ORIGINAL ARTICLE

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Density affects female and male mate searching in the fiddler crab, *Uca beebei*

Abstract In most species, only one sex searches for mates while the other waits. Models of sex-specific mate-searching behavior predict single-sex searching, but the factors that determine which sex searches are not understood. In this study, we examine the effects of density and predation risk on mate-searching behavior in the fiddler crab *Uca beebei*. *U. beebei* is one of the few fiddler-crab species in which both sexes search for mates. In a field experiment conducted in Panama, we manipulated crab density and perceived predation risk in replicate plots. Females searched more and males searched less at high densities. At high levels of perceived predation risk, both sexes similarly reduced their search rates. Observations of plots that naturally varied in crab density show that females were more likely to search for mates in areas of higher density, where there were more males. Females may preferentially search for mates in high-density areas because the abundance of nearby burrows, into which they can run to escape predators, decreases their costs of searching and because the abundance of males and male burrows facilitates comparisons and thus may increase their benefits from searching. Males at high densities decrease their mate-searching rate perhaps in response to the increase in female searching and to the corresponding increase in the intensity of their competitors' mate-attraction signals.

Keywords Mate searching · Sexual conflict · Density effects · Predation effects · Fiddler crabs

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Introduction

Sexually reproducing individuals must find and select appropriate mates. A game theoretic model of mate searching predicts a sexual division of labor for searching effort, with either males searching while females wait or vice versa, because both sexes encounter mates fastest if only one is mobile (Hammerstein and Parker 1987). Mate searching takes time and energy, and it may often expose searchers to an increased risk of predation. Hence, a conflict of interest arises over which sex should search and pay these costs. Male searching is predicted to be the more common solution to this game. Compared to females, males typically invest less into offspring and therefore have more time and resources for searching. Additionally, male mate searching may be common because selection more often favors multiple mating by males than by females. Indeed, in nature typically only one sex, usually males, searches for mates (Darwin 1874; Ghiselin 1974). For example, males search in most arachnids, insects, reptiles, and mammals, while females search in lek mating species, in most birds, and in species in which males provide stationary resources (Darwin 1874; Jacobson 1972; Thornhill and Alcock 1983). However, a few species exhibit a mixture of male and female searching as in some anurans, Lepidoptera, and ocypodid crabs (Crane 1975; Wells 1977; Greenfield 1981; Henning 1990; Rutowski 1991).

Because females search in some species, reproductive investment cannot be the only factor affecting mate-searching roles. Population density, predation level, and resource distribution are likely to contribute to the

search-related payoffs for each sex (Rowe 1994; Rowe et al. 1994; Lucas and Howard 1995; Srivastava and Dunbar 1996; Gotthard et al. 1999). Factors that affect sampling costs also may alter search-related payoffs and the assessment behavior of searching females (Real 1990; Luttbeg 1996). If sampling costs are high, females may even stop mate searching. The costs and benefits of searching vary with sex as well as with ecological conditions; together these factors may determine which sex searches for mates. Because of the larger zone of attraction to male searching that is identified in the Hammerstein and Parker mate-searching game discussed earlier, male searching is the likely default condition (Hammerstein and Parker 1987). We predict that females should take over the searching role when their search costs are low, their benefits are high, or their costs of not searching are substantial. This study examines whether population density and predation risk affect the frequency of male and female searching in the fiddler crab *Uca beebei*.

Among fiddler crabs, which are sexually dimorphic, semi-terrestrial crabs of the genus *Uca*, species differ in which sex searches for a mate. When females search, males wave their enlarged claws and use other displays to attract females into their burrows, which males then plug. Underground mating in male burrows has yet to be observed directly, but there is strong indirect evidence that it occurs (e.g., Christy 1982; Yamaguchi 1998). Females typically stay in these burrows while they incubate their eggs (Christy 1982, 1987a). In some species with searching females, females select mates based on male traits, burrow features, or both (Christy 1983, 1987b; Christy and Schober 1994; Backwell and Passmore 1996; deRivera 1999; Latruffe et al. 1999). Searching female *U. annulipes* have been reported to visit up to 24 males and travel 28 m before making a choice (Backwell and Passmore 1996), and *U. crenulata* females have been seen to visit over 100 males (C. deRivera, unpublished data). In male-searching species, males mate with females on the surface near the female's burrow opening, and females use their own burrows while they incubate their eggs (deRivera and Vehrencamp 2001). Searching males rarely wave prior to mating, and they do not travel far in search of mates (Crane 1975). In fact, they often mate with neighboring females (e.g., Yamaguchi 1971; Christy 1987b; Salmon 1987; Goshima and Murai 1988; Murai 1992). However, in some species males court females that are several meters away from their own burrows, and other males leave their burrows and court females before establishing new burrows (Salmon 1984; Koga et al. 1999). In addition, some males locate and mate with females while feeding far away from the burrowing area (Burkenroad 1947; Nakasone et al. 1983). In this paper we focus on the relative mobility of the sexes, that is, which sex approaches the other. We consider a crab to be searching for a mate when it approaches a member of the opposite sex. The searching crab may travel short or long distances, encounter few or many potential mates, and may or may not permanently leave its burrow.

U. beebei and several other fiddler crabs show intraspecific variation in searching behavior (Crane 1975; Nakasone et al. 1983; Salmon 1987; Murai et al. 1995). A single population of *U. beebei* exhibits both female and male searching and is therefore ideal for experimentally investigating the ecological factors that affect which sex searches (Christy 1987b). In this study, we examined how density affects female searching. We predicted that more females would search when densities were high for three non-exclusive reasons. First, since females can potentially benefit more from selective mate choice than males can (Bateman 1948), high male density may increase the benefits that females receive if they search. When densities are high, searching females can compare mates and their burrows more directly and immediately. Therefore, females may be better at differentiating between males and at selecting high-quality males and resources when they search in high-density areas. For example, female *U. annulipes* may be able to assess clustered males better than dispersed males because they use relative waving rate to compare courting males within groups (Backwell et al. 1998). This benefits hypothesis assumes that males or the resources they control vary in quality and thus in the fitness benefits they provide to their mates. Second, high male density can decrease the time and/or distance that females must travel to find a mate. This would reduce the energy costs of searching and the amount of time females are exposed to predators, which would be especially important if females are more vulnerable while searching than when at their own burrows. Moreover, searching females have a nearby place to retreat from predators when burrows are at high density. An increase in predation risk has been shown to decrease the frequency of burrow mating relative to mating on the surface in this species (Koga et al. 1998), which implies a decrease in female searching relative to male searching due to female search costs. Third, high density may increase male-female aggression rates, thereby causing females to leave their burrows (T. Koga, personal communication). Females lack the enlarged claw and are generally smaller than males, and are therefore less competitive in agonistic encounters over burrow ownership. Evicted females that are ready to mate and need a burrow for incubation may then search for mates and male burrows. Females have been found to search for mates following high aggression levels in two other fiddler crab species (Murai et al. 1987, 1996). Male harassment may trigger female mate searching in many animals (Clutton-Brock and Parker 1995) and may be especially common when females and males directly compete for limited food or burrow-site resources.

We predict that males will not approach females for copulation when females search because, as indicated in the Hammerstein and Parker mate-searching model (1987), males should avoid search costs if females are searching and because males probably have a higher assurance of paternity when they attract females to their burrows than when they copulate on the surface. Evidence suggests that female fiddler crabs fertilize their

eggs with the last sperm they receive (Murai et al. 1987; Diesel 1991; Koga et al. 1993). A male that attracts a female to his burrow ensures he is the last mate but, because both sexes mate with multiple partners within each breeding cycle when mating is on the surface, males have no such assurance if they approach a female for surface copulation. Therefore, a male should only search when he is unlikely to attract a mate to his burrow, perhaps because he lives in a low-density area.

In this study, we document the effects of natural and experimentally manipulated variation in crab density on male and female mate-searching behavior. We also replicated the predation-risk experiments of Koga et al. (1998). Because we did not know whether density or predation risk would be more important in affecting searching behavior and because density and predation risk could interact in unpredictable ways, we examined the effects of density and predation at both natural and manipulated levels of risk.

Methods

Study population

We studied *U. beebei* on a mudflat, about 200 m², on the west bank of the Panama Canal near its Pacific entrance. Combined male and female burrow density varies on a small scale across the flat and ranges from 50 to 200 burrows/m² in higher density areas (Christy 1988a). Why fiddler-crab burrows have a clumped distribution is unknown, but it may be related to drainage patterns. The sex ratio at this site is nearly equal (Christy 1987b; C.E. deRivera, personal observation). An average adult male *U. beebei* has a carapace width of 11 mm and a major cheliped length of 17 mm; an average adult female is 8 mm wide and lacks the enlarged male claw (Crane 1975; Christy 1988a). Males attract females to their burrows by waving their claws. Crabs breed year-round and with a low degree of synchrony throughout each biweekly, tidal amplitude cycle (Christy 1987b; Morgan and Christy 1995). Tidal amplitude cycles vary in length from 13 to 16 days, and very few matings occur during the 3 consecutive days of each cycle when the tide is low around dawn and dusk. Crabs are inactive during rainfall and at night. When inactive, crabs remain in and typically plug their burrows; plugged burrows are undetectable by the human eye. This population is subject to high levels of predation, chiefly by the great-tailed grackle, *Quiscalus mexicanus*. Crabs retreat to their burrows when grackles or other predators approach.

Experimental design

Density and predation-risk manipulations: enclosures and control plots

We enclosed 1 m×2 m plots with 0.25" mesh hardware cloth fences and manipulated the density of the crabs within to determine whether density affected searching behavior. The fences were 23 cm tall, with the bottom 12 cm buried in the mud. The upper 4 cm of each fence was covered by smooth plastic to prevent crabs from escaping. We established 12 high- and 12 low-density plots. Both high- and low-density plots were placed in areas that initially had low, medium, and high natural densities to verify that density, not an unmeasured factor correlated with density, was responsible for behavioral changes. We removed crabs from low-density plots until ten males and ten females were present on the surface. When necessary, we added crabs to high-density enclosures, obtaining surface densities of 50 males and 50 fe-
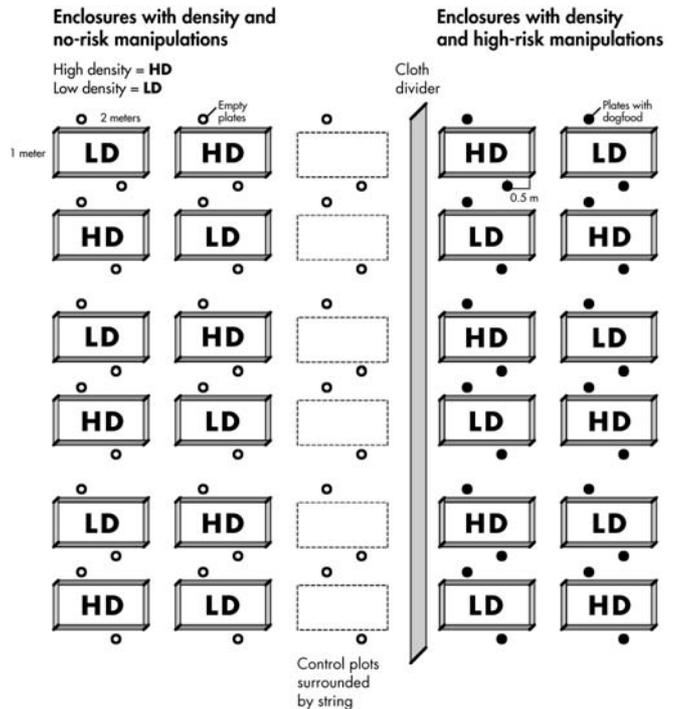

Fig. 1 Diagram of study site during the first set of risk manipulations. The cloth divider and dog-food locations were moved to the left for the second set of manipulations

males. Because some crabs were underground, the number of crabs on the surface during a daily observation period varied from the target densities and yielded a continuous distribution of plot densities. To minimize disturbances, we did not add crabs to plots after the start of observations.

To determine whether the fencing procedure or the confinement of crabs affected mate-searching behavior, we established twelve 1 m×2 m string-demarcated plots as controls. Six of these control plots were between the enclosures and the other six were on either side of the enclosures. The control plots varied in density and crabs could move freely in and out of them. We did not use the results from the observational plots discussed below to test for enclosure effects because we watched these plots at another time, and crab behavior varies unpredictably between tidal amplitude cycles.

Observations commenced 3 weeks after inserting the hardware cloth enclosures, and 6 days after adjusting the density. On 12 high-activity days (24 April to 2 May, 10–13 June 1998), we observed 12 high-density enclosures, 12 low-density enclosures, and 12 control plots. One of each kind of plot was observed daily, and each plot was observed only once. Crabs experienced natural levels of predation, which we refer to as the low-risk level. Even high natural predation levels (up to 5.3 birds/h) were lower than the manipulated levels of the high-risk treatment discussed below (10.7–38.3 birds/h).

We then manipulated the level of perceived-predation risk (hereafter referred to only as risk) in the same density-manipulated enclosures to determine the joint roles of risk and density on searching. Half of the enclosures were subjected to a high-risk treatment for 2 weeks (Fig. 1), followed by 2 weeks of a no-risk treatment. Meanwhile, the other half of the enclosures had the reverse order of risk treatments. We continued to use the six string-delineated control plots that were between enclosures, and these were never exposed to high risk.

We attracted grackles to the high-risk side of the mudflat by placing 2 plates of dog food outside of each of the 12 enclosures on that side, following protocols established by Koga et al. (1998).

Every point inside the enclosures was less than 1.12 m from a plate. Using this method, crabs encountered and responded to predators much more frequently than in unmanipulated populations, but actual predation rates did not change substantially because the birds ate the dog food, not the crabs. Hence, the predation risk perceived by the crabs increased dramatically while the density levels in the plots were not decreased by predation.

A cloth divider (0.5 m high×10 m long), which was put into place each day as soon as the water receded from the mudflat, kept crabs on the no-risk and control side from seeing grackles foraging on the ground. Plates were set around enclosures as in the high-risk manipulation but on this side they did not have dog food. Occasionally a grackle attempted to land on the no-risk side but was chased away, almost always before it landed, by shouts or by small projectiles that did not visibly affect crab behavior or hurt the birds. Many fewer grackles landed on or flew low over the no-risk manipulation than landed or flew low over crabs during the natural, low-risk session.

On each observation day from 8 May to 8 June 1998, a control plot and a plot from each of the four risk-density combinations were observed. Each enclosure was observed four times when we manipulated risk, twice under the no-risk treatment and twice under the high-risk treatment. Plots did not differ significantly between observations within a treatment for any of the variables (paired t-tests: t always <0.78, P always >0.4439). Therefore, we averaged the values of each variable for each plot within a treatment. This averaging yielded one high-risk value and one no-risk value for each variable from each enclosed plot. The six central control plots were observed four times each during the risk manipulations but always under the no-risk treatment. Each set of two observations was averaged, yielding two sets of no-risk data for these six control plots.

No manipulations: observational plots

From 26 March to 4 April 1998, before we built the enclosures, we observed crabs in plots without manipulating crab density or predation risk. Our objective was to determine the searching patterns in areas that naturally differed in density. During a period of high activity, we chose twelve 1 m^2 low-density plots, each with fewer than 30 crabs active on the surface daily (range=8–27), and twelve 1 m^2 high-density plots, each with at least 30 crabs active daily (range=33–88). Each low-density plot was paired with a high-density one situated less than 0.5 m from it. The pairs of plots were dispersed across the mudflat, and searching females typically travel much further than the distance between several of these plots (J. Christy and U. Schober, unpublished data). We delineated each plot with string. During observation periods, we framed each plot with 3 cm wide, flat white plastic ribbons which made it easier for us to see and hear crabs as they entered and left each plot. Crabs moved freely in and out of these plots.

Mobile females that eventually occupy a burrow alone primarily investigate female-owned burrows, empty burrows, and burrows with no occupant on the surface, whereas females that eventually stay with males avoid these burrows and instead typically only approach waving males (Christy 1988b; C.E. deRivera, personal observation). Therefore, to help distinguish between females that were looking for burrows and those that were searching for mates, we made false burrows about 10 mm deep and 8 mm wide at 10-cm intervals along the plastic ribbons. Females that approached and entered false burrows and female burrows were categorized as burrow-seeking females, whereas females that ignored these burrows and approached only waving males were considered to be searching for a mate. During observations, only four females entered both false burrows and burrows belonging to waving males. We categorized these females according to the type of burrow they investigated most often as they traveled.

Each plot was observed for one daytime low-tide period (2.88±0.53 h, mean±SD, range 2.0–3.5 h). We started observations when crabs first became active on the surface, from 0852 to 1445 hours; start times were dictated by the time of the diurnal low tide.

Behavioral observations

Two experienced fiddler-crab researchers, who had spent a day watching fiddler crabs together to ensure consistency and who had 100% agreement in observations, made all behavioral observations, usually with binoculars. The observers sat about 0.5 m from the closest plot, far enough away to avoid causing crabs to retreat into their burrows, and 6.5 m from the farthest plot. Plots were set close enough together in the density and risk-manipulation experiment that an observer on top of a ladder could effectively watch four enclosures and a control plot simultaneously, as required by the experimental design. Typically, only one crab in the five plots searched at any given time. Observations were made only on days when crabs were fully active (not on rainy days or days with crepuscular low tides). All observations were recorded in 0.5-h intervals throughout the 2.0- to 4.0-h period that the crabs were active on the surface each day.

For each plot, we recorded both behavioral and density variables. We counted and sexed the crabs on the surface, and counted the number of waving males three times per half-hour. We used the daily maximum number from each set of counts to obtain female and male surface densities, as well as waving-male density. Each half-hour, we kept a running tally of the number of grackles that caused crabs to retreat into their burrows, the number of male-female fights (except in risk manipulations), the number of searching males (males that approached and started to court females, whether or not the female allowed the male to mate), the number of females that left their burrows to mate search and the ones that left to seek a burrow, the number of burrow-seeking females walking in the plot (females that entered false burrows or female burrows), the number of mate-searching females (females that entered burrows of waving males), and the number of burrow matings (searching females who stayed in male burrows at least until the next diurnal low tide). The number of searching females is a good indicator of burrow mating in enclosures (n=49, r=0.77, t=8.29, P<0.0001) and in observational plots (n=24, r=0.53, t=2.89, P=0.0084), so we only report female searching in the results. For observational plots, we also tallied the number of females entering and leaving the plot. We always recorded the date, time of each half-hour observation period, and number of days into the project.

Statistical analyses

The variables used in the analyses are described in Table 1. We log or square-root transformed continuous variables to meet the assumptions of normality. We used the day's maximum recorded number of females, males and, where indicated, waving males on the surface of a plot. We used the day's total tally for each of the other observed behavioral variables. Searching behavior was quantified, not only by the plot's total number of searching males or females that day, but also as a per capita rate to control for the effects of daily density and activity levels. Fights were evaluated on a per capita basis as well. A final variable, searching sex, indicated which sex searched during each mate-searching event in each plot. For this variable, we included all observed searching males and searching females to determine whether and how many individuals of each sex searched.

Male density, an independent variable in many of the analyses, was tightly correlated with female density in enclosures and in observational plots (r>0.8 for both), so the effects of male density could not be separated from the effects of female or overall density. We used male, not female or total, density because we think it is the density factor most likely to affect male and female searching decisions.

Each analysis examined how independent variables and covariates affected a dependent searching variable. We used logistic regression when the dependent variable was nominal or ordinal, and analysis of covariance (ANCOVA), multiple regression, or simple linear regression when the variable was continuous. The interactions between the independent variables were included in

Table 1 Descriptions of the variables used in four kinds of statistical analyses: control, long-term trends, experimental enclosure, and observational plot analyses

Variable name	Form	Description (before transformation)
Variables used to test for differences between enclosures and controls		
Dependent, searching variables		
Searching females per capita	Continuous	Day's total no. females that approached waving males÷day's max. no. females on the surface of the plot. Values from high- and no-risk treatments were averaged across two observation days for each plot
Searching males per capita	Continuous	Day's total no. males that approached and attempted to mate with females÷day's max. no. of males on the surface of the plot. Values from high- and no-risk treatments were averaged across two observation days for each plot
Searching sex	Nominal	Which sex searched in each mate search (approach of male to surfaced female or of female to waving male) within a plot. Values from high- and no-risk treatments were averaged across two observation days for each enclosure
Independent variables		
Male density	Continuous	Max. no. of males on the surface of the plot that day. Values from high- and no-risk treatments were averaged across two observation days for each enclosure
Plot type	Nominal	Whether the plot was a control or an enclosure
Risk	Ordinal	Perceived predation risk: no risk (almost no predators approached the area during the observation week), low risk (predators not manipulated)
Variables used to test for long-term trends in enclosures during no- and low-risk manipulations		
Dependent variables		
Female density	Continuous	Max. no. of females on the surface of the plot that day
Male density	Continuous	Max. no. of males on the surface of the plot that day
Searching females per capita	Continuous	Day's total no. females that approached waving males÷day's max. no. females on the surface of the plot
Searching males per capita	Continuous	Day's total no. males that approached and attempted to mate with females÷day's max. no. of males on the surface of the plot
Independent variable		
Day of tidal cycle	Continuous	Observation day (1–12) within each biweekly, tidal amplitude cycle
Plot	Nominal	Each high-low density pair of enclosures. Plots were not used when they were subject to the high-risk treatment
Tidal amplitude cycle	Ordinal	The study spanned four tidal-amplitude cycles. Each cycle included 12 high-activity observation days between consecutive neap tides and 2–3 low-activity days during neap tides
Variables used to analyze experimental enclosure data		
Dependent, searching variables		
Searching females per capita	Continuous	Day's total no. females that approached waving males÷day's max. no. females on the surface of the plot. Values from high- and no-risk treatments were averaged across two observation days for each plot
Searching males per capita	Continuous	Day's total no. males that approached and attempted to mate with females÷day's max. no. of days males on the surface of the plot. Values from high- and no-risk treatments were averaged across two observation for each plot
Searching sex	Nominal	Which sex searched in each mate search (approach of male to surfaced female or of female to waving male) within a plot. Values from high- and no-risk treatments were averaged across two observation days for each enclosure
Independent variables		
Male density	Continuous	Max. no. of males on the surface of the plot that day. Values from high- and no-risk treatments were averaged across two observation days for each enclosure
Plot	Nominal	Each high-low density pair of enclosures (plot is also used throughout the text to refer to each of the observational, control, or enclosure areas observed during this study)
Risk	Ordinal	Perceived predation risk: no risk (almost no predators approached the area during the observation week), low risk (predators not manipulated), high risk (many predators approached the area daily during the observation week, and were attracted by dog food)
Variables used to analyze observational plot data		
Dependent, searching variables		
Females per capita that left their burrows then sought new ones	Nominal	Two categories: 0, ≥0.03; day's total no. females on the surface that left their own burrows on a plot then approached false burrows and female burrows÷day's max. no. females on the surface of that plot

Table 1 (continued)

Variable name	Form	Description (before transformation)
Females per capita that left their burrows then mate searched	Ordinal	Three categories: 0, 0.03–0.07, 0.1–0.13; day's total no. females on the surface of an observational plot that left their own burrows then approached waving males÷day's max. no. of females on the surface of the original plot
Male searching level per capita	Ordinal	Three categories: 0, 0.02–0.18, 0.36–0.60; day's total no. males that approached and attempted to mate with females÷day's max, no. males on the surface of the plot that day
Searching females	Continuous	Day's total no. females that entered a plot and visited burrows of waving males
Independent variables		
Male density	Continuous	Max. no. of males on the surface of the plot that day. Values from high- and no-risk treatments were averaged across two observation days for each enclosure
Male-female fights per capita	Continuous	No. of male-female fights÷day's max. no. females on the surface of the plot
Male fights per capita	Continuous	No. of male-male fights÷day's max. no. of males on the surface of the plot
Predator rate	Continuous	The day's total no. grackles that approached the observed plot÷no. observation hours
Searching females	Continuous	Day's total no. females that entered a plot and visited burrows of waving males
Searching males	Continuous	Day's total no. of males in a plot that approached and attempted to mate with females on the surface
Waving males	Continuous	Max. no. of males that waved in the plot that day

the original models, but each interaction term was removed because none showed a strong or a statistically significant effect ($P>0.24$ in all cases).

Separate analyses were conducted on the control, enclosure, and observational plots. We compared the control plots (12 plots from the low-risk observations plus 2 sets of observations during no- and high-risk manipulations on the 6 control plots between the enclosures) to the enclosure plots to evaluate whether the fences significantly affected the major searching variables. The independent variables in these analyses included type of plot (control plot vs enclosure), risk, and male density (Table 1). Data from the high-risk treatments were not included in these analyses because the control plots were never subjected to a high level of perceived-predation risk. The no- and low-risk enclosures also were analyzed to detect possible confounding long-term trends in the variables. The independent variables included plot, tidal amplitude cycle, and number of days into each tidal amplitude cycle (Table 1). Experimental enclosure data provided information on the simultaneous effects of plot, risk, and male density on the searching variables (Table 1). Data from the observational plots were used to evaluate the effects of male density and predator rate on females entering plots (Table 1). Similarly, male density, predator rate, male-female fights per capita and searching males in observational plots were used to predict whether, per capita, females active on the surface that day leave their burrows to mate search or to burrow seek (Table 1). Finally, the observational plot variables, searching females, male density or waving males, predator rate, and male fights per capita were used to predict male search levels on the surface that day (Table 1).

Statview was used for the linear regressions, and JMP (an SAS software package) was used for all other statistical tests. We report the likelihood ratio chi-square value of the logistic regressions, the F value of the ANCOVAs, the student t-values of the linear regressions, and the student t-values and standardized beta values (partial regression coefficients) of the multiple regressions. The t-values of the multiple regressions are based on tests of the standardized beta coefficients, which give the independent effects of each independent variable, partialling out all other variables.

Results

Control and long-term trends

Control plots did not vary significantly from the enclosures in searching males per capita (ANCOVA: $F=0.51$, $n=72$, $P=0.4781$), or searching sex (logistic regression: $\chi^2=1.42$, $n=96$, $P=0.2342$). However, because females from outside the area can enter a string-delineated plot but not a fenced one, control plots had more searching females per capita than enclosures (ANCOVA: $F=9.90$, $n=72$, $P=0.0025$). Descriptive statistics for controls and treatments are given in Table 2.

Over the course of the experimental manipulations, which lasted four biweekly, tidal amplitude cycles, values of female density, male density, number of searching females, and number of searching males did not significantly change in enclosures when we excluded the high-risk observations (Table 3). These values also did not fluctuate greatly during the observation days within each tidal amplitude cycle (Table 3).

The effects of male density and risk on which sex searches in enclosures

Male density was an average of 3.3 times higher and female density 2.7 times higher in high-density enclosures than in low-density ones (Table 2). Females were more likely than males to search as male density increased regardless of risk level (Table 4). In the low-density enclosures, female searching accounted for only 21.9±0.69% (mean±SE, $n=19$, no crabs searched in 17 observations of low-density enclosures) of all the searching, whereas in the high-density enclo-

Table 2 Summary statistics for the perceived predation risk and density manipulations in enclosures and corresponding control plots. Means and standard deviations are followed by the sample sizes (number of plots) in parentheses. There were 12 low-density and 12 high-density enclosures, each of which was observed at no, low (risk not manipulated), and high risk levels (3 sets of observations on each of 12 low-density and 12 high-density enclosures); the corresponding 2 m^2 control plots were never subject to high risk (1 set of observations on each of 12 control plots and 2 sets of observations on the 6 central control plots). Values from the low- and high-density enclosures are averaged for each risk-level column (1 set of observations on the 24 high- plus low-density enclosures for each risk level)

Variable	No risk	Low risk	High risk	Control	Low density (=18 males)	High density (>18 males)
Birds/h high risk	–	–	24.98±7.53 (24)	–	25.56±7.32 (12)	24.40±8.02 (12)
Birds/h low risk	–	2.09±1.59 (24)	–	2.14±1.62 (12)	2.20±1.58 (12)	1.98±1.66 (12)
Birds/h no risk	0.03±0.06(24)	–	–	0.03±0.07 (12)	0.04±0.08 (12)	0.02±0.05 (12)
Female density	20.46±12.71 (24)	19.58±10.30 (24)	21.29±13.59 (24)	23.21±9.85 (24)	11.01±4.48 (36)	29.88±9.76 (36)
Male density	21.54±14.48 (24)	24.63±13.68 (24)	19.21±12.44 (24)	19.85±9.24 (24)	10.22±3.81 (36)	33.36±9.09 (36)
No. searching females	1.23±1.51 (24)	1.67±1.86 (24)	0.33±0.62 (24)	2.79±2.49 (24)	0.31±0.89 (36)	1.85±1.63 (36)
No. searching males	0.81±0.91 (24)	0.75±0.85 (24)	0.23±0.33 (24)	1.06±0.98 (24)	0.58±0.81 (36)	0.61±0.76 (36)
Searching females per capita	0.06±0.05 (24)	0.07±0.06 (24)	0.02±0.03 (24)	0.10±0.06 (24)	0.02±0.05 (36)	0.07±0.05 (36)
Searching males per capita	0.19±0.18 (24)	0.14±0.16 (24)	0.09±0.12 (24)	0.21±0.17 (24)	0.18±0.19 (36)	0.10±0.10 (36)

Table 3 Analyses of covariance showing the effects of plot, biweekly tidal amplitude cycle, and day of the tidal amplitude cycle on the variables: female density, male density, searching females, and searching males

Source	Dependent variables											
	Female density			Male density			Searching females per capita			Searching males per capita		
	df	F	P	df	F	P	df	F	P	df	F	P
Plot	11	1.25	0.2788	11	0.40	0.9497	11	1.35	0.2220	11	1.44	0.1829
Tidal cycle	3	0.07	0.9782	3	0.91	0.4422	3	0.38	0.7672	3	1.91	0.1386
Day of tidal cycle	1	0.01	0.9473	1	0.13	0.7163	1	2.46	0.1223	1	0.83	0.3652
Error	56			56			56			56		

Table 4 Logistic regression and analyses of covariance showing the effects of male density, risk, and plot on the searching variables: searching sex, searching females per capita, and searching males per capita

Source	Dependent variables								
	Searching sex			Searching females per capita			Searching males per capita		
	df	χ^2	P	df	F	P	df	F	P
Plot	11	17.29	0.0995	11	1.53	0.1456	11	1.52	0.1500
Risk	2	0.45	0.7976	2	6.79	0.0023	2	3.86	0.0268
Male density	1	23.44	<0.0001	1	28.52	<0.0001	1	9.61	0.0030
Error	61			55			55		

sures, female searching accounted for 75.3±0.49% (n=32, no crabs searched on 4 occasions) of all the searching.

Changes in both female and male search behavior accounted for the increased likelihood that females did the searching at higher male densities. Per capita, searching females increased while searching males decreased with increasing male density (Table 4, Fig. 2). It was rare for any females to search in low-density enclosures, but about 1 out of 12 females searched in high-density ones, throughout a range of high male densities. In contrast, about 1 in 15 males searched in low-density plots, whereas about 1 in 42 males searched for mates in high-density plots.

Though the sexes responded differently to density, they reacted similarly to perceived predation risk. Both searching females per capita and searching males per capita decreased as risk increased (Table 4, Fig. 3). Females searched less per capita when risk was high than when it was low or near zero (Fisher's PLSD post-hocs: no vs low P>>0.10, no vs high and low vs high P≤0.01), and males searched much less per capita when risk was high than when it was close to zero (no vs low P>0.10, no vs high P<0.05, low vs high P>0.10). Male and female searching per capita both depended on male density and risk. However, risk did not affect which sex searched more because both sexes similarly reduced their searching at high levels of risk.
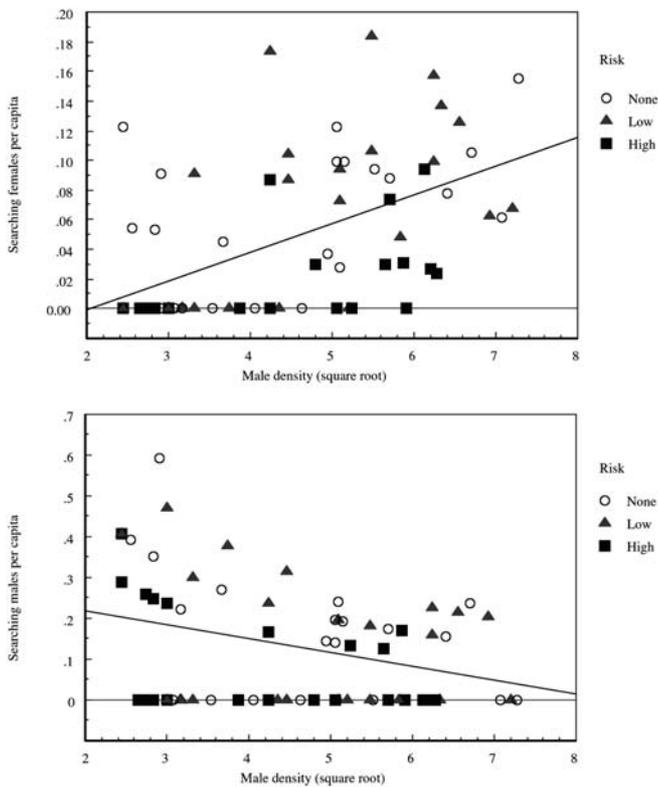
Fig. 2 Plots of searching females per capita (*upper plot*) and searching males per capita (*lower plot*) versus male density (square root) in enclosures. Each risk treatment [no, low (natural), and high risk] has its own *symbol*, but data are pooled to determine the overall regression line. The regression line equations are: searching females per capita=–0.04+0.02*male density, r^2=0.29; searching males per capita=0.29–0.03*male density, r^2=0.10

Fig. 3 Bar charts showing the mean and standard deviation of searching females per capita (*upper plot*) and searching males per capita (*lower plot*) at different male density and risk levels in enclosures. See Table 4 for relevant statistics

No manipulations – observational plots

Females entering observational plots

There were 2.5 times more males in the high-density observational plots than the low-density ones. More searching females entered high-density observational plots than entered the low-density plots (Fig. 4), and this behavior was independent of predator rate (multiple regression: n=24; male density β=0.61, t=3.48, P=0.0022; predator rate, P=0.5415).

Females that leave observational plots

More females per capita left their burrows and sought new burrows when predator rates were naturally low; neither male density nor male-female fights per capita affected the departure of females who sought new burrows (Table 5). In contrast, more mate-searching females per capita left their burrows when they lived in plots that had high male density, but females did not leave at higher rates to mate search when predator rate was low or male-female fights per capita were high. Adding an extra
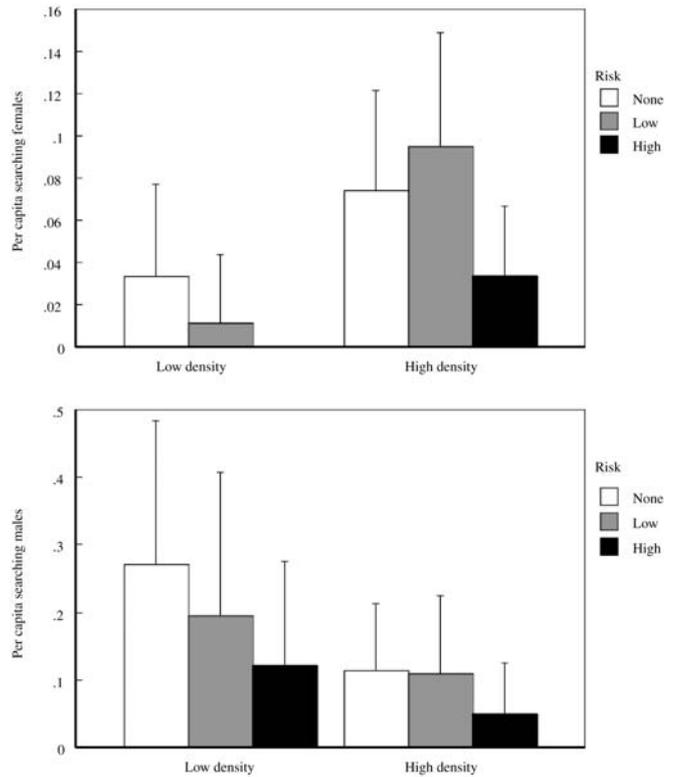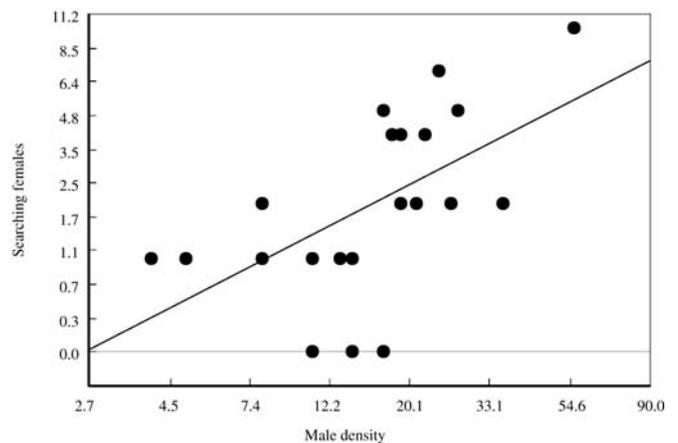
Fig. 4 Plot of searching females versus male density in observational plots. Each low-density plot was adjacent to a high-density plot. Searching females=–0.59+0.61 male density, r^2=0.36. See text for further statistics

independent variable, searching males, to the above model showed reduced male searching, which occurs at high density, was not the trigger for females to leave their burrows to mate search (Table 5). Each of the above results was qualitatively the same when female mate searching and burrow seeking were examined

Table 5 Logistic regression analyses showing the effects of male density, predator rate, and male-female fights on female leaving rate for non-receptive burrow-seeking females and receptive mate-searching females in observational plots. The final column also incorporates searching males in the model and so has four independent variables ($n=24$ in all 3 analyses)

Source	Dependent variables					
	Females per capita that left their burrows then sought new burrows		Females per capita that left their burrows then mate-searched (3×variables)		Females per capita that left their burrows then mate-searched (4×variables)	
	χ^2	P	χ^2	P	χ^2	P
Male density	1.26	0.2608	5.52	0.0188	5.29	0.0214
Male-female fights per capita	0.27	0.6060	2.33	0.1266	2.37	0.1238
Predator rate	4.82	0.0282	0.29	0.5877	0.12	0.7243
Searching males					0.09	0.7617

overall instead of per capita (ordinal, divided into 0, 1, ≥2 females left).

Male-female fights per capita did not increase with increasing density (linear regression: $n=24$, $r^2<0.01$, $t=0.14$, $P=0.8864$).

Male searching in observational plots

Male searching was rare in plots visited by searching females, but male searching level per capita was not affected by inter-male aggression or predator rate (logistic regression: $n=24$; searching females $\chi^2=3.42$, $P=0.0644$; male density $\chi^2=2.81$, $P=0.0939$; predator rate $\chi^2=2.28$, $P=0.1311$; male fights per capita $\chi^2=0.004$, $P=0.9475$). Substituting the number of waving males for male density reveals that the number of males waving to attract females affects male searching level per capita even more strongly than does the number of searching females ($n=24$; searching females $\chi^2=5.79$, $P=0.0161$; waving males $\chi^2=6.68$, $P=0.0097$; predator rate $\chi^2=2.95$, $P=0.0860$; male fights per capita $\chi^2=0.13$, $P=0.7198$).

Per capita, male fighting increased only slightly as male density increased (linear regression: $n=24$, $r^2=0.08$, $t=1.35$, $P=0.1920$).

Discussion

This study examined the effects of natural and experimentally manipulated levels of density and perceived predation risk on mate searching in *U. beebei*. Both sexes search in this species, but the level of female and male searching depends on the ecological and social context. Female searching increased and male searching decreased with increasing crab density. Both sexes reduced searching when the perceived predation risk was manipulated to be very high but the ratio of male to female searching did not change. Females may search more often at high densities because as density increases, search costs decrease, the benefits of searching increase, or the costs of not searching increase.

Three lines of evidence suggest that female *U. beebei*'s mate-searching costs decrease with increasing density. Searching females were more likely to enter high-density observational plots than low-density plots adjacent to them. By moving directly to and searching in a high-density area, females may reduce their travel or search time and thus lower their energetic costs and predation risk (Real 1990). An increase in density may decrease the predation risk of searching females in another way as well. Mate-searching females escape predators by entering burrows along their search path (personal observation). An aggregation of closely spaced burrows affords more nearby burrows into which a female can retreat if a predator appears. At lower density, females would have to travel farther to reach a burrow and escape predation, and the nearest burrow might be too far away to see (Zeil and Layne 2003). If predation risk is extremely high, however, even high burrow density may fail to allow a female to leave her burrow and start mate searching. Comparisons of mate-searching and burrow-seeking females that have left their own burrows also suggest that mate searching may be relatively less costly than burrow seeking. We found that burrow-seeking females, who typically are denied even temporary access to male burrows, only left their own burrows on days in which predators were very rare locally. In contrast, mate-searching females initiated searching even on days with locally moderate and high natural levels of predator visits. Therefore, without access to a burrow, the cost of traveling is probably high, but the risk of predation for female mate searching, especially in a high-density area, is probably low throughout natural levels of predation. This is further supported by our experimental enclosure results that show females did not search less when perceived predation risk increased from no predation to natural levels of predation risk. Enclosed females only decreased their searching when predation risk was manipulated to be very high.

Both males and females reduced their searching effort in plots to which we attracted many grackles, regardless of the density of crabs in those plots. The extremely high perceived risk may have confined crabs to their burrows and decreased searching. Because both sexes decreased their searching similarly at high risk, predation risk did not affect which sex searched. Koga et al. (1998) found

that high levels of risk reduced female searching relative to surface copulations (a measure of male searching), though both female searching and surface copulations decreased with increasing perceived risk. We propose three reasons for why our results differ from those reported in Koga et al. (1998). First, female searching at no and low predation risk was higher in the Koga et al. study (1998) than in the current study because we used enclosures that prevent searching females from entering a plot. Therefore, the earlier study found a greater reduction in searching females when predation increased than ours did. Our enclosure data indicate whether or not females will start mate searching given local density and predation conditions. Second, because the studies were investigating searching for different reasons, they used slightly different measures of relative searching by gender and of male searching. The earlier work measured the ratio of sampling females to surface copulations (requires both sexes search in the plot) while the present study examined which sex searched (accounts for searching when only one sex searches). Moreover, the earlier work measured surface copulations while the present study measured all male searching, surface copulations plus searches in which males approach and start to court females but do not succeed in mating. If the difference in definition of searching males is responsible for the greater reduction in male searching found in the present study, it implies that searching males are more successful at high levels of perceived risk. Third, Koga et al. (1998) did not consider the possible confounding effects of male density, which we found to be a strong determinant of female searching. If fewer crabs were active on the surface when perceived predation risk was high, the density-dependent effects that we identified could have caused a spurious predation effect in the Koga et al. (1998) study.

Female benefits from searching also might influence which sex searches for mates. Females that search instead of wait for a mate can gain access to a better incubation burrow, one they do not have to create and maintain, and perhaps a better mate. Females may benefit more from searching when density is high because they can more effectively and directly compare clustered males and resources. As mentioned above, searching females preferentially entered high-density observational plots. Females encountered 2.5 and 3.5 times more males in high-density observational plots and enclosures, respectively, compared to low-density ones. We did not monitor any aspect of mate quality or reproductive success in this study, so we cannot say whether searching in high-density areas increases female fitness. Nor did we identify whether females show more mate discrimination in high-density areas, as predicted (Crowley et al. 1991). Future experiments should document whether high male density causes females to increase their selectivity and change which males they accept as mates, as is found in pine engraver beetles (Reid and Stamps 1997), and whether higher densities enable females to better compare males. Females of another fiddler-crab species reduce their acceptance thresholds for males as remaining

breeding time dwindles (Backwell and Passmore 1996), and thresholds may change with density as well.

We did not find support for the third outlined hypothesis, which suggests females search when the cost of being a resident increases due to a density-related increase in male-female aggression. Per capita, aggression did not increase the likelihood that females left their burrows and aggression per capita did not increase with density. However, before eliminating aggression as a potential explanation for female searching, it must be shown that the number of fights an individual female has at her burrow is not related to whether she stays or leaves. We only examined the number of fights in an entire plot, not the number of fights experienced by each female.

Males may vary their searching levels in direct response to or independently of female behavior. We examined which factors were correlated with male searching to identify proximate cues of male searching and to determine whether male searching patterns were consistent with our prediction that males should not search if searching females approach. Males were less likely to leave their burrows to mate with neighboring females when searching females entered the plots, especially if many of their neighbors were waving. Male mate searching was not affected by density, unmanipulated predator rate, or aggression level. Male *U. beebei* that fail to attract a mate to their burrows, perhaps due to living in a low-density area, can increase their chances of paternity above zero by mate searching for receptive females. If females search, males do not and so can secure even higher paternity.

The reasons for female and male searching discussed above are not exhaustive. Density could have other effects on searching. Females may move directly to high-density areas because large groups of males provide a larger stimulus (see Parker 1983). Factors such as spatial separation of feeding and breeding sites may lead to female searching as well (Christy 1982, 1983).

Other studies similarly found that density plays a role in determining the searching sex. For example, in a *Pteroptyx* firefly species, males searched for mates when densities were very low; otherwise females always searched (Lloyd 1979). A comparative study of anurans showed the opposite trend: males searched at high densities, but females searched at low densities (Wells 1977). This difference, discussed in depth elsewhere (deRivera and Vehrencamp 2001), may be due to the fact that male distribution and breeding-resource distribution are not correlated in anurans but are correlated in fiddler crabs. Breeding-resource density is determined by male density in fiddler-crab species that mate in and incubate their eggs in male-constructed burrows (Crane 1975; Greenspan 1980; Christy 1982, 1983, 1987a; Backwell and Passmore 1996; deRivera 1999, 2003). Female fiddler crabs, like moths (Greenfield 1981), may search when search costs are low because breeding resources are clumped or at high density.

Further research is needed to determine what density-related cues cause females to initiate mate searching. We

can eliminate some potential cues: neither a lack of searching males nor a high level of fights per capita, per plot increased the rate that females left their burrows to find a mate.

In summary, females searched at high densities, and density influenced which sex searched more than did perceived predation risk. In addition, mate-searching females preferentially entered high-density areas. We suggest that more females search for mates at high male densities because many closely spaced male burrows reduce searching costs and facilitate comparison of males and, perhaps, breeding sites. Females may be less able to defend their own burrows against aggressive, competitive males, but our results did not support aggression as a factor that influenced female searching. At high density, males decreased their search rate in response to the increase in female searching and to the accompanying increase in competitors' waving. Males benefit from responding to increased female searching because attracting females to their burrows minimizes their search costs and maximizes their paternity assurance.

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