

Male versus female mate searching in fiddler crabs: a comparative analysis

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We present a comparative analysis of mate searching in fiddler crabs, genus *Uca*. Several ecological factors determine which sex will search for mates and how complex male signaling will be. Female searching is most tightly correlated with mating in male burrows. Female searching is associated with high burrow density, small body size, and large soil size. These factors explain variation in a female's need for male-defended incubation sites. Female searching also is correlated with short eyestalks. In species in which females search for mates, males use a more complex mate attraction signal than in species in which males search. *Key words:* courtship display, density, mate signaling, mobility game, operational sex ratio, searching sex, *Uca*. [*Behav Ecol* 12:182–191 (2001)]

Males and females of sexually reproducing species must find appropriate mates to pass on their genes. Searching for a mate takes time and energy and increases exposure to predators (Daly, 1978; Pomiankowski, 1987; Reynolds and Gross, 1990). These costs of searching bring the sexes into conflict over which one must search for a mate. A game theory model called the Mobility Game examines this conflict and predicts that either females search while males wait, or that males move while females wait (Hammerstein and Parker, 1987). This model reflects the tendency in nature for only one sex to search for mates in a population. Hammerstein and Parker (1987) suggest that males typically will be the searching sex because the greater gametic investment by females leaves males with excess time and energy to search for mates. Male searching is very common, but female searching occurs in most bird species, anuran amphibians, orthopterans, and some lepidopterans (Darwin, 1874; Ghiselin, 1974; Gibson and Langen, 1996; Gwynne, 1982; Henning, 1990; Howard, 1978; Nishida et al., 1996; Ryan, 1985; Simmons, 1988). Clearly gametic investment alone does not identify which sex will search. Ecological and life history factors also must affect the relative costs and benefits of searching for males and females.

Earlier comparative reviews of taxa with variable searching sex have linked the searching pattern to factors such as resource distribution, population density, and breeding season duration. For example, male Lepidoptera search for females when larval food is patchily or regularly dispersed and mate searching is costly, whereas females search for mates when the larval food is hyperdispersed and mate searching is not as energetically demanding (Greenfield, 1981). Male Orthoptera, typically long-distance callers that attract searching females, will search without signaling when they live in dense, sedentary colonies (Alexander, 1975). Alexander suggests that males search either because the patchy microhabitat structure makes it easy for females to locate resources and for males to locate females or because high population density causes in-

creased competition by interloper males (Alexander, 1975). Wells (1977) noted that male anurans usually search for mates when the breeding season is short, which produces a more equal operational sex ratio, and when density is high. Female anurans search when the breeding season is long, perhaps because mating is asynchronous and they benefit from choosing among many competing males. In all of these cases, females only search when either the costs of searching are low, and/or the benefits of searching are high. Males search when females do not.

In this article, we use a comparative approach to examine the ecological, life history, and behavioral correlates of searching strategies in fiddler crabs. The fiddler crab genus, *Uca*, is ideal for comparative studies of mate searching because males search in some species and females search in others and because crabs in this genus are sexually dimorphic, with females lacking the male's enlarged claw (Crane, 1975). There are approximately 70 species which are divided into nine subgenera (Crane, 1975). A recent phylogeny based on a 16S rDNA analysis of 27 species regroups species into three clades and suggests that the Ancestral clade (which contains the subgenera *Afruca* and *Uca*) is basal to both the Indo-West Pacific clade (*Amphiuca*, *Australuca*, some of *Celuca*, *Deltuca*, and *Thalassuca*) and the Derived American clade (*Boboruca*, most of *Celuca*, and *Minuca*) (Levinton et al., 1996; Sturmbauer et al., 1996). Fiddler crabs are semi-terrestrial, intertidal crabs that excavate individual burrows into the muddy or sandy substrate. Females mate, brood the eggs in a burrow or otherwise carry them for several weeks, then release the eggs as larvae into a nocturnal ebb tide. Fiddler crab reproductive biology, including searching sex and mate choice, is therefore likely to be influenced by factors such as tide cycle, the part of the intertidal zone occupied, substrate type, burrow density and quality, clutch size, and female synchrony (Salmon and Zucker, 1988). Information on most of these variables and descriptions of display, searching, and mating behaviors have been reported by the many researchers drawn to the conspicuous claw-waving of male fiddler crabs. Building on the reviews of Crane (1975) and Salmon and Zucker (1988), we extracted these ecological and behavioral variables from the literature and looked specifically for associations with searching sex using both species- and phylogenetic-based analyses.

Based on the principles of the mobility game and the findings from the comparative studies on other taxa, we predicted

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that factors increasing operational sex ratio, such as large clutch size and low female breeding synchrony, should be associated with male searching. Substrate and burrow characteristics were expected to affect the benefits females might obtain from breeding and brooding site selection. Population density could affect searching sex in several ways, so it is difficult to make a specific prediction. High density could reduce the costs of searching, which would favor female searching and inspection of males; alternatively high density could increase the competition among males, which would favor interference scrambles for receptive females. Our analyses suggest that density and soil size affect which sex searches, and that searching sex, in turn, affects claw-waving display complexity.

METHODS

Variables

We conducted a thorough search of the fiddler crab literature and abstracted physical and biological variables. We gathered information on intertidal zone, salinity, soil size, eyestalk length, carapace width, clutch size, burrow density, mating location, searching sex, display lightening (a male's ability to move pigments), and wave form (see Figure 1 and Table 1). We organized many of these into discrete categories because different researchers reported a range of values for the same species, used different methods to collect the data, or only reported non-numeric information about the variable. The small sample sizes required us to lump nominal variables into only two categories. Each of the factors is described next.

We divided the intertidal zone into low- to mid-tidal and high- to supra-tidal areas. Each species was assigned to the intertidal area that contains most of the burrows for that species. We also used Salinity as a habitat variable. Crabs that live in fresh, brackish, or euryhaline—but primarily fresh to brackish—water were lumped into a low salinity category, while crabs that live in estuaries or saltier water were categorized as high salinity species. We categorized Soil size as fine, for crabs that live in mud to muddy sand, and large, for crabs that, at least in some instances, live in sand or larger grained soils.

Eyestalk length was divided into short to medium stalks or long stalks. Shorter eyestalks are separated by a larger distance relative to body width, a larger frontal width, than are longer eyestalks (Crane, 1975). We used the Carapace width (in mm) of the largest measured male of each species as a general indicator of body size.

Clutch size is the number of eggs in a clutch of an average-sized female. We excluded *U. subcylindrica* from clutch size analyses because this species has atypical egg development and egg volume (Rabalais and Cameron, 1983; Thurman, 1985). In other species egg diameter averages 0.25 ± 0.02 mm (mean \pm sd) and egg size is not correlated with female size (Thurman, 1985).

Burrow density is a common measure of population density for fiddler crabs. We used the highest reported number of burrows per square m. The Mating location is the place where the majority of matings occur. We separated mating location into matings that occur on the surface (surface matings) and matings that occur inside male burrows (burrow matings). We categorized Searching sex into male, for species in which males search in over half to all of the cases, or female, for species, including the mixed searcher *U. beebei*, in which females primarily or always search. Species exhibiting low levels of searching by one sex have been coded as both sexes searching as well as being assigned a primary searching sex.

Display lightening describes the males' tendency to move pigments and thus partially or fully whiten their claws, cara-

paces, or both while they wave for mates. We noted display lightening as present or absent. We classified Wave form of male crabs as either simple or complex. Simple waves include vertical waves and semi-unflexed waves. In vertical waves the male slightly elevates his flexed major cheliped then returns it to resting position; in semi-unflexed waves the male lifts a partially opened claw then returns it to resting. The complex waves are lateral-straight or lateral-circular. Lateral-straight waves entail a complete opening then closing of the cheliped in addition to vertical lift and return. When crabs use lateral-straight waves they appear to be beckoning. In lateral-circular waves the crab holds his claw at a different height when opening the wave than when closing and thus the tip of the claw moves in circles. When a crab species uses both simple and complex displays, we categorized it as a complex waver.

Analysis

We first examined the associations between searching sex and the other morphological, ecological, and behavioral variables using each species as an individual data point (species analyses) using univariate tests. We then used two methods, multiple regression and analyses in a phylogenetic context, to tease apart causation from correlation.

For univariate species analyses, we used Fisher's exact tests when the variables were categorical, and logistic regressions when the independent variable was continuous. We log- and power-transformed the continuous variables to approximate normal distributions. For some of the variables, data were available on species not included in Figure 1 and Tables 1–3. The tests reported in the article were executed using only the species in these tables, but the qualitative results of these tests never differed from ones run for all species with available data.

We conducted an informal path analysis to examine the relationship between the various factors. We standardized the variables, even the dichotomous ones, so that each had a mean of 0 and a variance of 1. Then, using data on each species, we conducted a series of multiple regressions. We started with wave form as the dependent variable, and the remaining variables as independent variables. We removed all variables with slopes close to zero. We then conducted similar backwards stepwise regressions using all potential independent variables except for ones that had already been included as dependent variables in earlier levels. When the model was complete, we were able to construct a flow chart showing the relationships between the variables. Partial regression coefficients were used to identify the strength of the correlations and to verify the model as a whole. We multiplied the correlation values for all of the links in each path and compared this to the observed correlation between the first and last variables in that path (Sokal and Rohlf, 1995). Finally, we ran a univariate phylogenetic test, using the methods detailed below, for each path.

We looked for correlations between searching sex and the other variables using a 16S rDNA phylogeny of 27 of the fiddler crab species (Levinton et al., 1996; Sturmbauer et al., 1996). There are several soft polytomies in the published tree, so we obtained the sequence data from the authors and then used neighbor joining in PAUP to generate the most likely trees. We analyzed the six most likely trees in MacClade (Maddison and Maddison, 1992) and in CAIC (Comparative Analysis by Independent Contrasts, Purvis and Rambaut, 1995). We report results from both species and phylogenetic analyses because each type of analysis provides valuable information.

We used MacClade's concentrated-changes test to investigate associations between the categorical variables and searching sex. This test is dependent on parsimony reconstruction

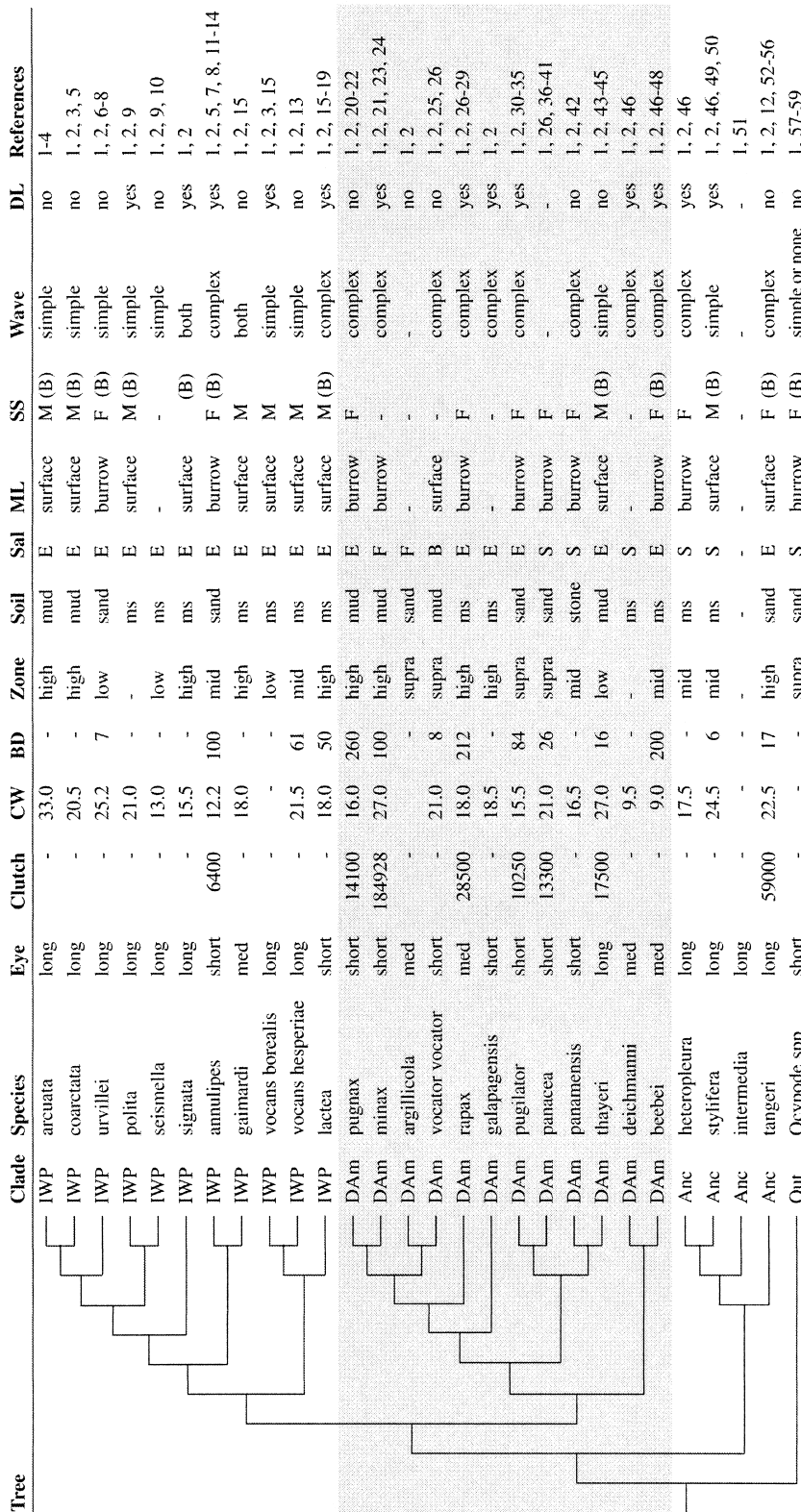


Figure 1
 Current *Uza* phylogeny and the states of the morphological, ecological, and behavioral variables for each species. Tree = one of the six most likely trees that was generated in PAUP from the Sturmbauer et al. sequences; eye = eyestalk length; clutch = number of eggs in clutch; CW = carapace width in mm for large males; BD = burrow density; zone = intertidal zone inhabited; soil = soil size: ms = mud-sand; sal = salinity; B = brackish, E = estuarine, F = fresh, S = saline; ML = mating location; SS = searching sex; M = males search, F = females search, (B) = both sexes search and the sex that searches most of the time is noted first; wave = wave form; DL = display lightening. For References, see Table 1.

of ancestral states. The concentrated-changes test examines whether the number of gains and losses observed in the dependent variable varies significantly between areas of the tree where the independent variable is assigned one or the other character state. For example, to determine if there is a significant association between searching sex and intertidal zone, the test counts the number of changes to female search and the changes to male search that occur in areas of the tree reconstructed to be in the lower tidal zones, and compares these to the number of changes in the whole tree. We examined the number of changes in searching sex on branches assigned the character states high intertidal zone, high salinity, large soil size, long eyestalks, and burrow mating. In addition, we evaluated the changes in wave form and in display lightening that occurred on female-search branches and compared these to changes that occurred on all branches.

When branches or ancestral states were equivocal, we performed the concentrated-changes test twice. First, we looked at the number of changes that occurred on branches that were coded for the state in question. Then we looked at the number of changes that occurred on the above branches and on equivocal ones. The six trees with their different resolutions to equivocal branches yielded either six or 12 different concentrated-changes tests for each pair of factors. We report the number of tests performed for each pair of factors and the average p values from these tests for each pair of factors.

We used CAIC to analyze the associations between searching sex and each of the continuous variables, carapace width, burrow density, and clutch size. We assumed equal branch lengths (i.e., a model of punctuated evolution). Though CAIC does not require a fully resolved tree, fewer soft polytomies lead to more contrasts, so we used the six most likely trees in this program as well. This yielded six sets of contrasts. We analyzed the contrasts generated in CAIC with one-sample t tests to test for deviations from a mean contrast value of zero (Purvis and Rambaut, 1995).

RESULTS

Typically both sexes searched in the Ancestral clade, males searched in the Indo-West Pacific and females searched in the Derived American clade (Figure 1 and Table 1, summarized in Table 2). However, several Indo-West Pacific and Derived American species showed the less typical search pattern for their clades. Both sexes searched at some time in nine of the 14 Indo-West Pacific species in which searching sex was documented; two of these species primarily had searching females. Males searched some to most of the time in three of the 15 Derived American species.

The data in Table 2 are re-arranged in Table 3 to show how the variation in searching sex can be partly explained by several of the physical and biological variables documented in this study. Statistical tests are presented in Table 4. Females tended to search when burrow density was high, carapace width was small, eyestalks were short, and mating occurred in male burrows. With few exceptions, either males used complex waves, females searched, and crabs mated in male burrows, or males used simple waves, searched for mates and mated on the surface. The relationships between the variables are diagrammed in a flow chart that is supported by multiple regression and by a series of univariate phylogenetic analyses (Figure 2). This figure shows all the strong correlations between variables that have support from both species and phylogenetic analyses.

Burrow densities varied substantially between those species with searching males and those with searching females (Figure 1 and Tables 1 and 3). Increased burrow density and decreased carapace width were correlated with female searching

in species analyses but not in phylogenetic ones (Table 4). They were important predictors of searching sex because of their indirect effects on searching: burrow density affects mating location, and smaller body width was correlated with higher burrow density.

In the species analyses, eyestalk length was correlated with searching. The Indo-West Pacific crabs primarily grow long eyestalks and the Derived American species mostly grow shorter eyestalks, so the phylogenetic analysis was not significant. However, several species in each clade posed exceptions to this rule and these same uncharacteristic species showed the atypical searching pattern (Figure 1 and Table 1). For example, in the Indo-West Pacific species *U. annulipes*, eyestalks were short and females searched more than males, and in the Derived American *U. thayeri*, eyestalks were long and males searched more often than females.

Fiddler crabs live in soils ranging from clay to stones, but most species inhabit mud or sand (Crane, 1941, 1975). Any species may live in a range of soil types, but soil size is an important factor controlling the distribution of fiddler crab species (Chakraborty and Choudhury, 1992). There was a trend toward female searching in larger soils and male searching in finer-grained soils, and this was especially evident in species with the atypical searching sex for each clade (Figure 1 and Tables 1 and 4).

The supra-tidal zone has only been invaded by female-searching species of the Derived American clade. However, intertidal zone was not correlated with searching sex (Table 4), but it was correlated with wave form (Figure 2). Display lightening also was not correlated with searching sex but was weakly correlated with wave form.

Clutch size increased with increasing female carapace width within a species (deRivera, 1999; Goshima et al., 1996; Salmon, 1984, 1987; Thurman, 1985) and with increasing female carapace volume across species (regression: $r^2 = .48$, $n = 17$, $t = 3.70$, $p = .002$). The ratio of clutch size to female volume showed a slight, non-significant negative correlation with body size ($r = -.33$, $p = .20$). Clutch size was not correlated with searching sex or with the other variables (Table 4 and Figure 1). Likewise, salinity was not correlated with either searching sex or other variables.

In summary, we found that female searching was most strongly correlated with mating in male burrows and with complex wave form. Female searching also correlated with high population density, small carapace width, short eyestalks, and living in larger-grained soils.

DISCUSSION

We identified a number of variables that were significantly correlated with which sex searches for mates in fiddler crabs: mating location, soil size, burrow density, carapace width, wave form, and eyestalk length. We used informal path analysis (Sokal and Rohlf, 1995) to construct a plausible diagram of the causative relationships among these variables (Figure 2).

Mating location was a nearly perfect predictor of searching sex. When males searched, the crabs mated on the surface and females maintained their own burrows. When female crabs searched, they left their own burrows and mated and incubated in male burrows. Both soil size and burrow density were correlated with mating location, and therefore were indirect predictors of searching sex. Large soil size was associated with mating and incubating in male burrows. Even within a species, mating males burrow in larger-grained soils than non-mating males and females (deRivera, 1999). The functional explanation for this association may be that larger-grained soils transmit more oxygen than finer-grained soils, and oxygen is needed for successful subsurface egg develop-

Table 1
Data for key factors for all *Uca* species that are not in the partial phylogeny but that have documented search form or burrow density

Clade	Species	Eye	Clutch	CW	BD	Zone
IWP	<i>acuta</i>	long	—	16.0	17	—
IWP	<i>dussumieri</i>	long	—	29.8	17	mid
IWP	<i>rosea</i>	long	—	20.5	31	high
IWP	<i>tetragonon</i>	long	7192	21.0	25	low
IWP	<i>triangularis</i>	medium	3990	13.0	21	high
IWP	<i>vocans vocans</i>	long	—	23.0	12	high
IWP	<i>v. vomeris</i>	long	8119	18.0	—	mid
DAm	<i>burgersi</i>	short	1782	10.4	—	supra
DAm	<i>crenulata</i>	short	3477	13.2	264	high
DAm	<i>latimanus</i>	short	—	13.4	—	—
DAm	<i>longisignalis</i>	short	20000	17.4	182	low
DAm	<i>musica terpsichores</i>	medium	—	7.0	—	mid
DAm	<i>saltitanta</i>	medium	—	7.0	—	—
DAm	<i>speciosa</i>	short	—	11.5	—	—
DAm	<i>spincarpa</i>	short	9000	15.5	47	supra
DAm	<i>stenodactylus</i>	medium	—	13.0	—	high
DAm	<i>subcylindrica</i>	short	627	16.0	25	supra
DAm	<i>virens</i>	short	—	17.5	34	supra
Anc	<i>maracoani</i>	long	—	32.0	—	low

Numbering is continued from Figure 1. See Figure 1 legend for column headings. References for Table 1 and Figure 1: 1. Sturmbauer et al., 1996. 2. Crane, 1975. 3. Huang et al., 1989. 4. Murai, 1992. 5. Pearse, 1912. 6. Takeda and Murai, 1993. 7. Frith and Brunenmeister, 1980. 8. Backwell PRY, personal communication. 9. von Hagen, 1993. 10. Salmon, 1984. 11. Altevogt, 1955. 12. Feest, 1969. 13. Icely and Jones, 1978. 14. Backwell and Passmore, 1996. 15. Jones and Morton, 1994. 16. Yamaguchi, 1971. 17. Murai et al., 1987. 18. Goshima and Murai, 1988. 19. Severinghaus and Lin, 1990. 20. Aspey, 1978. 21. Montague, 1980. 22. Greenspan, 1982. 23. Gray, 1942. 24. Salmon, 1965. 25. von Hagen, 1970. 26. Thurman, 1984. 27. Salmon, 1967. 28. Greenspan, 1980. 29. Genoni, 1991. 30. Connell, 1963. 31. Christy, 1978. 32. Hyatt and Salmon, 1978. 33. Christy, 1982. 34. Christy, 1983. 35. Salmon and Hyatt, 1983. 36. Novak and Salmon, 1974. 37. Powers, 1975. 38. Barnwell and Thurman, 1984. 39. Thurman, 1987. 40. Caravello and Cameron, 1991. 41. Thurman, 1994. 42. Vehrencamp SLV, personal observation. 43. Warner, 1969. 44. von Hagen, 1973. 45. Salmon, 1987. 46. Crane, 1941. 47. Christy, 1987. 48. Christy, 1988. 49. Altevogt, 1969. 50. deRivera CED, unpublished data. 51. Von Prahl and Toro, 1986. 52. Altevogt, 1959. 53. von Hagen, 1987. 54. Wolfrath, 1992. 55. Klaassen and Ens, 1993. 56. Wolfrath, 1993. 57. Hughes, 1973. 58. Powers, 1977. 59. Schober and Christy, 1993. 60. Chakraborty and Choudhury, 1992. 61. Murai et al., 1996. 62. Murai et al., 1995. 63. Goshima et al., 1996. 64. Murai et al., 1983. 65. Nakasone et al., 1983. 66. Christy and Salmon, 1984. 67. Gibbs, 1974. 68. Zucker, 1981. 69. Salmon and Atsides, 1968. 70. Thurman, 1982. 71. Mouton and Felder, 1995. 72. Mouton and Felder, 1996. 73. Zucker, 1974. 74. Zucker, 1984. 75. Christy et al., 1996. 76. Salmon et al., 1979. 77. Müller, 1986. 78. Rabalais and Camaron, 1983. 79. Thurman, 1985. 80. Salmon and Kettler, 1987. 81. Crane, 1958.

ment in crabs (Chakraborty and Choudhury, 1992; Murugan and Vivek Raja, 1993; Whiting and Moshiri, 1974). Females incubating in male burrows remain buried under ground for most of the incubation period, whereas females of surface-mating species carry their eggs while continuing to forage. The advantages of enclosure in a deep burrow defended by the male may therefore only be feasible in oxygen-rich soils.

High burrow density was strongly associated with female searching and mating in male burrows. Furthermore, in a study of a bisexual searcher, *U. beebei*, experimental manipulations of density affected which sex searched for mates, with females searching at high densities (deRivera, 1999). High density could favor burrow mating and female searching for several reasons. High density decreases the cost of searching, allowing females to examine more males and exercise greater mate choice. When females search, they selectively choose longer, deeper male burrows for mating (Backwell and Passmore, 1996; deRivera, 1999). In addition, high density may deter the small-clawed females from maintaining their own burrows for incubation because of the increased risk of aggression and eviction (Christy, 1988; deRivera, 1999; Murai et al., 1987, 1996; Zucker, 1977). We also found that density was correlated with carapace width, with smaller crab species living at higher densities. The combined effects of small body size, high density, and coarse-grained soil appear to result in important benefits to females of inhabiting male burrows and searching for the best burrow sites.

Courtship display complexity, as measured by wave form, was correlated with searching sex, carapace width, and inter-

tidal zone. When females search, they exert strong selective pressure on male display traits, and displays become more elaborate. When males locate mates, male waving displays are less dramatic and mostly are used in territory defense. Low waving vigor is found in the Ancestral clade so this is probably not a derived trait, as was suggested by Crane (1957, 1975). Instead, it seems that males in some Indo-West Pacific species and in a few species from other clades use simple waves because they are not attracting searching females with these waves. Male signal complexity has been linked to searching sex in other animals (Greenfield, 1981; Wells, 1977) and, in general, the signaling sex is the non-searching, waiting sex (Bradbury and Vehrencamp, 1998). When females search, male signaling serves as a basis for females to choose mates as well as locate them; when males search, females usually will signal to advertise their receptive status (Christy, 1987; Gibson, 1996; Greenfield, 1981; Phelan and Baker, 1990; Thornhill, 1979). Which sex searches sets the stage for how males will compete for mates.

Even after correcting for the searching sex effect, however, there are small but significant effects of body size and intertidal zone on wave form. Large species tend to have simple waves. Male claws are large, often 1.5 times longer than the carapace width; larger species may avoid using complex waves to prevent expending the energy required to constantly extend such a large claw or because complex waves may cause large-clawed males standing on moist soils to lose their balance.

Fiddler crab species inhabiting the upper intertidal zones

Table 1, extended

Soil	Salinity	ML	SS*	Wave	DL	References
mud	estuarine	—	—	—	no	2, 15, 60
mud	estuarine	—	M	simple	no	2, 6, 15, 60
mud	estuarine	surface	(B)	simple	no	2, 61
pebbles	saline	surface	M (B)	simple	no	2, 6, 13, 62, 63
ms	brackish	surface	M	both	yes	2, 3, 12, 60
ms	estuarine	surface	M (B)	simple	yes	2, 6, 7, 64–65
sand	estuarine	surface	M (B)	simple	yes	2, 10, 66
sand	euryhaline	burrow	F	complex	no	2, 27, 67
ms	estuarine	burrow	F	complex	yes	2, 50
ms	fresh	burrow	F	complex	yes	2, 46, 68
sand	fresh	—	—	complex	yes	37, 69–72
sand	saline	burrow	F	complex	yes	2, 46, 50, 73–75
mud	saline	burrow	F	complex	yes	2, 46
mud	euryhaline	burrow	F	complex	yes	2, 38, 76
sand	euryhaline	—	—	complex	yes	2, 26, 39, 41, 71, 72, 76
ms	saline	burrow	F (B)	complex	yes	2, 46, 77
sand	fresh	—	—	—	—	2, 26, 78, 79
sand	euryhaline	—	—	complex	yes	37, 69, 80
mud	estuarine	burrow	F (B)	complex	no	2, 81

use complex waves, whereas low tidal-zone species are more likely to use simple waves. Perhaps, only the species that live higher in the intertidal zone have enough foraging time both to meet their basic energy demands and to wave in a more complex, more energetic manner.

We hypothesized that operational sex ratio should affect which sex searches. According to the mobility game, male searching should be associated with a more strongly male-biased operational sex ratio. Variation in operational sex ratio is caused by two primary parameters: female synchrony and relative gametic investment of the two sexes. When females

are synchronously receptive, the operational sex ratio approaches equality, whereas asynchrony results in a more male-biased operational sex ratio. An increase in female gametic investment relative to male investment results in a longer reproductive cycle length for females and therefore a more male-biased operational sex ratio.

In this study we measured two variables that potentially affect operational sex ratio. The tidal zone inhabited by a species affects female synchrony: species in the upper intertidal breed more synchronously than lower intertidal species (Morgan and Christy, 1995). We did not, however, find a strong

Table 2
Summary data of variables for each clade

Variable	Character state	Clade		
		Indo-West Pacific	Derived American	Ancestral
Continuous				
Burrow density		34.1 ± 28.7 (10)	112.2 ± 97.4 (13)	11.5 ± 7.8 (2)
Carapace width		25.2 ± 6.4 (18)	21.0 ± 7.8 (22)	35.6 ± 10.9 (4)
Clutch size (×10 ³)		6.7 ± 1.7 (5)	27.7 ± 52.8 (11)	59.0 (1)
Categorical				
Display lightening	No	10	6	2
	Yes	8	15	2
Eyestalk	Long	14	1	5
	Short	4	22	0
Intertidal zone	Lower	8	5	3
	Upper	7	14	1
Mating location	Surface	13	2	2
	Burrow	2	14	2
Salinity	Fresh	11	11	1
	Salty	7	12	3
Searching sex	Only males	5	0	0
	Mostly males	7	1	1
	Mostly females	2	2	2
	Only females	0	12	1
Soil size	Fine	13	13	3
	Large	4	10	1
Wave form	Simple	12	1	1
	Complex	5	19	3

Mean ± standard deviation followed by sample size in parentheses are reported for each continuous variable. Totals for the categorical variables may differ because of missing data.

Table 3
Summary data of variables for searching sex

Variable	Character state	Searching males	Searching females
Continuous			
Burrow density		26.0 ± 19.3 (8)	130.0 ± 105.0 (9)
Carapace width		26.9 ± 5.6 (14)	22.9 ± 10.6 (18)
Clutch size (×10 ³)		9.0 ± 5.1 (5)	17.2 ± 18.8 (8)
Categorical			
Clade	Indo-West Pacific	12	2
	Derived American	1	13
	Ancestral	1	3
Display lightening	No	7	6
	Yes	7	11
Eyestalk	Long	12	4
	Short	2	14
Intertidal zone	Lower	7	7
	Upper	6	8
Mating location	Surface	13	1
	Burrow	0	16
Salinity	Fresh	7	5
	Salty	7	13
Soil size	Fine	12	10
	Large	2	8
Wave form	Simple	11	1
	Complex	3	16

Mean ± standard deviation followed by sample size in parentheses are reported for each continuous variable. Totals for the categorical variables may differ because of missing data.

association between intertidal zone and searching sex. Female clutch size (relative to body size) is a good measure of gametic investment. Assuming that male investment in sperm is constant across species, a larger clutch size means a stronger skew in investment and a more strongly male-biased operational sex ratio. Clutch size clearly affects cycle length in fiddler crabs: females of large-clutch species reproduce at most every four to six weeks, whereas females of small-clutch species may reproduce every other week (Christy and Salmon, 1984, 1991). However, clutch size was not associated with searching sex. In fiddler crabs, clutch size and female synchrony are intercorrelated in a way that cancels out their influences, which may explain why we did not detect an effect of either of these variables. Smaller fiddler species tend to have relatively larger clutch sizes (increasing operational sex ratio) and to inhabit higher tidal zones (greater synchrony, decreasing operational

sex ratio). Since operational sex ratio is a result of the combined effects of relative cycle lengths and female synchrony, the overall operational sex ratio, which we could not extract from the literature, may not vary much among fiddler crab species.

Eyestalk length may not be as important as Salmon and Zucker (1988) had thought based on their comparison that was made before a molecular phylogeny was available. We found eyestalk length to be correlated with searching sex only in the species analysis. If eyestalk length does affect searching or wave form, the variable with which it is most highly correlated, it may be because of some mechanistic relationship between these variables. Eyestalk length affects vision: crabs with longer eyestalks can resolve objects in the vertical plane better and at farther distances than can crabs with shorter eyestalks (Zeil et al., 1986). Long eyestalks may be better for

Table 4
Summary of associations between searching sex and the other variables from the univariate species and phylogenetic analyses

Variable	Species analyses			State	Phylogenetic analyses			
	χ^2	<i>n</i>	<i>p</i>		Mean <i>t</i> (<i>n</i>)	Mean <i>p</i>	No. of trees <i>p</i> < .05	State
Burrow density	5.33	17	.02	high	1.65 (3)	.25	0/6	
Carapace width	3.27	32	.07	small	1.74 (5)	.16	0/6	
Clutch size	0.35	13	.55		— (1)	—	—	
Display lightening		31	.48			.23 ± .14	0/6	
Eyestalk length		32	.001	short		.24 ± .02	0/6	
Intertidal zone		28	>.99			.07 ± .04	6/12	
Mating location		30	<.0001	male burrow		.003 ± .001	12/12	male burrow
Salinity		32	.28			.44 ± .14	0/12	
Soil size		32	.12			.01 ± .001	12/12	large
Wave form		31	<.0001	complex		.01 ± .01	6/6	complex

State = character state correlated with female searching. The continuous variables (burrow density, carapace width, and clutch size) were analyzed with logistic regression and with CAIC, while the remaining, nominal variables were analyzed with Fisher's exact tests and with McClellan's concentrated changes test.

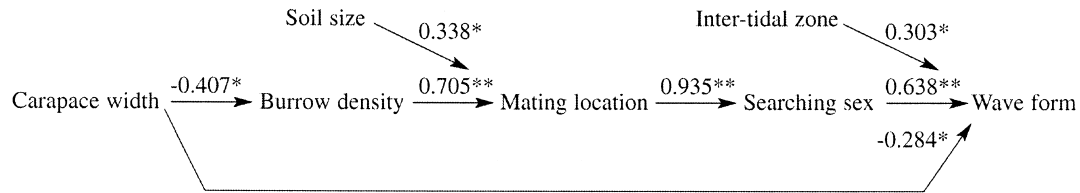


Figure 2

A model suggesting how key factors affect which sex of fiddler crab searches for a mate and which wave form males will use. Regression coefficients and p values are from multiple regressions. The regression coefficients are reported above the line connecting the variables. * $p < .05$, ** $p < .001$. All of these relationships are also statistically significant to the $p < .05$ level in univariate phylogenetic analyses.

low-density species with searching males that have to detect females over longer distances, as opposed to the high-density species in which females inspect males at close range because they are examining burrow characteristics as well.

In summary, variables affecting operational sex ratio do not appear to determine which sex searches in fiddler crabs, as it does in anurans. Density, on the other hand, was associated with searching sex in fiddlers (female searching at high densities), but in the opposite direction to the pattern found in orthopterans and lepidopterans (male searching at high densities). A taxon's ecology and life history details are important determinants of the costs and benefits of searching for each sex. The burrowing habits and female egg-carrying parental strategy of fiddler crabs are clearly critical adaptations that affect male and female mating strategies. We found that high density and large soil size lead to mating in male burrows, and therefore to searching by females. However, it seems that across animals, males generally search unless the species' ecology requires that females search for male-controlled resources or females gain large benefits from selectively choosing mates while searching.

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