

Behavioral and ecological correlates of female mate searching in the fiddler crab *Uca crenulata*

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Investigating factors that influence which sex searches for a mate helps to identify how and why mating location and the degree of selectivity for mates change with ecological conditions. Several ecological factors that are thought to affect which sex searches — density, sediment size, and predation — were measured in two populations of the fiddler crab, *Uca crenulata*. At one of these populations, two additional factors, clutch size and larval release synchrony, also were measured because these factors may affect females' reliance on male-defended stationary resources. Females produced clutches that protruded beyond their abdomens and they released larvae synchronously at biweekly intervals throughout the breeding season. Density, sediment size, and predation levels varied between the two populations. Only females searched for mates at the high-density, predator-free, sandy site, while both sexes searched at the low-density site that contained more silt and predators. Females did not stop searching when density was lowered in experimental enclosures set in the sandier area. This suggests that density is less important in determining which sex searches when sediment grain and clutch size are both large.

KEY WORDS: burrow structure, fiddler crab, larval release synchrony, mate search, population density, sediment.

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INTRODUCTION

In order to mate, males and females of sexually reproducing species must locate one another. To find each other, one sex typically signals to attract mates while the other sex travels to find a mate (HAMMERSTEIN & PARKER 1987, BRADBURY & VEHCENCAMP 1998, DERIVERA & VEHCENCAMP 2001). In most animals, males search while females broadcast attractive signals (DARWIN 1874, GHISELIN 1974, BRADBURY & VEHCENCAMP 1998). Female mate searching and male mate-attraction signaling is common, however, among birds and several other taxa. Males of these female-search species often have elaborate songs or showy displays (DARWIN 1874), and the complexity of mate-attraction signals may depend on which sex searches for a mate (ALEXANDER & BORGIA 1979, DERIVERA & VEHCENCAMP 2001). Which sex searches may also affect how selective females are while choosing a mate, how long courtship persists, and which sex offers parental care, if any is given (BRADBURY & VEHCENCAMP 1998).

Relative reproductive investment between the sexes was the first identified factor that affects which sex searches (HAMMERSTEIN & PARKER 1987). Lower male than female investment partly explains why male searching is more common than female searching. HAMMERSTEIN & PARKER (1987) suggest that because males are rarely the limiting sex, a male that fails to join other males in mate searching will be less likely to attain a mate than a similarly aberrant female. Because females search for mates in species that have higher female than male investment, however, reproductive investment cannot be the only factor that affects which sex searches; ecological factors may also be important.

Recent studies suggested several ecological factors influence which sex searches for a mate. A comparative literature study of the genus *Uca*, the fiddler crabs, provided the first statistical examination of the effects of ecological factors on searching sex (DERIVERA & VEHCENCAMP 2001). This comparative study found that female fiddler crabs search when they mate in male burrows, and this burrow mating most often occurs when density is high or when the sediment is composed, at least in part, of sand or larger grains. Population density is correlated with searching sex in frogs, fireflies, moths, and crickets as well, perhaps because density affects the economic feasibility of female mate searching and of male resource defense in all of these animals (WELLS 1977, LLOYD 1979, GREENFIELD 1981). Sediment size may be important to searching sex in fiddler crabs because their burrows, critical to adult and egg survival, may be more variable in larger grained sediments than in silt (CRANE 1975, CHRISTY 1983). An experiment that manipulated predator risk in the Panamanian fiddler crab, *U. beebei*, demonstrated that predation also might affect mate searching because fewer females moved to male burrows to mate when predation risk was high (KOGA et al. 1998). Further experimental manipulations of *U. beebei* supported the hypothesis that density plays an important role in influencing which sex searches for mates but did not find strong support for the role of predation: females primarily searched when density was high and males searched more when density was low, while increased predation decreased the amount of searching by each sex but did not induce a switch from female to male searching (DERIVERA et al. 2003).

Large clutch size and synchronous larval release also could contribute to female mate searching in fiddler crabs because these factors may increase females' need to use specialized burrows for incubation. Females of fiddler crab species with small clutch to body size ratios can cover their eggs with their abdomens and

therefore can incubate on the surface or in shallow burrows without desiccating their eggs (CHRISTY & SALMON 1984, SALMON 1984). Female fiddler crabs with larger clutches may need to incubate in a deeper burrow to protect their eggs. If a male creates, maintains, and defends a burrow suitable for incubation, mate-searching females can build smaller burrows. Moreover, intertidal crabs face selection pressure to release their larvae at the nocturnal tide with the greatest tidal flow (CHRISTY 1982, 1986). Larvae released during this period of maximum nocturnal tidal flow out of the estuary disperse quickly and are afforded many hours of relative safety from diurnal planktivorous fish and other predators (CHRISTY 1982, CHRISTY & STANCYK 1982, MORGAN & CHRISTY 1995). Synchronous larval release requires that all the eggs, those in the center of the sponge and those on the periphery, face similar conditions during development. Furthermore, releasing on a targeted day requires that eggs develop at a certain rate. Mating just before the previous syzygy combined with using specific incubation chambers may allow females with protruding clutches to time larval development so all of their eggs hatch the next nocturnal maximum-amplitude tide (DERIVERA in review).

This study documents all the named variables — mate searching, population density, sediment size, predation level, clutch size relative to body size, degree of larval-release synchrony, and burrow size — in a population of the California fiddler crab, *Uca crenulata*, so that this population can be compared to other populations and species. Enclosure experiments reported in this study further examine the effect of density on which sex searches, this time on sand instead of the silt sediment used in the *U. beebei* experiments. Some sediment, density, predation and burrow measurements, and searching sex observations are given for a secondary *U. crenulata* population as well to determine if these factors naturally vary across habitats in which this species lives.

METHODS

Species

Uca crenulata is a small, sexually dimorphic, semi-terrestrial crab of Mexico and California. Males average 14.5 mm and females average 14.2 mm in carapace width (DERIVERA 1999). As with all fiddler crabs, female *U. crenulata* have two small chelipeds while males have a small cheliped for eating and a major cheliped, 1.1 to 2.3 times carapace width, used for fighting and waving (DERIVERA 1999). *Uca crenulata* inhabits the mid to upper intertidal zone of estuaries and salt lagoons (CRANE 1975, LEIJA-TRISTAN et al. 1990, DERIVERA personal observation), from Pt. Conception, California (~ 34°N) to Tenacatita Bay in Jalisco, Mexico (~ 19°N; CRANE 1975).

Both male and female *U. crenulata* build, maintain, and defend individual burrows in which they spend a majority of their time. An average female emerges on less than 1/2 of the days during the breeding season while an average male emerges on 2/3 of these days (DERIVERA 2003). Furthermore, these crabs are only active on the surface during diurnal low tides. Like other fiddler crabs, *U. crenulata* insert a plug of sediment into their burrow entrances before the tide rises. Burrows may not be visible to the human eye when they are plugged.

Female *U. crenulata*, like many other fiddler crabs, have locally decalcified opercula so can mate throughout the breeding season without molting. At the Sweetwater River estuary, crabs mate throughout the week before each biweekly maximum amplitude tide from late May through late August (DERIVERA 2003). After mating, females ovulate and attach their eggs to their pleopods.

Study sites

This study was conducted at two sites in San Diego County, California, a primary site used for most of the investigations and a secondary site that provided information on a different population. The primary study site included a range of intertidal elevations at the mouth of the Sweetwater River. Most of the waving, mate searching, and breeding occurred in the upper and upper-mid intertidal zones, in a 33×13 m area (DERIVERA 1999). Waving and breeding tapered off to either side of this area, and no waving or breeding was observed in the lower intertidal zone. The entire breeding area was uncovered by the tide for at least 7 hr during the day, and the lower intertidal burrows were emersed for at least 4 hr. Sex ratio is biased in the breeding area, with 3.4 males per female while the site averages 1.6 males per female (DERIVERA 2003). The second site, where Tecolote Creek opens into Mission Bay, offers only a small stretch of suitable habitat, 633.2 m², and hosts a much smaller population of *U. crenulata*. The entire habitat is always covered by the rising tide and remains emersed for a 3.5 to 5-hr period at each low tide.

Clutch size and larval release

I brought 38 ovigerous females from the Sweetwater estuary population to the lab in July 1998 and July 1999. I measured their carapace widths to the nearest 0.1 mm using vernier calipers. Following established protocols, I placed each female in a mesh-bottomed container that was suspended over an Erlenmeyer flask filled with saltwater (see CHRISTY 1982). I noted the day of release relative to the nearest maximum amplitude tide then reduced the water to 150 ml and, after stirring, counted the larvae in three 10 ml samples. Using these counts, I estimated the total number of larvae in each clutch. Crabs could not be removed from the Tecolote Creek population so were not used in this part of the study.

Observations of Sweetwater River females yielded information on breeding synchrony. From 18 May through 29 June 1997, I counted the first 50 females I saw on the surface and noted whether or not each female carried a clutch of eggs. Too few ovigerous females (one) were seen in the Tecolote Creek population for analysis.

Population density, burrow measurements, predation, and sediment grain

Field assistants and I counted and measured burrows along two transects at the Sweetwater site in April 1997. We established a 42 m transect, with 42 1×0.5 m quadrats, perpendicular to the tide and a 41 m, 41-quadrat transect parallel to the tide, bisecting the breeding area, about 80% of the way from the mean low water mark to the upper limit of the flat. We watched crabs emerge to identify which sex inhabited each burrow in a quadrat. We then noted whether the burrow had a hood or rim around it ("exterior architecture") and measured with vernier calipers the diameter of the burrow opening ("aperture") to the nearest 0.1 mm. To determine burrow length, we fed a piece of tubing down the shaft of each burrow and measured the tubing to the nearest 0.5 cm. Repeated measurements yielded values within ± 0.1 mm for aperture and ± 0.5 cm for length.

We estimated population density at the Tecolote Creek site in April 1999 by counting every burrow and dividing by the entire inhabited area. Because crabs at this site live in a narrow (< 10 m) strip of habitat and because there was no obvious pattern in the distribution of the sexes, we did not use transects. We recorded the aperture, length, and architecture of male and female burrows in 14 randomly-located 1 m² plots.

We scanned for predators once every 30 min during observation days at each site in 1999. In addition, we looked for predation in a less regimented way on every observation day and recorded each occurrence of predation.

Substrate from the Sweetwater transect parallel to the tide and from the Tecolote Creek site was sieved for grain size analysis, following BUCHANAN (1984). To present this data, we

transformed the Wentworth scale to obtain phi: $\phi = -\log_2$ particle diameter (mm) (BUCHANAN 1984). I used 7 samples from randomly selected quadrats within the Sweetwater breeding area and 7 samples from quadrats that lay outside the breeding area, plus 11 samples randomly selected from the Tecolote Creek site.

Mate searching and burrow use observations

Observations of free-ranging crabs at the Sweetwater River site yielded information on which sex searched for mates, search distance, and duration of time females stayed in male burrows. Field assistants and I observed crabs at the Sweetwater site for 3-4 hr per day almost every day from 1 May through 25 July 1997, from 17 June through 7 September 1998, and from 27 May through 3 September 1999. We also observed crabs on over half of the days from 27 April to 27 May 1999. We noted all occurrences of mate searching, which is defined as a female approaching waving males or a male approaching and courting at least one female. In July 1999, we recorded the distance covered by 9 females that stayed with a male at the end of their mate searches. These distances represent only a fraction of each search since we always detected females in the midst of their search. Therefore, these data yield a conservative estimate of search distance.

To determine how long females carried their eggs and how long females remained in their mate's burrow, we marked the burrow selected by a mate-searching female and retrieved her later, when possible. We marked shafts of burrows that females stayed in by sliding a plastic string through the entrance. We dug for the female 6 to 19 days later by sliding a piece of tubing down the shaft of each marked burrow and removing the surrounding sediment until we found the female. We recovered 40 females that we had seen enter male burrows.

Field assistants and I observed crabs at the Tecolote Creek site for 3 hr per day on 7 high-activity days from 12 through 26 May 1999 and on 20 additional days during the breeding seasons of 1998 and 1999. We noted search distances and durations and the sex of the searching crab.

Enclosure experiment

In May 1997 we built enclosures at Sweetwater and manipulated the density (high and low) and sex ratio (male-biased and female-biased) of the crabs within to determine whether mating behavior was affected by these factors. We established twelve 1 × 1.5 m plots in areas that had initially high natural densities, and interspersed treatments using a randomized block design. We enclosed each plot with partially buried hardware cloth fencing topped by aluminum siding to prevent crabs from escaping. We labeled the crabs within the enclosures then rearranged and removed crabs until we had 3 plots of each density/sex ratio combination. The 6 high-density enclosures held 231 crabs each while each low density one held 33 crabs. Because we found 1.73 males per female in enclosures before we moved crabs, we established a similar sex ratio of 1.75 males per female in half of the high-density and half of the low-density enclosures (21 males and 12 females, or 147 males and 84 females), and the opposite sex ratio, 1.75 females per male, in the other enclosures. We observed every treatment daily for 16 days (26 July-19 August 1997) from 0.5 hr before to 1.5 hr after low tide (= 32 hr per treatment).

Statistical analyses

I conducted several parametric and nonparametric statistical analyses, all 2-tailed, using the software program Statview. The parametric tests met the assumption that each vari-

able, once it was transformed, approximated the normal distribution. I report the standard error to directly compare the group means of data used in these analyses. When the data were not normally distributed, even after transformation, I used the non-parametric Mann-Whitney test to analyze the untransformed data, and I report the median and range.

To identify whether females released their clutches synchronously, I used a Matlab program designed especially for circular-linear correlation (J. TRACEY unpublished) following BATSCHLET (1981: 191-196). The dependent variable, proportion of females on the surface with eggs, was linear while the independent variable, day of the biweekly lunar/tidal-amplitude cycle, was circular. The circular variable was scaled to an angular scale (BATSCHLET 1981, ZAR 1984).

RESULTS

Clutch size and larval release synchrony

Each female's clutch of eggs extended well beyond her abdomen. Clutch size of females in the Sweetwater estuary population averaged $3,357.8 \pm 1693.5$ eggs ($n = 38$) and larger females produced larger clutches (Fig. 1; $r^2 = 0.17$, $n = 38$, $t = 2.70$, $P = 0.0105$). Eggs were 0.35 mm in diameter ($n = 6$ females). Clutch size was not evaluated for females in the Tecolote Creek population, but the clutch of the observed ovigerous female protruded beyond her abdomen and below her body.

Females released their clutches synchronously. The proportion of females with eggs was highest just before maximum amplitude nocturnal tides and declined just after such tides in the Sweetwater population (Product-moment correlation coefficient for circular-linear regression: $r = 0.70$, $n = 29$). In addition, the median release date of ovigerous females that I brought into the lab was the maximum amplitude nocturnal tide, though some females released their clutches up to 2

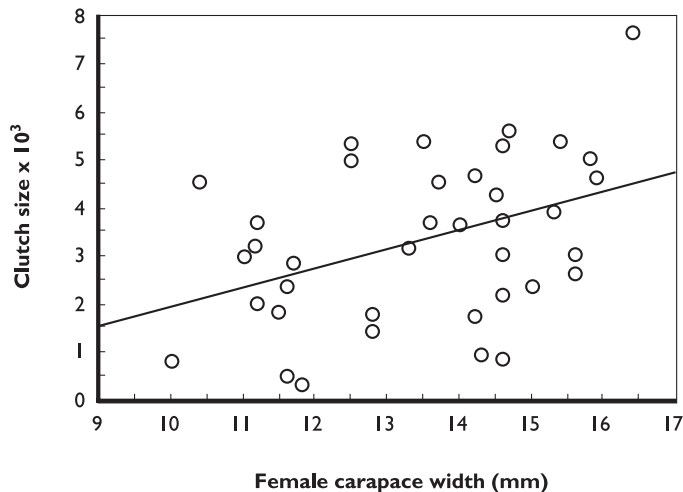


Fig. 1. — Clutch size increases with female carapace width. Clutch size = $-2014.14 + 398.89 \times$ Female carapace width (mm), $r^2 = 0.17$.

nights before or after the maximum amplitude tide (Fig. 2; n = 25). Females in the lab released their clutches between 22:00 hr and 07:00 hr. A female’s entire clutch was released on 1 night.

Population density, predation, and sediment size

A median of 40, from 2 to 156, crabs surfaced per m² in quadrats along transects throughout the 42 × 41 m section under study at the Sweetwater estuary (n = 83 quadrats from 2 transects). The primary breeding area held a median burrow density of 45, from 22 to 88 (n = 46 sampled quadrats) surface active adult crabs per m² and 27, from 10 to 62, active mature males per m². The population size and density were lower at Tecolote Creek: 2192 crabs surfaced at this site in 1 day and density averaged 3.5 crab burrows per m² (Table 1).

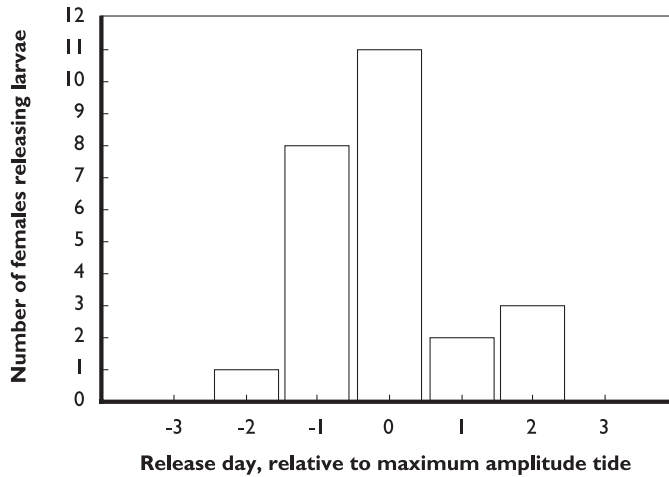


Fig. 2. — Bar chart showing when 25 females, which were brought into the lab when ovigerous, released their eggs relative to the maximum amplitude nocturnal tide of each biweekly tidal cycle.

Table 1.

Comparison of the two populations with respect to several key variables that relate to which sex searches for a mate.

Variable	Sweetwater River	Tecolote Creek
Population density	high, 44 burrows/m ²	low, 4 burrows/m ²
Predation	none seen	present
Sediment	19% silt	36% silt
Separate breeding area	yes	no
Burrow dimorphism	male burrows longer	sexes build similar burrows
Mate searching sex	female	primarily male

We never observed or found any evidence of predation on fiddler crabs at the Sweetwater estuary ($n = 459$ scans across 70 days, plus observations on 158 other days) although many birds that typically eat crabs frequented the site and its surroundings. In contrast, we twice saw willets prey upon male crabs at the Tecolote Creek site, and people and cars frequently passed by and caused crabs to retreat into their burrows (Table 1, $n = 112$ half-hourly scans across 18 days, plus observations on 9 other days).

The median particle size diameter of sediment in the breeding area of the Sweetwater population ($Md \phi = 2.97$, interquartile range, $Q \phi = 1.29$) was larger than the surrounding area ($Md \phi = 3.38$, $Q \phi = 0.55$), and the median size of Tecolote Creek population was intermediate ($Md \phi = 3.13$, $Q \phi = 1.25$; Fig. 3). The Sweetwater site was sandier than the Tecolote Creek site (Mann-Whitney U: $U = 116$, $n = 25$, $P = 0.0328$): a median of 73.0% of the breeding area sediment, 79.8% of the surrounding area sediment, and only 64.2% of the Tecolote sediment was composed of very fine grained sand or larger particles (Fig. 3).

Burrow dimorphism

Male burrows were longer than female ones in the Sweetwater estuary's breeding area (Fig. 4a) and its surrounding area, and burrows in the breeding area were longer and wider than burrows in the surrounding areas (Table 2). The Tecolote Creek population lacked the sex-based burrow dimorphism found in the Sweetwater estuary population. Male burrows at Tecolote Creek averaged 29.46 ± 1.49 cm (mean \pm SE, $n = 52$) in length, twice as long as male burrows at Sweetwater, and this was not significantly longer than female burrows, which averaged

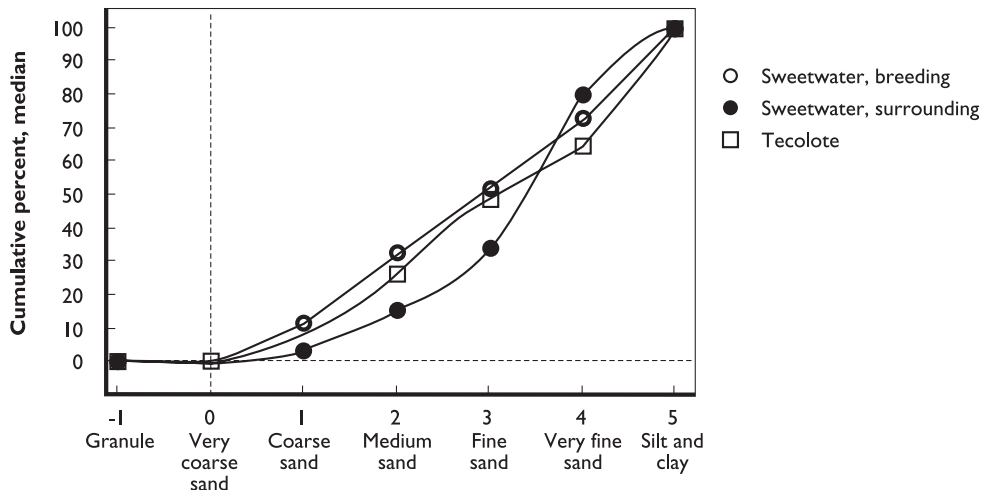


Fig. 3. — Cumulative frequency curves of sediment particles, separated with a graded series of sieves, from the Sweetwater River populations breeding and surrounding areas and the Tecolote Creek population. A logarithmic transformation was applied to the Wentworth scale to obtain ϕ : $\phi = -\log_2$ particle diameter (mm).

26.41 ± 1.54 cm (Fig. 4b; n = 53; t-test: t = 1.43, df = 103, P = 0.1572). Male Tecolote Creek burrow aperture (14.98 ± 0.21 mm, n = 38) did not vary from female burrow aperture (14.99 ± 0.25 mm, n = 41; t-test: t = - 0.03, df = 77, P = 0.9796).

At the Sweetwater estuary site, just over half (239/463) of males in the plots in the primary breeding area built exterior architecture — hoods or elevated rims — around their burrow entrances during the breeding season, and male burrows

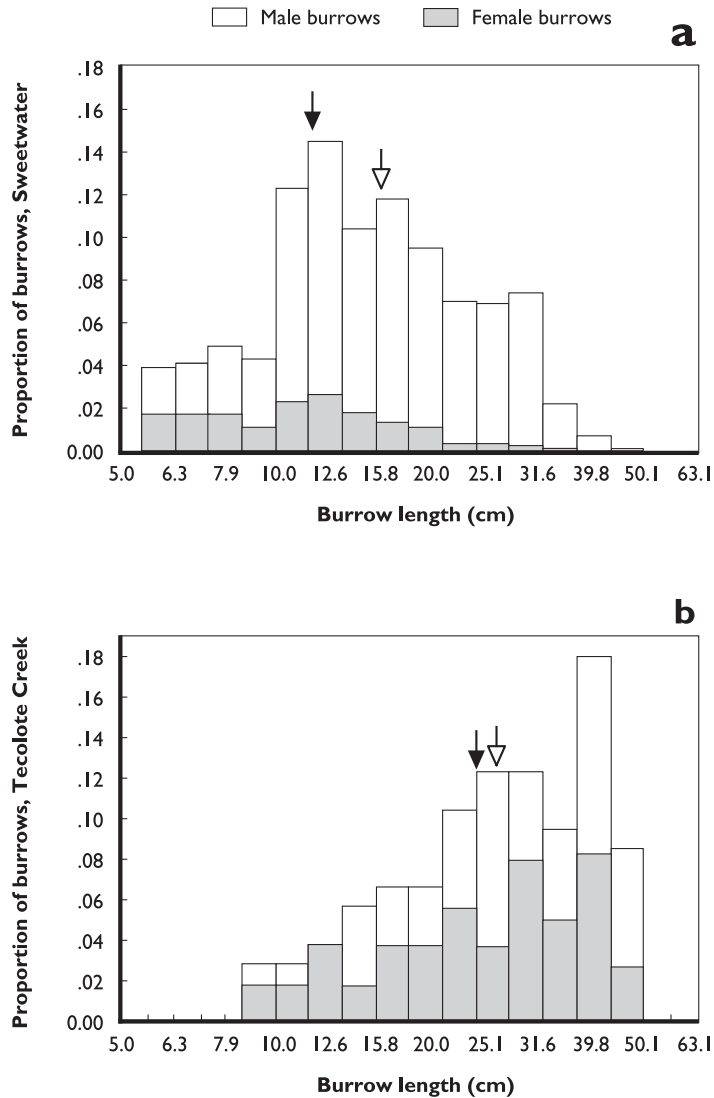


Fig. 4. — Frequency distribution histograms of male and female burrow lengths at (a) the Sweetwater river population and (b) the Tecolote Creek population. Open arrows indicate the means for male burrows while filled arrows indicate female means.

Table 2.

Descriptive statistics and results from an ANOVA comparing male and female burrow length and aperture in the primary breeding and surrounding areas of the Sweetwater estuary population.

Variable	Burrow length (cm)			Aperture (mm)		
	Mean	SE	n	Mean	SE	n
Male, breeding area	17.26	0.31	578	10.85	0.05	538
Male, surrounding area	12.36	0.50	111	10.67	0.16	106
Female, breeding area	12.72	0.49	126	10.75	0.16	115
Female, surrounding area	10.54	0.27	231	10.43	0.09	233
	df	F	P	df	F	P
Area (breeding vs surrounding)	1	50.68	<0.0001	1	5.37	0.0207
Sex	1	45.89	<0.0001	1	2.43	0.1191
Area × sex	1	6.50	0.0109	1	0.41	0.5226
Residual	1085			988		

with exterior architecture were 26% (4.0 cm) longer than male breeding area burrows lacking this architecture (Fig. 5; t-test on transformed data: $t = -5.88$, $df = 445$, $P < 0.0001$). Females never built such architecture around their burrow openings (0/512 female burrows). Crabs never built hoods or rims at Tecolote Creek.

Mate searching and burrow use

Females always searched for mates ($n = 226$), entering the burrows of waving males only, and remained in male burrows ($n = 92$) in the Sweetwater estuary population, and no matings were seen on the surface. Females traveled 1.5 to 15.0 m (median = 5.0 m, $n = 9$) from the place we first noticed them to the male burrows in which they remained.

Females with eggs were found in their mates' burrows up to 16 days after they entered ($n = 40$), but none were found after 17 to 19 days ($n = 9$). Not all females remained in male burrows for the entire incubation period, however; out of 97 observation days that did not include the day of or just prior to larval release, a median of 12.0% (from 0 to 100%, the latter after a rainstorm) of the females walking on the surface carried eggs. Oviparous females on the surface dug burrows or entered uninhabited burrows.

At the Tecolote Creek site, males approached neighboring females and started to court them on the surface in 11 of 13 observed non-aggressive approaches between the sexes. Males approached females, courted them, and eventually mated with them on the surface ($n = 2$) or did not mate ($n = 9$) because the female repeatedly kicked her suitor ($n = 4$) or because the crabs retreated to their burrows after birds flew over or people passed by ($n = 5$). These males never traveled more than 1.0 m in search of a mate. Two females approached and stayed in the burrows of neighboring, waving males that burrowed just 0.3 and 1.1 m from the female's burrow.

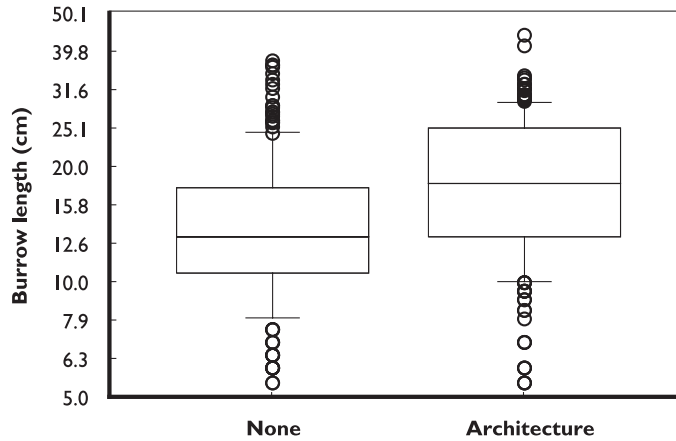


Fig. 5. — Box plots showing that in the breeding area of the Sweetwater River population, male burrows with exterior architecture ($n = 231$) were longer than male breeding area burrows lacking this architecture ($n = 216$).

Enclosure experiment

Manipulations of density and sex ratio in enclosures at the Sweetwater estuary population did not affect which sex mate searched or where mating occurred. Females always searched for mates in enclosures: 20 females searched for mates in the high density, predominantly male enclosures; 8 females searched in the high density, female-biased enclosures; 7 females searched in the low density, male enclosures; and 9 females mate-searched in the low density, female-biased enclosures.

DISCUSSION

This study examined the behavioral and ecological characteristics of a population of fiddler crabs, *Uca crenulata*, with female mate searching. Females produced clutches that protruded beyond their bodies and they released their eggs synchronously. Only females searched at this high density, sandy, predator free site. Females searched even when density was experimentally lowered in enclosures at this site. In contrast, a limited set of observations at a second, lower density, silty site with predators, revealed male searching. The populations varied in burrow structure as well. Males of the densely populated, sandy site built longer burrows than females did. Both male and female burrows at the sandy site were shorter than burrows, which did not vary by sex, at the site with more silt and fewer crabs.

Large clutch size in these intertidal crabs may necessitate incubation in a specialized burrow. Females must ensure that their exposed eggs do not desiccate, and incubation in burrows is typical of fiddler crabs that have protruding clutches

(FEEST 1969, PILLAY & NAIR 1971, RABALAIS & CAMERON 1983, BARNWELL & THURMAN 1984, CHRISTY & SALMON 1984, TAKEDA & MURAI 1993). Due to the small body size of females and the large size of each of the 3,000 or so eggs, the clutch of *U. crenulata* protruded beyond each female's abdomen, and, at the Sweetwater estuary site, females remained in their mates' long burrows for most to all of the time they carried their clutches. This pattern and the low number of ovigerous females on the surface suggest that females not only mate but also incubate in their mates' burrows in this population. Burrows of both sexes at Tecolote Creek were very long and females may incubate in their own or their mate's burrow at this site.

Synchronous larval release at a nocturnal tide of maximum amplitude, which has been identified for many fiddler crab species (CHRISTY 1978, 1982; DECOURSEY 1979; BERGEN 1981; CHRISTY & STANCYK 1982; SALMON 1984; MORGAN & CHRISTY 1995), also may mandate that females either build or find burrows that offer a stable environment. Female *U. crenulata* released their larvae synchronously at night around the maximum amplitude tides and each female released all of her eggs at one time. The short time period during which a female *U. crenulata* releases her eggs may require that she incubate all of her eggs in a similar environment during development. Therefore, both large clutch size relative to body size and synchronous release are likely to increase a female's reliance on a specialized incubation burrow, but the burrow may be her own.

Large sediment size may influence whether female fiddler crabs with protruding clutches benefit from using male burrows. Eggs are lost when burrows crumble or flood (CHRISTY 1980, 1983), and large sediment size probably increases the degree to which burrows within a population vary in gas exchange, structural stability, and resistance to flooding. If a female leaves her own burrow to search for a mate and his burrow, she can use a burrow that will meet her incubation criteria without having to build, maintain, and defend it. A majority of the sediment at the female-search site was sand and the breeding area averaged even larger-grained sand than the surrounding areas. The fact that males build burrows in the sandiest spots suggests that burrows in these areas, if properly built and maintained, provide the best incubation chambers. At the site with male searching, the sediment contained a larger fraction of silt. Moreover, burrow size varied by sex in the sandy, female-search population but not in the silty male-search one. In addition, females were more selective, as measured by search length, while searching for a mate than were the few observed females from the site with more silt.

Population density has been suggested as a key factor in determining female mate searching (DERIVERA 1999, DERIVERA & VEHCENCAMP 2001). Experimental work on an *U. beebei* population that lacked sex-based dimorphism in burrow length (CHRISTY & SCHOBBER 1994) and that lived on a silty mudflat showed that females reduced their searching in low-density experimental enclosures (DERIVERA et al. 2003). Contrasting the low-density, male search with the high-density female search *U. crenulata* populations of the present study is consistent with a positive correlation between population density and female mate searching. However, these sites varied in all measured variables, not just density. Moreover, enclosure experiments at the sandy site showed that density alone cannot explain which sex searches. Unlike in *U. beebei*, density reduction in enclosures did not decrease the proportion of searching done by females. Perhaps density has less of an effect on searching when the sediment is large grained. When burrows are necessary for incubation and sediment grain size is large, females may search throughout densities because their burrows are not suitable for incubation while male-created and defended bur-

rows are. When silt dominates the sediment composition, burrows may not differ as much so females could rely on their own burrows for incubation. In silt, females may search when density is high or because they are evicted from their own burrows, such as in *U. lactea* and *U. rosea* (MURAI et al. 1987, 1996). An alternative explanation is that density is still important to searching on sandy sediment, but the shift to male searching does not occur until density is very low, lower than the surface density of the experimental enclosures.

Only females search for mates in some *Uca crenulata* populations while males search in nearby populations, showing that local ecology, not just differences between the sexes and history, can affect searching sex. Given the potential advantage to females of using specialized incubation burrows, a male could attract more mates if he modified his burrow into one that was better for incubation, such as the male breeding burrows at the sandy site. His mates would be free to create small burrows and live near a better food supply or in areas with less fighting for burrow possession. In addition to building small burrows, most females in the high-density, sandy population burrow in different areas than breeding males (DERIVERA 2003). Females should be selective when choosing a burrow if burrows affect incubation success. Indeed, the searching females in the high-density, sandier population searched further for mates and male burrows than the few females that traveled to mates in the low density, siltier population.

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