

ARTICLE

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Causes of a male-biased operational sex ratio in the fiddler crab *Uca crenulata*

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Abstract This research investigates the causes of a male-biased operational sex ratio in a population of the California fiddler crab, *Uca crenulata*. Mensurative studies revealed there were almost twice as many adult males as females, mating occurred across half of the days within the breeding season, and females had much longer individual reproductive cycles than males. Therefore, many more males than females were available for mating on each breeding day. Perhaps as a consequence, males spent a large proportion of their time fighting with neighbors and rapidly waving their large claws when females passed by.

Key words Fiddler crab · Mating synchrony · Operational sex ratio · Reproductive cycle · *Uca*

Introduction

Sexual selection is likely to be intense when one sex limits the reproductive opportunities of the other and reproductive success is highly skewed (Darwin 1874; Emlen and Oring 1977). Both of these conditions may be met when there are fewer females than males available as mates at a given time (Emlen and Oring 1977). Such a male-biased operational sex ratio can be caused by three key factors. First, the adult sex ratio itself can be biased toward males as a result of factors unrelated to breeding, such as higher levels of predation on females. Second, asynchrony of receptive females – when different females are available for breeding throughout a breeding cycle – further accentuates the male operational sex ratio bias (Emlen and Oring 1977).

If females have asynchronous reproductive periods and mate guarding is brief or absent, most of the males but only a fraction of the females can mate at any time. Third, differential reproductive investment between the genders biases the operational sex ratio. Females typically invest more into each offspring than males do (Bateman 1948). These females will take longer to recover from producing offspring and will be available for mating less often than a reproductive male. In some species, male signaling and resource defense increase male reproductive expenditure but these investments often are at least partially balanced by the corresponding mate-searching efforts of females and generally do not reduce male availability to the level of female availability. Long or dangerous mate searching by males, large gamete contributions, such as is found in some crabs (Kendall et al. 2001), or male parental care, however, can bring male investment up to or beyond the level of female reproductive investment in some species.

Sexual selection is thought to be strong in fiddler crabs, intertidal, burrowing crabs in the genus *Uca* (family Ocypodidae), because males, but not females, have a grossly enlarged claw that they use to defend their territories and to attract females (Crane 1975). In some species, such as the sand fiddler crab, *U. pugilator*, more males than females are available as mates, and males vary in their reproductive success (Christy 1980, 1982). *U. pugilator* males attract multiple mates to their burrows, which they defend and provide as an incubation-site resource for females, though females build their own burrows (Christy 1982). Similarly, males of the California fiddler crab, *U. crenulata*, seem to outnumber receptive females and attract females to their burrows (Leija-Tristan et al. 1990; deRivera 1999).

The California fiddler crab, the focus of this article, inhabits estuaries from Pt. Conception, California (about 34°N), throughout Baja California and the corresponding coastline of mainland Mexico, to Tenacatita Bay in Jalisco (about 19°N), and perhaps even farther south in Mexico, as well (Crane 1975). It is the only fiddler crab found in the western United States, but it is joined by several other congeners in Mexico. In California, *U. crenulata* are subject to much cooler surface temperatures during their breeding

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season than most other fiddler crabs, since most species live in the tropics (Crane 1975). Low temperatures reduce crab activity and may influence the breeding cycle in the northern part of the range (Crane 1975). As is typical for temperate zone crabs, California *U. crenulata* hibernate in their individual burrows through the winter and feed and mate in the warmer months. Some information on the breeding biology of this species has been reported for a population toward the southern end of the range (Leija-Tristan et al. 1990). No data on the mating site, breeding synchrony, or reproductive investment are available for this species, and data on the operational sex ratio are lacking for most fiddler crab species.

In this article I examine three causes of a male-biased operational sex ratio in the California fiddler crab and compare these to values reported for other fiddler crab species.

Materials and methods

Species

Uca crenulata is a small, sexually dimorphic crab that lives in the mid to upper intertidal zone of estuaries and salt lagoons (Crane 1975; Leija-Tristan et al. 1990; personal observation). Males average 14.5 mm and females average 14.2 mm in carapace width (deRivera 1999). As with all fiddler crabs, females have two small chelipeds, whereas the major cheliped of male *U. crenulata* is very large. On average, the major propodus length is 1.56 times longer than the carapace width (deRivera 1999). Males use their large claw to push and grapple with opponents and also wave this claw in a beckoning motion to attract females to their burrows.

Both male and female *U. crenulata* build, maintain, and defend individual burrows that do not connect underground. Male burrows average 15.9 cm and may have multiple terminal chambers, whereas female burrows average 10.7 cm in length and have at most a single chamber (deRivera 1999). The crabs retreat into their burrows when there is movement nearby. They remain in their burrows when the tide covers the burrows, when it rains, and when it is night, except when females release their larvae. In addition, they hibernate in their burrows throughout the winter. Like other fiddler crabs, *U. crenulata* insert a mud plug into and below their burrow entrances before the tide rises. Burrows may not be visible to the human eye when they are plugged.

When females search for mates, they leave their burrows and walk for up to 22 m, passing through groups of males (C. deRivera, unpublished manuscript). Males wave and eventually enter their burrows when females approach. Females then may partially or fully enter the male burrow or continue on. Females enter an average of almost four burrows through each meter of their mate search. Searching females eventually remain in a male burrow and presumably mate there. While within their mate's burrow,

females release their eggs and attach them to their pleopods. Females carry their clutch of eggs, which protrudes well beyond the apron (abdomen), until they release the clutch as larvae into an outgoing, nocturnal tide (deRivera 1999).

Males do not search for mates in this population and breeding males may remain in their burrows for the entire mating season (deRivera 1999).

Study site

The study site was located at the mouth of the Sweetwater River, Chula Vista, California. The population, which contains well over 150,000 individuals (unpublished data), continued about 400 m upstream and 400 m along the shore of the San Diego Bay. The study area was the most densely populated section of the estuary, averaging 43.9 ± 26.7 (mean \pm SD) surfacing crabs per square meter throughout the 42×41 -m section under study (deRivera 1999). This site contains thick stands of pickleweed, *Salicornia virginica*, under which crabs burrow, and muddy-sand areas that are unvegetated but also house crabs. Only the unvegetated areas were used for observations and measurements. Crabs built burrows through a range of intertidal elevations. The tide covered the crabs living high on the mudflat only for about 2 h during the highest amplitude tides and not at all during low amplitude ones, while it covered crabs living further down the beach for up to 16 h a day. Breeding burrows were found neither at the lower tidal areas nor in other moist areas (deRivera 1999). Most of the breeding occurred in an area that spanned 33×13 m.

Observations of free-ranging crabs

Observations of free-ranging females yielded information on breeding season duration and breeding cycles. Because crabs were only active outside of their burrows during diurnal low tides, a majority of fiddler crab aboveground activity can be recorded by observing crabs for several hours each day. Field assistants and I observed crabs for 3–6 h per day almost every day from 21 March through 7 September in 1997 and 1999 and from 17 June through 7 September in 1998. We sat still during observations but did not use a blind because crabs over 0.5 m from us were fully active on the surface and because a blind would have limited our ability to watch mobile crabs without interruption. We used binoculars when crabs were difficult to see clearly with the unaided eye, typically whenever crabs were over 5 m from us. We recorded the temperature every observation day and recorded the amount of waving in 1997.

We recorded all observations (all-occurrence sampling) of females entering in and staying in male burrows, noting the time and whether the female already carried a clutch of eggs. Eggs are orange, red, or maroon, and clutches protrude well beyond the female body, so they can easily be detected at a distance. When a mate-searching female – a mobile female that primarily visited burrows of waving

males – remained in a male burrow for 15 min, we assumed she mated with the burrow owner. In every case, neither occupant was seen for at least 15 min. Well before other crabs plugged their burrows, one of the occupants plugged the mating burrow from within and enclosed the pair or the male waved on the surface for up to 1 h before he plugged the burrow.

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 down through the entrance. The terminal chamber was marked by dropping several beads down the burrow shaft. We dug for the female 6–19 days later. We unearthed these females after we completed observations for the day but before most burrows were plugged that day. Immediately before digging, we slid a piece of 0.63 cm diameter, flexible tubing down the shaft of each marked burrow. Using a trowel, we removed the sediment surrounding the tubing. As we dug, we made sure the tubing touched the plastic string. We continued carefully digging until we found the female and the beads. When crabs had moved the beads, we only included a female in the data set when the tubing led right to her, when she was in a terminal chamber, and when we did not encounter a mud plug between the surface and the female. These methods helped distinguish the correct female from other females in chambers nearby. We returned the sediment to the burrow as best we could. However, these burrows were greatly damaged by our digging and were not used by us again.

All unearthed and trapped (see enclosure observations below) crabs were measured. Each crab was weighed to the nearest 0.025 g using a 5-g precision spring scale accurate to $\pm 0.3\%$. Carapace width and propodus length of the male major cheliped were measured to the nearest 0.1 mm using vernier calipers.

We observed focal crabs (focal sampling) and groups of crabs (instantaneous scan sampling) to document gender-based differences in key behaviors. Randomly selected focal males and females were observed for 30 min each on 7 days from 8 to 29 May 1997. We observed at least 1 male and 1 female on each observation day for a total of 12 individuals of each gender. Two females were excluded from analyses because they walked out of view before 10 min had passed. To increase sample size for statistical purposes, on 16 May 1997, we also scanned a small area at the lower edge of the primary breeding area throughout the high activity period. At 10-min intervals we recorded the number of males and females that were fighting, waving, or performing other behaviors. This yielded 26 sets of observations with a total of 263 observations of males (1 of the 11 males entered and plugged his burrow after 3 observations; because an observer does not know what behaviors are conducted by a crab in its burrow, this male was excluded from the remaining scans) and 234 observations of females.

A glance at the study area reveals that many more males than females live in the higher, breeding area, whereas such a male bias is not present lower in the intertidal zone. To

quantify this pattern and to estimate the sex ratio, we observed crabs along two transects. In April 1997, we established 42 consecutive 1×0.5 -m quadrats along a 42-m transect that ran perpendicular to the tide. We also established a similar 41-quadrat transect that ran parallel to the tide 27 m above the mean low tide water line. We watched crabs emerge from their burrows and identified which gender inhabited each burrow. We only conducted this study one time, but one would not expect the distribution of the genders nor the sex ratio to fluctuate greatly right before or during a breeding season because this is a large, well-established, resident population, crabs need their burrows to survive and rarely construct new burrows during the breeding season, predation on crabs is probably very low, and recruitment occurs after the breeding season. Our data on reproductive cycles are from the same year as the sex ratio data, and the mating synchrony data did not significantly differ between years (see Results), so our estimation of the operational sex ratio in 1997 should not be affected even if the sex ratio changed at the study site across years.

Enclosure observations

We built and observed enclosures in 1997 to gather information on individuals over time and to establish the sex ratio of all crabs in plots, not just crabs that surface on one day. We established three 1×1.5 -m plots in areas that had similar numbers of burrows as other parts of the breeding area, then enclosed each plot with hardware cloth fencing. The fences were 23 cm tall; the upper 4 cm was covered by aluminum siding to prevent crabs from escaping; the bottom 12 cm was buried in the mud. To track individual crabs across days as well as to determine density, we labeled all of the crabs within the enclosures by gluing waterproof labeling tape, marked with a unique number code, onto their backs using superglue. We picked crabs up from the ground or trapped them with non-destructive, sliding traps to collect them for labeling.

To determine the percentage of females and males that surfaced each day and the frequency with which individual males and females surfaced, we observed the enclosures throughout the whole time the crabs were active daily from 25 May to 4 July and sporadically until 20 August 1997 for a total of 57 observation days. We noted when individuals surfaced and when each female carried and released eggs. The sample sizes of the analyses on individual crab behavior are lower than the number of crabs in the enclosures because data were used only for crabs that were identifiable for an extended period. I analyzed male data based on 250 randomly selected males in the three enclosures. Of these 250, 196 retained their tags and were seen across at least 10 days.

Statistical analyses

To test whether male waving rate is independent from female mate searching, I conducted a chi-square analysis on

a contingency table, following Zar (1984). The log-likelihood ratio, *G*, test could not be used because one of the cells contained a zero. I used counts of nominal data for both variables. Male waving was categorized as “no to low” when no males waved or a small proportion of the males waved sporadically and slowly, as “moderate” when up to half of the males in the breeding area waved and waving was at times fast, and as “high” when most males waved rapidly for at least part of the activity period. Two levels of female searching, no searching versus some searching, were used in this analysis.

An analysis of variance (ANOVA) examined whether males and three categories of females, all from the enclosures, spend different proportions of time underground. I compared males, ovigerous females, females that had been ovigerous but had released their eggs (“previously ovigerous females”), and females that were not seen with eggs. I transformed this proportion data using the arcsine square-root transformation to approximate even more closely the normal distribution. The differences between the four variables were further examined with Tukey–Kramer post hoc tests.

Data from instantaneous scans identified whether the genders spent different proportions of time fighting and waving. All male fights were tallied, as were all female fights (the observed values). As shown in Table 1, I obtained the expected value for males by multiplying the proportion of observations of males by the total number of fights. To determine the proportion of observations that were of males, I multiplied the number of scans times the number of males, then divided this product by the total number of observations (number of scans times number of individuals). The same procedure was repeated for females to determine the expected number of female fights. These data were analyzed using a chi-square goodness of fit test after performing the Yates correction for continuity. I analyzed the waving data using the same method.

For all statistical tests, I used two-tailed analyses and used $\alpha = 0.05$ to judge significance. When the distribution of a variable approximated the normal distribution, I report the mean and standard deviation, unless otherwise noted. I report the standard error when directly comparing the group means.

Results

Sex ratio

The adult sex ratio of this population in 1997 was male biased, but it varied with location of the study site. Observations of the number of crabs that surfaced in quadrats along transects revealed that males built their burrows higher up on the beach than females did (Fig. 1). Male burrows outnumbered female ones throughout the primary breeding area – the upper central part of the field site – with 3.37 surfacing adult males per female (46 quadrats, 684 males, 203 females). Across the entire study site, the sex ratio was less biased, with 1.59 surfacing adult males per female (83 quadrats, 827 males, 521 females). Because the enclosures were in the lower part of the breeding area and because we counted all crabs in the quadrat, not just those that surfaced during one day of observations, we found 1.73 males for every female we captured and marked in enclosures.

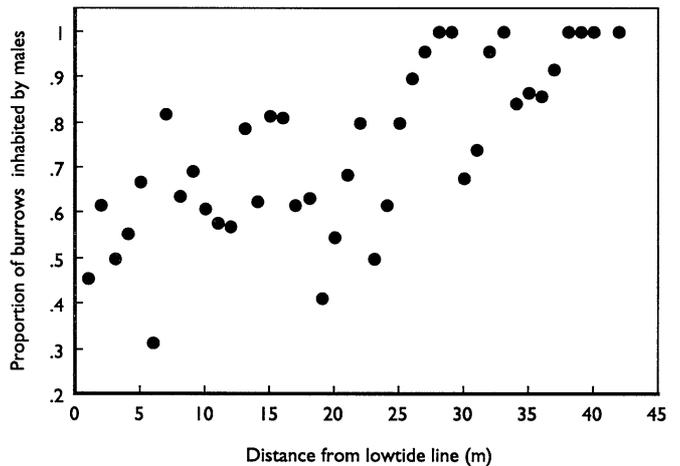


Fig. 1. A greater proportion of burrows were inhabited by males as distance from the low tide line increased

Table 1. Observed and chi-square values from instantaneous scan samples comparing the tendency of males versus females to conduct competitive behaviors, fighting and waving. *Behavior* state behavior, fighting or waving, being performed at time of scan; *class* category of animals, males or females, being observed during scans; *scansxclass size* the number of scans (26) × the number of males (11 during 3 scans, 10 thereafter) or females (9) that were observed during each instantaneous scan; *proportion* proportion of all observations (scansxclass size) that were of males or females; *observed no. behaviors* number of times males or females were seen fighting or waving during a scan, totaled across scans (followed in parentheses by the adjusted value, adjusted by the Yates correction for continuity); *expected proportion* total number of observed behaviors; χ^2 chi-square goodness of fit comparing genders, obtained using the adjusted observed and the expected values

Behavior	Class	Scansxclass size	Proportion	Observed no. behaviors	Expected	χ^2	<i>P</i> value
Fighting	Males	263	0.5292	25 (24.5)	15.88	9.95	0.0016
	Females	234	0.4708	5 (5.5)	14.12		
	Total	497		30			
Waving	Males	263	0.5292	92 (91.5)	48.68	79.98	<0.0001
	Females	234	0.4708	0 (0.5)	43.32		
	Total	497		92			

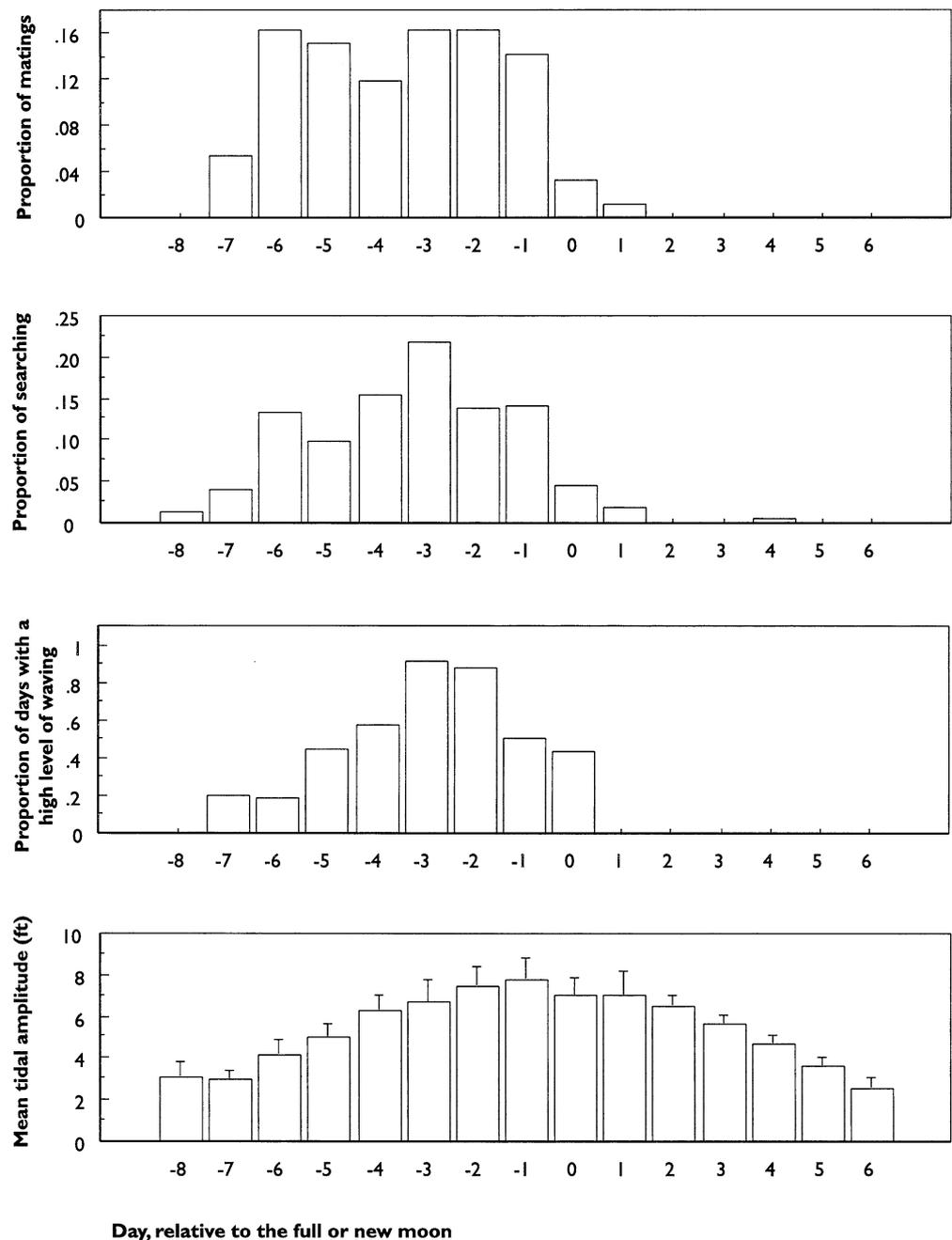
Temporal breeding patterns and mating synchrony

California fiddler crabs did not breed uniformly throughout the breeding season – the first to the last time females were observed to enter and stay in male burrows. The breeding season lasted 18.3 weeks in 1997, from 28 April to 2 September. Data from 1998 are fragmentary, and in the cool *la niña* year, 1999, the breeding season only lasted 10.7 weeks, from 28 May to 10 August. Reproduction peaked during the first week in July in all years, and there was an equally large peak in the last week of May in 1997. Reproductive timing was related to temperature; crabs did not breed or search for mates when the temperature above the surface was below

18.9°C. The average temperature of the time periods when mating occurred was $22.7 \pm 2.3^\circ\text{C}$ (mean \pm SD).

This population mated on several days within each semi-lunar cycle, and thus females show moderate but not complete mating synchrony. Almost all observed mate searching (88.1%, $n = 226$) and mating (90.2%, $n = 92$) occurred from 6 days to 1 day before a high amplitude tide (Fig. 2). Mating synchrony did not vary across the 3 years of the study (two-way ANOVA on transformed values, with year and days relative to moon (here categorized as either 1–6 days before new or full moon or other days) as nominal independent variables: $n = 86$; proportion of searching females: year $F = 1.24$, $P = 0.2952$, interaction $F = 0.55$, $P = 0.5814$; pro-

Fig. 2. Mean tidal amplitude (\pm SD), the proportion of days during which males waved at a high level, the proportion of mate searching (226 females mate searched), and the proportion of matings (92 females remained in male burrows) across 86 days divided into six semi-lunar cycles (14 or 15 days each) from 1997 and 1999. *Negative numbers* represent days before the full or new moons; *positive numbers* represent days after the full or new moon



portion of matings: year $F = 1.87$, $P = 0.1613$, interaction $F = 2.57$, $P = 0.0829$).

Mate searching and mating were moderately synchronous within a day as well, and the timing of these mating activities varied with the time of the low tide. Mate searching occurred only between 1100 and 1412 hours, and low tides on these days ranged from 0941 to 1629 hours. Mate searching occurred from 2.2 h before to 4.2 h after low tide. Females concluded their searches and stayed in male burrows from 1.5 h before to 2.9 h after low tide.

Male mate-attraction behavior closely corresponded with female searching. All of the males in enclosures surfaced on at least one of the days that females searched for mates during each biweekly breeding cycle. Furthermore, males waved at higher rates on days when females searched for mates than on days when females did not search (contingency table: $\chi^2 = 25.54$, $df = 2$, $n = 83$, $P < 0.0001$, Fig. 2). Almost every male on the surface in or out of enclosures waved at a high rate when a mate-searching female passed within 0.5 m of him. On days when females did not search, males rarely waved, never waving at the high pace typical of mate attraction, and spent their time fighting, maintaining their burrows, and eating.

Differential reproductive investment and individual reproductive cycles

Females had longer individual reproductive cycles than males did. Females carried their eggs from 12 to 16 days after they mated, based on females unearthed in 1997 and on labeled enclosed females also in 1997. Females did not remate while they carried eggs or soon thereafter. No female that entered and remained in a male burrow had eggs when she first entered ($n = 92$ females), and no searching females carried visible eggs ($n = 226$). After releasing a clutch of eggs, females in enclosures ate on the surface for 3.6 ± 2.5 days (mean \pm SD, 0–7 days, $n = 22$). These females then remained underground for 17.5 ± 9.2 (4–33) consecutive days. Ovigerous females spent the greatest percentage of their time underground ($88.5 \pm 2.5\%$, 12; mean \pm SE, n), followed by previously ovigerous females ($75.4 \pm 3.9\%$, 13), females not seen with eggs ($57.4 \pm 1.8\%$, 137), and then males ($37.0 \pm 1.2\%$, 196; ANOVA: $F_{3,354} = 60.29$, $P < 0.0001$; Tukey–Kramer post hoc test: all groups significantly different from each other except ovigerous from recovering females). Female surfacing seemed to be affected by weather as well as reproductive stage. Females rarely surfaced when it rained or when it was overcast and less than 18°C.

As a result of the long time females required for gamete production and recovery, individual female reproductive cycles spanned two to three semi-lunar cycles. During the 12 weeks we watched the three unmanipulated enclosures, 42 of the females were seen carrying eggs and 2 of these produced a second clutch. The second clutches appeared 30 days after the first in both cases. Therefore, the female individual reproductive cycle was at fastest 4 weeks, and probably more often lasted at least 6 weeks. In the 18-week

breeding season of 1997, a female could produce three to four clutches per year. No female would be expected to produce more than two clutches in the shorter, 1999 breeding season.

Male recovery time took somewhere between part of a day and 3 days, based on post-mating behavior. Males resurfaced and resumed courting soon after they attracted a mate to their burrow; 14.3% of 63 observed males that mated in their burrows were courting new searching females the same day and 61.9% had unplugged their burrows and were actively courting within 3 days.

Some males attracted multiple females to their burrows, and this also indicates rapid recovery time. Digging up marked chambers of 71 male burrows revealed some males attracted more mates than others. One male burrow contained four ovigerous females in its terminal chambers, two male burrows housed three mates each, 18 male burrows (25.4%) housed two females, and 50 burrows (70.4%) had just one female. Unmarked terminal chambers housing females are easily missed. Therefore, these numbers underestimate the number of male burrows with females in other terminal chambers.

Males invest more than females in non-mating intra- and inter-sexual behaviors. Males observed during 30-min focal observations spent 7.3% (0–38.7%, $n = 12$) of their time fighting to maintain possession of their burrows and 31.6% (0–84.1%) of their time waving their claws. In contrast, females spent 1.5% (0–14.4%, $n = 10$) of their time fighting. No female was ever observed waving at this site. Data from instantaneous scan sampling further emphasize these gender-based differences in time spent on fighting and waving (Table 1).

Operational sex ratio

More males than females were available for mating on every day within a breeding peak because of the male bias to the adult sex ratio, the availability of different receptive females over multiple days within a breeding cycle, and the relatively long female reproductive cycle. In 1997, 1.73 adult males per female were found in enclosures, males could attract females over 6 days during each biweekly breeding cycle, and males could potentially mate during two to three times more breeding cycles within the breeding season. If we multiply the values of these variables together to obtain a rough estimate of *U. crenulata*'s operational sex ratio at this site in 1997, we find that 20 to 32 (i.e., $1.73 \times 6 \times 2$, or $\times 3$) times more males than females were available for mating. A more extreme measure comes from comparing the number of waving males to the number of mate-searching females for each day on which mating occurs. This estimate suggests that 80 times more males than females were available for mating (i.e., 29.7 males surface each day per square meter in the breeding area \times 429 m² breeding area \times about 80% males on the surface and waving while a female passes \div 3.75 observed searching females per day during the peak days in the approximately 1/34 of the breeding area observed at a time \div 34).

Discussion

I examined the causes of a male-biased operational sex ratio in a population of *Uca crenulata*, the California fiddler crab. I found more adult males than females lived at the study site, females were available for mating on half of the days within each breeding cycle, and females took much longer to recover from reproduction than males did. As a result of these conditions, many more males than females were available for mating at any given time. I expect the three identified factors that contribute to a strong male operational sex ratio are common for other related fiddler crabs. Such a large male bias to the operational sex ratio yields polygynous mating systems and provides the opportunity for strong sexual selection (Emlen and Oring 1977).

A male bias to the adult sex ratio could contribute to a male-biased operational sex ratio and to polygyny because an abundance of males sets the stage for more breeding males than females and increased competition for mates. Almost twice as many adult males as females inhabited the study site. Other populations of *U. crenulata* have a similar sex ratio (Leija-Tristan et al. 1990; C. deRivera, unpublished data). Most examined fiddler crab species, in fact, have a strong male bias to their adult sex ratio (Valiela et al. 1974; Powers 1975; Ahmed 1976; Frith and Brunenmeister 1980; Thurman 1985; Severinghaus and Lin 1990; Spivak et al. 1991; von Hagen 1993; Wolfrath 1993; Emmerson 1994), though one American species had an equal sex ratio (Zuker 1984) and a population of *U. vocans*, an Indo-west Pacific species, had as few as 0.4 males per female (Salmon 1984). As was suggested by Montague (1980), some of the male bias may be explained by the methods used in some studies: using the number of surfacing males and females may overestimate the number of males relative to females because males, of *U. crenulata* at least, surfaced more often than females did. More accurate estimates can be obtained from digging or observing labeled crabs over time, methods that have been used in many fiddler crab studies (e.g., Ahmed 1976; Frith and Brunenmeister 1980; Leija-Tristan et al. 1990; Severinghaus and Lin 1990; Spivak et al. 1991; Emmerson 1994). A male-biased adult sex ratio may truly be common to fiddler crabs because some avian predators typically eat the easier-to-handle females (Bildstein et al. 1989). Because it is male biased in most fiddler crab species, adult sex ratio must not be a key determinant of differences in the breeding biology of fiddler crab species even though it affects the operational sex ratio.

When different females mate on multiple days within a breeding cycle, males can breed with multiple females within each cycle (Emlen and Oring 1977). *U. crenulata* mated on half of the days within each semi-lunar cycle. In addition, these crabs mated throughout many hours each day. Therefore, males had the opportunity to court and mate with multiple females within a semi-lunar cycle. Almost one-third of the males that mated attracted multiple mates.

Greater female than male reproductive investment lengthens the reproductive cycles of individual females relative to individual males and further increases the num-

ber of males available per breeding female (Emlen and Oring 1977). Female *U. crenulata* required much more time than males to recover from reproduction. Females spent long stints underground during and after egg carrying, and their inter-mating intervals lasted 4 weeks or longer. Each female, therefore, could produce two or three clutches per year. A male, on the other hand, could attract females each consecutive biweekly cycle throughout the breeding season. Furthermore, most males waved to attract new mates 1–3 days after mating, and males devoted over one-third of their time while the tide was out to mate attraction and fighting. Males of a related species, *U. pugilator*, took 1–3 days to remate because they never re-surfaced until their mates produced eggs (Christy 1978). Mated male *U. crenulata* that resurface by the next day potentially attract up to five females within each semi-lunar cycle. Some males come close to this, as we found four mates in one male burrow. If a preferred male can attract an average of three mates per breeding cycle, he has the opportunity to have his sperm fertilize 27 clutches within an 18-week breeding season and thus contribute to 9 times more clutches than a female.

The abundance of males in the population, the availability of different receptive females on multiple days each breeding cycle, and especially the difference between the genders in reproductive cycle length biased the operational sex ratio toward males. Combining the sex ratio, female availability, and reproductive cycle data yielded an estimate of 32 available males per breeding female. A second estimate that used the number of waving males and searching females in the primary breeding area yielded an even greater male bias, 80 available males per female. The difference between the two estimates combined with the low proportion of enclosure females that produced a second clutch suggests that most females bred less often than the possible one time every two to three semi-lunar cycles. Perhaps a large fraction of the females in the population bred only during the first peak-breeding episode or once during this peak and one more time, after variable recovery times, during the breeding season.

The male-biased operational sex ratio and a high level of male competition may be typical of the clade to which *U. crenulata* belongs, the derived American clade (Levinton et al. 1996), formerly the broad front fiddler crabs (Crane 1975). Other derived American species follow similar semi-synchronous, semi-lunar mating and breeding activity patterns (Christy 1978; Wheeler 1978; Greenspan 1982; Salmon 1987) that facilitate male remating within a breeding cycle. Moreover, a similar pattern to *U. crenulata*'s – each male courts during most prime breeding days while each female mates only once every 4 or more weeks – was found in *U. pugilator* (Christy 1979).

Species belonging to the Indo-west Pacific clade of fiddler crabs (primarily the former narrow fronts) also probably have a bias toward males but a less extreme one due to the greater equality between male and female reproductive cycles. At least one Indo-west Pacific species had nearly continuous breeding (Salmon 1984). In other species in this clade, such as *U. tetragonon* and *U. vocans*, females mate

while they carry eggs (Salmon 1984; Goshima et al. 1996). This brief female recovery time combined with longer male mating intervals that result from mate guarding (Goshima et al. 1996) may neutralize any male bias to the operational sex ratio created by other factors such as asynchronous breeding across females.

The large claw of males, used for territorial fighting and mate signaling, is a probable outcome of a high level of competition between males in all fiddler crab species. Mating with multiple females within a breeding season, also found in most fiddler crabs, is another likely outcome of these conditions.

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