

# Density affects mating mode and large male mating advantage in a fiddler crab

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Received: 12 June 2009 / Accepted: 23 September 2010 / Published online: 8 October 2010  
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**Abstract** Fiddler crabs show two different mating modes: either females search and crabs mate underground in male burrows, or males search and crabs mate on the surface near female burrows. We explored the relationship between crab density, body size, the searching behavior of both sexes, and the occurrence of both mating modes in the fiddler crab *Uca uruguayensis*. We found that crabs change their mating mode depending on their size and crab density. Crabs mated mostly on the surface at low densities, and underground at high densities. The proportion of wandering receptive females but not courting males accounted for the variation in mating modes. This suggests that whether crabs mate underground (or on the surface) is determined by the presence (or absence) of searching females. We found that the change in the mating mode affected the level of assortative mating; males mating underground were bigger than those mating on the surface, suggesting active female choice. Given that fiddler crabs experience multiple reproductive cycles, they are prone to showing behavioral plasticity in their mating strategy whenever the payoffs of using different mating modes differ between reproductive events. Our results suggest that the incorporation of different levels of environmental

variability may be important in theoretical models aimed at improving our understanding of the evolution of alternative mating tactics and strategies.

**Keywords** *Uca uruguayensis* · Alternative mating strategies · Mating tactics · Behavioral plasticity

## Introduction

When sexual selection is strong and promotes high variance in reproductive success, alternative mating strategies are likely to arise (Shuster and Wade 2003). The underlying mechanisms through which behavioral and/or morphological variation is established within the population have been a matter of controversy. Several models have been proposed to explain the evolution of alternative mating strategies. Frequency-dependent selection models ascribe trait variability to the control of genetic polymorphism (Gross and Charnov 1980; Ryan et al. 1992; Gross 1996). Status-dependent or environmental threshold models propose that the variability is due to individual phenotypic plasticity (Hazel et al. 1990; Gross 1996), where traits are viewed as different tactics performed by a single genotype. The evolution of alternative mating strategies by frequency-dependent selection or by environmental threshold models may depend on how individuals perceive the environmental grain (Levins 1968). This perception is a function of the number of mating opportunities during the lifetime, the payoff of different mating tactics among different mating opportunities, and the predictability of such changes (Lively 1986; Hazel et al. 1990, 2004). Hence, species in which individuals experience multiple reproductive events during their lifetimes, and in which payoffs of different tactics differ in each reproductive event, are

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Communicated by Libby Marschall.

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expected to evolve phenotypic plasticity in behavior (Schlichting and Pigliucci 1998).

In most species, alternative mating tactics involve different behaviors, generally performed by individuals of the same sex. For example, males may or may not be aggressive (e.g., insects, Carroll 1993; pupfishes, Kodric-Brown 1996; squirrels, Koprowski 1993), guard females (e.g., insects, Thornhill and Alcock 1983; lizards, Zamudio and Sinervo 2000; wrasses, Alonzo and Warner 2000), or show differentiated phenotypes (e.g., hooknose and jacks in salmon species, Tanaka et al. 2009). However, in a small group of species, including fiddler crabs (genus *Uca*), alternative mating tactics seem to be associated with a change in the sex that searches for mates (deRivera 2003).

Fiddler crabs comprise a group of nearly 100 species (Rosenberg 2001), and engage in two general mating modes. In surface mating, males approach neighboring females, use tactical courtship signals, and mate on the surface beside the opening to the female's burrow. After mating, each crab returns to its burrow (e.g., Christy and Salmon 1984; von Hagen 1993). In underground mating, females leave their burrows, stop briefly at the burrows of several courting (visual and seismic signals) males, and finally stay in one male burrow. The chosen male and the female mate underground in the male's burrow (e.g. Greenspan 1982; Christy and Salmon 1984; Christy and Schober 1994) and stay together for 2–3 days (Christy 1978) until the female lays a clutch of eggs. The male then leaves the burrow and finds a new one or he continues to use the burrow shaft and digs a new terminal chamber (Christy 1982), sealing the female off in the original terminal chamber, where she stays to incubate her eggs. Most species use only one of these mating modes, but some species have been reported to use both (e.g., Yamaguchi 1971; Nakasone et al. 1983; Christy 1987; Murai et al. 1996). A comparative analysis among 27 fiddler crab species (deRivera and Vehrencamp 2001; deRivera 2003) suggests that high burrow density, small carapace size, and coarse soils are the major factors associated with female searching and, thus, underground mating in male burrows.

Who searches and who waits may depend on the relative fitness payoffs to be gained by using each mating mode in particular environmental and social conditions. In the context of environmental threshold models, conditional strategies are viewed as environmentally cued threshold traits (Hazel et al. 1990, 2004). Changing the searching sex suggests that males and females experience different searching costs and benefits across different environmental conditions (deRivera 2003). In this way, environmental cues promoting the change in the searching sex should be strongly linked to the searching costs and benefits.

In this study we explored the role of population density and body size as determinants of whether to mate

underground or on the surface in the fiddler crab *Uca uruguayensis*. We studied the relationship between the searching behavior of both sexes and the occurrence of both mating modes. We also evaluated the relationship between mating mode and the level of size-assortative mating to explore possible mate-choice consequences of using each mating mode. We studied body size because it may impose mechanical constraints on underground mating. A female must enter a male's burrow to mate with that male, and she cannot enter burrows that are too narrow. We studied the effect of crab density because it may influence the risks as well as the efficiency of searching (deRivera and Vehrencamp 2001; deRivera 2003; Koga et al. 1998). At low densities, burrows become widely spaced, which increases searching time and thus the probability of undergoing physiological stress or being eaten by a predator (Booksmythe et al. 2008).

## Methods

### Study site, species and natural densities

The study was conducted near the mouth of the San Clemente tidal creek (eastern Samborombón Bay, 36° 22' S, 56° 45' W, Argentina), an area affected by low amplitude (<1.4 m) semidiurnal tides. *U. uruguayensis*, a medium-sized fiddler crab (up to 16 mm carapace width; Crane 1975), occurs in the middle to upper intertidal flats near the fringe of an extensive *Spartina densiflora* marsh, and is active on the surface from September to April, showing lower activity during the rest of the year (personal observation). Fiddler crabs dig burrows that are used for underground mating, egg incubation by females, and as temporary refuges from predators and physiological stress. During the flood tide, crabs plug their burrows until the next ebb tide (de la Iglesia et al. 1994). The density of fiddler crabs is highly variable (Ribeiro et al. 2005); across an area of 2 km, crab density can range between 10 and 90 crabs m<sup>-2</sup>. Based on previous work (Ribeiro et al. 2005), we designated low-density areas as those that showed a mean density of 10–30 crabs m<sup>-2</sup>, and high-density areas as those with mean densities of between 70 and 90 crabs m<sup>-2</sup>.

### Population density and mating mode

We observed the behavior of crabs from November 2001 to March 2002, encompassing the entire reproductive season (Bogazzi et al. 2001). Like many estuarine organisms, fiddler crabs show semilunar cycles of reproductive activity (Skov et al. 2005). The fiddler crab *U. uruguayensis* concentrates its mating activity around days during which the low tide occurs between 9:30 and 16:30 (personal

observation). For this reason, we performed the observations during such days, thus avoiding possible confounding effects of nonreproductive behaviors.

Using binoculars (10 × 50), and at a distance of 5 m, we monitored the surface activity from 4 h before low tide (when crabs begin to emerge) up to 4 h after low tide (when crabs begin to close their burrows; Ribeiro et al. 2003). We used iron stakes to demarcate plots (3 m width and 2 m length) in which we counted the number of males feeding, the number of males courting females, the number of females owning a burrow, and those wandering. A wandering female was considered to be receptive when it approached only males, inspecting their burrows for some seconds. Receptive females generally show a standing upright posture (body clearly separated from soil and unflexed legs) and develop a characteristic green-colored carapace. Unreceptive females as well as exclusively feeding males adopt a more cryptic dark-gray color and flexed articulations. In addition, females that approached other females' burrows (sometimes aggressively) or were feeding a large amount of the time were not considered to be receptive, even if they were seen inspecting a male's burrow. Each plot was observed only once during the study. We observed each plot for 1 h before moving to another, randomly selected plot. We observed high- and low-density areas on the same days and for the same amount of time.

To quantify the relative occurrence of surface matings at both densities, we counted the number of surface matings detected within each plot during the monitoring. To quantify the relative occurrence of underground matings at both densities, we randomly sampled 1,000 burrows of each density and dug up those that were plugged. A mating pair was assumed when a male and a female were found in a plugged burrow (see Yamaguchi 1998). This was done during low tide to avoid the confounding effect of crabs closing their burrows due to the incoming tide (approximately 4 h after low tide).

We used a  $\chi^2$  test (Zar 1999) to evaluate whether the proportional occurrence of surface matings was similar between densities. Under the null hypothesis of no change in an individual's likelihood of surface mating with a change in population density, we would still expect that the actual number of surface matings occurring will increase with the total number of crabs observed in a sample, and thus should increase with population density. For this reason, using the number of crabs counted while monitoring the surface activity, the expected values for the  $\chi^2$  test were calculated based on the density differences between areas as follows:

$$SM_i = \frac{C_i \times SM_t}{CT},$$

where  $i$  denotes density,  $SM_i$  is the expected number of surface matings at density  $i$ ,  $SM_t$  is the total number of surface matings at both densities,  $C_i$  is the number of crabs counted at density  $i$ , and  $CT$  is the sum of the number of crabs at both densities.

We used a  $\chi^2$  test (Zar 1999) to evaluate whether the occurrence of underground matings was similar between densities. Given that we explored an equal number (1,000) of burrows, our sampling efforts were the same at both densities, and thus we did not need to correct the expected values as for surface matings.

#### Searching behavior and mating mode

We used the data from the previous section to evaluate whether male courtship and female searching activity were related to the occurrence of both mating modes.

Given that crabs concentrate their courtship and mating activity around the low tide (personal observation), we restricted the analysis to the information from 2 h before until 2 h after low tide. For each day and density, we calculated the mean proportion of wandering receptive females and the mean proportion of courting males. The number of surface and underground matings observed at each density were divided by the mean density of crabs active on the surface. By fitting linear regressions (Zar 1999) separately for both densities and for the pooled data, we evaluated the relationship between both the number of underground and surface matings per crab  $m^{-2}$ , and the proportions of courting males and wandering receptive females.

We used  $t$  tests (Zar 1999) to test for differences in the mean proportions of wandering receptive females and courting males between densities.

#### Experimental evidence that density affects mating mode

We conducted a field experiment to explore whether the relative occurrence of mating modes depends on crab density. The experiment lasted for 3 months (from 15 October 2005 to 15 January 2006), beginning 1 month before the crabs began their reproductive activity, and encompassed four reproductive cycles. The experiment was set up within an area naturally inhabited by a low density of fiddler crabs (mean of 10–30 crabs  $m^{-2}$ ). We increased the densities of such low-density areas up to values similar to those of high-density areas (mean of 70–90 crabs  $m^{-2}$ ) without modifying the sex ratio of the population. To stop crabs escaping from the treated areas, we constructed circular enclosures (2 m diameter) delimited by a plastic mesh that was 15 cm above the surface and

buried 25 cm deep. We found circular enclosures to be the best shape (personal observation) for preventing other coexisting crab species (e.g., *Neohelice granulata*) from making their burrows outside but against the mesh, decreasing the stability of the enclosures. To increase the density we captured crabs from a neighboring low-density area 10 m from the experiments. Once the densities had been increased, no more additions were needed, as the densities remained stable throughout the experiment (see “Results”). We opted for crab additions rather than crab removals to avoid disrupting the sediment structure. At high crab density, burrows are densely packed and digging would have caused the sediment to collapse.

The experiment had the following treatments, with six replicates each: (1) open areas: natural low-density areas with neither density increases nor fence delimitation, (2) high-density enclosures: fenced, naturally low-density areas to which crabs were added, and (3) low-density enclosures: fenced area with naturally low densities in which crabs were replaced with an equal number of crabs collected from the same area as those added in high-density enclosures. Crabs from low-density enclosures were extracted using a core (10 cm diameter, 20 cm depth) or by digging at one side of the burrow opening, which caused crabs to emerge. Sediment cores were relocated in the same place and the crab burrows were closed. Given that the distances between burrows were large (30–50 cm), this extraction procedure did not significantly disrupt the sediment structure. As in increased-density areas, new crabs were released and pursued to construct new burrows. This crab removal and replacement procedure was done to control for the effect of crab importation in high-density enclosures. The enclosures or areas were separated from each other by at least 5 m and were located at the same tidal height.

Using binoculars (10 × 50) at a distance of 5 m from the experimental areas, we performed hourly censuses of each enclosure from 3 h before low tide to 3 h after low tide. In each census we counted the occurrence of surface matings, the number of males, the number of feeding females, and the number of wandering receptive females (criteria described previously). The occurrence of surface matings was compared between treatments with the  $\chi^2$  test by calculating the expected values based on the density differences between treatments (as described previously).

We did not dig up plugged burrows in order to search for underground matings, because this would have disturbed crab behavior and sediment structure, making enclosures inoperative for subsequent observations. Instead, we studied the change in the proportion of wandering receptive females. The number of wandering receptive females was positively related to the occurrence of underground

matings but negatively related to the occurrence of surface matings (see “Results”). Thus, the relative occurrences of these mating modes may depend on the proportion of wandering receptive females. Therefore, we studied the change in the proportion of wandering receptive females between treatments. For each reproductive cycle and for each enclosure, we chose the maximum number of wandering receptive females and its associated number of foraging females. A generalized linear model (Lindsey 1997) with a binomial distribution and a logit link function was used to compare whether the proportion of wandering receptive females was higher in high-density enclosures than in low-density enclosures and open areas.

#### Size of crabs and mating mode

To assess for differences in the sizes of crabs from populations of different densities, we sampled 30 plots (0.5 × 0.5 m) each from high-density and low-density areas and measured the carapace widths (accuracy 0.01 mm) of all male and female crabs. After square-root transforming the carapace-width data to fit parametric assumptions, we used a two-way ANOVA (Zar 1999) to test for the effect of density and sex on carapace width. We also measured the carapace widths (accuracy 0.01 mm) of all males and females, from surface and underground matings, that could be collected during observations. After square-root transforming the data, we used two-way ANOVAs to test for the effects of mating mode and density on carapace width for each sex separately.

We calculated the correlation between the sizes of males and females within mating pairs to explore the degree of size-assortative mating in relation to the adopted mating mode. We calculated the Pearson coefficient of correlation (Zar 1999) between the male and female carapace width, but did not evaluate whether the coefficients differed from zero. As surface matings occur between neighboring crabs, the spatial clumping of individuals of similar size will promote matings between similar sized crabs, producing  $r$  values  $\neq 0$ . Since females must enter male burrows for underground matings to occur, females cannot mate with males who own burrows with opening diameters that are too narrow for the female to enter. Instead, we ran two different computer simulations of male–female matings to construct the appropriate null hypotheses of randomness following the restrictions imposed by the spatial distribution of neighboring crabs for surface matings (spatially restricted model) and the diameter of burrow openings for underground matings (burrow-restricted model). For both models, the population size distributions of males and females were estimated from the previously sampled plots. The minimum male mating size was set as the smallest male observed from mating pairs; the minimum female

mating size was set as the smallest female observed to be ovigerous (Bogazzi et al. 2001).

For the burrow-restricted model, the program generated pairs randomly, with the only restriction being that the opening of the male burrow was always equal to or bigger than that of the female. A linear regression (Zar 1999) was fitted between carapace width (accuracy 0.01 mm) and the diameter of the burrow opening (accuracy 0.05 mm) for both males ( $n = 324$ ) and females ( $n = 171$ ). The program performed the following steps: (1) randomly selected a female from the size–frequency distribution and used the regression between female carapace width and burrow opening diameter to predict its burrow diameter. This prediction was not necessarily the mean value estimated from the regression line but a value from the normal distribution around the expected mean value; (2) randomly selected a male from the size–frequency distribution and used the regression between male carapace width and burrow opening diameter to make a prediction of its burrow diameter (as for females); (3) designated the female from step 1 and the male from step 2 as a burrow mating pair when the predicted female's burrow was as wide as or narrower than that of the male; (4) repeated steps 1–3 to designate  $n$  mating pairs, where  $n$  was the sample size of correlations from the collected underground matings at each density, and; (5) calculated the correlation coefficient between male and female carapace width. After repeating steps 1–5 10,000 times, we determined whether the correlation values for field mating pairs were included within the 95% confidence limits of the simulated distributions under random mating.

In the spatially restricted model, the program simulated the clumping of crabs, obtaining each pair from the same sampling unit (of any of the 30 plots). The program performed the following steps: (1) randomly selected a plot; (2) randomly selected a female and a male from the same plot; (3) designated the female and male from step 2 as a surface mating pair; (4) repeated steps 1–3  $n$  times, where  $n$  was the sample size of the correlations from the collected surface matings at each density, and; (5) calculated the correlation coefficient between male and female carapace width. After repeating steps 1–5 10,000 times, we determined whether the values of the correlation values for field mating pairs were included within the 95% confidence limits of the simulated distributions under random mating.

Using the data from the simulations, we also evaluated whether the mean sizes of males and females mating on the surface or underground were similar to those expected from the restrictions imposed by the spatial distribution of neighboring crabs for surface matings (spatially restricted model) and the diameter of burrow openings for underground matings (burrow-restricted model). For this, we calculated the mean and the 95% confidence limits for the

crab size obtained from the simulations, and determined whether the mean values from the collected mating pairs were included within these confidence limits.

## Results

### Population density and mating mode

During the sampling period, we saw more surface matings in low-density areas ( $n_{\text{low}} = 62$ ) than in high-density areas ( $n_{\text{high}} = 39$ ,  $\chi^2 = 27.81$ ,  $P < 0.0001$ , the expected values calculated based on density differences were 36.5 for low density and 64.5 for high density). Conversely, we found more underground matings in high-density areas ( $n_{\text{high}} = 75$ ) than in low-density areas ( $n_{\text{low}} = 32$ ,  $\chi^2 = 17.28$ ,  $P < 0.0001$ ).

### Searching behavior and mating mode

The number of underground matings per crab  $\text{m}^{-2}$  was positively related to the proportion of wandering receptive females for both densities as well as for the pooled data (Fig. 1a; Table 1). The number of surface matings per crab  $\text{m}^{-2}$  was negatively related to the proportion of wandering receptive females for high density as well as for the pooled data (Fig. 1c; Table 1). The number of underground matings per crab  $\text{m}^{-2}$  (Fig. 1b) and the number of surface matings per crab  $\text{m}^{-2}$  (Fig. 1d) were not related to the proportion of courting males (Table 1). The proportion of wandering receptive females was higher at high densities (Fig. 1a, c;  $t$  test with separate variances:  $t = 7.93$ ,  $df = 27.3$ ,  $P < 0.0001$ ). The proportions of courting males were similar between densities (Fig. 1b, d;  $t = 0.69$ ,  $df = 38$ ,  $P = 0.6270$ ).

### Experimental evidence that density affects mating mode

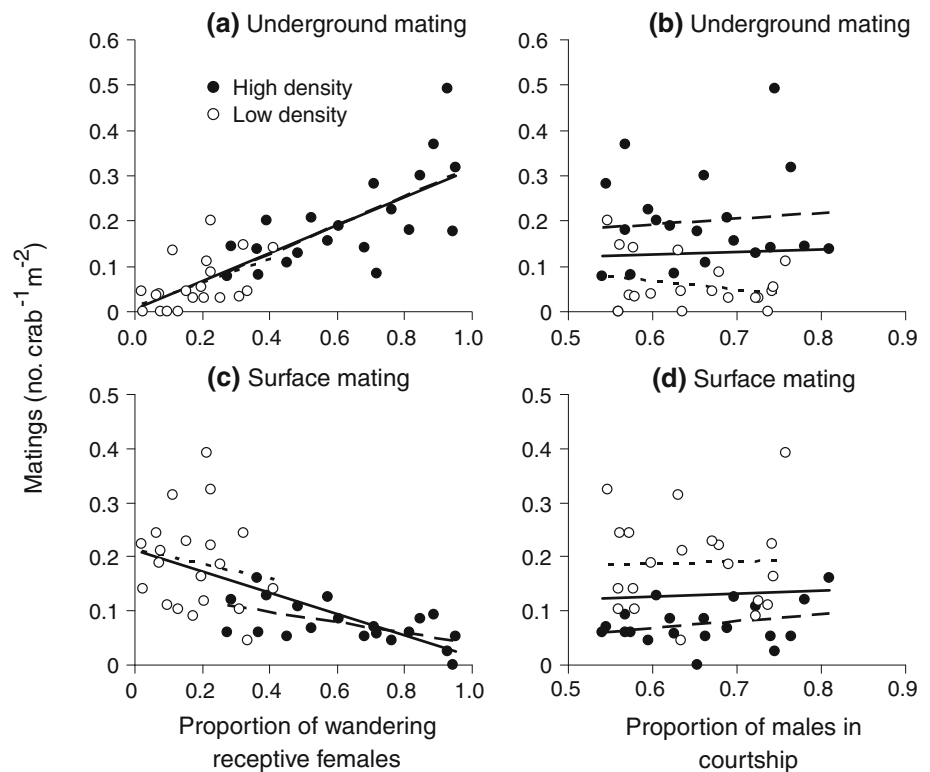
The density of crabs was 2–2.5 times higher in the high-density enclosures, and was relatively constant throughout the experiment (Fig. 2a). For the four reproductive cycles, the proportion of wandering females differed between the treatments (Fig. 2b; Table 2), being higher in high-density enclosures than in low-density and open enclosures. Surface matings (Fig. 2c) were more frequent in low-density and open enclosures than in high-density enclosures (Table 3).

### Size of crabs and mating mode

Within a population, males were larger than females, and both were smaller in high-density than in low-density



**Fig. 1** Relationships between the proportion of wandering receptive females and the occurrence of **a** underground and **c** surface matings of fiddler crabs (*Uca uruguayensis*) in San Clemente tidal creek (Samborombón Bay, Argentina) from November 2001 to March 2002. Relationships between the proportion of males in courtship and the occurrence of **b** underground and **d** surface matings. Mean values for pooled data (solid lines), high-density areas (dashed lines, filled circles), and low-density areas (dotted lines, open circles) are shown



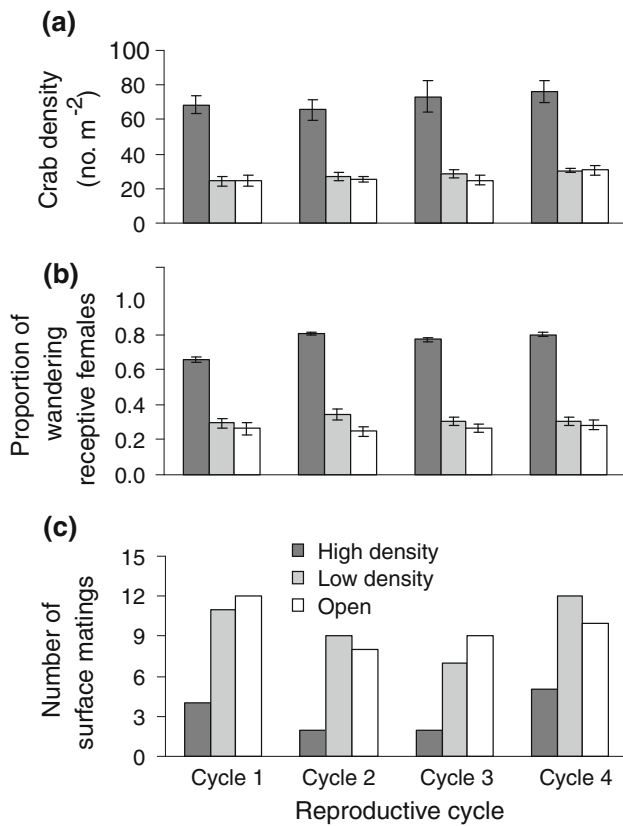
**Table 1** Summary statistics for an analysis of the relationships between the number of underground (UM) or surface matings (SM) per crab  $m^{-2}$  and the proportion of wandering receptive females (Fw) or the proportion of males in courtship (Mc)

	UM per crabs $m^{-2}$				SM per crabs $m^{-2}$			
	F	MSE	P	$r^2$	F	MSE	P	$r^2$
High density								
Fw	15.98	0.0063	0.0008	0.47	8.54	0.0011	0.0091	0.32
Mc	0.16	0.0118	0.6965	0.01	1.52	0.0014	0.2334	0.08
Low density								
Fw	5.76	0.0026	0.0274	0.24	0.49	0.0079	0.4939	0.03
Mc	1.09	0.0033	0.3085	0.06	0.01	0.0081	0.9179	0.001
Pool								
Fw	72.72	0.0043	<0.0001	0.66	26.46	0.0047	<0.0001	0.41
Mc	0.06	0.0124	0.8109	0.001	0.02	0.0080	0.8908	0.001

areas (Table 4; Figs. 3, 4). Males that mated underground were larger than those that mated on the surface (Table 5; Fig. 3), and males that mated in low density areas were larger than those that mated in high-density areas (Table 5). Females that mated underground were similar in size to those that mated on the surface (Table 5; Fig. 4), and females that mated in low-density areas were larger than those that mated in high-density areas (Table 5).

The burrow-restricted model could explain the carapace size correlation between females and males within mating

pairs (Fig. 5a, c) from underground matings in low-density areas but not at high densities (Table 6). The mean size of females mating underground was similar to that obtained by the burrow-restricted model (Fig. 5b, d). The mean size of males that mated underground was larger than that obtained by the burrow-restricted model (Fig. 5b, d). The spatially restricted model could explain the carapace size correlation between females and males within mating pairs for both densities in surface mating (Table 6). The mean sizes of males and females within surface matings were similar to those obtained by the spatially restricted model



**Fig. 2** **a** Density of crabs (mean ± SE) in the experimental enclosures and **b** proportion of wandering receptive females (with bootstrap 95% confidence limits) during the peak day of activity of each reproductive cycle. **c** Number of surface matings during each reproductive cycle. Each reproductive cycle occurs within a semilunar cycle (14.8 days), with 3–5 peak activity days occurring generally around spring tides. High-density enclosures (dark-gray bars) are fenced and are naturally low-density areas with artificially increased density; low-density enclosures (light-gray bars) are fenced and are naturally low-density areas without artificially increased density; open areas (open bars) are naturally low-density open areas with neither artificially increased density nor fence delimitation

**Table 2** Statistics for generalized linear models (binomial distribution and logit link function) that compare the proportions of wandering females in high-density enclosures (HD), low-density enclosures (LD), and open areas (OA)

	Scaled deviance	Deviance change	Overdispersion scale parameter	P
Cycle 1	48.27	36.82	1.25	<0.0001
Cycle 2	111.75	90.79	1.09	<0.0001
Cycle 3	108.8	92.23	1.14	<0.0001
Cycle 4	110.13	90.11	1.12	<0.0001

(Fig. 5b, d). The parameters of the linear regressions fitted to the relationship between carapace width and the diameter of the burrow opening were

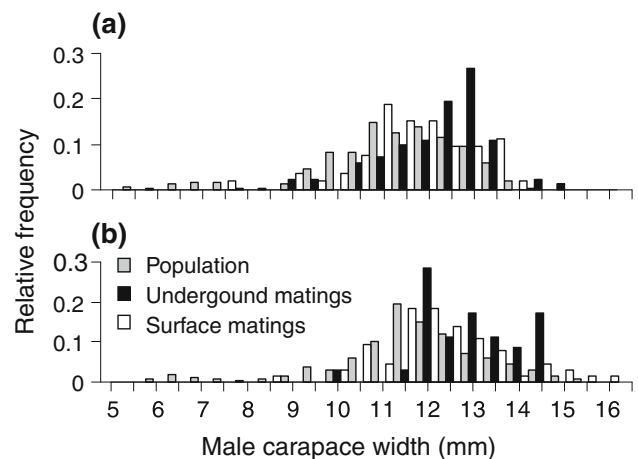
- Males: elevation = 3.64 ± 0.40; slope = 0.51 ± 0.03; MSE = 1.1768; n = 324

**Table 3** Expected values calculated based on density differences, and  $\chi^2$  statistics for the comparison between the number of surface matings in high-density enclosures (HD), low-density enclosures (LD), and open areas (OA)

	Expected values			Statistics	
	HD	LD	OA	$\chi^2$	P
Cycle 1	15.77	5.59	5.64	21.20	<0.0001
Cycle 2	10.58	4.33	4.09	15.73	0.0004
Cycle 3	10.39	4.07	3.54	17.28	0.0002
Cycle 4	14.99	6.00	6.01	15.32	0.0005

**Table 4** Summary statistics of the two-way ANOVA for the comparison of crab carapace width between densities (high and low) and sexes

	SS	df	MS	F	P
Sex	1.4190	1	1.4190	26.52	<0.0001
Density	0.4282	1	0.4282	8.00	0.0048
Sex × density	0.0106	1	0.0116	0.19	0.6565
Error	42.5901	796	0.0535		

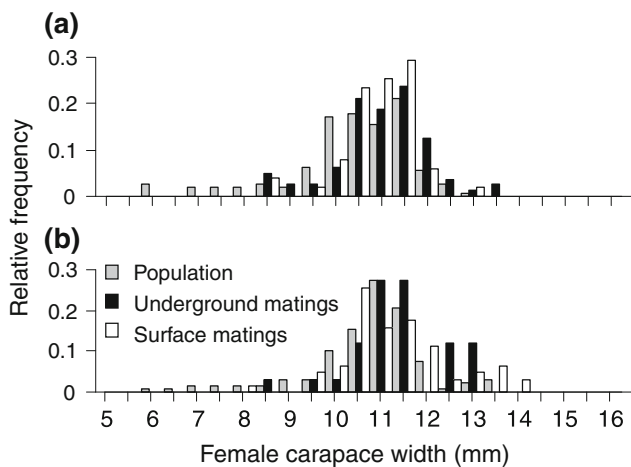


**Fig. 3** Size–frequency distribution based on carapace width of males from the whole population (gray bars), males mating underground (filled bars), and males mating on the surface (open bars) in **a** high- and **b** low-density areas

- Females: elevation = 3.20 ± 0.50; slope = 0.53 ± 0.04; MSE = 0.9889; n = 171

**Discussion**

*U. uruguayensis* mated underground and on the surface with different frequencies depending on crab density. Underground matings were more common at high density,



**Fig. 4a–b** Size–frequency distribution based on carapace width of females from the whole population (*gray bars*), females mating underground (*filled bars*), and females mating on the surface (*open bars*) in **a** high- and **b** low-density areas

**Table 5** Summary statistics of the two-way ANOVA for the comparison of carapace widths of males and females between densities (high and low) and mating modes (underground and surface mating)

	SS	df	MS	F	P
<b>Males</b>					
Mating mode	0.5137	1	0.5137	15.39	0.0001
Density	0.4114	1	0.4114	12.32	0.0005
Mating mode × density	0.0003	1	0.0003	0.01	0.9229
Error	7.7098	231	0.0334		
<b>Females</b>					
Mating mode	0.0095	1	0.0095	0.3843	0.5359
Density	0.1656	1	0.1656	6.6817	0.0104
Mating mode × density	0.0030	1	0.0030	0.1198	0.7296
Error	5.7235	231	0.0248		

while surface matings were more common at low density. These results were expected given the results from previous studies (deRivera and Vehrencamp 2001; deRivera 2003). We also found that large males mated underground more often than did small ones, while males of all sizes seemed to mate on the surface equally often. Given that crab size increases with age (Crane 1975), it is likely that males are more likely to mate underground as they age.

The proportions of wandering receptive females differed between densities, and this explained much of the variation in the occurrence of each mating mode. In contrast, the proportions of males that courted neither differed between densities nor explained the variation in occurrence of each mating mode. Hence, whether crabs mate underground or on the surface is determined mainly by whether or not females search for mates. Thus, we think the change in the occurrence of the two mating modes reflects a change in

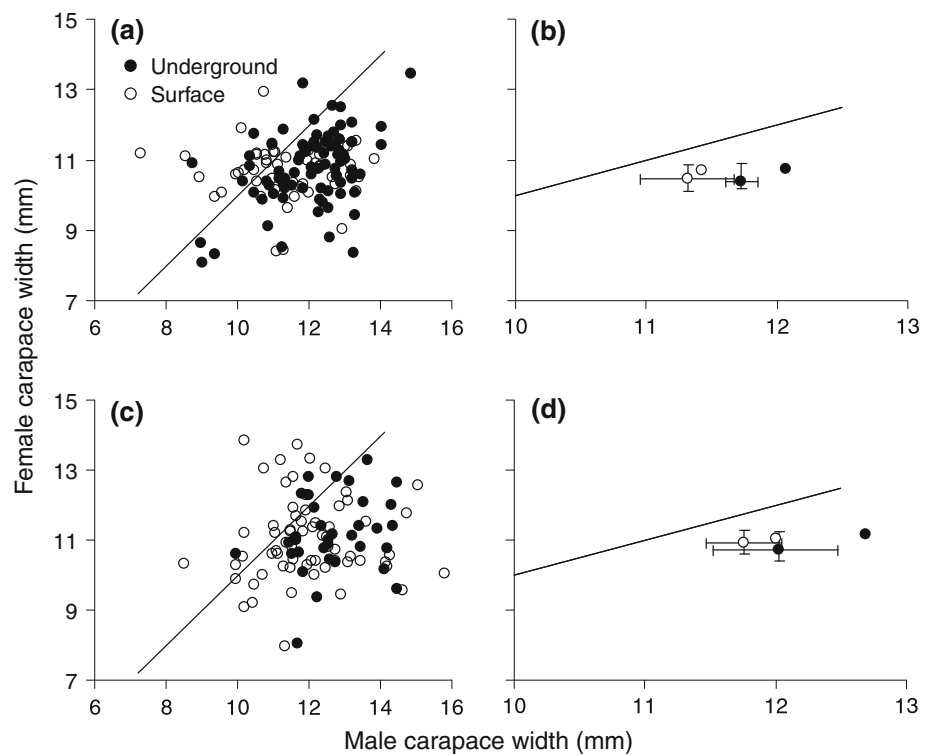
the frequency with which individual crabs flexibly engage in the two modes.

Understanding why females decide to wander for underground mating is the cornerstone to understanding the change in mating mode. Judging from the absence of a difference in size between the females that mated underground and those that mated on the surface, it is likely that the initiation of female wandering is linked to social context or physical characteristics of the environment. When wandering and searching for mates, females leave the area and discard their own burrows to mate inside male burrows. Wandering places females at enhanced risk of mortality through predation (Ribeiro et al. 2003) and desiccation (Booksmythe et al. 2008). In some species, wandering is a consequence of an increased aggressiveness of males towards females (e.g., Murai et al. 1987; but see deRivera 2003), but during our experiment we saw too few instances of male aggression towards females to evaluate the effect of such interactions on female wandering. Thus, at high densities, females may benefit from searching because they avoid male aggression by leaving the area, and they find a mate and a new burrow. At high densities, the costs of searching may be lower, as male burrows are closer together (Booksmythe et al. 2008), which means that the females are exposed to enhanced risks of predation and desiccation for only a short time while moving between males (deRivera et al. 2003).

Characteristics associated with a female's burrow or its position may determine whether it is adequate as a breeding site, and therefore whether the female leaves and searches for a mate and breeding site. The stability of the burrow depends on sediment characteristics (Christy 1980, 1987) and perhaps on burrow density (Christy and Salmon 1984). In addition, the quality of the surrounding surface sediment for feeding should also be important. The association of female searching with species living in coarse sediments (deRivera and Vehrencamp 2001) suggests that females may adopt searching when sediments are relatively food poor. Furthermore, an experiment evaluating the effect of food addition on the courtship of *Uca lactea* (Kim et al. 2008) found that food-supplemented males attempted to mate more often on the surface than in a control situation. Thus, if females depend on the food quality of the surrounding sediment in order to develop a successful brood, then females will leave if they are in a poor food area. Food depletion is more likely to occur in areas with high crab densities than in areas with low densities. In addition, the fact that crabs in low-density areas are generally larger than those in high-density areas may be due to food differences between areas. Given the high heterogeneity of the environment inhabited by *U. uruguayensis* (Ribeiro et al. 2005), the potential relationships between



**Fig. 5** Correlations between the carapace sizes of males and females within mating pairs in **a, b** high- and **c, d** low-density areas. **a, c** Mean sizes of females and males from mating pairs collected on the surface (*open circles*) or underground (*filled circles*), and **b, d** 95% confidence limits obtained from simulation models. *Solid lines* indicate the 1:1 relationship



**Table 6** Coefficients of correlation (*r*) evaluating size-assortative mating, and the 95% confidence limits for the *r* values from the simulations of random mating under burrow and spatial constraints

	Observed values		<i>r</i> value from simulated mating pairs	
	<i>n</i>	<i>r</i>	Mean	95% confidence limits
High density				
Underground mating	82	0.4159	0.1304	−0.0894, 0.3418
Surface mating	53	−0.0039	0.0906	−0.1748, 0.3417
Low density				
Underground mating	35	0.2071	0.1249	−0.2176, 0.4450
Surface mating	65	0.0329	0.1267	−0.1590, 0.3862

body size, density, and female mating mode warrant further research.

In contrast to females, males that mated underground were larger than males that mated on the surface. This change in male size in relation to the mating mode may be due to changes in the level of female choice and to the effect of mechanical and spatial constraints on the encounter rates of crabs of different sizes. Due to the mechanical constraint imposed by burrow diameter, large males have a larger pool of potential mates than small males. On the other hand, given that surface mating occurs between neighboring crabs, the pool of potential mates will depend on the size–frequency distribution of neighboring crabs. Size-assortative mating may result without female choice if similar sizes of crabs are clumped in space. Thus, the ecological characteristics under which both mating

modes occur may potentially affect the level of size-assortative mating, even without female choice. In this way, computer simulations showed that burrow diameter constraints on the sizes of crabs in mating pairs explained the correlation between the sizes of mated pairs at low but not at high densities. This suggests that there is no mate choice in underground matings at low densities. However, this may be an artifact, given the small range of males that mated underground at low densities, and considering that the magnitude of a correlation depends on the ranges of the correlated variables (Pascual and Iribarne 1993). In addition, at both densities, the mean size of males that mated underground as obtained from computer simulations was significantly smaller than that observed from the collected mating pairs. This means that males that mated underground were larger than they needed to be for females to be

able to enter their burrows, indicating some level of female choice for large males beyond the potential effects of mechanical constraints. In contrast, computer simulations showed that random mating between neighbor crabs may explain crab size as well as the correlation between male and female size within pairs, indicating that there is no size-based female choice in surface matings.

The difference in the level of size-based mate choice between mating modes may be related to differences in the resources that females receive from males in each mating mode. The change from surface to underground mating implies a change from the absence to the presence of the male's burrow as a resource. In surface matings, because the female incubates her egg in her own burrow, the only resource clearly provided by males is sperm. Thus, if females choose males in surface mating, the choice would be based on indirect benefits (e.g., sperm quality, good genes). Given the low level of size-assortative mating in surface matings, female choice based on indirect benefits seems to be weak or uncorrelated with male size. In contrast, in underground matings, the male guards the female and, when the female extrudes the eggs, the male leaves the burrow to the female for egg incubation (Christy 1982, 1987; Christy and Salmon 1984). In some species, females choose males based on burrow stability and depth, in order to avoid burrow collapse and to provide a good thermal environment for egg development (Christy 1980, 1987; Backwell and Passmore 1996; deRivera 2005). Hence, when mating underground, females may be choosy about their mates to ensure a high-quality burrow for egg incubation. Large males may hold large burrows and they may be able to defend high-quality territories in which they dig their burrows (Milner et al. 2010). Thus, female choice may be based directly on male size or on other characteristics of males or burrows that are correlated with male size (Backwell and Passmore 1996). This means that sexual selection by females based on male size may be strong in sites where crab density is high, where underground mating is more common. As a consequence, the overall result of the action of sexual selection on the whole population will depend on how the density variation is represented within the whole population. We think this may be important in fiddler crab species that live at variable densities in the same area (*Uca beebei*, deRivera 2003; *U. uruguayensis*, Ribeiro et al. 2003) or meta-populations with subpopulations of different densities, connected by larval flow (also *U. uruguayensis*, Bogazzi et al. 2001).

Among the almost 100 species of fiddler crabs known, no more than 15 are known to use both mating modes (e.g., Yamaguchi 1971; Nakasone et al. 1983; Christy 1987; Murai et al. 1996). The reasons for the majority of species of fiddler crabs using only one mating mode may be associated with low variability in the environmental

context during their lifetimes (e.g., relatively stable settlement density) and/or the influence of other factors (e.g., predatory levels, Kim et al. 2007) on each species, which may have selected for the fixation of only one mating mode.

In theory, the evolution of behavioral plasticity depends on how individuals perceive the environmental grain (Levins 1968). In fact, multiple mating events during a lifetime plus the ability to predict changes in payoffs when using different tactics (Schlichting and Pigliucci 1998) are expected to favor behavioral plasticity instead of the establishment of genetically differentiated tactics (see Shuster and Wade 2003). Given that fiddler crabs experience several reproductive cycles, whenever the social context changes substantially between reproductive events they are expected to show behavioral plasticity in their mating strategy. Our experimental results may support this. In addition, the change in the occurrence of mating modes with density also suggests that payoffs of different mating modes may change with density. Thus, for some individuals, mating underground in high density areas may give a higher payoff than mating on the surface, with the opposite being true for low densities. This means that different level of densities may function as refuges for the maintenance of different mating modes. Therefore, the incorporation of different levels of variability in the environmental context (Formica and Tuttle 2009) may be important for theoretical models of the evolution of alternative mating strategies.

**Acknowledgments** We thank John H. Christy, Libby Marschall, Taewon Kim and two anonymous reviewers for their suggestions on previous drafts of this work. We thank Laura Farisé for her help in field work. We are grateful to the Club Social de Pesca Náutica y Fomento, San Clemente del Tuyú, for allowing us to use their facilities. This work was supported by grants from Agencia Nacional de Promoción Científica y Tecnológica to P.D.R. (PICT 2007-01488) and to O.O.I. (PICT 2007-01472), and a grant from CONICET to O.O.I. (PIP 112-200801-00174).

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