males on each of 7 50 by 50 cm square plots (Rodman flat) that were defined by a twine grid. A different plot (7–13 males) was observed each day (15–21 Aug. new moon on 16 Aug.) beginning about 1 h before LT. I recorded for each male if and when it built a pillar and scored its activity with respect to 9 behavioral categories (Table 2; and Table 2 in CHRISTY 1988).

### Behavior of Wandering Females

To examine the role of pillars as guideposts that receptive females may use to find the burrows of courting males, I recorded and compared the responses of wandering sexually receptive females to males that courted from burrows with and without pillars. No obvious behavioral or morphological cues distinguished receptive and non-receptive females before they stopped wandering. I therefore observed both. Wandering females were located by visually scanning the Rodman flat until a female was seen that was moving relatively quickly and was not obviously returning to a burrow. I then dictated a narrative of her behavior into a tape recorder until she chose a mate or I judged her to be non-receptive. A non-receptive female is one which either defended and fed by (for at least 10 min) or entered and plugged a burrow she dug, won in a fight with another crab or found empty. I documented each female's behavior with respect to five responses and the context in which each was given (Table 1). I made additional comments when necessary.

A tendency for females to more often approach and descend the burrows of pillar building males might be due to the effects of pillars alone on female behavior, the affects of more vigorous or otherwise attractive courtship display by pillar builders, or both. Since it would be difficult to control for possible differences in the courtship behavior of the two classes of males, I examined the role of pillars alone as orientation cues in another context — escape from predators.

### Pillars and Predator Escape Behavior

I frequently saw great-tailed grackles (*Cassidix mexicana*) catch and eat *U. beebei* on the Rodman flat. Grackles foraged by landing on the flat and walking slowly until they apparently spotted a potential prey. They then ran rapidly, often 2 to 5 m, and caught the crab on the surface. Burrow-holding crabs readily escaped by entering their burrows. Wandering crabs attempted to escape by running, often a meter or more, into an empty burrow or one occupied by another crab. If pillars affect the ability of wandering females to find a burrow then, when chased by a predator, females

Table 1: Responses and contexts used to score the behavior of wandering receptive and nonreceptive female *Uca beebei*

Response	Description and contexts
Pass	Female is approached closely (< 10 cm) by a courting male but does not alter her path and move toward the male or his burrow. Contexts: male with or without a pillar.
Threat	Female receives a threat from another crab. Contexts: other crab is a courting male with or without a pillar, a female or a small non-courting male.
Check	Female probes a depression in the mud or partially enters a burrow. Contexts: burrow is empty, belongs to another female, belongs to a courting male, with or without a pillar and the male is or is not courting on the surface when the female checks.
Enter	Female enters a burrow. Contexts: as for check.
Dig	Female digs a new burrow or removes material from an existing burrow. Contexts: female creates a burrow by digging at a depression, female digs at an empty burrow or one belonging to another female or a small noncourting male.
Other behavior recorded as needed: ousting a crab resident at a burrow; closing a burrow with a sand plug; feeding by and defending a burrow; remaining with male in burrow to mate.	

should escape more often into burrows with pillars than into burrows without pillars. I did an experiment in which I simulated attempts at predation on wandering females and provided equal numbers of burrows with and without pillars into which females could escape.

I removed all crabs, destroyed their burrows and smoothed the surface of a roughly circular level area, 2 m in diameter, on the Rodman flat. I made a shallow depression in the center of the area and added 16 artificial burrows equally spaced (approx. 15 cm between burrows) around the circumference of a circle 40 cm in radius and centered on the depression.

Artificial burrows were made by forcing cylindrical glass vials (1.5 cm diameter, 5 cm long) vertically into the mud until their rims were about 1 cm below the surface. I removed pillars from the burrows of courting male *U. beebei* and placed one on the side of the opening most distant from the center of the circle of every other artificial burrow. I added a small amount of mud to some pillars so all were about 2 cm high [mean height of pillars built by males =  $2.1 \pm .40$  cm; (CHRISTY 1988)]. I lightly scribed a circle with a 10-cm radius around the central depression. Females were captured from the surface or dug from their burrows and were released singly in the depression. When the female crossed the scribed circle 10 cm from the depression, I rapidly moved a stuffed skin of a female grackle or a black plastic foam model of a grackle toward the female. The simulated predator was mounted on the end of a 3 m long, thin white pole and was moved just above the surface starting from a distance of about 5 m from the female. I recorded whether the female ran out of the arena, entered a burrow with a pillar or one without a pillar. Each female was used once. The experiment was run on four days and began each day during the hour following the time of LT.

Statistical tests and procedures for data analysis follow those in SOKAL & ROHLF (1981), ROHLF & SOKAL (1981) and ROHLF (1984). An alpha level of 0.05 was used for all tests of statistical hypotheses. Means are given  $\pm 1$  S. D.

Hereafter, the abbreviations P male and NP male will refer to males that built pillars and males that did not build pillars respectively.

## Results

### Courtship Behavior

CRANE (1941, 1975) described the wave display and courtship behavior of *U. beebei* in Panama. My observations largely agree with hers, though I noted two displays she did not describe. The wave display is a smooth raise, full lateral

extension and return of the enlarged cheliped with little or no pause between successive waves (Fig. 1 a). During peak periods of display, and when females were near, males waved about twice per s for several min with only infrequent short pauses. Males waved and fed at the same time ("wave-feed") or waved without feeding ("wave"). Crane often saw males revolve in front of the females they courted, revealing the iridescent blue-green anterior band on their carapace and the bluish-purple surfaces on their ambulatories. I saw males court females in all orientations and did not note this as a distinctive or characteristic movement. Waving males closely approached wandering females that were moving slowly within about 20–30 cm of their burrows. Two to three males often simultaneously courted the same female. I saw up to 10 waving males arrayed in a rough circle around a female. When a wandering female moved more rapidly, waving males usually moved alternately toward their burrow and then back slightly toward the moving female as if leading the female to their burrow. Males usually stopped waving when a female approached their burrow directly. Instead, they kept their large chela flexed close to their front, raised the carpus to its highest extent and oriented toward the female such that the dark brownish-purple ventral surface of the nearly vertical cheliped was revealed (Fig. 1 b). They then alternately moved a few mm toward their burrow and slightly lowered their inclined

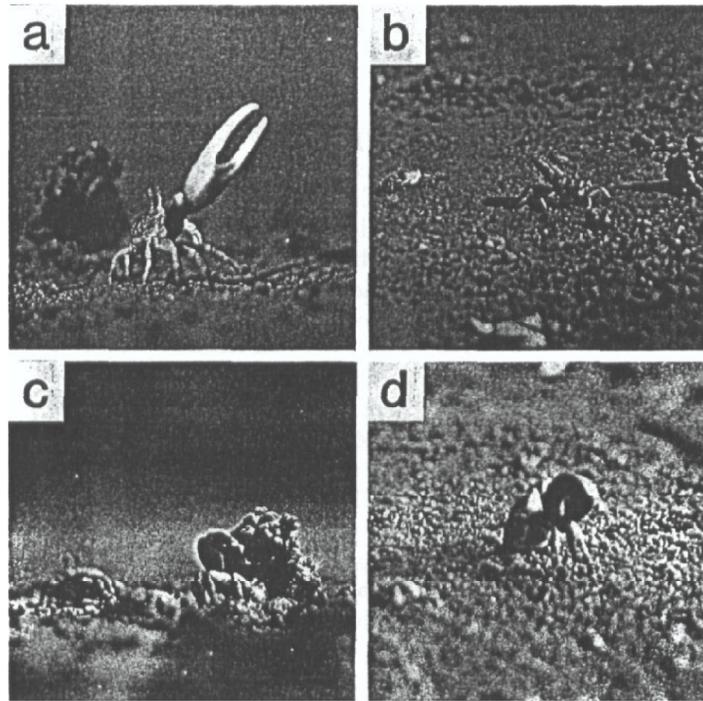


Fig. 1: Courtship behavior of *Uca beebei*. a: waving male with pillar; b: male with pillar giving raised carpus display to approaching (ovigerous) female; c, d: male with and male without a pillar giving the raised carpus display as they descend their burrows

chela, and then back toward the female and raised it again. These movements were rapid and their amplitude small. This raised carpus display (not noted by CRANE) usually was the last males gave as they entered their burrows. Pillars and the dark, nearly vertical ventral surface of a male's chela revealed by this display appear similar to me (Fig. 1c, d). Males usually disappeared from the surface before females reached their burrow. Females either stopped at the entrance of the burrow or entered it at the end of their approach. If the female left the burrow the male usually returned to the surface within a few s, followed the female for a short distance and waved. Less often, the male ran rapidly past the female, stopped about 20–40 cm away, paused, extended and raised his chela so that the tips of the pollex and dactyl pointed up, ran back toward the female and his burrow, stopped at the burrow entrance and lowered his chela. On the run back to the burrow males sometimes altered their path slightly so that they approached the female directly. This behavior is nearly identical to the dash-out-back display of *Uca pugilator* (CHRISTY 1980) though it seemed to be less common in *U. beebei* (also not noted by CRANE). Females often behaved as if they were startled by the display. They either moved rapidly away from the male and his burrow or into it, in which case the male would follow the female. I saw one male plug his burrow after giving this display and following the female below. I do not know if the pair mated.

#### Timing of Wandering, Mating and Pillar Building

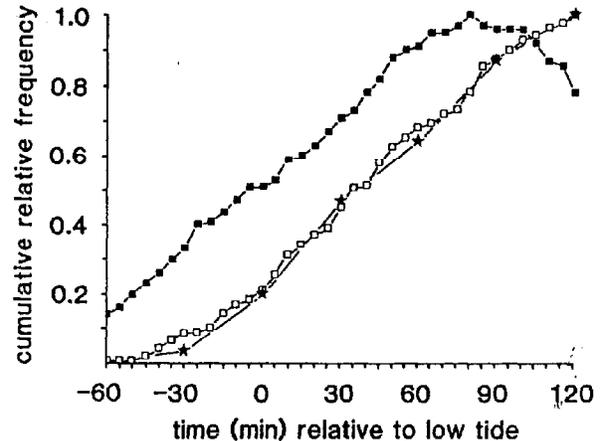
I saw 138 cases where wandering females either stopped at or entered ("sampled") the burrows of the males that courted them on the 10 0.75 by 0.75 m square plots. Courting male densities ranged from 19–47 males/plot. I recorded the times that 30 females entered and stayed in the burrows of courting males. Males at all but one of these burrows plugged their burrow entrances with sand and these burrows remained plugged for at least one day. I assume the crabs mated underground (CHRISTY 1987 b). The exception occurred when a female entered a male's burrow, the burrow was not plugged and then the male emerged about 1.5 h later and left the burrow. About 1 h after the male left I dug up the burrow and found a female with a freshly laid clutch of eggs at its bottom.

There is no significant difference (Kolmogorov-Smirnov two sample test:  $D_{\max} = 0.0637$ ,  $p > 0.90$ ) between when females sampled males and burrows and when they chose mates during the activity period (Fig. 2). Males built pillars up to 2 h past LT. However most pillars were built before most females chose mates (timing of pillar building and sampling compared:  $D_{\max} = 0.3018$ ,  $p < 0.001$ ; timing of pillar building and mate choice compared:  $D_{\max} = 0.3119$ ,  $p < 0.001$ ). For example, 51 % of all pillars were built by the time of LT when only about 20 % of the females had chosen mates.

#### Male Time Budgets

The activity of 51 NP males and 22 P males was recorded at 5-min intervals over 3–3.5 h periods beginning 1-h before low tide. All P males courted during the activity period. In contrast, 20 NP males did not court. There was consider-

Fig. 2: Timing of pillar building (solid squares), female sampling (open squares), and mating (stars) during the low tide activity period. The number of pillars began to decline 90 min after LT because some males destroyed their pillars and others ceased to repair them when they were damaged by wandering crabs



able variation among males in how they apportioned their time among 9 behavioral categories (Table 2). Time spent wave-feeding was least variable among P males across the activity period and time spent feeding was least variable among NP males. These data are highly heteroscedastic and could not be normalized with the arcsine transformation. I therefore did not analyze the data statistically.

Inspection of the data (Table 2) suggests the following general contrasts. NP males spent 30–35 % of their time in their burrows while P males usually spent less than 5 % of their time underground. P males fed less during the middle than at the beginning and at the end of the activity period. NP males fed much more than P males at all times and showed only a slight depression in feeding activity during 2 h following LT. P and NP males differed consistently and strikingly in the proportion of time they spent courting. P males courted about 60–75 % of the time (wave-feed and wave) during the 2 h following LT when 75 % of the females chose mates. NP males spent only about 15–20 % of their time courting during this period. In particular, NP males waved, at most, about 2 % of the time while P males waved about 20 % of the time during the peak courtship period. In general, P males allocated more time to courtship than did NP males and they courted most when most females sampled and chose mates. Temporal changes in the time budgets of NP males did not follow changes in the abundance of receptive females during the tidal period.

#### Behavior of Wandering Females

*Non-social behavior.* Only 5 of the 23 receptive females that I observed until they chose mates checked, entered or dug at depressions, empty burrows or burrows occupied by other females. These five females showed a total of 11 such responses — about 7 % of the responses of all types by receptive females. By definition, all of the 53 non-receptive females checked, entered or dug at depressions or burrows. I recorded 147 such responses, 34 % of the 433 total responses scored for these females. Non-receptive females behaved as if they were seeking burrows and feeding sites, receptive females did not.

Table 2: Hourly time budgets of 22 male *Uca beebei* that built pillars on their burrows (P) and 51 males that did not build pillars (NP). Entries are means  $\pm$  S.D. of the % time spent in each of 9 behavioral categories. (See also CHRISTY 1988, Table 2). CV: coefficient of variation

Behavior	Pillar?	1 h before LT	1 h after LT	1-2 h after LT	2-3 h after LT	Mean CV
Male in burrow	P	11.54 $\pm$ 17.77	4.34 $\pm$ 10.99	1.08 $\pm$ 2.78	3.77 $\pm$ 9.82	231.3 %
	NP	30.97 $\pm$ 30.69	34.23 $\pm$ 40.73	30.30 $\pm$ 41.10	35.65 $\pm$ 44.86	119.9 %
Male removing mud from inside burrow	P	5.32 $\pm$ 11.74	3.09 $\pm$ 5.66	0	0	201.9 %
	NP	4.70 $\pm$ 12.60	1.96 $\pm$ 6.83	1.32 $\pm$ 4.34	0.55 $\pm$ 2.74	360.9 %
Male building pillar	P	9.62 $\pm$ 9.58	4.05 $\pm$ 6.00	0.38 $\pm$ 1.77	0	236.7 %
Self-maintenance behavior	P	4.69 $\pm$ 9.11	3.78 $\pm$ 4.48	0.70 $\pm$ 2.27	0	212.4 %
	NP	2.50 $\pm$ 5.98	1.50 $\pm$ 4.84	0.88 $\pm$ 2.54	0.29 $\pm$ 2.10	391.1 %
Feeding	P	34.21 $\pm$ 29.23	18.87 $\pm$ 16.42	10.12 $\pm$ 10.84	31.88 $\pm$ 35.76	97.9 %
	NP	49.10 $\pm$ 31.37	43.16 $\pm$ 36.42	40.64 $\pm$ 33.97	45.16 $\pm$ 40.98	80.7 %
Waving and feeding	P	15.66 $\pm$ 15.57	41.14 $\pm$ 18.56	65.22 $\pm$ 17.36	51.28 $\pm$ 28.60	56.6 %
	NP	3.45 $\pm$ 7.31	13.46 $\pm$ 21.24	21.35 $\pm$ 25.37	15.63 $\pm$ 27.68	166.4 %
Waving	P	6.80 $\pm$ 10.12	18.67 $\pm$ 19.77	13.12 $\pm$ 19.53	7.39 $\pm$ 15.74	153.9 %
	NP	0.40 $\pm$ 2.02	0.94 $\pm$ 3.00	1.89 $\pm$ 5.52	0	372.1 %
Give or receive threat	P	10.70 $\pm$ 12.97	6.01 $\pm$ 7.81	9.20 $\pm$ 8.81	5.06 $\pm$ 11.27	142.4 %
	NP	7.05 $\pm$ 10.81	3.19 $\pm$ 6.82	3.22 $\pm$ 8.72	2.53 $\pm$ 7.61	234.7 %
Fight with another male	P	0.97 $\pm$ 2.49	0	0.32 $\pm$ 1.51	0	364.3 %
	NP	0.97 $\pm$ 3.53	0.18 $\pm$ 1.27	0.12 $\pm$ 0.84	0	589.8 %

*Aggressive behavior.* Both receptive and non-receptive females received threats (see Table 2 in CHRISTY 1988) from courting males when they passed their burrows. Females sometimes gave what appeared to be lateral merus displays (WRIGHT 1968) to the males that threatened them, but I did not record this behavior systematically. The frequencies with which P and NP males courted or threatened females depended on whether females were receptive (Table 3; 3-way interaction:  $G$  [Williams] = 4.624, 1 df,  $p < 0.05$ ). P males threatened receptive females in 4 % and non-receptive females in 22.8 % of their interactions ( $G$  = 12.041, 1 df,  $p < 0.001$ ). There was no difference in how NP males interacted with the two kinds of females ( $G$  = 1.935, 1 df,  $p > 0.10$ ). I do not know if these

Table 3: Aggressive and non-aggressive interactions of wandering receptive and non-receptive female *Uca beebei* with males that built pillars and males that did not build pillars

Male	Interaction	Wandering female	
		receptive	non-receptive
Pillar	aggressive	3	21
	non-aggressive	67	71
	% aggressive	4.3 %	22.8 %
No pillar	aggressive	16	51
	non-aggressive	59	120
	% aggressive	21.3 %	29.8 %

differences are due to differences in the way receptive and non-receptive females responded to the two kinds of males or vice versa.

*Non-aggressive responses to courtship.* The frequencies with which females passed or approached courting P and NP males depended upon whether females were receptive (Table 4). Receptive females significantly more often approached courting P than NP males. Non-receptive females also approached courting P males more often than courting NP males, but the difference is not significant (Table 4). Receptive females significantly more often entered the burrows of courting P than NP males. Non-receptive females also more often entered P than NP males' burrows, but again the difference is not significant. Once receptive females entered a burrow they were as likely to stay and mate in burrows with or without a pillar. The relative frequency with which receptive females mated in the two kinds of burrows did not differ from the relative frequency with which they entered them (G test of goodness of fit:  $G$  [Williams] = 0.065, 1 df,  $p > 0.50$ ). From a male's viewpoint, if he courts from a burrow with a pillar, then 57 % of the receptive females he courts will follow him into his burrow and about 27 % will stay and mate. If he courts from a burrow without a pillar, then about 20 % of the receptive females he encounters will enter his burrow and 9 % will stay and mate.

#### Pillars and Escape From Predators

Two of 151 females did not respond to approach of the stuffed or model grackle by running out of the arena or entering a burrow. Both simply froze motionless in slight depressions in the mud surface. The openings of the artificial burrows occupied 9.6 % of the circumference of the test arena. Yet, 67 % (100/149) of the females that ran from the simulated predator entered burrows, indicating that females oriented to and entered burrows nonrandomly (G test of

Table 4: Responses of receptive and non-receptive female *Uca beebei* to courtship from males with and males without pillars on their burrows. G-tests (Williams correction) were used to compare the responses of the two classes of females and the responses of each class of females to the two kinds of males

Female	No. of courtships	Pass	Approach check enter	Mate	% Approach	% Enter if approach	% Mate if enter
<b>Receptive</b>							
Male and pillar	67	2	27	38	18	97 % *** <sup>1)</sup>	58 % ** <sup>2)</sup> n.s. <sup>3)</sup>
Male only	59	20	27 *** <sup>4)</sup>	12	5	66 %	31 % 42 %
<b>Non-receptive</b>							
Male and pillar	71	38	21	12	—	47 % n.s. <sup>5)</sup>	36 % n.s. <sup>6)</sup>
Male only	120	77	31	12	—	36 %	28 %

<sup>1)</sup>  $G = 22.620$     <sup>4)</sup>  $G = 11.728$     \*\*  $p < 0.01$   
<sup>2)</sup>  $G = 7.519$     <sup>5)</sup>  $G = 2.080$     \*\*\*  $p < 0.001$   
<sup>3)</sup>  $G = 0.115$     <sup>6)</sup>  $G = 0.601$     n.s.  $p > 0.05$

goodness of fit:  $G = 293.9$ , 1 df,  $p < 0.001$ ). Although burrows with and burrows without pillars were equally available to females, females significantly more often (66/100, 66 %) entered burrows with pillars ( $G$  test of goodness of fit:  $G = 10.422$ , 1 df,  $p < 0.005$ ). Most females were moving slowly when they first crossed a point 10 cm from the depression in the center of the arena and the simulated predator was moved toward them. When the predator approached, they ran rapidly toward the circumference of the arena. Females that entered burrows followed curved or distinctly angular paths suggesting that they located the burrows visually as they were running, not before they ran.

### Discussion

The effects of male waving and other courtship behavior upon female behavior and mate choice in fiddler crabs are not known (SALMON 1983). Female choice in *U. pugilator* (CHRISTY 1983) and *U. beebei* (CHRISTY 1987b), is based, at least in part, on the quality of the burrows males defend as breeding sites. Yet male reproductive success in these and other species that mate in males' burrows, is probably also affected by a male's ability to compete with its neighbors at attracting females into its burrow. It is likely that the wave, at minimum, identifies the species of the courting male (eg. SALMON et al. 1978; VON HAGEN 1983, 1984). But the wave and other courtship behavior such as the dash-out-back and raised carpus displays described here, herding (CRANE 1975) or directing (ZUCKER 1983), and carrying (ALTEVOGT 1969) may also increase the probability that a female will enter a male's burrow and subsequently mate.

Here I present evidence that both the courtship behavior of male *U. beebei* and pillars affected the movement of females to burrows. Rapid movement into a burrow probably is the best way for crabs to escape an attack by an avian predator. I assume, therefore, that the females I chased in the test arena were at least as motivated to find and enter a burrow as were wandering receptive females. Yet receptive females significantly more often approached and entered burrows when they were courted (82 %) than did females that were chased by the simulated predator (67 %) ( $G$  [Williams] = 8.616, 1 df,  $p < 0.005$ ). This difference implicates the presence of cues in male courtship that facilitate oriented movement of females to males' burrows. When chased by the predator, females had only cues associated with burrows themselves to find a burrow. In this context, females significantly more often entered burrows with pillars than burrows without pillars. Pillars clearly provide females with cues that better guide their movements to burrows than the cues available from unadorned burrow openings.

When courted by P and NP males, wandering receptive females significantly more often approached and entered burrows with pillars than burrows without pillars. This difference could have arisen because P males court in ways that are more attractive to females, because females are better able to locate burrows with pillars, or for both reasons. P males more often waved without feeding than did NP males, suggesting that behavioral differences that could affect the attractiveness of the two classes of males are likely.

I suggest that pillars are guideposts — physical signals that increase the probability that receptive females will enter a male's burrow and mate — and that pillar building by courting males has evolved in the context of competitive courtship signaling.

#### Pillars as Guideposts and Icons

The function of pillars as guideposts is consistent with what is known about the orientation behavior of fiddler crabs (HERRNKIND 1983, and references) and their vision (CRONIN 1986; ZEIL et al. 1986). Fiddler crabs do not use vision, at least as the primary sense, to relocate their burrow. Instead, they integrate the distances and angles they move away from their burrow (up to about 1 m) and return quickly along a straight path (idiothetic orientation). If their burrow is blocked, or they are momentarily displaced from the surface and returned, they move in a zigzag path to locate their burrow even though it may be only a few cm away (VON HAGEN 1967). Burrow openings apparently do not provide reliable visual cues crabs use to orient their movements, at least directly toward a burrow. Female *U. beebei* found and entered burrows without pillars when they were chased by the simulated predator and had no opportunity to establish an idiothetic map of the location of a burrow. They usually followed a curved or angular path suggesting that they first perceived the burrows while moving, perhaps because of the relative movement of the image of the pillar or burrow opening in their visual field.

When wandering on the surface, fiddler crabs will orient consistently to stationary two-dimensional shapes. From distances of several m, crabs tend to approach vertical rectangular silhouettes and avoid silhouettes shaped like predators. In the laboratory, at distances of a few cm and when burrows are not available, vertical rectangular shapes elicit spontaneous approach more consistently than do horizontal rectangles or other shapes of equal area (LANGDON & HERRNKIND 1985). Crabs moving on the surface away from burrows may approach vertical shapes because this usually will bring them to cover provided by trees, grass, and mangrove proproots or pneumatophores.

The eyes of fiddler crabs appear to be especially well designed to resolve objects in the vertical plane. ZEIL et al. (1986) have shown that two species of *Uca* (*U. flammula*, *U. sp.*) have narrow vertical corneal pseudopupils with interommatidial angles as low as  $0.42^\circ$  on the eye equator yielding an acute zone of high vertical resolving power. This accords with earlier work showing that interommatidial angles in *U. pugnax* are smallest in the central third of a vertical transect through the eye (CLARK 1935). The eyes of *U. beebei* when viewed from the front show a narrow vertical pseudopupil indicating that their ommatidia are similarly arranged and that their visual acuity is best in the vertical plane (CRONIN 1986; ZEIL et al. 1986).

The use by females of vertical structures as guideposts to burrows is further indicated by the form and use of the raised carpus display. Although I do not know how this display affected the behavior of females, males used it only when females began to move toward them and their burrows — when a guidepost might most effectively orient and sustain the female's approach. As CRANE (1975)

suggested, when NP males enter their burrows they leave no additional cue an approaching female could use to locate the entrance to their burrow. When a P male vanishes from the surface as a female nears his burrow, the pillar remains as a visual cue of the burrow's location. Pillars appear to be icons of the raised carpus display to which the guidepost function of courtship is wholly transferred when males enter their burrows at the end of the courtship sequence.

#### The Context of Pillar Building

Is the context in which males build pillars consistent with their function as guideposts during courtship?

Males began to build pillars before receptive females began to sample males and burrows (Fig. 2). However, some males did not fully anticipate when females would sample as they built their pillars after many females chose mates. In addition, some males either knocked over or failed to repair their pillars before females stopped wandering at the end of the activity period (Fig. 2). Neither behavior is consistent in a simple way with the function of pillars as courtship signals that significantly increase the attractiveness of courting males. Likewise, it is difficult to explain why some males that otherwise court passing females vigorously do not build pillars. These observations imply that, for some males, the costs of building or owning a pillar exceed the evident benefits due to increased attractiveness.

Pillar building probably is not a particularly expensive behavior because it takes males only about 9.5 min to build a pillar (CHRISTY 1988) and the activity must surely cost less energy (per activity period) than waving. Once a male builds a pillar, however, his burrow probably becomes more apparent (perceptible) not only to receptive females but also to wandering non-receptive females and males that are wandering and fighting for burrows. When courted, non-receptive females did more often approach burrows with (47 %) than burrows without (35 %) pillars (Table 4). I did not make the observations necessary to compare the relative frequencies with which P and NP males fought with wandering males. P males may incur considerably greater costs than NP males in time, energy and risk of burrow loss due to the greater frequency with which crabs other than receptive females orient to their burrows.

As in other fiddler crabs (eg. CRANE 1958; ZUCKER 1976, 1978; CHRISTY 1978; GREENSPAN 1984), individual male *U. beebei* probably exhibit cyclical changes in their allocation of time and energy to reproductive and other activities. The contrasts in the time budgets of P and NP males (Table 2) show that pillar building is associated with an increased expenditure of time and energy on courtship at the expense of feeding without waving (and other behavior), especially when most females sample and choose mates. P males evidently can afford to devote more time and energy to courtship than can NP males. Some males may build pillars "late" in the activity period, knock them down "early" or fail to build them at all because they have not fed sufficiently to absorb the social costs of having a pillar and still be able to court.

Unlike many other species of fiddler crabs, *U. beebei* appears to lack clear lunar-related cycles of male courtship, pillar building and mating at the colony

level (CHRISTY 1987 b, 1988; but see ZUCKER 1978). On a given day, males in a colony may be at any stage of their individual reproductive cycles. Some may spend most of their time feeding or in their burrows and never court (about 40 % of the NP males), others may court but not build pillars, and still others may build pillars and spend most of their time courting. The failure of some courting males to build pillars may not be inconsistent with their function as a courtship signal but may merely reflect variation among individuals in their reproductive schedules.

Although the proportion of males that build pillars on a given day may reflect the degree of phase synchrony among individuals in their underlying reproductive cycles, few pillars are built on days with heavy cloud cover and when it rains (CHRISTY 1988). Rain destroys pillars and probably prevents males from building new ones. It is less obvious why few pillars are built on heavily overcast days. Fiddler crabs have apposition eyes that best resolve detail under high light intensities and tend to be found in decapods that live in bright habitats (CRONIN 1986). Perhaps *U. beebei* do not build pillars on dark cloudy days because females see them poorly at low light intensities and they therefore are not effective as guideposts that orient female movements to burrows. Alternatively, cool temperatures on cloudy days may generally depress crab activity including female wandering, courtship and mating.

#### Pillars, Attractiveness and Female Choice

Has the differential attractiveness of P males and their burrows to females evolved because P males are genotypically and phenotypically superior mates and their burrows are especially good breeding sites? The data presented here and in CHRISTY (1987 b) suggest that there are no differences in quality between P and NP males or their burrows. The key observation is that once females entered both kinds of burrows they were equally likely to stay and mate (Table 4). Females apparently find both combinations of male and burrow of equal value. The quality of male burrows as breeding sites is strongly (positively) correlated with burrow length and depth. These two burrow features (among four measured) are the best predictors of female choice while the presence of a pillar is the worst (CHRISTY 1987 b). Further, there are no significant differences in either the lengths ( $t_s = 0.4775$ , 13 df,  $p > 0.50$ ) or the depths ( $t_s = 0.0979$ , 13 df,  $p > 0.90$ ) of the burrows of P and NP males females chose as breeding sites. Hence, there are no apparent differences in the quality of the burrows of P and NP males. Since females found the two combinations of males and burrows of equal value, it follows that there are no differences in the quality of P and NP males that have affected female breeding decisions.

P male *U. beebei* may be exploiting the ability of females to resolve and their tendency to orient to vertical structures when wandering away from their burrows. It is likely that this perceptual ability and orientation behavior has evolved and is maintained due to heavy predation on crabs, including receptive females, moving on the surface between burrows. P males probably are setting out a "sensory trap" (WEST-EBERHARD 1984; EBERHARD 1985), quite literally to

catch receptive females. The trap is set due to signal competition among males to attract females and the trap works probably because females that do not readily orient to burrows with pillars spend more time exposed to and less often escape predators as they move between males and burrows than those that do. The attractiveness of P males and their burrows may have evolved due to fitness gains to females as they sample potential mates and breeding sites apart from any gains as a consequence of choice of P males and their burrows.

#### Interspecific Comparisons

The courtship and orientation behavior of species of *Uca* that build semi-domes or rims suggests that these low, massive structures do not function as guideposts. Male *U. pugilator* (semidomes) use the dash-out-back display relatively often after a female has entered their burrow briefly and left. I have seen males of this species end the display several centimeters from their burrow entrance, especially when they have tripped while carrying their large chela aloft on their return (CHRISTY 1980). Such males executed the zigzag search typical of crabs that have had their idiothetic map disrupted. Some males relocated their burrows, others did not and attempted to obtain new burrows by fighting former neighboring males. Semidomes evidently do not provide cues males, and by inference, females can use to find burrows. Semidomes are low wide structures while pillars are relatively tall and narrow. Height probably is the key feature of pillars that makes them functional as guideposts.

Male *U. pugilator*, *U. tangeri* (semidomes) and *U. panacea* (rims) wave during the day at wandering females. When females approach, males retreat to just inside their burrow entrances and rap their large chelae on the sand. Females sense the substrate vibrations rapping produces. Rapping is the primary courtship signal when crabs occur in dense vegetation and the sole courtship signal at night (ALTEVOGT 1959; VON HAGEN 1962; SALMON et al. 1978 and references; MÜLLER 1983). It is not known how rapping affects the behavior of wandering receptive females of these species. The context in which rapping occurs, and the fact that females can sense the substrate vibrations rapping produces argue strongly for a guidepost function for this courtship signal.

Males of 7 of the 8 species of *Uca* that build pillars or hoods are known to produce substrate vibrations by stridulating or striking parts of their bodies or the substrate with their major cheliped (CRANE 1975, p. 644). In some of these species [perhaps not in *U. beebei* (VON HAGEN 1968)], production of substrate vibrations appears to be an integral part of courtship signaling (MÜLLER 1986). The function of hoods and pillars has been studied in detail in only one other of the 8 species of fiddler crabs known to build them. ZUCKER (1974, 1981) found that the hoods built by male *U. musica* produce effects on male spacing, space use and rates of aggression that implicate a function in male-male competition (ZUCKER 1974, 1981). Nevertheless, female *U. musica*, and the other species as well, probably can perceive the pillars and hoods males build and might well use them to find males' burrows whatever additional functions these structures might have. It appears that the production of signals females can use to find males' burrows is an

important component of courtship of fiddler crabs and that such guideposts may be presented visually, through substrate vibration or via both modalities in some species.

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