

Variable sex-specific mortality due to shorebird predation on a fiddler crab

Pablo D. Ribeiro, Oscar O. Iribarne, Luciano Jaureguy, Diego Navarro, and Eugenia Bogazzi

Abstract: Male fiddler crabs compete for access to mates mainly by displaying an enlarged claw. One cost of this large claw is presumed to be higher exposure to predators. The fiddler crab *Uca uruguayensis* is used as a food source by several Neotropical migratory shorebirds. We investigated whether crab density and male claw-waving behaviour increase predation by shorebirds. The sex ratio of crabs on the surface was strongly male biased. Male crabs showed a daily succession of feeding–waving–feeding activities and their dry mass at the site decreased with a high density of crabs, suggesting stronger male–male competition than at sites with a low density of crabs. Sex-specific predation varied according to shorebird species. The Ruddy Turnstone (*Arenaria interpres*) preyed intensively on male crabs when they were courting and at sites with a high density of crabs, the Black-bellied Plover (*Pluvialis squatarola*) and the Lesser Golden Plover (*Pluvialis dominica*) preyed on crabs of both sexes, and the Whimbrel (*Numenius phaeopus*) foraged intensively on females. When estimating the net effect of all predators, we found that the four shorebird species together were able to consume between 0.1 and 0.2% of the crab population, and consumption did not differ between the sexes of crabs. These mortality rates indicate a low source of mortality, likely unable to produce deviations in the sex ratio of the population. Thus, our results indicate that a trait thought to be sexually selected does not necessarily lead to a disproportionate increase in mortality due to predation.

Résumé : Les crabes violonistes mâles font compétition pour les femelles principalement en exhibant leur pince élargie. Un des coûts associés à cette grande pince est sans doute une exposition accrue aux prédateurs. Le crabe violoniste *Uca uruguayensis* sert de nourriture à de nombreux oiseaux de rivage migrants néotropicaux. Nous avons vérifié si la densité des crabes et le comportement d'agitation de la pince par les mâles augmentent la prédation par les oiseaux de rivage. Le rapport mâles : femelles des crabes à la surface favorise nettement les mâles. Les crabes mâles ont une succession journalière d'activités d'alimentation, d'agitation de la pince, d'alimentation et ils ont une masse sèche plus faible au site où la densité des crabes est la plus grande, ce qui fait croire à un niveau de compétition entre les mâles plus élevé qu'à des sites à faibles densités de crabes. La prédation spécifique au sexe varie selon les espèces d'oiseaux. Le tourne-pierre à collier (*Arenaria interpres*) fait une forte prédation des crabes mâles pendant leur comportement de cour et aux sites de fortes densités de crabes, le pluvier argenté (*Pluvialis squatarola*) et le pluvier doré d'Amérique (*Pluvialis dominica*) se nourrissent de crabes des deux sexes et le courlis corlieu (*Numenius phaeopus*) fait une chasse intense des femelles. En estimant l'effet net de tous les prédateurs, nous avons découvert que l'ensemble des oiseaux de rivage arrive à consommer entre 0,1 et 0,2 % de la population de crabes, sans différence entre les sexes. Ces valeurs de mortalité indiquent qu'il s'agit d'une source de mortalité trop faible pour expliquer les déviations du rapport mâles : femelles de la population. Nos résultats montrent aussi qu'une caractéristique qu'on croit être soumise à la sélection sexuelle ne mène pas nécessairement à un accroissement disproportionné de la mortalité due à la prédation.

[Traduit par la Rédaction]

Introduction

In species where the females make the major reproductive investment, it is common for males to develop courtship displays (Andersson 1994). Courtship displays are thought to be an outcome of sexual selection (Darwin 1874; Andersson 1994) and have a function in stimulating females before mating (see Halliday 1983) and in assessing genetic benefits

(Alcock 1989; Andersson 1994) by the production of visual signals that may indicate mate quality (Zahavi 1987). In all cases, courtship displays involve conspicuous characteristics or behaviours that make the male that produces them more detectable and thus more available to predators.

Given that predation risk is often high for species with conspicuous courtship displays (Trivers 1985; Krebs and Davies 1993), individuals may adjust their risk-taking be-

Received 28 October 2002. Accepted 20 May 2003. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 26 August 2003.

P.D. Ribeiro,^{1,2} O.O. Iribarne,² L. Jaureguy, D. Navarro. Departamento de Biología, Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG Mar del Plata, Argentina.

E. Bogazzi.² Instituto Nacional de Investigación y Desarrollo Pesquero, Paseo Victoria Ocampo N° 1, P.O. Box 175, B7602HSA Mar del Plata, Argentina.

¹Corresponding author (e-mail: pdribeir@mdp.edu.ar).

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET).

haviour in relation to the expected mating probabilities (Kålås et al. 1995), which results in a trade-off between mating and avoiding predators (Magnhagen 1991; Koga et al. 1998). However, mating success also depends on the level of intrasexual competition and the probability of encountering mates (Kålås et al. 1995). Thus, as the operational sex ratio becomes more male dominated, males expend more energy in courtship activities (Riechert 1988; Iribarne 1996), usually increasing their exposure to predators.

Fiddler crabs provide a good example of the use of visual courtship displays. They exhibit an extreme sexual dimorphism (Crane 1975; Christy and Salmon 1984), males having a single enlarged claw that often accounts for more than 30% of body mass (Crane 1975; Hyatt and Salmon 1978). The males wave the claw as a signal to attract females and use it as a weapon in male–male combat (Hyatt and Salmon 1978; Greenspan 1980; Christy 1983). The size of the claw is likely to benefit individuals during courtship and thus this dimorphism can be the product of sexual selection (Darwin 1874; Andersson 1994). However, the increased visibility (due to the dimensions and colour of the enlarged claw) is likely to reduce the survival of males because they are conspicuous to predators and it may hinder their escape (Montague 1980). In contrast, although there are species in which the females are brightly coloured (e.g., *Uca flammula*; Crane 1975), most females are not conspicuous and thus are less visible to predators. As a result, if a predator bases its ability to capture prey on the visibility or detectability of the prey, a female-biased sex ratio would be expected. However, many fiddler crab species have a strong male-deviated sex ratio (e.g., Thurman 1985; Spivak et al. 1991; Emmerson 1994), which may be due to greater predation on females. Given the heavier exoskeleton of males, which leads to a lower relative energy content than that of females (Zwarts and Blomert 1990), and the presence of the enlarged claw, which increases handling time and the possibility of injury, it is likely that males are not the best prey for some predators (Bildstein et al. 1989). Thus, a predator maximizing its capture rate may feed on males when they are in good supply, but a predator maximizing prey quality may search for females (Koga et al. 2001).

The fiddler crab *Uca uruguayensis* is the southernmost Atlantic species of the genus (Crane 1975) and ranges from southern Brazil (33°S) to the northern coast of Argentina (38°S; Crane 1975). Several Neotropical migratory shorebirds (those that breed in the northern hemisphere) such as the Lesser Golden Plover (*Pluvialis dominica*), Black-bellied Plover (*Pluvialis squatarola*), Ruddy Turnstone (*Arenaria interpres*), and Whimbrel (*Numenius phaeopus*) are their main predators (Iribarne and Martínez 1999). Each shorebird species has a particular feeding strategy that leads to the capture of different prey. The Lesser Golden Plover captures mostly juveniles, the Black-bellied Plover and Whimbrel capture mostly females, and the Ruddy Turnstone captures mostly large male crabs (Iribarne and Martínez 1999). The reason for these differences is still not well understood. In this study, we explored whether differential exposure of the sexes due to courtship by male crabs accounts for sex-specific predation by the four shorebird species. We were interested to determine whether the density at which crabs occur is related to the level of male–male competition, and

thus to the level of exposure to predation. Finally, we explored whether sex-specific predation was the outcome when the effects of predation by the four shorebird species were combined.

Materials and methods

Study area

The study was conducted near the mouth of the San Clemente tidal creek (eastern Bahía Samborombón, Argentina, 36°22'S, 56°45'W), an area affected by low-amplitude (<1.4 m) semidiurnal tides. This bay is an important stop-over for migratory shorebirds (Morrison and Ross 1989; Botto et al. 1998). The southernmost permanent population of *U. uruguayensis* inhabits this area and reaches densities of up to 140 individuals/m² (Iribarne and Martínez 1999). They occur in the upper levels of the tidal flats near the fringe of an extensive *Spartina densiflora* marsh. They are active on the surface from September to April, remaining inside their closed burrows the rest of the time (Spivak et al. 1991).

A beach (1000 m long and 100 m wide at low tide) with large settlements of *U. uruguayensis* was selected for observing shorebirds and crabs. Based on previous information (Iribarne and Martínez 1999) we identified, at the same intertidal level, three areas (2760, 3100, and 5380 m²) with a high density of crabs (50–140/m²) (hereinafter high-density sites) and three areas (2150, 3240, and 3710 m²) with a low density of crabs (10–40/m²) (hereinafter low-density sites). At these sites we observed the behaviour of shorebirds and crabs during five 3-day periods during the summer of 1999. The five sampling periods were the 11–13 and 26–28 January, 8–10 and 22–24 February, and 9–11 March. These periods encompassed most of the time during which migratory shorebirds are in the region.

Behaviour of *U. uruguayensis*

Seasonal changes in behaviour

We explored whether crabs at the high-density and low-density sites behaved similarly during the summer in relation to (i) the sex ratio on the surface and (ii) the proportion of male crabs engaging in courtship activities. At low tide on the first day of each set of sampling periods we counted the open burrows in 10 randomly located squares (0.5 × 0.5 m) at each of the three high-density and three low-density sites. The number of burrows is an indicator of crab activity on the surface. During the first day of each sampling period we made scanning observations of crabs at low tide using a 36× spotting scope and from a distance of 20 m. Five samples were obtained from a high-density site and five from a low-density site, in which we counted the crabs of each sex within the focal length of the scope (0.40 m²). In the case of male crabs, we also noted if they were waving their enlarged claw. Daily samples were pooled.

The sex ratio of crabs on the surface (i.e., those available to shorebirds) may differ from that of the whole population. We therefore estimated the population sex ratio in January 1999 by digging five samples at one site of each density (0.5 × 0.5 × 0.5 m deep; crab burrows are not deeper than 0.30 m (P. Ribeiro, personal observation)), sieving the sedi-

ment through 0.5-mm mesh and counting all *U. uruguayensis*. Similar procedures were performed in December 1998, January 1999, and February 1999 to estimate the proportion of ovigerous females within a high-density site.

To evaluate the crabs' condition, adult males and females (carapace width larger than 9 mm) were sampled and measured (maximum carapace width; precision 0.02 mm), then dried at 70°C for 48 h and weighed (precision 0.001 g). Given that male crabs have an enlarged claw, we analyzed the sexes separately.

Crab behaviour in relation to low tide

We explored whether crabs at the high-density and low-density sites behaved similarly during the tidal cycle in relation to (i) the sex ratio on the surface and (ii) the proportion of males engaging in courtship activities. We performed hourly focal observations during the whole tidal cycle on the first day of the 26–28 January sampling period at one site of each density. We divided the tidal cycle into 9 tidal moments, determined as the number of hours since low tide (during ebbing = -4, -3, -2, -1 h, low tide = 0; during flooding = +1, +2, +3, +4 h). The tidal amplitude between 0 and 4 tidal moments is 0.8–0.9 m. During each tidal moment, five samples were obtained in which we counted the crabs of each sex within the focal length of the scope (0.40 m²). In the case of males, we also noted whether they were waving their enlarged claw. Hourly samples were pooled.

Behaviour of shorebirds

Habitat use by shorebirds

We assessed whether shorebirds used the sites differently in relation to the behaviour of crabs. For this, during the 3 days of all sampling periods we censused shorebirds hourly (using 10 × 50 binoculars) from emersion to submersion of the sites, dividing the tidal cycle into 9 tidal moments. Species were identified using Narosky and Yzurieta's (1993) field guide. To evaluate habitat use by shorebirds during the summer, we calculated the daily mean number of shorebirds of each species that were feeding at each site during each sampling period. Based on the observed behaviour of crabs during the summer (see Results), we identified a courtship season when more than 70% of male crabs were waving their enlarged claw during low tide (11–13 and 26–28 January sampling periods) and a non-courtship season when fewer than 5% of male crabs were waving their enlarged claw during low tide (8–10 and 22–24 February and 9–11 March sampling periods). In addition, for the courtship season, based on the observed behaviour of crabs during the tidal cycle (see Results), we identified tidal moments when more than 60% of male crabs were engaged in waving behaviour and tidal moments when more than 70% of male crabs were engaged in feeding behaviour. To evaluate habitat use by shorebirds in relation to the waving–feeding behaviour of male crabs, we used the census from the courtship season. From the numbers of shorebirds present while male crabs were feeding for each day and each shorebird species we calculated the mean for the three sites of each density during the tidal moments when the proportion of male crabs engaged in courtship was lower than 0.3 (tidal moments -4,

-3, +3, and +4). From the numbers of shorebirds present while male crabs were waving their enlarged claw, we used a similar procedure for the tidal moments when the proportion of male crabs engaged in courtship was higher than 0.6 (tidal moments -2, -1, +1, and +2). We did not include tidal moment 0, to keep the number of censuses the same as for feeding behaviour.

Foraging behaviour of shorebirds

To evaluate whether changes in the foraging rates of shorebirds were related to changes in the behaviour and density of crabs, we performed focal observations of shorebirds during the complete tidal cycle in all sampling periods. Observations were made at high-density and low-density sites using a 36× spotting scope at least 50 m from the observed area, and the data were recorded on audiotape. Each bird was observed for 5–10 min and the number of male and female *U. uruguayensis* captured was recorded. When performing a focal observation we also recorded the percentage of male crabs waving their enlarged claw. Thus, as was done for the censuses of shorebirds, the observations of the foraging rates of shorebirds on male and female crabs were divided into three behavioural categories: waving behaviour, feeding behaviour, and feeding behaviour during the non-courtship season. In all behavioural categories, females were feeding; however, we also divided the foraging rates of females according to the behaviour of males.

Mortality of *U. uruguayensis* caused by shorebirds

Given that not all shorebirds prey equally on crabs of each sex, we explored whether crab mortality was sex-biased when the effects of all predators were pooled. For this purpose we calculated the percentages of male and female crabs eaten by all shorebirds during the summer.

We first estimated the proportion of crabs (mortality rate) that were eaten in 1 day. We discriminated between the courtship season and the non-courtship season. If the mortality rate was for 1 day within the courtship season, we divided the estimate into two terms, one for the moments of feeding behaviour and other for the moments of waving behaviour. The estimates were of the following form:

$$M_{h,j,k} = (\sum_i F_{i,h,j,k} T_{i,j,k}) / (N_{h,j,k})$$

where M is the mortality rate, F is the foraging rate, T is foraging time spent by the shorebirds, N is the number of crabs at the site, and i denotes shorebird species, h the sex of the crab, j the site density, and k the behaviour of the crab.

Foraging rates were obtained from the focal observations of shorebirds described above. The number of crabs at each site was estimated by digging 25 random samples (1 m² and 0.30 m deep) in each area and multiplying the number of crabs by the dimensions of the areas. The time that each shorebird species spent foraging was estimated from the censuses. As the census resolution was 1 h, each individual counted was interpreted as equal to 1 h of foraging by the respective shorebird species. As a result, the units of T were transformed to a standardized time unit that estimates the time expended in foraging activities. For each day of the courtship season and for each shorebird species we added the number of individuals counted while waving (tidal moments -2, -1, 0, +1, and +2), which constitutes a sample of

$T_{i,j}$ for the waving behaviour. Similarly, we added the number of individuals counted while feeding (tidal moments -4 , -3 , $+3$, and $+4$), which constitutes a sample of $T_{i,j}$ for the feeding behaviour. For each day of the non-courtship season and for each shorebird species we added the number of individuals counted during all tidal moments, constituting a sample of $T_{i,j}$ for the non-courtship season.

We employed a resampling method (Manly 1998), choosing values for $F_{i,h,j,k}$ and $N_{h,j,k}$ randomly. Similarly, we chose $T_{i,j,k}$ values randomly, but kept together the $T_{i,j,k}$ values for different shorebird species from the same day to avoid overestimating the maximum number of shorebirds foraging at each site and to maintain the structure of shorebird occurrences (i.e., we do not know whether there is a correlation between shorebird species). $M_{h,j}$ values for the courtship season were estimated, adding a $M_{h,j}$ value for the waving behaviour plus a $M_{h,j}$ value for the feeding behaviour; both were calculated from $T_{i,j,k}$ values for the same day. Finally, the level of predation pressure was calculated by adding a $M_{h,j}$ value for the courtship season multiplied by the total number of days in the courtship season plus a $M_{h,j}$ value for the non-courtship season multiplied by the total number of days in the non-courtship season. This yielded $M_{h,j}$ values for the whole summer. Based on our observations, we assigned 3 months to the courtship season (November, December, and January) and 2 months to the non-courtship season (February and March). We also counted the days on which crabs were not available to predators because of (i) rain or (ii) a southeasterly wind that prevented the emersion of the tidal flats. As a result, the courtship season included 70 days when crabs were available to predators and the non-courtship season included 45 days. This is an approximation, but serves as an indicator of predation pressure. Standard normal confidence limits (Manly 1998) were constructed to evaluate significant differences in the percentage of crabs eaten in relation to sex and density.

Statistical analysis

To evaluate significant differences between means, we employed ANOVA (Neter et al. 1991). In cases of unbalanced designs, Type III sum of squares was employed. Factors were always fixed and we used a repeated-measures design when the levels of a factor were paired or were obtained from the same sampling unit. Scheffé's test was used for all a posteriori testing. Analysis of covariance (ANCOVA) was employed to assess differences between regression equations (Neter et al. 1991). Differences between frequencies or proportions were evaluated by means of contingency tables (Zar 1999). In cases of multiple testing, we corrected P values for Type I error bias by applying the sequential Bonferroni technique (Rice 1989). We used a 0.05 level of significance in all cases.

Results

Behaviour of *U. uruguayensis*

Seasonal changes in behaviour

The mean number of open burrows ranged between 60 and 100/m² at high-density sites and between 20 and 40/m² at low-density sites (Fig. 1A). The sex ratio of crabs on the

surface was significantly male biased initially, but this declined over the season, and more rapidly at low-density sites (Fig. 1B). The level of courtship activity was significantly higher during January, declined abruptly in February, and was zero during March (Fig. 1C).

The sex ratio of the *U. uruguayensis* population obtained by digging was significantly male biased (1.40 at high-density sites; $\chi^2_{[1]} = 4.67$, $P < 0.05$; 1.42 at low-density sites; $\chi^2_{[1]} = 3.98$, $P < 0.05$), but ratios were similar between densities ($\chi^2_{[1]} = 0.003$, $P > 0.9$). The proportion of ovigerous females (Fig. 1C) decreased significantly from 50% in January to less than 5% in February ($\chi^2_{[2]} = 41.81$, $P < 0.001$).

Male crabs at the low-density sites were significantly heavier than those at the high-density sites ($F_{[1,336]} = 4.75$, $MS_{\text{effect}} = 0.02129$, $P < 0.05$, square-root transformation; Fig. 2A). However, females showed no differences ($F_{[1,178]} = 0.18$, $MS_{\text{effect}} = 0.00008$, $P > 0.6$; Fig. 2B) between densities.

Crab behaviour in relation to low tide

Crabs remained inside burrows when the areas were covered by high tide (and when it rained). Then, as the burrowing areas were uncovered (Fig. 3A), crabs emerged (Fig. 3B) and remained active on the surface until a few minutes before the areas were flooded again by the incoming tide. The sex ratio on the surface was strongly male biased during the hours of low tide, and was less biased in moments near to high tide (Fig. 3C). This cyclical trend was significant at high-density sites ($\chi^2_{[8]} = 37.79$, $P < 0.0001$) but not at low-density sites ($\chi^2_{[8]} = 13.86$, $P > 0.08$). The proportion of males engaged in courtship was higher during the hours of low tide and was almost absent during moments near to high tide (high-density sites: $\chi^2_{[8]} = 3.68$; low-density sites: $\chi^2_{[8]} = 98.72$, $P < 0.0001$ for both; Fig. 3D). The sex ratio and proportion of males engaged in courtship did not differ significantly between densities.

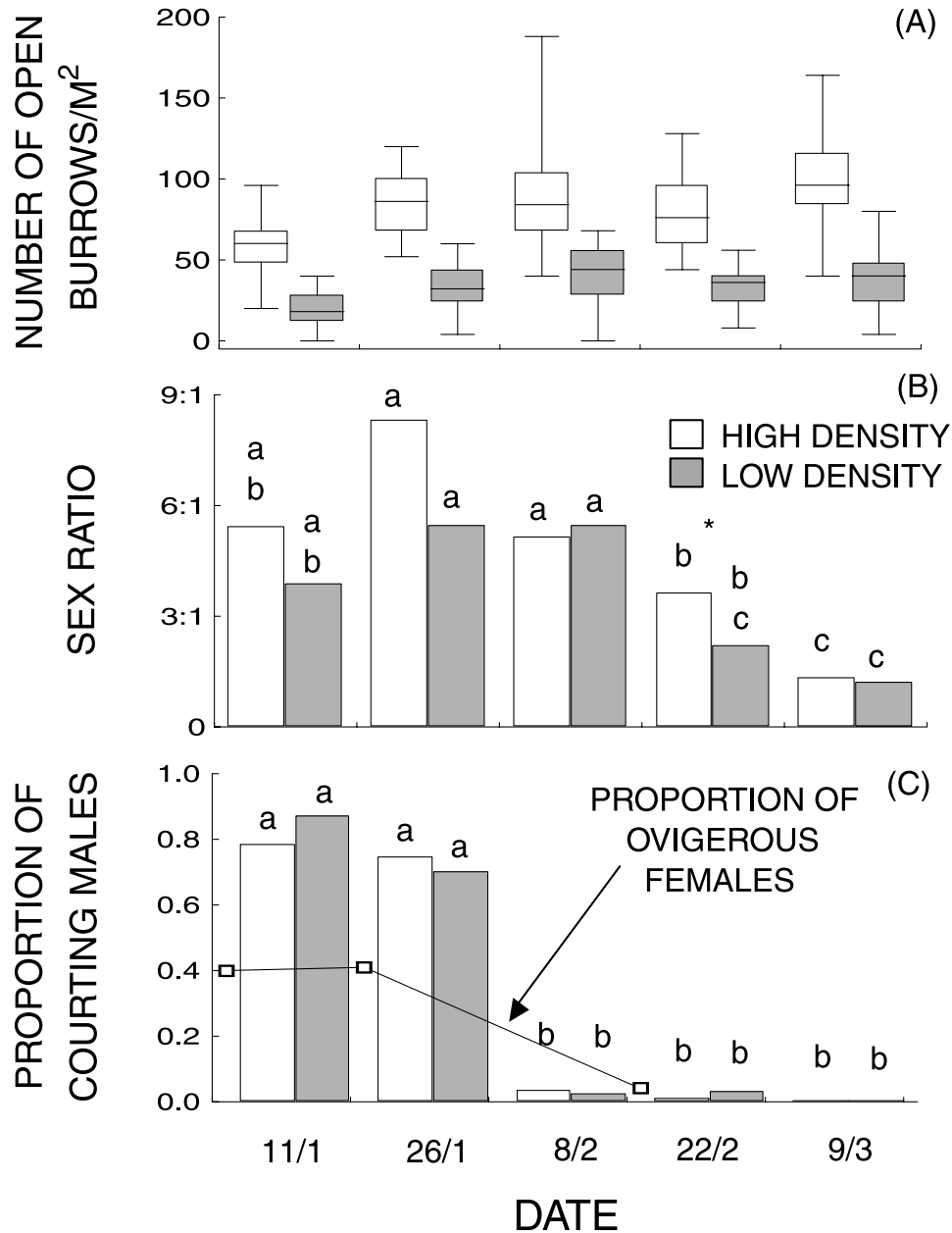
Behaviour of shorebirds

Habitat use by shorebirds

Field observations of shorebird activity were performed for a total of 114 h. The shorebirds observed feeding on *U. uruguayensis* included the Ruddy Turnstone, Whimbrel, Black-bellied Plover, and Lesser Golden Plover. Except for the Whimbrel, which preyed exclusively on *U. uruguayensis*, the other shorebirds also preyed on other infaunal organisms such as polychaetes, small molluscs, and scyphozoan medusae. The Hudsonian Godwit (*Limosa haemastica*), the Gull-billed Tern (*Sterna nilotica*), and the resident Great Kiskadee (*Pitangus sulphuratus*) occasionally preyed on *U. uruguayensis* but, given their sporadic occurrence, they were not included in the analysis.

During the summer, the abundance of shorebirds at high-density sites was higher than at low-density sites, and there was a significant interaction between shorebird species and date (Table 1, Fig. 4). Within the courtship season the abundance of shorebirds was also higher at high-density sites than at low-density sites, but did not differ between waving and feeding behaviour nor between shorebird species (Table 2, Fig. 5).

Fig. 1. Seasonal behaviour of fiddler crabs (*Uca uruguayensis*) according to date (day/month). (A) Density of open burrows. (B) Sex ratio of crabs on the surface. The asterisk indicates differences between densities. (C) Proportions of courting males (bars) and proportions of ovigerous females (squares). In B and C, different lower-case letters indicate differences within densities.

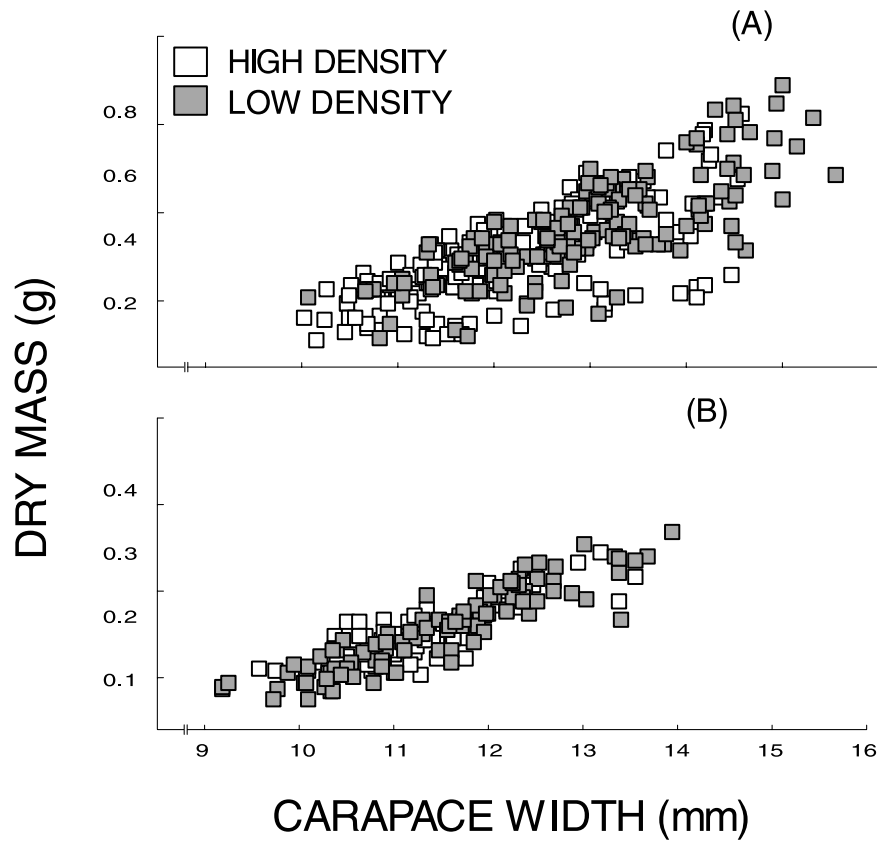


Foraging behaviour of shorebirds

Focal observations of 62 Ruddy Turnstones were performed for a total of 245 min. During the courtship season this species foraged at both high-density and low-density sites when male crabs were either waving or foraging. Foraging behaviour consisted of continuous walking (92% of foraging time) over the entire area. This walking took the crabs away from the vicinity of their burrows. Most captures were made on the surface (90.3%, $n = 56$) and the enlarged claw was rarely eaten (6.4%, $n = 4$). The remaining captures included individuals trapped in holes or burrows. These were individuals that tried to enter a neighbouring burrow, but could not enter completely because of their large size. Con-

sequently, they could be extracted by shorebirds, commonly with violence, leaving signs of disturbance at the burrow entrance. There was a significant interaction effect between sex, behaviour, and density of *U. uruguayensis* on the foraging rate of Ruddy Turnstones (Table 3). In general, during the courtship season, Ruddy Turnstones captured mostly males at high-density sites, but also foraged on females at low-density sites and during the non-courtship season (Fig. 6A).

Focal observations of 35 Whimbrels were performed for a total of 95 min, and *U. uruguayensis* was the only prey captured. Given that most foraging Whimbrels (88.6%, $n = 35$) were observed during the courtship season of the crabs, we

Fig. 2. Relationships between dry mass and carapace width of male (A) and female (B) *U. uruguayensis*.**Table 1.** Summary of three-factor repeated-measures ANOVA evaluating the abundance of shorebirds in relation to density of fiddler crabs (*Uca uruguayensis*) at a site (high and low), shorebird species, and date.

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	4	30.3093	18.66*
Species	3	12	4.2022	3.25 ns
Date	4	16	14.3174	7.72**
Density × species	3	12	0.8769	0.68 ns
Density × date	4	16	1.8291	0.99 ns
Species × date	12	48	2.2945	3.46**
Density × species × date	12	48	0.5737	0.87 ns

Note: Shorebird species is included as a repeated-measures factor. Data are square-root transformed to fit sphericity. *, $P < 0.05$; **, $P < 0.01$; ns, not significant.

restricted the analysis of foraging behaviour to this season. This species walked slowly, with short periods of inactivity (18% of the 95 min of foraging time). Whimbrels captured most prey by probing inside crab burrows with their large curved bill, but they captured some crabs on the surface (11.4%, $n = 4$). Whimbrels foraged mostly on females, and showed no differences according to density or crab behaviour (Table 4, Fig. 6B).

Focal observations of 51 Black-bellied Plovers were performed for a total of 253 min. This species made short runs and stops, performing a stop–run–stop sequence. While stopped, they inspected the area for available prey. Then

Table 2. Summary of three-factor repeated-measures ANOVA evaluating the abundance of shorebirds in relation to shorebird species and behaviour (feeding and waving) and density of *U. uruguayensis* at a site (high and low).

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	20	8.7505	13.68**
Behaviour	1	20	0.0023	0.003 ns
Species	3	60	0.1189	0.68 ns
Density × behaviour	1	20	0.1553	0.24 ns
Density × species	3	60	0.1623	0.92 ns
Behaviour × species	3	60	0.1307	0.74 ns
Density × behaviour × species	3	60	0.3017	1.71 ns

Note: Shorebird species is included as a repeated-measures factor. Data are $x^{(0.25)}$ -transformed to fit homoscedasticity. **, $P < 0.01$; ns, not significant.

they ran quickly, captured a crab, and moved to a new waiting position (they were inactive for 71% of foraging time). They also caught crabs (9.8%, $n = 5$) that were plugging their burrows with mud when the flooding tide was covering the area. The foraging rates of Black-bellied Plovers did not change with density. However, there was a significant interaction between sex and behaviour of crabs (Table 5, Fig. 6C): males were more preyed upon than females when they were waving but less preyed upon than females when they were feeding.

Fifty-five Lesser Golden Plovers were observed for a total of 233 min. The foraging behaviour of this species was simi-

Fig. 3. Behaviour of *U. uruguayensis* according to the tide. (A) Tidal cycle. The broken lines show intertidal levels. (B) Densities of crabs on the surface. (C) Sex ratios of crabs on the surface. (D) Proportions of courting males. In C and D, different lower-case letters indicate differences within densities.

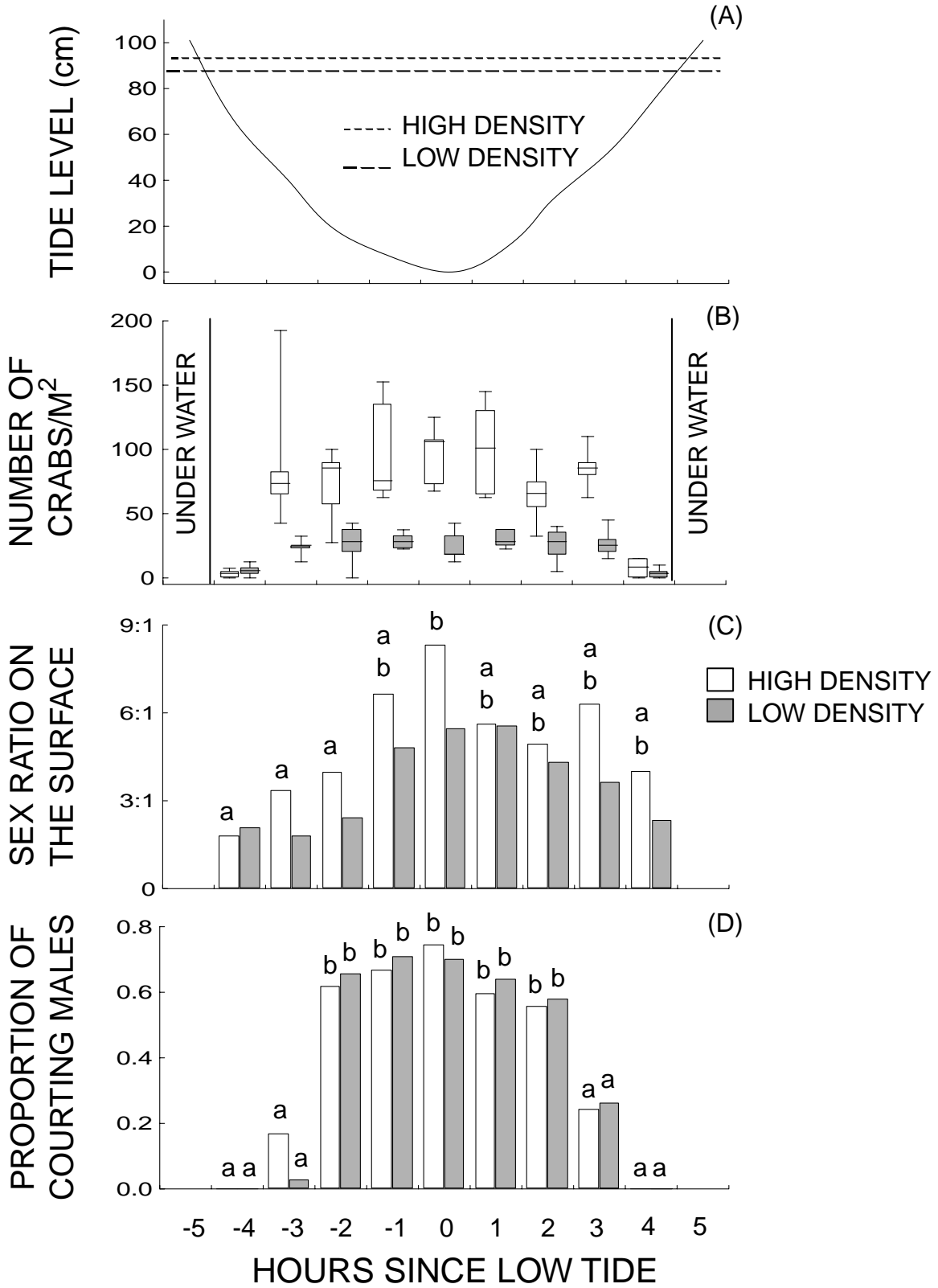


Fig. 4. Occurrences of shorebird species during the summer by date (day/month). The limits of the whiskers are the 0.99 and 0.01 percentiles and the marker is the median. RT, Ruddy Turnstone; W, Whimbrel; BBP, Black-bellied Plover; LGP, Lesser Golden Plover. Different lower-case letters indicate differences in occurrence for the shorebird species × date interaction.

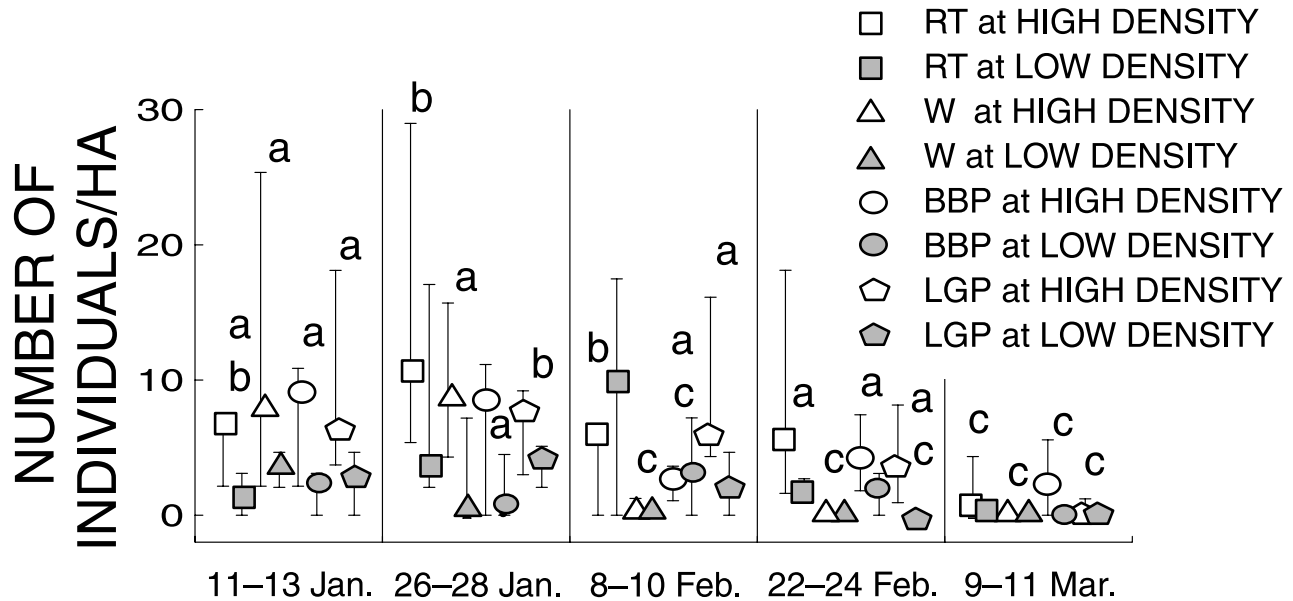
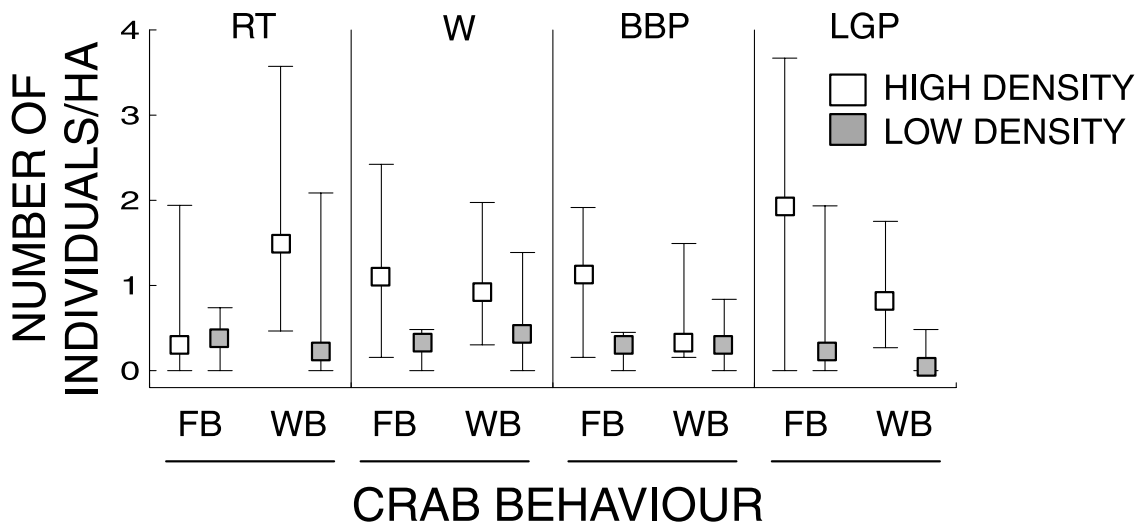


Fig. 5. Occurrences of shorebird species during the courtship season in relation to the density and behaviour of *U. uruguayensis*. FB, feeding behaviour; WB, waving behaviour; RT, Ruddy Turnstone; W, Whimbrel; BBP, Black-bellied Plover; LGP, Lesser Golden Plover.



lar to that of the Black-bellied Plover but with shorter periods of inactivity (62% of foraging time; χ^2 test comparing both species: $\chi^2_{(1)} = 141.39, P < 0.01$). However, they were never observed foraging at sites when crabs were engaged in waving behaviour. Lesser Golden Plovers always ate similar numbers of male and female crabs (Table 6, Fig. 6D).

Mortality of *U. uruguayensis* caused by shorebirds

Estimated mortality rates indicate that shorebirds in Bahía Samborombón are able to consume, on average, between 0.1 and 0.2% of the population of *U. uruguayensis* (Table 7).

Confidence limits indicate that differences related to sex and density are not significant (Table 7).

Discussion

Behaviour of *U. uruguayensis*

While the population sex ratio was slightly male biased, the sex ratio on the surface was strongly male biased in January and this decreased by the end of summer. The proportion of ovigerous females decreased by February; ovigerous females stay in burrows until their eggs hatch (Bogazzi et al.

Fig. 6. Foraging rates of Ruddy Turnstones (A), Whimbrels (B), Black-bellied Plovers (C), and Lesser Golden Plovers (D). The limits of each box are the 0.75 and 0.25 percentiles, the vertical lines represent the 0.01 and 0.99 percentiles, and the line within the box is the median. FB, feeding behaviour during the courtship season; WB, waving behaviour during the courtship season; NCS, feeding behaviour during the non-courtship season. An asterisk indicates differences in foraging rate between male and female prey. Different lower-case letters indicate differences between crab densities and behaviours (within sex).

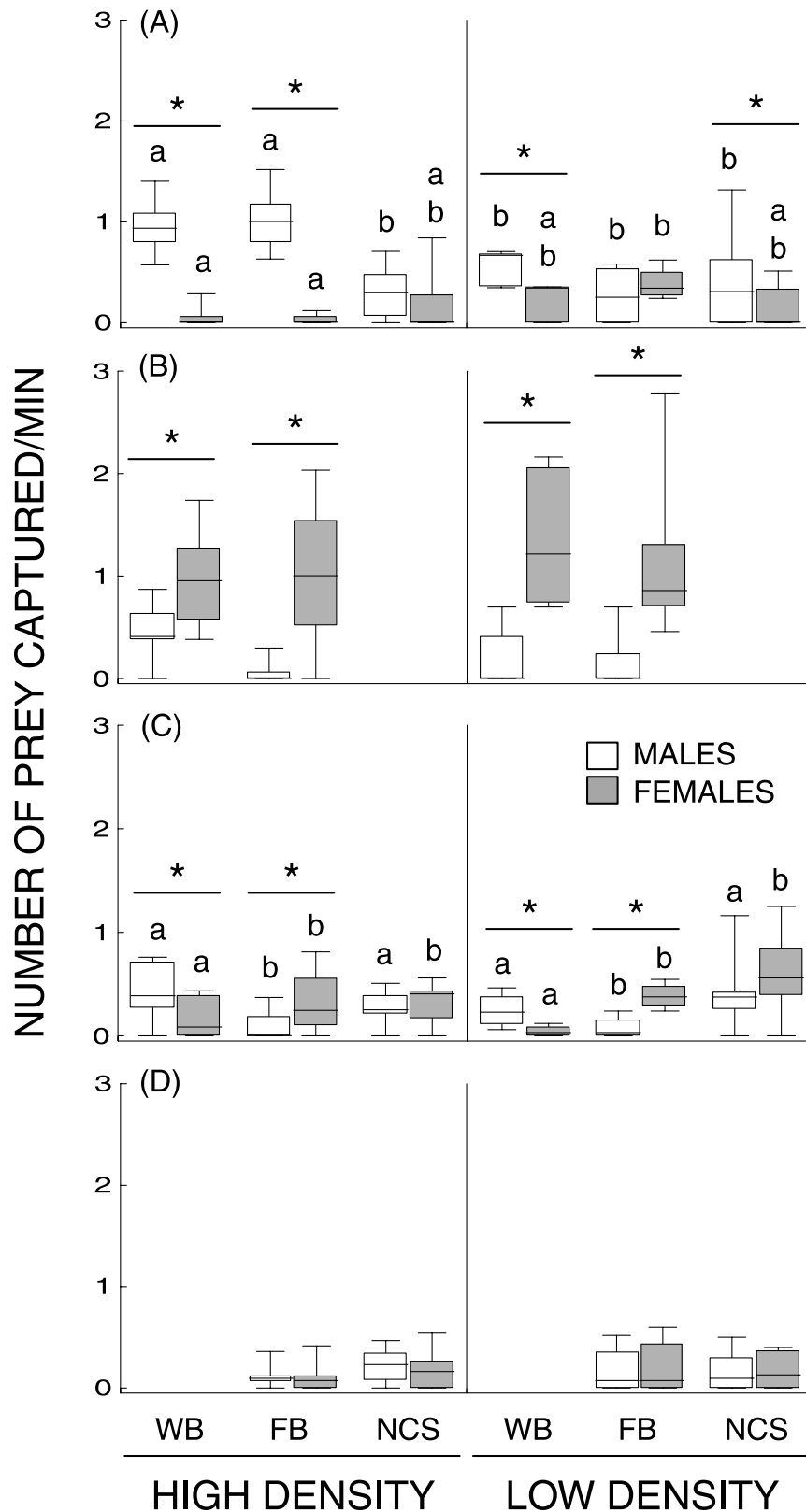


Table 3. Summary of Type III sum of squares three-factor ANOVA evaluating the foraging rate of Ruddy Turnstones in relation to the sex, density, and behaviour of *U. uruguayensis*.

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	40	0.0001	2.97 ns
Behaviour	2	40	0.0001	6.39**
Sex	1	40	0.0008	47.82**
Density × behaviour	2	40	0.00003	1.59 ns
Density × sex	1	40	0.0003	18.32**
Behaviour × sex	2	40	0.0001	5.41**
Density × behaviour × sex	2	40	0.0002	10.41**

Note: The ANOVA design incorporates two levels for the density factor (high and low density), three levels for the behaviour factor (feeding behaviour, waving behaviour, and feeding behaviour during the non-courtship season), and sex as a repeated-measures factor. **, $P < 0.01$; ns, not significant.

Table 4. Summary of Type III sum of squares three-factor ANOVA evaluating the foraging rate of Whimbrels in relation to the sex, density, and behaviour of *U. uruguayensis*.

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	20	0.00001	0.23 ns
Behaviour	1	20	0.0001	1.20 ns
Sex	1	20	0.0026	32.02**
Density × behaviour	1	20	0.000002	0.02 ns
Density × sex	1	20	0.0001	0.98 ns
Behaviour × sex	1	20	0.00002	0.24 ns
Density × behaviour × sex	1	20	0.0001	0.77 ns

Note: The ANOVA design incorporates two levels for the density factor (high and low density), two levels for the behaviour factor (feeding behaviour and waving behaviour), and sex as a repeated-measures factor. **, $P < 0.01$; ns, not significant.

Table 5. Summary of Type III sum of squares three-factor ANOVA evaluating the foraging rate of Black-bellied Plovers in relation to the sex, density, and behaviour of *U. uruguayensis*.

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	30	0.0002	0.17 ns
Behaviour	2	30	0.0054	4.07*
Sex	1	30	0.0002	0.15 ns
Density × behaviour	2	30	0.0017	1.26 ns
Density × sex	1	30	0.0002	0.13 ns
Behaviour × sex	2	30	0.0084	5.71**
Density × behaviour × sex	2	30	0.0001	0.06 ns

Note: The ANOVA design incorporates two levels for the density factor (high and low density), three levels for the behaviour factor (feeding behaviour, waving behaviour, and feeding behaviour during the non-courtship season), and sex as a repeated-measures factor. Data are square-root transformed to fit homoscedasticity. *, $P < 0.01$; **, $P < 0.01$; ns, not significant.

2001), which seems to cause the bias in the sex ratio on the surface observed during January. Courtship activity was observed during January, concurrent with the male-biased sex ratio, decreased in February, and did not occur in March, when feeding was the only activity. This pattern is also observed in other fiddler crabs (Zucker 1978; Wolfrath 1993).

Table 6. Summary of Type III sum of squares three-factor ANOVA evaluating the foraging rate of Lesser Golden Plovers in relation to the sex, density, and behaviour of *U. uruguayensis*.

Source of variation	df _{effect}	df _{error}	MS _{effect}	F
Density	1	24	0.0001	0.15 ns
Behaviour	1	24	0.0008	1.56 ns
Sex	1	24	0.0001	0.08 ns
Density × behaviour	1	24	0.0007	1.45 ns
Density × sex	1	24	0.0004	0.19 ns
Behaviour × sex	1	24	0.00002	0.01 ns
Density × behaviour × sex	1	24	0.00001	0.003 ns

Note: The ANOVA design incorporates two levels for the density factor (high and low density), three levels for the behaviour factor (feeding behaviour and feeding behaviour during the non-courtship season), and sex as a repeated-measures factor. Data are square-root transformed to fit homoscedasticity. ns, not significant.

Table 7. Estimates of the proportions of crabs eaten during one summer by the four shorebird species combined.

	Mean	Median	SD	−95% confidence limits	+95% confidence limits
High-density sites					
Males	0.1548	0.1364	0.0902	0.0355	0.4703
Females	0.1814	0.1622	0.1127	0.0367	0.5890
Low-density sites					
Males	0.1257	0.0968	0.1071	0.0074	0.8609
Females	0.2261	0.1908	0.1641	0.0352	0.8474

Note: Standard normal confidence limits were constructed after log-transformation.

Behaviour during the tidal cycle followed a foraging–waving–foraging pattern. As soon as the crab beds were uncovered, crabs emerged from their burrows and started feeding for a variable period, then male crabs shifted to courtship behaviour. Female crabs either continued feeding by their burrows or left their burrows in search of a mate. During the flooding tide, crabs reinitiated their feeding activities until the bed was again covered by the tide. At this point, all crabs sheltered in their burrows. The sex ratio showed the highest bias towards males during low tide. This pattern may be due to sex differences in feeding ability, given that males have a single feeding appendage and have to spend more time feeding than females, thus increasing their exposure to predators (Valiela et al. 1974). We found that this variation was significant only at high-density sites, indicating that changes in the sex ratio are greater. Given that the level of male–male competition (Kvarnemo and Ahnesjö 1996; Jirotkul 1999) is likely to be related to the bias in the sex ratio, greater variation in the sex ratio at high-density sites may result in higher variance in the level of competition. Furthermore, dry mass of males at low-density sites was higher than that of males at high-density sites, which may have been due to differences in both energetic condition and morphometric characteristics (e.g., differences in the length of the enlarged claw as a result of autotomy; Backwell et al. 2000). Both possibilities suggest a higher level of male–male competition at high-density sites, a pat-

tern expected in mating systems with sexual dimorphism (Bateson 1983). Given these results, we expected that those shorebirds which took advantage of exposure of male crabs during courtship would have higher foraging rates at high-density sites than at low-density sites.

Shorebird foraging behaviour

Birds that ate *U. uruguayensis* showed distinct foraging patterns that varied by species. Ruddy Turnstones, which walked continuously across the whole flat and ate crabs on the surface, varied their foraging behaviour according to crab density and behaviour. At high-density sites, Ruddy Turnstones preyed exclusively on male crabs when they were waving. However, these birds also captured females when they foraged at low-density sites or when the courtship season of crabs had finished. These differences indicate a relationship between prey availability and behaviour and may result from differential exposure of the sexes, given that when a predator is present, waving males stay longer on the surface than females or males that are not trying to attract females (e.g., Backwell et al. 1998; P. Ribeiro, personal observation). Whimbrels, which probe burrows as they travel slowly across the mud flat, showed no variations in their foraging rate according to crab density or behaviours. We do not know whether Whimbrels ate more females because they selected them; however, they did not take advantage of the exposure of male crabs while waving, which may in some way reflect the cost of preying on the most available but least profitable prey (Bildstein et al. 1989; Zwarts and Blomert 1990). The foraging behaviour of Black-bellied Plovers, which chased a crab on the surface, then stopped and looked before chasing a new one, did not differ between densities, but there was an interaction between crab behaviour and sex on the foraging rate of these plovers. Black-bellied Plovers mostly ate males when they were waving, and ate females when male crabs were feeding. This may be due to their preference for female crabs, but they may also take advantage of males when they are waving. The foraging behaviour of Lesser Golden Plovers, which showed a similar foraging strategy to Black-bellied Plovers, did not change with crab behaviour. However, during the crab courtship season, Lesser Golden Plovers did not forage when male crabs were waving, which in some way indicates differential habitat use. Further, Lesser Golden Plovers did not seem to take advantage of male vulnerability as was observed with Black-bellied Plovers, which may be evidence that male crabs are not a good prey item for them.

The shorebird–crab interaction

Intertidal areas are commonly used by migratory shorebirds as stopover sites (Adam 1990; Morrison and Ross 1989) and, given that the energy demands of moult and fat deposition are high (Schneider 1983), foraging rates are expected to be high. Thus, predation usually has an intense impact on intertidal organisms (Mercier and McNeil 1994), which is often episodic and predictable from year to year (Wilson 1991). This is not the pattern of predation on *U. uruguayensis* by migratory shorebirds in Bahía Samborombón. However, their effect on prey (measured as the mortality rate) was affected by several factors, including crab

foraging, crab sexual behaviours, and their own foraging patterns.

As expected, the rate of predation by shorebirds exploiting male crabs' vulnerability during courtship was higher when male crabs were waving and at high-density sites. This is a cost of courtship (Bell and Koufopanou 1986; Lima and Dill 1990; Magnhagen 1991), and for male crabs this cost is clear when the foraging rates of Ruddy Turnstones are observed (Fig. 6A). In Mauritania, the variable predation rate is related to whether crabs feed in droves or in burrowing beds (Ens et al. 1993). Here, male crabs' vulnerability is associated with their sexual display. While waving, males make short runs back and forth to their burrows. Males move up to 1 m away from their burrows (P. Ribeiro and O. Iribarne, unpublished observation) and thus they run the risk that a wandering crab (male or female) could displace them from their burrow. On some occasions, when a Ruddy Turnstone arrives, the generalized running-away behaviour of all crabs seems to confuse males that had moved farther from their burrows. These crabs lost the location of their burrows, began to wander, and attempted to shelter in other burrows. Large males face the problem that they have a lower probability of finding a burrow into which they can fit (there are few large burrows); furthermore, most burrows are defended by their inhabitants (Iribarne and Martínez 1999). If competition for mates is higher at high-density sites than at low-density sites, males may move farther from their burrows to find mates, and more crabs will lose their burrows and end up exposed to predation.

Our estimate of predation pressure indicates that the four shorebird species together would be able to capture, on average, between 0.1 and 0.2% of crabs of both sexes during one migratory season. The confidence limits of these values show no significant differences. However, even if they did, the values represent a small proportion of the population, and are unlikely to have significant effect on the population sex ratio. The sex ratio may be affected by an increase in the density of predators. Under this hypothetical scenario, the net effects of predation on the population sex ratio may be the result of the interaction between (i) the social context of the crabs, which may govern their exposure level, and (ii) the species and relative quantities of predators present. Thus, crab mortality would be sex-biased according to the occurrence of a predator such as the Whimbrel, which mainly consumes female crabs.

Prey are expected to respond in such a way as to minimize the impact of predation (Wilson 1991), potentially changing their behaviour patterns, such as reducing courtship by males and changing the location where copulation occurs (Koga et al. 1998). However, their predators have different feeding strategies, so it is likely to be difficult to develop antipredator behaviour specific to each predator. By increasing their efficiency in evading predators that use one strategy, their vulnerability to other predation strategies may increase. Thus, the general response of running into a burrow may be the best strategy regardless of the predator species (i.e., a bet-hedging response; Philippi and Seger 1989). However, the system is more complex in the case of fiddler crabs, which have an extreme sexual dimorphism and a mating system that consists of males competing for mates

(Christy and Salmon 1984; Zucker 1986), trading off reproduction against a high risk of predation. In such a situation, *Uca beebei* changed its courtship behaviour according to the predation risk (Koga et al. 1998). In the case of *U. uruguayensis*, we may expect no specific antipredator responses, given that the level of predation, at least by shorebirds, is not a substantial source of crab mortality; however, the historic predation pressure is unknown. The only other known predator is the burrowing crab *Chasmagnathus granulatus*. This crab preys on *U. uruguayensis* in areas where their distributions overlap (Daleo et al. 2003). However, these areas do not represent a considerable proportion of the distribution area of *U. uruguayensis*, and predation rates are low (Daleo et al. 2003). Thus, the evidence suggests that in this system, the benefits of display exceed the costs of predation, and that a trait commonly believed to be sexually selected, such as an enlarged male claw, does not (in this case) lead to a disproportionate decrease in the survivorship of the individuals that carry it.

Acknowledgements

We are indebted to J. Christy and C. deRivera for their invaluable contributions and suggestions on previous drafts. J.L. Gutierrez, J.P. Isacch, F. Botto, and two anonymous reviewers also provided valuable comments and suggestions that improved the work. This project was partially supported by grants from the Universidad Nacional de Mar del Plata, IFS-Sweden (A2501-2F), Fundación Antorchas (Argentina A013672), National Geographic Exploration Grants (No. 6487-99), and CONICET (PIP2851, all granted to O.I.). P.D. Ribeiro is supported by a scholarship from CONICET and this work is part of his doctoral dissertation.

References

- Adam, P. 1990. Saltmarsh ecology. *Camb. Stud. Ecol.*
- Alcock, J. 1989. *Animal behaviour: an evolutionary approach*. 4th ed. Sinauer Associates, Inc., Sunderland, Mass.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton, N.J.
- Backwell, P.R., O'Hara, P.D., and Christy, J.H. 1998. Prey availability and selective foraging in shorebirds. *Anim. Behav.* **55**: 1659–1667.
- Backwell, P.R., Christy, J.H., Telford, S.R., Jennions, M.D., and Passmore, N.I. 2000. Dishonest signalling in a fiddler crab. *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 719–724.
- Bateson, P. 1983. *Mate choice*. Cambridge University Press, Cambridge.
- Bell, G., and Koufopanou, V. 1986. The cost of reproduction. *Oxf. Surv. Evol. Biol.* **3**: 48–82.
- Bildstein, K.L., McDowell, S.G., and Brisbin, I.L. 1989. Consequences of sexual dimorphism in sand fiddler crab, *Uca pugilator*: differential vulnerability to avian predation. *Anim. Behav.* **37**: 133–139.
- Bogazzi, E., Iribarne, O.O., Guerrero, R., and Spivak, E. 2001. Wind pattern may explain the southern limit of distribution of a southwestern Atlantic fiddler crab. *J. Shellfish Res.* **20**: 353–360.
- Botto, F., Iribarne, O.O., Martínez, M.M., Delhey, K., and Carrete, M. 1998. The effect of migratory shorebirds on the benthic species of three southwestern Atlantic Argentinean estuaries. *Estuaries*, **21**: 700–709.
- Christy, J.H. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behav. Ecol. Sociobiol.* **12**: 169–180.
- Christy, J.H., and Salmon, M. 1984. Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biol. Rev. Camb. Philos. Soc.* **59**: 483–500.
- Crane, J. 1975. *Fiddler crab of the world: Ocypodidae: genus Uca*. Princeton University Press, Princeton, N.J.
- Daleo, P., Ribeiro, P., and Iribarne, O. 2003. The SW Atlantic burrowing crab *Chasmagnathus granulatus* Dana affects the distribution and survival of the fiddler crab *Uca uruguayensis*. *J. Exp. Mar. Biol. Ecol.* **291**: 255–267.
- Darwin, C. 1874. *The descent of man: and selection in relation to sex*. 2nd ed. A.L. Burt Co. Publishers, New York.
- Emmerson, W.D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, southern Africa. *J. Crustacean Biol.* **14**: 568–578.
- Ens, B.J., Klaassen, M., and Zwarts, L. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behaviour. *Neth. J. Sea Res.* **31**: 477–494.
- Greenspan, B.N. 1980. Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*. *Anim. Behav.* **28**: 387–392.
- Halliday, T.R. 1983. The study of mate choice. *In* *Mate choice*. Edited by P.P.G. Bateson. Cambridge University Press, Cambridge. pp. 3–33.
- Hyatt, G.W., and Salmon, M. 1978. Combat in the fiddler crab, *Uca pugilator* and *Uca pugnax*: a quantitative analysis. *Behaviour*, **65**: 182–211.
- Iribarne, O.O. 1996. Habitat structure, population abundance and the opportunity for selection on body weight in the amphipod *Eogammarus oclairi*. *Mar. Biol. (Berl.)*, **127**: 143–150.
- Iribarne, O.O., and Martínez, M.M. 1999. Predation on the southwestern Atlantic fiddler crab (*Uca uruguayensis*) by migratory shorebirds (*Pluvialis dominica*, *P. squatarola*, *Arenaria interpres* and *Numenius phaeopus*). *Estuaries*, **22**: 47–48.
- Jirotkul, M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. *Anim. Behav.* **58**: 287–294.
- Koga, T., Backwell, P.R., Jennions, M.D., and Christy, J.H. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proc. R. Soc. Lond. B Biol. Sci.* **265**: 1385–1390.
- Koga, T., Backwell, P.R.Y., Christy, J.H., Murai, M., and Kasuya E. 2001. Male-biased predation of a fiddler crab. *Anim. Behav.* **62**: 201–207.
- Krebs, J.R., and Davies, N.B. 1993. *An introduction to behavioural ecology*. 3rd ed. Blackwell Scientific Publications, London.
- Kvarnemo, C., and Ahnesjö, I. 1996. The dynamics of operational sex ratios and competition for mates. *Trends Ecol. Evol.* **11**: 404–408.
- Kålås, J.A., Fiske, P., and Sæther, S.A. 1995. The effect of mating probability on risk taking: an experimental study in lekking great snipe. *Am. Nat.* **146**: 59–71.
- Lima, S.L., and Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**: 619–640.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**: 183–186.
- Manly, B.F.J. 1998. *Randomization, bootstrap and Monte Carlo methods in biology*. 2nd ed. Chapman and Hall, London.

- Mercier, F., and McNeil, R. 1994. Seasonal variation in intertidal density of invertebrate prey in a tropical lagoon and effects of shorebird predation. *Can. J. Zool.* **72**: 1755–1763.
- Montague, C.L. 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. *Contrib. Mar. Sci.* **23**: 25–55.
- Morrison, R.I.G., and Ross, R.K. 1989. Atlas of Nearctic shorebirds on the coast of South America. *Can. Wildl. Serv. Spec. Publ. No. 2*. pp. 131–323.
- Narosky, T., and Yzurieta, D. 1993. Birds of Argentina and Uruguay: a field guide. Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Neter, J., Wasserman, W., and Kutner, M.H. 1991. Applied linear statistical models: regression, analysis of variance, and experimental designs. 3rd ed. Irwin, Boston, Mass.
- Philippi, T., and Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**: 41–44.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.
- Riechert, S.E. 1988. The energetic cost of fighting. *Am. Zool.* **28**: 877–884.
- Schneider, D.C. 1983. The food and feeding of migratory shorebirds. *Oceanus*, **26**: 38–43.
- Spivak, E.D., Gavio, M.A., and Navarro, C.E. 1991. Life history and structure of the world southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita Lagoon (Argentina). *Bull. Mar. Sci.* **48**: 679–688.
- Thurman, C.L., II. 1985. Reproductive biology and population structure of the fiddler crab *Uca subcylindrica* (Stimpson). *Biol. Bull. Camb. Philos. Soc.* **169**: 215–229.
- Trivers, R.L. 1985. Social evolution. Benjamin/Cummings Publishing Co., Menlo Park, Calif.
- Valiela, I., Babiec, D.F., Atherton, W., Seitzinger, S., and Krebs, C. 1974. Some consequences of sexual dimorphism: feeding in male and female fiddler crab, *Uca pugnax* (Smith). *Biol. Bull. Camb. Philos. Soc.* **147**: 652–660.
- Wilson, W.H. 1991. The foraging ecology of migratory shorebirds in marine soft-sediment communities: the effects of episodic predation on prey populations. *Am. Zool.* **31**: 840–848.
- Wolfrath, B. 1993. Observations on the behaviour of the European fiddler crab *Uca tangeri*. *Mar. Ecol. Prog. Ser.* **100**: 111–118.
- Zahavi, A. 1987. The theory of signal selection and some of its implications. *In* Proceedings of the International Symposium on Biological Evolution, Bari, Italy, 9–14 April 1985. *Edited by* V.P. Delfino. Adriatica Editrice, Bari, Italy. pp. 305–325.
- Zar, J.H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Inc., Englewood Cliffs, N.J.
- Zucker, N. 1978. Monthly reproductive cycles in three sympatric hood-building tropical fiddler crabs (genus *Uca*). *Biol. Bull. Camb. Philos. Soc.* **155**: 410–424.
- Zucker, N. 1986. On courtship patterns and the size at which male fiddler crab (genus *Uca*) begin to court. *Bull. Mar. Sci.* **38**: 384–388.
- Zwarts, L., and Blomert, A.-M. 1990. Selectivity of Whimbrels feeding on fiddler crabs explained by component specific digestibilities. *Ardea*, **78**: 193–208.