

## HOOD-BUILDING DYNAMICS AND MATING MODE IN THE TEMPERATE FIDDLER CRAB *UCA URUGUAYENSIS* NOBILI, 1901

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### ABSTRACT

Courting males of 18 species of fiddler crabs (*Uca* Leach, 1814) are known to build mud or sand structures at the entrances of their burrows. Females orient to these structures when seeking mates and, in some species, males sometimes orient to their own structures as well to relocate their burrows. We studied hood building in the temperate species *Uca uruguayensis* Nobili, 1901, the southernmost fiddler crab species, which mates both underground in males' burrows, especially at high densities, and on the surface at the entrance to females' burrows, a more common mode at low densities. *Uca uruguayensis* is relatively inactive during the winter and it was expected that the intensity of hood building would vary seasonally, with more hoods built when underground mating was more common. Courting male *U. uruguayensis* built nearly symmetrical cupped hoods of muddy sand, approximately half as high and two-thirds as deep as wide. Male courtship and mating occurred in summer from November 2001 to January 2002, but hood building was largely restricted to the last semi-monthly cycle, when the maximum number of matings were coincident with the maximum occurrence of hoods. The predominance of hood building at the end of the season may reflect the amount of time following winter inactivity that males need to feed before they exceed a threshold in the trade-off between allocation of resources to growth or reproduction. Contrary to expectations, males built more hoods at low densities where inter-burrow distances were greater. Males more often build hoods at lower densities because hoods enable them to venture further from their burrows to court both passing and burrow resident females. The temporal pattern of hood building by male *U. uruguayensis* may therefore reflect the mechanisms courting males use to relocate their burrows as well as variation in the social and spatial context of courtship and mate choice.

KEY WORDS: mating behavior, reproductive cycle

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### INTRODUCTION

Courting males of 18 species of fiddler crabs (*Uca* Leach, 1814) are known to build structures ("hoods," "semidomes," and "pillars") out of mud or sand at the entrances of their burrows (Beinlich and von Hagen, 2006; Christy, 2007). Although structure building in fiddler crabs has been known for decades (Crane, 1975) and several hypotheses proposed to explain its function (Matthews, 1930; Salmon and Atsades, 1968; Zucker, 1974, 1981), the effects of these structures on the males that build them has been explored experimentally in the field only relatively recently. Mud pillars in *U. beebei* Crane, 1941, sand hoods in *U. terpsichores* Crane, 1941, and semidomes in *U. lactea* (de Haan, 1835) have been found to attract females to males' burrows for mating (Christy, 1988a, b; Christy et al., 2002, 2003a, b; Kim et al., 2004; Zhu et al., 2012). These structures also serve as visual guideposts that males use to relocate their burrows when their non-visual mechanism based on path integration fails (Ribeiro et al., 2006), and as beacons marking "home," allowing males to move more freely when courting far from their burrows (Kim et al., 2010b; Kim and Christy, 2015). As Crane (1975) noted, females of

all these structure-building species follow males into their burrows for mating. Structures in most species may therefore function as sexual signals to which females orient visually, and variation in structure form may be related more to variation in the kinds of sediment used to build the structures rather than to interspecific differences in function. Indeed, female *U. terpsichores* (broad sand hoods) and *U. beebei* (narrow mud pillars) are equally attracted to males of their own species with replicas of the other species' structure when placed on their burrows (Christy et al., 2003a). Female *U. terpsichores* are equally attracted to males of their own species with hoods, hood replicas, stones, shells, and pieces of wood on their burrows (Christy et al., 2003b). Structures thus appear to elicit a very general orientation response to objects or landmarks (Herrnkind, 1983).

The intensity of structure building varies with the lunar or semilunar reproductive cycles of fiddler crabs, which are generally entrained to variation in tidal height and amplitude (Christy, 1978; Greenspan, 1982; Kim and Choe, 2003; Morgan and Christy, 1994, 1995; Skov et al., 2005; Yamaguchi et al., 2005; Masunari, 2012). Comparative studies (over 80 species; Christy, 2011) have shown that

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the timing of reproduction by fiddler and other brachyuran crabs leads to the hatching of eggs on large amplitude nocturnal ebb tides and the rapid dispersal of larvae away from abundant near-shore diurnal predators. Semi-lunar or lunar cycles of female sexual receptivity and mating in fiddler crabs are matched by coincident cycles of investment by males in courtship signalling (Christy, 1978; Zucker, 1978; Greenspan, 1982; Kim and Choe, 2003; Kim et al., 2010a; Kerr et al., 2014). While males of some species of fiddler crabs make structures every day when in court (e.g., *U. latimanus* Rathbun, 1893 (Zucker, 1978), *U. pugilator* (Bosc, 1801) (Christy, 1982)), males of other species invest in structures only on the few days at the peak mating period (*U. beebei* (Backwell et al., 1995), *U. terpsichores* (Christy et al., 2001)). It has been proposed that the abundance of hoods accurately indicates the intensity of mating, as in *U. terpsichores* (Christy et al., 2001) and *U. leptodactyla* Rathbun, 1898 (Masunari, 2012). The absence of hoods may not, however, indicate a lack of mating activity because factors other than the cyclic availability of sexually receptive females may affect structure building. Even in tropical species, with year-round reproduction, hood building activity varies seasonally and between reproductive cycles depending on the site (JHC, unpublished; Kim et al., 2010a). Similarly, in the temperate species *U. pugnax* (Smith, 1870) hood building increases during the summer breeding period (Greenspan, 1982), suggesting that the number of hoods in an area increases as juvenile males mature and begin to court late in the season (Greenspan, 1982). The experimental addition of food increased male courting intensity in *U. terpsichores* (Kim et al., 2010b), pillar building in *U. beebei* (Backwell et al., 1995) and semidome building in *U. lactea* (Kim and Choe, 2003). Variation in the energy that males have to allocate to courtship may thus also drive changes in the intensity of structure building. The amount of time crabs spend on different activities could also depend on temperature. In contrast to tropical fiddler crab species, temperate species usually suspend surface activity during winter and resume activity in early spring, during which crabs exclusively feed to recover, grow, and prepare to the forthcoming reproductive season. Males begin to court females from late spring to midsummer. In temperate species it is thus likely that seasonal changes in crab activity could also lead to more prominent changes in hood building intensity in comparison to tropical species with year-round reproduction.

In addition to seasonal changes, hood building intensity can be affected by social and spatial factors as density, sex ratio, inter-burrow distances, and mating mode. As in many fiddler crabs species (see de Rivera et al., 2001), *U. uruguayensis* Nobili, 1901 mates both on the surface and underground (Ribeiro et al., 2010). In surface mating, males approach neighbor females, use tactical courtship signals, and mate on the surface next to the opening to the female's burrow. Each crab returns to its burrow after mating. In underground mating, females leave their burrows, stop briefly at the burrows of several courting males (displaying waving and seismic signals), and finally stay in a male's burrow. The chosen male and female mate underground in the male's burrow and stay together

for 2-3 days until the female lays a clutch of eggs. The male then leaves the burrow. The frequency of surface mating is higher at low densities and, conversely, the frequency of underground matings is higher at high densities (Ribeiro et al., 2010). It has been suggested that at high densities inter-burrow distances could be shorter, decreasing searching costs for females, thus favouring underground mating mode (de Rivera et al., 2003; Ribeiro et al., 2010). Furthermore, in addition to their function as landmarks showing the location of the male's burrow, hoods could facilitate burrow defence against other males (Christy, 1982; Yamaguchi et al., 2005), which could be important at high densities. The relationship between inter-burrow distance and density, however, has not been documented. Given that male use hoods to attract, orient, and guide females to their burrows for underground mating (Christy et al., 2002, 2003b), proportionately more hoods would be expected at high densities where underground matings are more common.

Here we describe hood architecture and building dynamics in the temperate *U. uruguayensis*, the southernmost fiddler crab species. We describe the structures built by crabs in comparison to other fiddler crab species, explore seasonal changes in crab activity and hood building at two different population densities, and evaluate whether hood building could be explained by mating intensity and mating mode.

## MATERIALS AND METHODS

### Study Site and Sampling Period

The study was conducted near the mouth of the San Clemente tidal creek (eastern Samborombón Bay, Argentina (36°22'S, 56°45'W), an area with semi-diurnal tides of moderate amplitude (<1.4 m). Fiddler crabs inhabit the middle to upper intertidal flats near the fringe of an extensive *Spartina densiflora* Brongn. marsh. The density of crabs is highly variable (Ribeiro et al., 2005), with mean population density ranging 10-90 crabs m<sup>-2</sup> across an area of 2 km. These population densities are based on excavation sampling and include both crabs that are active on the surface and those that remain underground (e.g., ovigerous females, molting crabs). Crabs are active on the surface from September to April. Not all crabs from the population are active on the surface every day. The density of crabs on the surface thus vary across time, showing a general increase towards the end of the summer. This work explores differences in hood building and mating mode under two distinct crab population densities. Based on previous work (Ribeiro et al., 2005, 2010) we have identified areas with low (mean 10-40 crabs/m<sup>2</sup>) and with high population densities (mean 60-90 crabs/m<sup>2</sup>). Density of crabs on the surface at both type areas can change as described above but rarely overlap across sampling periods.

### Hood Architecture

We selected 100 hoods and measured their a) height, b) total width, c) depth, d) widest side at base, and e) tip shift, as the horizontal distance between the tip of the hood and the center of the burrow entrance (Fig. 1). When possible, we captured the owner of the burrow and recorded its sex and carapace width. In order to evaluate variability in hood architecture we compared the coefficients of variations in height, width, and depth ( $\chi^2$  test for CV comparisons; Zar, 2010). We used correlations to evaluate the relationships between height, width, depth, and the size of the builder male, and calculated two estimators of hood symmetry: a) hood asymmetry at base, as the proportion of the wider side at base from total width, and b) hood cup centring, as the proportion of tip shift from total width.

### Crab Density and Inter-Burrow Distance

To determine the relationship between density and inter-burrow distance (ID) we randomly selected 160 burrows, and counted the number of neighbouring burrows within a radius of 34 cm and measured the distance to

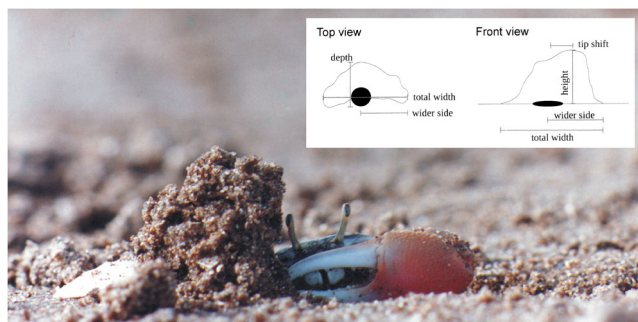


Fig. 1. A male fiddler crab (*Uca uruguayensis*) with a hood. Illustrations within the box show the measurements made on hoods. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/journals/1937240x>.

the nearest burrow. We evaluated whether inter-burrow distance decreased inversely with density by fitting the following model:

$$\text{Distance} = \left( \frac{a}{\sqrt{\text{Density}}} \right)$$

where parameter  $a$  is expected to equal 0.5 if inter-burrow distance varies randomly (Clark and Evans, 1954). We fit the model with Nonlinear Least Squares estimation and constructed confidence limits (95%) for parameter  $a$ .

#### Seasonal Patterns of Crab Activity and Hood Building

We observed crabs on a semi-monthly schedule following their semi-monthly reproductive cycles from October 2001 to March 2002, a period that spanned the entire reproductive season (Bogazzi et al., 2001). We observed crabs for five days during each cycle when crabs were most active (Ribeiro et al., 2010; Ribeiro and Iribarne, 2011); generally, days with low tides occurring between 0930 and 1630.

For each semi-monthly cycle we delimited 10 plots ( $2 \times 3$  m each) with wooden stakes. We positioned the plots so that five contained a low population density of crabs and the other five a high population density. Plots for each semi-monthly cycle were at different locations. Using binoculars ( $10 \times 50$ ) at a distance of 5 m we monitored crab activity within plots from 3 h before low tide to 2 h after low tide. Each hour we counted the number of: 1) males and females, 2) males courting with claw waving, and 3) hoods. The counts for all plots took 20-35 minutes. For the remainder of the hour period we continuously monitored all plots for surface matings and recorded the number observed. To quantify the occurrence of underground matings we scanned each plot for plugged burrows. Similarly to other fiddler crab species (e.g., Christy, 1978; Yamaguchi, 1998), males of *U. uruguayensis* plug their burrows when the attracted female enter and stay for mating underground (personal observation; Ribeiro et al., 2010). We therefore used the count of plugged burrows, with a male and a female inside, as a measure of the number of underground matings (see Christy et al., 2001; Ribeiro et al., 2010). We searched for plugged burrows 2-3 hours after low tide, early enough in the tidal activity cycle to avoid the confounding effect of males plugging their burrows without having attracted a female, which typically occurs 4-5 hours after low tide.

We studied seasonal changes in crab activity by evaluating seasonal changes in: 1) density of crabs on the surface, 2) sex ratio on the surface, 3) proportion of males in courtship, and 4) proportion of males with hoods. These analyses were conducted by fitting Linear Models (see below). For the sake of simplicity, for each semi-monthly cycle, we used the data from the day and the hourly count (usually the hour around the time of low tide; Ribeiro et al., 2003) with the highest activity and density of crabs on the surface.

**Seasonal Changes in the Density of Crabs on the Surface.**—We fit a two-way ANOVA (Zar, 2010) to evaluate changes in the density of crabs on the surface (dependent variable) in relation to date and population density class (explanatory variables). This analysis also allowed us to support whether our prior identification of high and low population density areas was appropriate.

**Table 1. Summary of the analysis of deviance for the generalized linear model, fitting the sex ratio on the surface (proportion of males on the surface to total crabs on the surface), in relation to date and density class (high and low). GLM was fit under binomial distribution and logit link function.  $D^2$  is the explained deviance. The overdispersion parameter was 9.77. Wald test for model goodness of fit:  $F = 11.26$ ,  $df = 23, 96$ ,  $p < 0.0001$ .**

Factor	Scaled deviance	df	$p$ -value	$D^2$
Date	285.33	11	<0.0001	72.20
Density	0.11	1	0.7384	0.03
Date $\times$ Density	7.61	11	0.7474	1.93
Residual	102.16	96		

**Seasonal Changes in the Sex Ratio on the Surface.**—We fit a Generalized Linear Model (GLM; McCullagh and Nelder, 1989) to evaluate whether changes in the sex ratio on the surface (dependent variable) could be explained by date and population density class (explanatory variables). The model incorporated an interaction term between date and density class. Sex ratio on the surface was measured as the proportion of males on the surface to total crabs on the surface. As the dependent variable was a proportion, we fit the model using binomial distribution, with logit link function, and including the number of observed crabs as weighting factor for the number of observed cases. Quasi-likelihood estimation was employed to control for over-dispersion (Hardin and Hilbe, 2012). The goodness of fit of the whole model was evaluated with a Wald test (Wasserman, 2004). The effect of each explanatory variable or of their interaction over the dependent variable was evaluated with Likelihood Ratio Tests (Wasserman, 2004). We calculated the explained deviance  $D^2$ , the equivalent to  $R^2$  for GLM models (Guisan and Zimmermann, 2000), of the whole model and of the contribution of each explanatory term.

**Seasonal Changes in the Proportion of Males in Courtship.**—We fit a GLM to evaluate whether changes in the proportion of males in courtship (dependent variable) could be explained by date, density class, and sex ratio on the surface (explanatory variables). To keep the model as simple as possible we only incorporated an interaction term between date and density, but not the triple interaction between sex ratio, date, and density because sex ratio did not vary interactively with date and density (see Table 1). We fit the model using binomial distribution, with logit link function, and including the number of observed males as weighting factor for the number of observed cases. Quasi-likelihood estimation was employed to control for over-dispersion (Hardin and Hilbe, 2012). The goodness of fit and the contribution of each explanatory term were evaluated with the Wald test, Likelihood Ratio tests, and the calculation of the explained deviance  $D^2$ .

**Seasonal Changes in the Proportion of Males With Hoods.**—We fit a GLM to evaluate whether changes in the proportion of males with hoods (dependent variable) could be explained by date, density class, and sex ratio on the surface (explanatory variables). To keep the model as simple as possible we only incorporated an interaction term between date and density, but not the triple interaction between sex ratio, date, and density because sex ratio did not vary interactively with date and density (see Table 1). We fit the model using binomial distribution, with logit link function, and including the number of observed males as weighting factor for the number of observed cases. Quasi-likelihood estimation was employed to control for over-dispersion (Hardin and Hilbe, 2012). The goodness of fit and the contribution of each explanatory term were evaluated with the Wald test, Likelihood Ratio tests, and the calculation of the explained deviance  $D^2$ .

#### Hood Building, Mating Intensity and Mating Mode

We hypothesise that if hoods have a function in the context of underground mating, then the variance in the proportion of males with hoods could be mainly explained by the occurrence of underground matings. Otherwise, if males build hoods under both underground and surface matings contexts, then both mating modes should explain a similar amount of variance in the proportion of males with hoods. Previous work (Ribeiro et al., 2010) found that underground matings are more frequent at high densities, whereas surface matings are more frequent at low densities. If changes in the occurrences of each mating mode are partly related to density differences, then the variance in the proportion of males with hoods would be also correlated to density class. We corroborated for the present data

whether the frequency of underground and surface matings varied with population density class. We used a  $\chi^2$  test (Zar, 2010) to compare the overall occurrence of underground and surface matings at both density classes during the whole study. The expected values for the  $\chi^2$  test were calculated in proportion to differences in the number of crabs counted while monitoring the surface activity at both density classes.

From data gathered in the sampling described in the previous section we obtained for each semi-monthly cycle and plot: *a*, the maximum number of hoods built in a day; *b*, the maximum number of males observed during the five days of each cycle; *c*, total number of underground matings observed during the five days of each cycle, and *d*, the total number of surface matings observed during the five days of each cycle. For each plot and semi-monthly cycle, we estimated the proportion of males with hoods by dividing *a* by *b*, the number of underground mating per male by dividing *c* by *b*, and the number of surface matings per male by dividing *d* by *b*. We fit a GLM to evaluate whether changes in the proportion of males with hoods (dependent variable) could be explained by density class, the number of underground matings per male, and the number of surface matings per male (explanatory variables). The model incorporated an interaction term between each mating mode and density. We fit the model using binomial distribution, with logit link function, and including the number of observed males as weighting factor for the number of observed cases. Quasi-likelihood estimation was employed to control for over-dispersion (Hardin and Hilbe, 2012). The goodness of fit and the contribution of each explanatory term were evaluated with Wald test, Likelihood Ratio tests, and the calculation of the explained deviance  $D^2$ .

#### Software for Statistical Analysis

All statistical analysis was conducted in the R environment (R Core Team, 2015).

## RESULTS

### Hood Architecture

*Uca uruguayensis* males built cupped hoods of muddy sand, approximately twice as wide as high and two-thirds deep as wide (Fig. 2). Hoods were more variable in depth than in width and height (CV width = 0.2213, CV depth = 0.2860, CV height = 0.2298;  $\chi^2 = 7.25$ ,  $df = 2$ ,  $p = 0.0267$ ). Wider hoods were deeper ( $r^2 = 0.53$ ,  $df = 98$ ,  $t = 10.54$ ,  $p < 0.0001$ ) and higher ( $r^2 = 0.34$ ,  $df = 98$ ,  $t = 7.11$ ,  $p < 0.0001$ ). Larger crabs built slightly wider hoods ( $r^2 = 0.05$ ,  $df = 84$ ,  $t = 2.02$ ,  $p = 0.0464$ ), but not deeper ( $r^2 = 0.01$ ,  $df = 84$ ,  $t = 1.07$ ,  $p = 0.2892$ ) nor higher ( $r^2 = 0.0002$ ,  $df = 84$ ,  $t = 0.13$ ,  $p = 0.8929$ ) than small crabs. Hoods were relatively symmetrical at base (Fig. 3A) and generally with a minor shift of their cups in relation to the opening of the burrow (Fig. 3B).

### Crab Density and Inter-Burrow Distance

The distance to the nearest neighbour (Fig. 4) decreased inversely as burrow density increased. The parameter *a* was estimated to be 0.57 (95% Confidence limits: 0.53, 0.60).

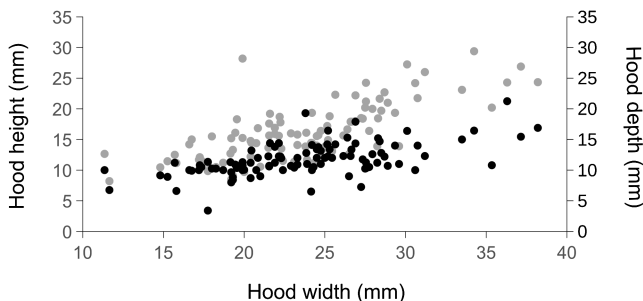


Fig. 2. Hood height (black circles) and depth (grey circles) in relation to hood width.

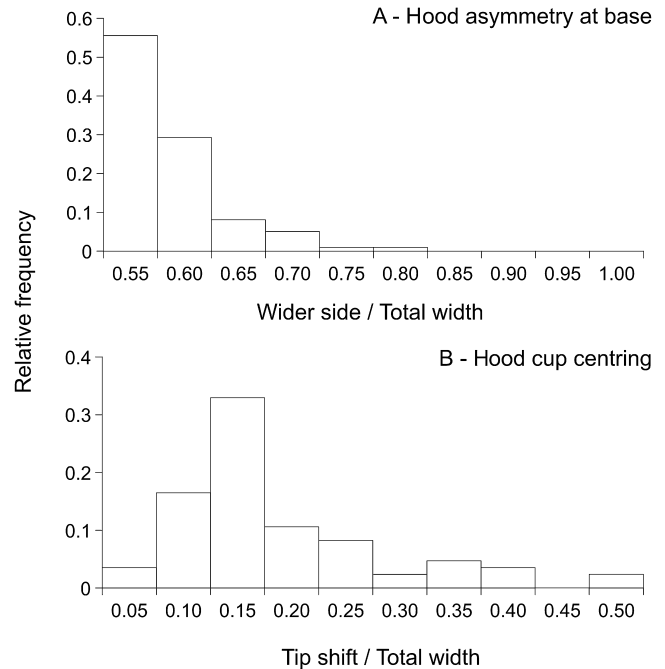


Fig. 3. Relative frequency distribution for (A) hood asymmetry at base, measured as the proportion of total width of the hood achieved by the wider side at the base of the hood and for (B) hood cup centring, measured as the proportion of tip shift from total width.

### Seasonal Patterns of Crab Activity and Hood Building

Density of crabs on the surface (Fig. 5A) varied across the time of the year and population density classes (two-way ANOVA: date  $\times$  density class interaction,  $F = 6.44$ ,  $df = 11, 96$ ,  $MSE = 109.46$ ,  $p < 0.0001$ ). The density of crabs on the surface did not overlap between high and low population density classes (Fig. 5A). Sex ratio on the surface (Fig. 5B) varied across the time of the year and was similar between densities (Table 1). The proportion of males in courtship (Fig. 5C) varied mainly across the time of the year (97% of the deviance; Table 2), being similar between densities, and with a small amount of variation explained by sex ratio (less than 1% of the deviance; Table 2). Male courted females predominantly (i.e. more than 50% of males in courtship) from early November through early January (Fig. 5C). Hood building (Fig. 5D) was more restricted in time, being observed primarily from late December through January, the latter half of the breeding season. The proportion of males with hoods thus varied across the time of year and densities

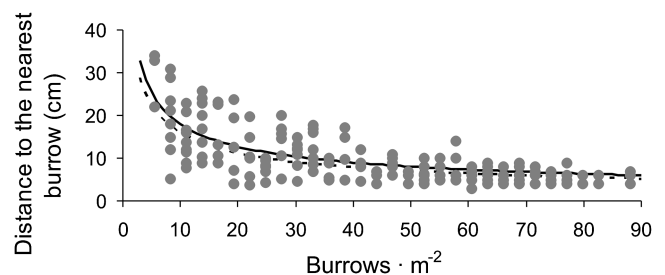


Fig. 4. Distance to the nearest burrow in relation to burrow density. Dotted line shows the expected curve given a random spatial distribution of burrows. Solid line shows the curve fitted to the data.

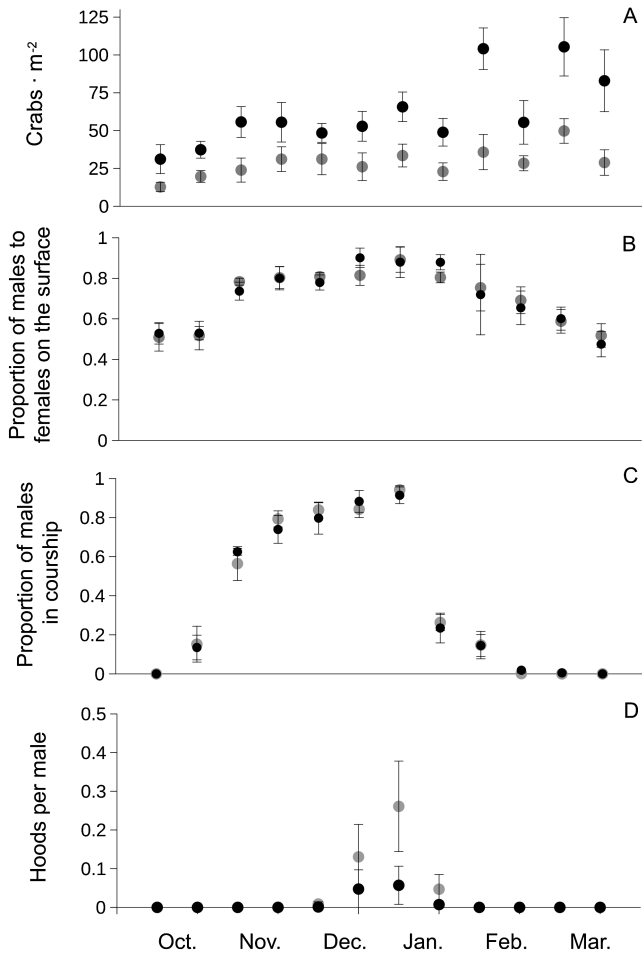


Fig. 5. Mean and SD for the density of crabs (A), sex ratio on the surface as the proportion of males to total crabs on the surface (B), proportion of males in courtship (C), and the number of hoods built within high (black) and low (grey) density plots.

(Table 3), but contrary to expectations, males built more hoods at lower densities (Fig. 5D).

**Hood Building, Mating Intensity and Mating Mode**

We found more underground matings (Fig. 6A) at high densities (118) than at low densities (38,  $\chi^2 = 4.57$ ,  $p < 0.0326$ ) throughout the study. Conversely, surface matings (Fig. 6B) were more common at low densities (108) than at high densities (69,  $\chi^2 = 66.38$ ,  $p < 0.0001$ ). Similarly

Table 2. Summary of the analysis of deviance for the generalized linear model, fitting the proportion of courting males in relation to date, density class (high and low), and sex ratio on the surface. GLM was fit under binomial distribution and logit link function.  $D^2$  is the explained deviance. The overdispersion parameter was 2.99. Wald test for model goodness of fit:  $F = 78.23$ ,  $df = 24$ ,  $95$ ,  $p < 0.0001$ .

Factor	Scaled deviance	df	p-value	$D^2$
Date	5349.57	11	<0.0001	97.67
Density	0.33	1	0.5637	0.01
Sex ratio	14.20	1	0.0002	0.26
Date × Density	16.00	11	0.1410	0.29
Residual	97.09	95		

Table 3. Summary of the analysis of deviance for the generalized linear model, fitting the proportion of males with hoods in relation to date, density class (high and low), and sex ratio on the surface. GLM was fit under binomial distribution and logit link function.  $D^2$  is the explained deviance. The overdispersion parameter was 2.51. Wald test for model goodness of fit:  $F = 8.22$ ,  $df = 24$ ,  $95$ ,  $p < 0.0001$ .

Factor	Scaled deviance	df	p-value	$D^2$
Date	585.38	11	<0.0001	72.25
Density	116.52	1	<0.0001	14.38
Sex ratio	2.34	1	0.1260	0.29
Date × Density	3.23	11	0.9873	0.40
Residual	102.79	95		

to the seasonal variation in male courtship, mating activity (Fig. 6) also occurred predominantly from early November through early January. The maximum number of matings, however, were observed during the semi-monthly cycle of late December and that of early January, which was coincident with the maximum in hood building (Fig. 5D). Parameter estimates and the constructed linear predictors for the GLM model (Table 4), indicated that the proportion of males with hoods increased with the occurrence of both underground and surface mating. More than 40% of the variation in the proportion of males with hoods was accounted by the occurrence of underground matings, whereas surface matings and density class had lower contributions (Table 5).

**DISCUSSION**

Hood building occurs almost exclusively in species of the subgenus *Leptuca* Bott, 1973 (Beinlich and von Hagen, 2006). We here report that males of the fiddler crab *Uca* (*Leptuca*) *uruguayensis* also build hoods in the context of mating.

Relative to crab size, the hoods built by *U. uruguayensis* are not as high as the hoods built by male *U. terpsichores* (Christy et al., 2001), but they probably are relatively higher than the semidomes built by male *U. lactea* (Kim et al., 2004). Larger males built wider but not higher or deeper

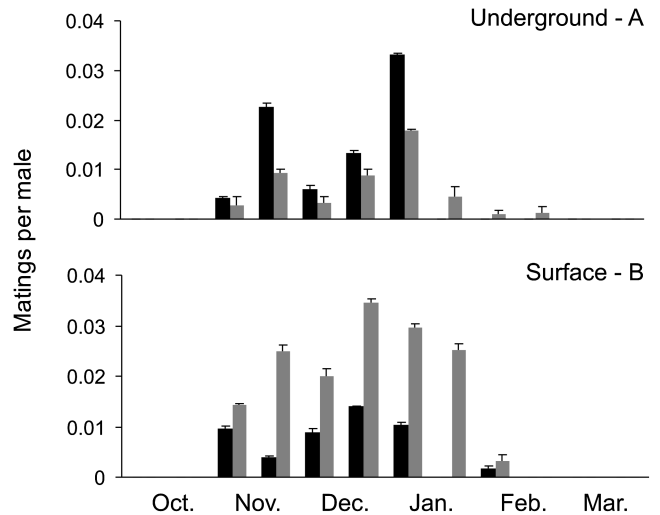


Fig. 6. Mean and SD for the number of underground matings per male (A), and the number of surface matings per male (B), within high (black) and low (grey) density plots in each semi-monthly cycle.

Table 4. Parameter estimates for the generalized linear model, fitting the proportion of males with hoods (PH) in relation to density class (high and low), the number of underground matings per male (UM), and the number of surface matings per male (SM). GLM was fit under binomial distribution and logit link function.

Parameter	Estimate	SE
Intercept	-8.08	1.14
Low density	0.04	1.66
Underground mating	73.12	20.89
Surface mating	264.87	84.77
Low density × Underground mating	92.50	40.66
Low density × Surface mating	-133.12	93.66

Linear predictor for high density:  $-8.08 + 73.12 \text{ UM} + 264.87 \text{ SM}$ . Linear predictor for low density:  $-8.03 + 165.62 \text{ UM} + 131.75 \text{ SM}$ . The mean proportion of males with hoods is obtained from  $\left(\frac{\exp(\text{Linear predictor})}{\exp(\text{Linear predictor})+1}\right)$ .

hoods. This contrasts with the strongly positive relationship between structure height and male size in *U. lactea* (Kim et al., 2004) and the weak correlation in *U. terpsichores* (Christy et al., 2001). These differences could be due to the greater variance in the dimensions of the hoods built by *U. uruguayensis*. For example, the CV in height for the hoods of *U. terpsichores* is 0.13624 (Christy et al., 2001), whereas the CV in hood height for *U. uruguayensis* is 0.2298.

Seasonal changes in the density of crabs on the surface, sex ratio, and intensity of courtship are as expected for a temperate species. Crab density on the surface is relatively low at the beginning of the spring when crabs are becoming active following the period of inactivity during the cold winter months. As reproduction begins, activity increases but incubating females remain underground producing the highly male-biased sex ratio (see Bogazzi et al., 2001; Ribeiro et al., 2003). Densities do not reach a maximum until February and March, the end of the summer when most crabs are active daily on the surface. At this time juvenile crabs recruit to the population which also increases crab density.

At least for females that mate underground in males' burrows, females breed in these burrows (personal observation). Based on the occurrences of underground matings (Fig. 6), *U. uruguayensis* could have 5-6 semi-monthly breeding cy-

cles during each reproductive season. Even when mating cycles show a semi-monthly rhythm, however, it is unlikely that all females breed during all cycles (Christy, 1978; Henmi, 2003). Embryonic development can take more than 15 days and females, especially those that remain underground during incubation, do not feed (Henmi, 2003), and need to accumulate energy reserves after they release their larvae. The intensity of mating and breeding thus varies between each of the bi-weekly breeding cycles. The temporal pattern of matings indicates that underground matings were most common in mid-November 2001 and in early January 2002. Hood building occurred almost exclusively during the last mating cycle in early January 2002, at the end of the reproductive season. Structures built by males of several species play a key role in attracting females to male burrows for underground mating (Christy, 1988a, b; Christy et al., 2002, 2003a, b; Kim et al., 2004; Zhu et al., 2012). Later in the season, male *U. uruguayensis* can have accumulated sufficient energy to engage in building structures and they timed their allocation to coincide with the late seasonal increase in female receptivity.

In some temperate species males have also been found to build hoods later in the reproductive season (e.g., *U. pugnax* (Greenspan, 1982) and *U. annulipes* Milne Edwards, 1837 in Mozambique and *U. mjobergi* Rathbun, 1924 in Darwin, Australia: P. Backwell, personal communication). *Uca uruguayensis* occurs further south than any other species of fiddler crab. The near restriction of hood building to the end of the season could reflect the long period needed to recover from the prolonged period of cold weather and inactivity. A comparison with hood building in populations of *U. uruguayensis* in warmer northern parts of its range where it breeds year round (Costa et al., 2006) should be informative.

Studies of hood building by *U. terpsichores* (Christy et al., 2001) and *U. lactea* (Kim et al., 2004) have failed to find a relationship between the number of hoods and crab density. Common density ranges of *U. terpsichores* and *U. lactea*, however, could be comparable to low densities plots of *U. uruguayensis*. We had expected that males would more often build hoods at higher densities where underground matings in males' burrows were relatively more common. In contrast, we found that more males built hoods at low densities, where surface matings were more frequent than underground matings. When we evaluated the effect of mating mode, however, we found that, as expected, underground matings explained more variation in the proportion of males with hoods than surface matings. Consideration of the mechanisms crabs use to orient to and find their burrows and the social and spatial context of courtship and mate choice suggest a possible explanation. Fiddler crabs are able to locate and orient to the opening of their burrow using vision. Due to perspective foreshortening and to the geometry and configuration of their eyes, however, fiddler crabs cannot see their burrow opening if they are more than about 10 body lengths away (Zeil and Layne, 2002). To orient to their burrows from greater distances, fiddler crabs use path maps based on an egocentric spatial frame of reference and an idiothetic source of information (Layne et al., 2003). A male that loses contact with the

Table 5. summary of the analysis of deviance for the generalized linear model, fitting the proportion of males with hoods in relation to density class (high and low), the number of underground matings per male, and the number of surface matings per male. GLM was fit under binomial distribution and logit link function.  $D^2$  is the explained deviance. The overdispersion parameter was 8.12. Wald test for model goodness of fit:  $F = 18.48$ ,  $df = 5, 114$ ,  $p < 0.0001$ .

Factor	Scaled deviance	df	p-value	$D^2$
Density	35.50	1	<0.0001	14.10
Underground matings	106.2	1	<0.0001	42.41
Surface matings	38.66	1	<0.0001	15.44
Density × Underground matings	5.05	1	0.0246	2.02
Density × Surface matings	2.29	1	0.1299	0.92
Residual	62.92	114		

surface during combat or that makes complex movements while courting could experience errors in its path map, leading to an off-target return to its burrow. More recent studies show how hoods could serve as landmarks that males use to relocate their burrows (Ribeiro et al., 2006) and as beacons marking home allowing males to move more freely when courting (Kim et al., 2010a; Kim and Christy, 2015). Our results thus suggest that hoods could play a key role for underground mating specially at low densities, putting males a premium on hood building for monitoring and relocating their burrows. As inter-burrow distances are greater at lower densities it is likely that males venture further from their burrows to court and attract passing females than they do to court and mate on the surface with neighbouring females. At high densities, even when underground matings are more common than surface matings, males may not need to go as far to court and attract females and they could be less likely to build hoods.

Although the proportion of males with hoods was mainly explained by underground matings, the function of hoods for male orientation is still likely to be important when males mate on the surface with females resident at more distant burrows. In fact, 15% of variation of hood building could be accounted by surface matings. Consideration of hoods both as sexual signals to females and as objects to which males orient to relocate their own burrows could be necessary to explain the pattern of hood building by male *U. uruguayensis*.

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