

## FEMALE CHOICE AND THE BREEDING BEHAVIOR OF THE FIDDLER CRAB *UCA BEEBEI*

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### ABSTRACT

Fiddler crabs have been divided into species that mate and breed in burrows that males court from and defend (e.g., *Uca pugilator*), and species in which crabs pair on the surface and females breed in their own burrows (e.g., *Uca vocans*). I studied the reproductive behavior of the fiddler crab *Uca beebei* at a site on the Pacific coast of Panama and found that this species exhibits both of these major modes of mating and breeding. Some females mated on the surface near burrows which they defended and used for oviposition and incubation. This may occur when females are large enough to defend their burrows successfully, when their burrows are suitable breeding sites, and when food is abundant nearby. Other females left their burrows, sampled the burrows of several courting males, then chose mates and breeding sites by remaining in males' burrows. These females did not select mates on the basis of size, nor did they prefer males that built pillars by their burrows. They consistently chose males whose burrows were longer (by 8%) and deeper (by 12%) than those they rejected. Long deep burrows may provide better thermal environments for incubation than short shallow ones.

Males of most American species of fiddler crabs (genus *Uca*) defend burrows from which they court females, while males of most Indo-West Pacific species wander from their burrows and court females on the surface (Crane, 1975; Christy and Salmon, 1984). Receptive females of the former species leave their burrows and briefly enter (sample) the burrows of several courting males before they choose a mate by remaining in a male's burrow. The chosen male then plugs the burrow and the pair mates. The amount of time the sexes remain together, how each uses the burrow, and patterns of female choice are known in detail for only one such species, *Uca pugilator* (Christy, 1978, 1982, 1983). Mated pairs of this species remain underground for 1-3 days until the female oviposits. The male then opens the burrow and either leaves or stays and courts other females. If he stays, he abandons the terminal chamber of the burrow to the female and digs a new one. The female stays in the chamber for about 12 more days while her eggs develop, finally emerging on the night her eggs hatch to release her planktonic larvae. Female *U. pugilator* prefer to mate and breed in relatively deep burrows and those that will not flood, collapse, and cause females to lose eggs during oviposition and incubation. Females do not choose large males as mates among those that defend burrows in which they prefer to breed.

Explanations of how sexual selection operates in fiddler crabs are based almost entirely on a comparison of the ecology and the mating and breeding behavior of *U. pugilator*, and *U. vocans* (Christy and Salmon, 1984), a species that typically mates on the surface near burrows that females defend (Salmon, 1984). Is the breeding behavior of other fiddler crabs that mate in males' burrows similar to that of *U. pugilator*, and do females of these species also choose mates primarily on the basis of the quality of males' burrows as breeding sites? Recent studies (Christy, 1987; Murai *et al.*, 1987) suggest that male courtship behavior, competition for mates, female choice, and the site of oviposition and incubation may vary considerably within and among species of fiddler crabs in which males court from burrows they defend.

*Uca beebei* is a relatively small (adult carapace width about 1 cm) fiddler crab that occurs on protected shores on the Pacific coast of tropical Central and South

America (Crane, 1975). Males court from and defend burrows at the entrance to which they often build a mud pillar (Zucker, 1981; Christy, in press a). Receptive females typically wander and sample several males and their burrows before they choose a mate. Females use pillars as guideposts to find males' burrows (Crane, 1941; Christy, in press b). Crane (1941) twice saw females pair on the surface near their own burrows with courting males that defended burrows nearby and Zucker (1978) saw five surface pairings in this species. Hence, *U. beebei* may exhibit, within a single colony, both kinds of mating association known in the genus (see also Yamaguchi, 1971; Murai *et al.*, 1987).

Here I further document in *U. beebei* the occurrence of matings on the surface and in males' burrows. I also describe burrow use by the sexes during breeding, mating preferences of individual females that mate in males' burrows, and patterns of female choice.

## METHODS

### Study Site

I studied the mating and breeding behavior of *Uca beebei* from mid-August through mid-November 1985 on an open muddy sand flat [Rodman flat (Christy, in press a)] located on the west bank of the Pacific entrance to the Panama Canal, about 1 km NNW of the Bridge of the Americas. The flat lies about 30 m seaward of a mangrove forest, is bordered by two small tidal creeks, and is about 100 m<sup>2</sup>. The density of courting males (daily counts from 13 August to 7 September 1985) averaged 50/m<sup>2</sup> on the gently sloping banks of the flat and 23/m<sup>2</sup> on its level top (Christy, in press a). The densities of females varied similarly across the flat but were not measured. The amplitudes of the semidiurnal tides ranged from about 2.5–6 m during the study. Crabs were active on the surface when the flat was exposed for about 4.5 h during each diurnal tide.

### Mating Sites and Burrow Use

I saw surface pairings of *U. beebei* while studying the behavior of crabs on small (0.25 m<sup>2</sup>) plots (Christy, in press a). I followed individual females that wandered away from their burrows in order to record pairings in males' burrows (Christy, in press b). I followed each female until she entered a male's burrow. The male then plugged the burrow, sealing himself and the female below. I recorded the dates and times at which females paired on the surface or entered and remained in males' burrows. The burrows at which each kind of mating association occurred were marked with numbered stakes. I observed crabs and their burrows daily during the study except when low tide occurred at dawn and dusk and when it rained heavily and few crabs emerged from their burrows. Daily observations usually began less than 1 h after crabs emerged and lasted until crabs plugged their burrows a few minutes before the rising tide covered them. On each day I recorded whether the marked burrows were open or closed and the sex, presence of eggs, and general behavior of crabs that were active on the surface and used these burrows as refuges. I dug up the marked burrows 2.5 h–11 days after the presumed matings and recorded the sex and reproductive state of the occupant(s). I assumed (with a few exceptions) that the crabs I saw use, and those I dug from, marked burrows were the same crabs that mated in these burrows.

### Mate Choice

I obtained data on mating preferences of individual females by scanning the flat until I saw a female enter and leave the burrow of a courting male. I used a

blowgun and small color-coded darts to mark the location of this burrow, the location of each courting male's burrow she subsequently sampled, and the one in which she remained. I may have missed some males and burrows that females sampled before I first observed them. The darts had no obvious effect on crab behavior. I noted the presence of a pillar on each marked burrow. After the female chose a mate and burrow, I forced a thin rubber tube (a catheter) into each burrow. I dug up each burrow further inserting the tube as I dug if it had not reached the bottom. I removed all crabs and measured (with vernier calipers having 0.02-mm precision) the female's carapace length, the males' carapace lengths, and lengths of the propodus (LP) of the males' large chelae. Burrow length was measured from the length of the tube that was inserted into each burrow. Burrow depth, the vertical distance from the surface to the bottom of each burrow, was measured with a ruler. A sample of mud was removed from the bottom of each burrow. Percentage of water content of the mud was determined by weighing the sample before and after it was dried for 5 days at 60°C.

To detect individual mating preferences, I compared the size (LP) of the male and the features of the burrow each female chose with those that the same female sampled and rejected (*t*-test; Sokal and Rohlf, 1981: 229). I used a runs test (Sokal and Rohlf, 1981: 782) to determine (1) whether the females entered the burrows of ever larger (or smaller) courting males as they sampled, and (2) whether the movements of females were correlated with spatial variation in the presence of pillars, burrow length, depth, or water content. Finally, I asked [single classification ANOVA (Sokal and Rohlf, 1981: 210)] whether there was variation among females in features of the burrows they entered (including those they chose) and in the sizes of the males that defended those burrows.

To detect mating patterns among female *U. beebei*, I compared (ANOVA) the sizes of the males and features of the burrows that all females chose with those sampled and rejected. I also used stepwise logistical regression (Dixon *et al.*, 1985; Fienberg, 1980) to examine the rank order and strength of each of the variables which I measured as predictors of female choice of mates and breeding sites (Gibson and Bradbury, 1985). Step selections for the model were based on iterative calculation of maximum likelihood ratios (Dixon *et al.*, 1985). Correlations were calculated among burrow depth, length, and moisture content to determine if each of these variables could be entered into the model as an independent variate. The runs test described above was used to determine if the sizes of the males and values of the features of the burrows which females sampled in sequence were statistically independent observations.

## RESULTS

### Surface Pairings

I observed twelve surface pairings, all between nonovigerous females that fed near and defended their burrows and males that defended burrows 7–40 cm (mean = 19 cm, *N* = 8) away. Half of the males had pillars on their burrows. All pairings occurred at the entrances to the females' burrows. All but one of the females were conspicuously larger than their mates. I saw one male pair twice with the same female within 20 min and one female pair with two different males during the same low tide period.

Surface pairings occurred when a male approached, with or without waving, a neighboring female, touched and then manipulated her with his walking legs so that the female was inclined slightly above the male and their abdomens were opposed. The male stroked and plucked the frontal, orbital, dorsal, and lateral

Table 1. Behavior and reproductive state of 12 female *Uca beebei* that paired on the surface. F = female fed by her burrow and was not ovigerous; FO = female fed by her burrow and was ovigerous; B = female remained underground in her plugged burrow during the diurnal low tide activity period; // = the female's burrow was excavated with the stated result; ? = observation of the female and her burrow ended and the burrow was not excavated. Sequences of the same behavior and reproductive state are underlined.

Female	Days after pairing on the surface												
	1	2	3	4	5	6	7	8	9	10	11	12	
1	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>FO</u>	<u>FO</u>	<u>FO</u>	<u>B</u>	<u>B</u>	// ovigerous
2	<u>F</u>	<u>B</u>	<u>B</u>	<u>FO</u>	<u>FO</u>	<u>FO</u>	<u>FO</u>	<u>FO</u>	<u>B</u>	<u>B</u>			// lost burrow shaft
3	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>			// lost burrow shaft
4	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>			?
5	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>			?
6	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>			// ovigerous
7	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>					// ovigerous
8	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>	<u>B</u>	<u>B</u>	<u>B</u>						// lost burrow shaft
9	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>						// not ovigerous
10	<u>F</u>	<u>F</u>	<u>F</u>	<u>B</u>									
11	<u>F</u>	<u>F</u>	<u>F</u>										
12	<u>F</u>												

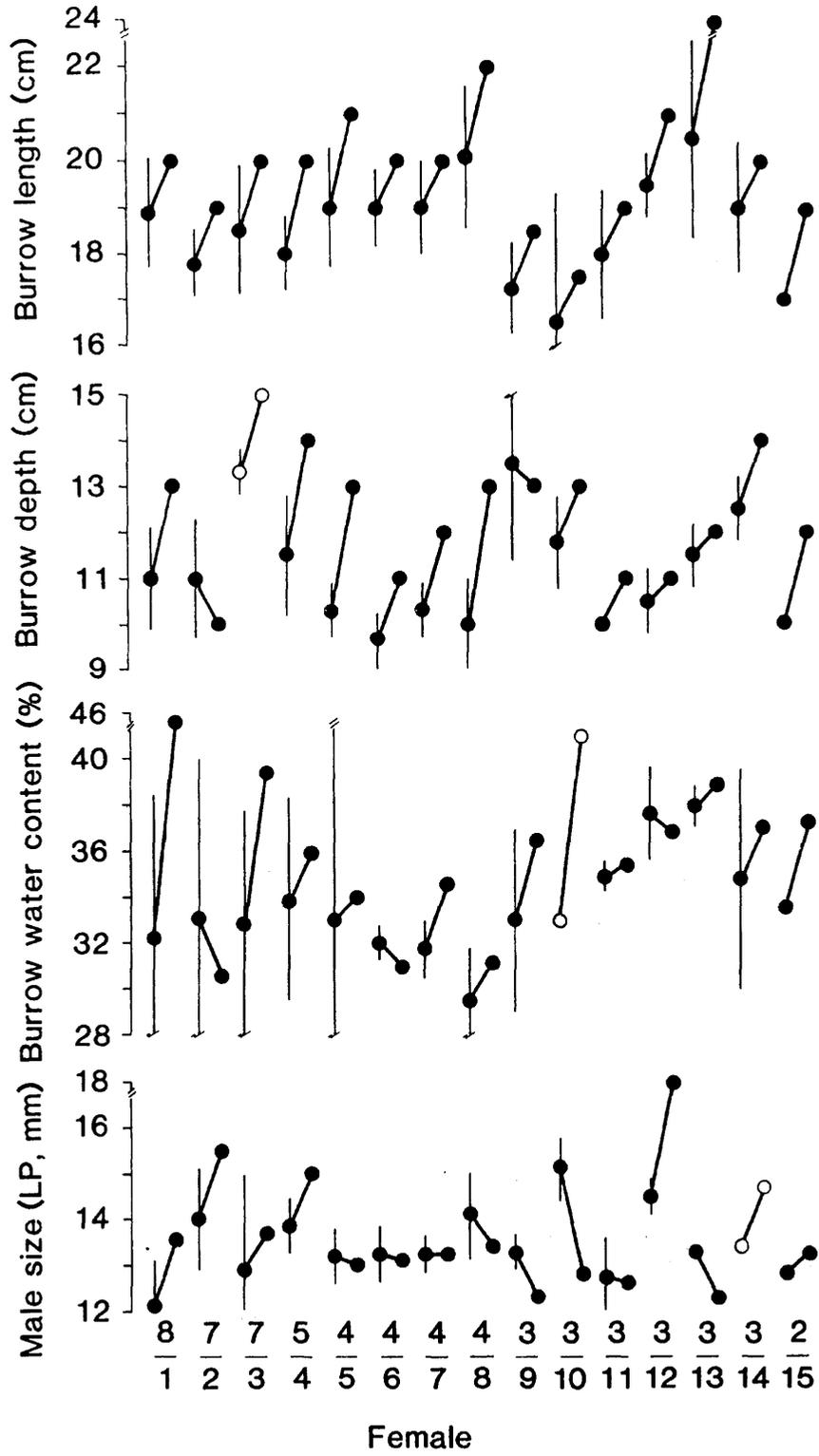
surfaces of the female's carapace with his minor chela. Both crabs opened their abdominal flaps in all such pairings, but I was not able to determine if intromission occurred. Pairings lasted 3–7 min (mean = 4.1 min,  $N = 9$ ).

After pairing on the surface, females fed near and defended their burrows for 1–6 days (mean = 3.9,  $N = 10$ ) before they remained underground in their plugged burrows for at least one day and oviposited (Table 1). I saw two females return to the surface and feed for 3 and 5 days while ovigerous. Both then remained underground in plugged burrows for two more days before I dug them up. All other females fed first for several days, then remained underground for 1–6 days before I excavated or stopped observing their burrows (Table 1).

#### Breeding in Male-Defended Burrows

I saw 32 females enter and remain in the burrows (22 with pillars, 10 without) of courting males. All males but one emerged 10–30 min later and plugged their burrows. In the exception, the male spent about 1.5 h underground with the female, then left. The female then plugged the burrow. About 1 h later I dug up the female and found that she had just oviposited. I dug up 28 of the remaining 31 burrows from 3–11 days (mean = 8.6 days) after the females entered them. I lost the shafts of 10 burrows. Fourteen of the 18 females I recovered were ovigerous.

Males that attracted females into their burrows did not court again from the same burrow. I saw two males open and leave their burrows 1 day after they attracted mates. The females in both burrows plugged them a few minutes after their mates left. In nine other cases I did not see males leave, but they apparently did. I saw ovigerous females emerge from and feed near these burrows 1–3 days (mean = 2.7 days) after they entered them. I do not know if these females opened their burrows themselves or if they emerged on the day their mates opened and



left the burrows. These females fed for an average of 1.1 days, and then plugged and remained in their burrows until I dug them up.

Males and nonovigerous females apparently sometimes used burrows containing ovigerous females. For example, one burrow was closed for 2 days after the resident male attracted a female, occupied by a small male for a day, then closed again for 5 days before I dug it up and found an ovigerous female below a second plug deep in the burrow shaft. Five other burrows that contained ovigerous females when I dug them up were used sequentially for one day only by 1–3 males or nonovigerous females.

#### Mating Preferences of Individual Females

I observed 15 receptive females sample and reject 1–7 males and their burrows before they chose a mate and breeding site. The carapace lengths of males and females in mated pairs are not significantly correlated ( $r$  (Pearson) =  $-0.19$ ,  $P > 0.80$ ). Females did not choose as mates males that differed significantly in size (LP) from those they rejected (Fig. 1). Nor did most females choose burrows that differed significantly in length, depth, or moisture content from those they rejected (Fig. 1). However, all 15 females chose longer burrows, 13 chose deeper burrows, and 12 chose wetter burrows than the mean of those they sampled (Fig. 1). Four females entered the burrows of 5–8 males. The sizes of the males they approached and the features of the burrows they entered varied randomly ( $P > 0.05$  for all runs tests) as they sampled. There was significant variation among females in the size (LP) of the males and the length, depth, but not the water content of the burrows they sampled (Table 2).

#### Patterns of Female Choice

Females chose significantly longer, deeper, and wetter burrows, but not larger males than those they rejected (Table 2). The depth of the burrows that females sampled was not significantly ( $P > 0.05$ ) correlated either with their length ( $r$  (Pearson) =  $0.04$ ) or with their water content ( $r$  (Pearson) =  $0.16$ ). Each of these features of burrows, the presence of a pillar (21 burrows with pillars, 8 chosen; 42 without, 7 chosen), and male LP were included as an independently varying predictor variable in the stepwise logistical regression. Burrow length entered the model first followed by burrow depth (Table 2). No other variable or interaction term significantly ( $P < 0.05$ ) improved the ability of the model to predict female choice of a mate and burrow, nor had a standardized coefficient greater than 2.

### DISCUSSION

#### Mating Associations

*Evidence of Mating.*—Two kinds of evidence indicate that male *U. beebei* mated (transferred sperm) with the females that entered and remained in their burrows and with those that paired with them on the surface. First, pairings were preceded

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 Fig. 1. Contrasts between the sizes of the males and the characteristics of the burrows that were rejected and chosen by 15 female *U. beebei*. The number above each female's number on the bottom of the figure is the number of males and burrows she sampled. Pairs of symbols show the means ( $\pm$ SD) of the sizes of the males and characteristics of the burrows females rejected (left-hand symbol) and those they chose (right-hand symbol). Open symbols show statistically significant differences.

Table 2. Patterns of female choice in *Uca beebei*.

Variable	Analysis of variance					
	$F_1$	$d.f.$	$P$			
I. Are there differences among females in the sizes of the males and features of the burrows they sample?						
Male size (LP) (mm)	2.21	14,48	<0.05			
Burrow length (cm)	3.14	14,48	<0.005			
Burrow depth (cm)	3.82	14,48	<0.001			
Burrow water content (%)	0.66	14,48	>0.75			
II. Are there differences between the sizes of the males and the features of the burrows females chose and those they sampled and rejected?						
Male size (LP) (mm)	1.16	1,61	>0.10			
Burrow length (cm)	11.22	1,61	<0.005			
Burrow depth (cm)	8.52	1,61	<0.005			
Burrow water content (%)	5.41	1,61	<0.025			
	Male size (mm)	Burrow length (cm)	Burrow depth (cm)	Burrow water (%)		
Chosen	13.7 ± 1.52	20.1 ± 1.55	12.5 ± 1.36	35.8 ± 4.94		
Rejected	13.4 ± 1.22	18.6 ± 1.44	11.2 ± 1.44	33.2 ± 4.86		
III. Which of the features of males and their burrows best predict female choice of mates and breeding sites?						
	Stepwise Logistical Regression					
Variable	Chi-square to enter, step 0 <sup>1</sup>	$P$	Entered step	Standardized coefficient <sup>2</sup>	Improvement chi-square <sup>3</sup>	$P$
Burrow length (cm)	10.23	0.001	1	2.80	10.23	0.001
Burrow depth (cm)	7.76	0.005	2	2.68	8.56	0.003
Burrow water (%)	5.22	0.022	NE <sup>4</sup>			
Pillar (yes/no)	3.40	0.065	NE			
Male (LP) (mm)	1.01	0.314	NE			

<sup>1</sup> Approximate chi-squared values to enter each variable in the model based on maximum likelihood ratios.

<sup>2</sup> Fitted coefficients divided by their standard errors.

<sup>3</sup> Tests the hypothesis that the addition of the variable improves prediction significantly.

<sup>4</sup> Not Entered because the standardized coefficient is <2 and the improvement chi-square has a  $P > 0.05$ .

either by male waving and other visual displays (Christy, in press b) or by tactile stimuli and manipulation, behavior that typically precedes mating in other species (Yamaguchi, 1971; Crane, 1975; Christy, 1980; Salmon, 1984, 1987). Second, I later saw or removed ovigerous females from the burrows where both kinds of pairings occurred. Thus, females that paired and subsequently oviposited probably received sperm when they paired.

**Mating and Breeding Behavior.** — The two kinds of mating associations of *U. beebei* differ in the location of mating, the precopulatory behavior of males and females, and in other aspects of crab breeding behavior. Females that mated on the surface, but not those that mated in males' burrows, tended to be larger than their mates. I did not measure the females that mated on the surface, but I noted that all also appeared to be large in absolute size. A recent study of *Uca lactea* (Murai *et al.*, 1987), the only other fiddler crab known to mate regularly on the surface and in males' burrows (Yamaguchi, 1971), suggests a possible explanation. Aggressive interactions and attempted matings by wandering and neighboring males often cause female *U. lactea* to abandon their burrows. Some such females mate in males' burrows while others dig or find new burrows. Male *U. beebei* also sometimes aggressively displaced females from their burrows. Large female *U. beebei* probably defend their burrows better than do small females. If so, then large

females would less often be forced to wander when they became receptive and they would more often mate on the surface with neighboring males than would small females.

Although aggressive interactions may contribute to female wandering, receptive females may leave their burrows for other reasons. I saw two females that mated on the surface emerge and feed for 3 and 5 days while carrying eggs. I saw seven females that mated underground feed while ovigerous; only one fed for more than 1 day. Ovigerous females that open their burrows to feed on the surface risk loosing their burrows in fights with neighbors and wandering crabs. Females that mated on the surface may have emerged and fed more often because they were larger and better able to defend their burrows than were the females that mated in males' burrows. However, some females that wandered and chose mates also were large, yet they seldom emerged and fed. Female size and competitive ability may interact with the quality or abundance of food near females' burrows and affect where they mate. Females may more often breed in their own burrows when they are large enough to defend them successfully and when food is abundant nearby, providing a resource which they can exploit profitably while incubating (Christy and Salmon, 1984; Salmon, 1984, 1987).

Wandering receptive females sampled and rejected several males and their burrows before making a choice, and they predictably chose long deep burrows. Male burrows apparently differ in quality as breeding sites and it is likely that female burrows do as well. (Although it would seem a simple matter for any crab to dig a long deep burrow, complex spatial variation in soil texture, including the presence of large stones and shells, as well as the labyrinth of existing burrows and chambers of *U. beebei* and other benthic animals, probably prevents this.) Some females, regardless of their size and competitive ability, may wander and mate in males' burrows because their own burrows are not suitable for breeding. The presence of both modes of mating within a colony of *U. beebei* may reflect variation in the ability of females to defend their burrows (Murai *et al.*, 1987) and in the quality of their burrows as feeding and breeding sites.

Size-related differences in the costs of the two modes of mating may also contribute to the apparent correlation between female size and surface mating. Great-tailed grackles (*Cassidix mexicana*) and other avian predators of *U. beebei* feed primarily on crabs wandering away from their burrows (Christy, in press b). In general, the larger the female, the longer she may wander before she encounters a male with a burrow that is large enough for her to enter and that is a high quality breeding site. The longer a female wanders before choosing a mate, the greater may be her cumulative risk of predation. Moreover, large wandering female crabs probably are more conspicuous than small ones and may be preferred prey (high net profitability) for most avian predators. The risk of predation to large females during surface mating probably is considerably less than during wandering. On several occasions I saw pairs break up, apparently prematurely, when grackles foraged nearby. The females rapidly escaped into their burrows which never were more than a few centimeters away. A high risk of predation on large wandering females may put a selective premium on surface mating and defense and use of their own burrows for breeding.

Fiddler crabs reproduce when their carapace is fully hardened from the deposition of calcium salts (the intermolt stage; Hartnoll, 1969; Crane, 1975). Hartnoll (1968) found that the vaginas of female *U. rapax* in a preserved sample were occluded by immobile opercula. He suggested that mating and oviposition would be possible only when the vaginal opercula are decalcified. Field studies of *U. rapax* (Greenspan, 1980), *U. pugilator* (Christy, 1982), *U. pugnax* (Greenspan,

1984), and *U. thayeri* (Salmon, 1987) showed that the vaginal opercula of these species are mobile (decalcified) for 3 days or less. Females oviposit soon after they mate, within a single "window" of receptivity. These species mate and breed in males' burrows, though *U. thayeri* also mates on the surface (compare Crane, 1975, p. 113, and Salmon, 1987). In contrast, adult female *U. vocans* (Salmon, 1984) and *U. lactea* (Murai *et al.*, 1987) can mate and ovulate at most times during the breeding season, since their vaginal openings are only rarely blocked by hardened opercula. Surface matings are much more common than matings in males' burrows in both of these species.

Female *U. beebei* probably are continuously receptive. Females that entered males' burrows oviposited within 2.5 h–3 days, a pattern similar to those species in which females mate in males' burrows, and are receptive for short periods. However, females that mated on the surface fed for 1–6 days before they plugged their burrows and oviposited, suggesting that females are receptive for a longer time. I examined the vulvas of 75 nonovigerous and 20 ovigerous female *U. beebei* (collected at the site of this study). I easily inserted the tip of a probe into the vaginas of all females and there was no visual evidence of calcified (opaque) opercula in any female.

Protracted sexual receptivity would allow females that mate on the surface to "sample" several potential mates as the identities of their male neighbors change, and to copulate at any time in their reproductive cycles. Lengthy and perhaps asynchronous periods of receptivity among females may also explain why densities of courting males at the study site did not vary cyclically over the lunar or semilunar cycle (Christy, *in press a*; but see Zucker, 1978). Extended female receptivity and weak male courtship rhythms also occur in *U. vocans* (Salmon, 1984).

#### Female Choice

*Male Phenotype.*—Receptive female *U. beebei* that leave their burrows could base their choice of mates and breeding sites both on the phenotypes (morphological and behavioral) of the males they sample and on features of their burrows. I examined female choice for two aspects of male phenotype: the length of the large cheliped (LP) and the presence of a pillar on the male's burrow. I consider pillars to be part of a male's phenotype because they function as courtship signals (Christy, *in press b*). Hence, they are not a feature of a male's burrow that could affect female reproductive success. I chose male LP as a measure of male size because it probably is positively correlated with male competitive ability (Hyatt and Salmon, 1978; Christy, 1980), age (Colby and Fonseca, 1984), and, by inference, general fitness (Trivers, 1976). Females that choose large males may gain immediately, because large males may defend better breeding sites and may better repulse crabs that open burrows and disturb mating pairs than small males (Christy, 1983). To the degree that male size is heritable and correlated with general and reproductive fitness, females that choose large males also may gain by producing especially fit offspring.

Individual female *U. beebei* that mated in males' burrows did not consistently (7 of 15 females) choose males that were larger than those they rejected. Consequently, chosen and rejected males did not differ significantly in size. Eleven of the 12 females that mated on the surface paired with males smaller than themselves. These females appeared to be large in absolute size and they could have rejected even smaller males that courted them. Nevertheless, the consistent relative size difference in these pairs speaks against a strong female preference for

large males. Female choice of large males has been studied but not found in two other fiddler crabs (*U. pugilator*, Christy, 1983; *U. vocans*, Salmon, 1984). Size-based homogamy may occur in *U. rapax*, but the pattern is questionable because only 11 pairs were measured (Greenspan, 1980). The costs and benefits of female choice of large males in fiddler crabs have not been determined. Costs due to predation on wandering females that sample long enough to be able to select both a large male and a high quality breeding site may be high (Christy, 1983). Coupled with small immediate (especially to females that mate on the surface) and heritable (Salmon, 1984; Jones, 1987) benefits of choosing large males, such costs may limit choice to burrow quality alone.

The presence of pillars on males' burrows did not significantly affect female choice of mates and breeding sites among those they sampled (Table 2). This accords with the results of a previous study (Christy, in press b) which showed that once females enter males' burrows, they are equally likely to remain and breed in burrows with and without pillars. However, males that build pillars are significantly more likely to attract females into their burrows than those that do not. Both pillars and the courtship behavior of pillar builders may contribute to this difference in attractiveness. Neither pillars nor the courtship displays of pillar builders flag preferred males or breeding sites, but they strongly increase the probability that a female will sample a male and his burrow, and they thereby increase a male's chance of mating. In the broadest sense, pillars do affect female choice in *U. beebei*. But their effect is through their attractiveness to females rather than through their use as a criterion by which females compare males and burrows and make breeding decisions (Parker, 1982, 1983).

*Burrow Features.*—Female *U. beebei* consistently chose burrows that were longer and deeper than those they sampled and rejected; both factors were good predictors of female choice (Table 2). Burrow depth also was an important factor in female choice of breeding sites in *U. pugilator* (Christy, 1983) and in competition among males for burrows (Christy, 1980). Maximum soil temperatures and diurnal temperature variation decline rapidly with depth in fiddler crab habitats (Powers and Cole, 1976; Christy, 1980). Female fiddler crabs may prefer relatively deep burrows because they provide stable thermal environments that yield constant embryo developmental rates and do not alter precise schedules of larval release (Christy, 1978, 1982; Christy and Salmon, 1984; Forward, 1987). Burrow length may be important because a long burrow would descend through the thermal gradient more gradually than a short one of the same depth. Females incubating in relatively long burrows could position themselves precisely with respect to the thermal gradient as it changed over the diurnal and tidal cycles. By selecting appropriate incubation temperatures, females could accelerate or retard developmental rates of embryos and compensate for "errors" in the timing of oviposition. Such behavior is possible in *U. beebei* because males always left their burrows after their mates oviposited. Hence, females had exclusive use of the entire burrow for incubation except when other males and females temporarily occupied the upper burrow shaft. Experiments are needed to determine if and how female reproductive success is related to the length and depth of the burrows in which they breed. Females discriminated small absolute differences in both burrow features. They chose burrows that averaged only  $1.5 \pm 0.67$  cm (8%) longer and  $1.3 \pm 1.11$  cm (12%) deeper than those they rejected.

Female *U. beebei* choose mates and breeding sites in two very different ways, yet males appear to adopt a primary mating strategy of resource defense as in *U. pugilator* and probably most other American fiddler crabs (Crane, 1975; Christy

and Salmon, 1984). A similar duality in modes of female choice coupled with male resource defense-behavior occurs in *U. lactea* (Murai *et al.*, 1987) and may prove to be common, since surface matings have been noted in many other species in which females also wander and choose mates (Crane, 1975: 502). Further study of such species could address two important questions: why some females mate on the surface while others wander and chose mates, and why males follow resource-defense mating strategies when they might wander and seek mates as do males of most Indo-West Pacific species that mate on the surface.

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