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Evaluating the potential impact of bird predation on the SW Atlantic fiddler crab *Leptuca uruguayensis*

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Abstract

The southernmost permanent population of the fiddler crab *Leptuca uruguayensis* occurs along the Samborombón Bay (36°22'S, 56°45'W, Argentina), an important feeding site for many bird species, including ruddy turnstones (*Arenaria interpres*), whimbrels (*Numenius phaeopus*), grey plovers (*Pluvialis squatarola*), american golden plovers (*Pluvialis dominica*) and gull-billed terns (*Gelochelidon nilotica*). Although all these birds are known to prey on many fiddler crab species worldwide, there is no estimation of their joint predation impacts, probably due to the difficulty in conducting experiments on an appropriate spatial scale. In these situations, computer simulation methods are useful tools. By using Monte Carlo methods and field data, we modeled the decrease of a fiddler crab population due to bird predation. The model found that under current bird occurrences and crab densities, birds do not consume more than 0.03% of the studied fiddler crab populations. Birds only consume more than 10% of the population if crab density is below 0.02 crabs m², or if bird occurrences are at least 3 orders of magnitude higher than currently observed. Both situations are unlikely, as mean crab density is 140 crabs m², and bird density is never so high. Furthermore, by monitoring three different fiddler crab patches, we found that bird predation cannot account for temporal density changes, suggesting that other population processes are more important than bird predation. In conclusion, even though fiddler crabs may exhibit strong predator-avoidance behavior, direct lethal effects of bird predation are currently small.

Keywords: Fiddler crabs, *Uca uruguayensis*, *Leptuca uruguayensis*, Predation impact, Shorebird predation, Computer simulation

Background

Soft-bottom environments such as mudflats and marshes are important sites for biological conservation, largely because they are feeding areas for both local and migratory bird species [1]. Indeed, most migratory shorebird species obtain most of their prey from these environments (e.g. [2]), and these habitats are thus subjected to annual events of episodic predation [3] due to high densities of shorebirds stopping along their migratory path to rest and feed [4–9].

Investigations on the role of predators in soft-bottom communities (reviewed in [10]) have often reached

contradictory conclusions [11]. Predators have negligible effects in some areas (see [12, 13]) while they significantly decrease prey abundances in others [7, 14], and/or modify their size frequency structure [3, 15, 16]. Therefore, it seems that in soft bottom intertidal habitats there are conditions or sites where predation may act as a strong selective force while in others it is negligible [11, 17]. Given logistic constraints, experiments designed to measure the impact of predation are generally performed on a much smaller spatial scale than the study system [18], providing results that may deviate considerably when extrapolated to the scale of the natural system [19–21]. Extrapolation of predation impacts from low spatial scale experiments to the system scale should therefore be used with caution [21–24]. Another way of inferring the impact of predation is through the use of computer model simulations (e.g. [18]). Even when they

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do not always incorporate experimental data (i.e. predator exclusion experiments), computer simulations are still powerful tools because they can easily incorporate observational field data into models on the scale of the system. For example, computer simulations based on field observations of predator and prey behaviors may be used to model the predator-prey interaction during a given time frame and on the scale of prey patches.

The fiddler crab *Leptuca uruguayensis* (previously *Uca uruguayensis*) is a small (up to 16.5 mm carapace width; see [25]) intertidal species found from southern Brazil (33°S) to the northern coast of Argentina (38°S; [25, 26]). The southernmost permanent population occurs along the Samborombón Bay (36°22'S, 56°45'W, Argentina; see [27]), where it is found mainly on exposed wet mudflats from the middle to upper intertidal flats near the fringe of an extensive *Sporobolus densiflorus* (previously *Spartina densiflora*) marsh. This area is an important stopover site for many non-tropical birds [28–30], where fiddler crabs provide food for several species, including ruddy turnstones (*Arenaria interpres*), whimbrels (*Numenius phaeopus*), grey plovers (*Pluvialis squatarola*), american golden plovers (*Pluvialis dominica*) and gull-billed terns (*Gelochelidon nilotica*; see [31]). In some areas, fiddler crabs may be the main food source for several bird species (e.g. [32, 33]), suggesting that predation impact on fiddler crabs should be considerable. In addition, each bird species has different feeding tactics and rates, leading to the consumption of different proportions of female and male crabs [31, 34, 35]. The global effect of predation on crab population size and sex ratio would therefore depend on both the number and relative occurrence of each bird species.

In this context, we constructed a mathematical model and applied Monte Carlo computer simulations to evaluate the potential predation impact of birds on a South-western Atlantic fiddler crab population of the species *Leptuca uruguayensis*. Using bird and fiddler crab field observations, we (1) evaluated the potential impact of predation under different fiddler crab population densities and under natural bird occurrences, (2) evaluated how predation impact would change if bird occurrences were higher than currently observed in nature and, (3) compared the density changes due to bird predation expected by the model to the population density changes of three fiddler crab patches monitored in the field.

Methods

Study site

The study used a database obtained from field observations at intertidal mudflats near the mouth of San Clemente tidal creek (eastern Samborombón Bay, 36°22'S, 56°45'W, Argentina), an area with low-amplitude (up to

1.4 m) semidiurnal tides. Fiddler crabs settle forming extensive patches with densities of up to 140 crabs m⁻² [36]. Data were obtained from an area along a 1000-m long × 100-m wide intertidal beach, within which we identified six fiddler crab patches (mean = 1175.5 m²) separated by interpatch clear areas without settlements (52.98% of the observation area). The edge of each fiddler crab patch was demarcated with 1 m wooden sticks. We considered fiddler crab patches as population units and explored their population size changes due to bird predation using Monte Carlo methods [37].

Bird and fiddler crab data

In the study area, the fiddler crab *Leptuca uruguayensis* is commonly preyed upon by ruddy turnstones, whimbrels, grey plovers, american golden plovers and gull-billed terns (see [31]). The model used the data from crab and bird surveys and observations performed during different field trips (3 to 5 days each), during 1999, 2000 and 2001. On each trip, we measured the size of each of the six fiddler crab patches. Each day, surveys of birds in each of the identified fiddler crab patches were carried out on an hourly basis, beginning 5 h before the diurnal low tide and ending 5 h after it, encompassing the time frame during which the mudflats were exposed. In addition, hourly surveys of fiddler crab activity were carried out by taking 5 samples (in each fiddler crab patch) and counting the number of male and female crabs within a 5 m × 1.5 m focal area. Focal observations over 207 individual birds, totaling 884 min of audio-tape recordings provided data to compute their feeding rates. During each observation, the observer continuously reported all behaviors of the focal individual, including prey capture attempts and outcomes, and prey items captured. Male fiddler crabs were easily identified from females when captured by the red color of their enlarged claw. Data on bird occurrences, feeding rates and the used methodology have been partially published [34, 35, 38].

Fiddler crabs dig burrows that are used for mating, egg incubation by females, and as temporary refuges from predators and physiological stress (e.g. high or low temperatures, high tides). For the study site (a temperate zone) fiddler crabs show a succession of surface activity over a year, from mid-September up to mid-March, represented by 3 different periods: (1) feeding only, (2) reproduction and feeding, and (3) feeding only. Thus, with the arrival of spring, fiddler crabs resume surface activity, feeding and growing exclusively for about 2 months; after which they initiate the reproductive period, which may last 2–3 months, and finally return to feeding only for about 2 months before completely halting surface activities when winter begins. This time frame coincides with the presence of migratory bird

species that use fiddler crabs as a prey item [30, 31]. Crab activity follows the semilunar cycle (14 days long), with maximum surface activity on days with spring tides, and minimum surface activity on days with neap tides [39]. During a typical spring tide, crabs may be active on the surface 5–7 h per day [34], with peak activity generally towards or around the time of the low tide. During high tide, crabs remain inside their plugged burrows [40]. During the reproductive period, the sex ratio of crabs active on the surface can be extremely male biased (e.g. 80% males; see [34]), after mating females produce egg masses that they incubate while remaining inside their plugged burrows for about 15 days [41]. The proportion of ovigerous females (rarely seen active on the surface; pers. obs.) fluctuates throughout the reproductive period, with a mean value of 0.34% ovigerous females (SD = 0.18; maximum observed value = 0.77; unpublished information obtained from 42 weekly random samples, 1 × 1 m square and 0.4 m depth). Overall, fiddler crabs are active on the surface during 14 semilunar cycles; with up to 6 of those cycles devoted to reproduction (see [42]) and the remaining 8 to non-reproductive activities (i.e. feeding, new burrow digging or burrow maintenance).

Model structure

The model simulated that joint consumption by birds can reduce the density of the fiddler crab population every day at a given rate, the Joint Density Consumption Rate (*JDCR*). The model integrates the *JDCR* across days throughout an entire fiddler crab-bird interaction season. The proportion of the fiddler crab population consumed by birds at time T can thus be viewed as:

$$C_T = \frac{\sum_{t=1}^T JDCR_{ft} * E_{ft} + JDCR_{mt} * E_{mt}}{D_0}, \quad (1)$$

were C_T is the proportion of crab population consumed at the end of the fiddler crab-bird interaction period, which lasts T days, D_0 is initial fiddler crab density, $JDCR_{ft}$ and $JDCR_{mt}$ Joint Density Consumption Rate of females and males, respectively, during day t , and E_{ft} and E_{mt} are exposure times on the surface of females and males, respectively, during day t .

Given that birds may prey at different rates under different crabs densities [34, 35] and due to the non linear semilunar cycles of crab density on the surface over time [39], the Eq. 1 is not easy to solve analytically. Alternatively, the equation can be solved numerically by estimating iteratively day by day the density of female and male crabs active on the surface and applying an appropriate *JDCR* value in accordance to crabs densities. The variation in surface activity of crabs across days may be modeled as a sine wave [39] so, the density of females and

males active on the surface for each day throughout the crab-bird interaction period can be estimated with the wave equation:

$$D_s = D_p \left[\frac{A}{2} + \frac{A}{2} \times \sin(t \cdot f \cdot 2\pi + \varphi) \right], \quad (2)$$

where D_s is the density of active crabs on the surface, D_p is the population density, t is a day from the crab-bird interaction period, A is amplitude, f is frequency (set as 1/14 days), and φ is phase, which, for the sake of simplicity, can be set as $-\pi/2$ so that a semilunar cycle of activity also starts at day 1.

Amplitude A may be viewed as the maximum proportion of crabs that can be active on the surface, which for males can be set as always 1 (disregarding the probability of molting crabs) and for females will depend on the proportion of ovigerous females within the population, which can be set as 0 during the non-reproductive cycles and 0.34 during the reproductive cycles (see “[Bird and fiddler crab data](#)” section for the estimation of this value). Equation 2 for males all time and for females during the non-reproductive period can thus be reduced to:

$$D_s = 0.5 \cdot D_p + 0.5 \cdot D_p \times \sin(t \cdot \pi/7 - \pi/2), \quad (3)$$

and for females during the reproductive period to:

$$D_s = 0.33 \cdot D_p + 0.33 \cdot D_p \times \sin(t \cdot \pi/7 - \pi/2), \quad (4)$$

Exposure times and *JDCR* values

Exposure times on the surface differ between sexes, with males generally being active on the surface for more time than females. Although the density of crabs active on the surface varies strongly over the semilunar cycle [39], the time that crabs are active on the surface may not substantially change over the days. Therefore, on different days, different numbers of crabs may be active on the surface, but with similar exposure times each day. Using the hourly surveys of fiddler crab activity, we computed the maximum density of females and males active on the surface, and calculated the proportion of female and male densities observed during each of the 9 hourly surveys. By integrating the 9 hourly proportions, we obtained an estimator of daily exposure time. Estimated mean daily exposure time was 5.08 h (5 h 4' 48'') for females and 6.24 h (6 h 14' 24'') for males.

The *JDCR* in a given patch at a given time may depend of many factors, including: (1) the density of crabs active on the surface, which is a function of the population density and the semilunar cycle, (2) the feeding rates of each bird species, and (3) the occurrence of each bird species. Using our database, we applied a Monte Carlo method to obtain empirical measures for *JDCR* as a function of the density of crabs active on the surface. The

empirical measures for *JDCR* estimate the mortality of crabs $\text{h}^{-1} \text{m}^{-2}$, produced by the 5 bird species feeding at the same time and at different fiddler crab densities.

An empirical measurement for *JDCR* was obtained by performing the following steps: Step 1: select randomly from the database a date, a fiddler crab patch and a bird survey to extract the occurrences of each of the five bird species counted during the selected hourly census. Step 2: select randomly a value of the density of females and males on the surface, provided it corresponds to the same patch, date and hour of the selected bird survey in Step 1. Step 3: select randomly a feeding rate for each of the individuals of each of the bird species, provided it corresponds to the same patch, date and time of the selected bird survey in Step 1. Step 4: break down each of the feeding rates from Step 3 into feeding rate on females and on males, and apply the following equation separately to each sex.

$$JDCR = \frac{\sum_{s=1}^5 \sum_{i=1}^N FR_{si}}{A}, \quad (5)$$

where *JDCR* is the Joint Density Consumption Rate (crabs consumed $\text{h}^{-1} \text{m}^{-2}$), *A* is patch area, *N* is number of individuals for the bird species *s* counted in the patch, and FR_{si} feeding rate assigned to bird individual *i* of the species *s*.

The procedure was repeated 100,000 times and the empirical measures of *JDCR* for females and males were plotted in relation to the density on the surface of females and males, respectively (obtained in Step 2). These plots showed how *JDCR* may change in relation to the density of crabs active on the surface and were used to estimate the consumption of fiddler crabs during the crab-bird interaction period.

Monte Carlo model estimation

We applied the model Eq. 1 to estimate the proportion of a fiddler crab population consumed by birds. The model simulated the outcomes of predation on 100,000 population over the crab-bird interaction period, which was set as *T* to 196 days (14 semilunar cycles \times 14 days each cycle), and consisted of a sequence of 4 non-reproductive semilunar cycles, 6 reproductive semilunar cycles, and 4 non-reproductive semilunar cycles. Each population had an initial density (D_0) ranging from 0.0005 to 140 crabs m^{-2} , in order to evaluate the potential effect of bird predation on fiddler crab populations with different densities. The initial sex ratio for each population was set as 0.62 (proportion of males; see [27]).

To solve Eq. 1 numerically, we performed the following steps. Step 1: estimate the density of females and males active on the surface by applying Eqs. 3 and 4, as

applicable. Step 2: select randomly a *JDCR* value for females and a *JDCR* value for males that corresponds to a density interval centered on the female and male density on the surface $\pm 0.05\%$ of density range of the empirical measures distribution. Step 3: multiply *JDCR* female and male values by exposure times of females and males, to obtain the daily density decrease of female and male population, respectively. Step 4: update female and male population densities by extracting values from Step 3 to the prior population densities. Step 5: repeat Steps 1 to 4 up to $t=196$ and compute the proportion of consumed population and the sex ratio shift (SRS) using the initial density values of females and males and those achieved at the end of the crab-bird interaction period ($t=T=196$). The SRS was calculated as the proportion of males in the total population at the end of the crab-bird interaction period minus the initial proportion of males in the total population. Therefore, positive SRS values signified that consumption by birds increased the proportion of males in relation to females, and the inverse if negative. The 95% percentile-based confidence limits [37] for the proportion of consumed population and the sex ratio shift were calculated.

Occurrence of birds and potential predation impact

In the previous section, the model explored how birds, under their current natural occurrences, may consume a given proportion of fiddler crab populations of different densities. As was found (see “Results”), bird predation seems to be unimportant for fiddler crab populations with densities above 0.01 crabs m^{-2} . This may be in part due to the fact that bird occurrences are generally low for the study site (see Fig. 1). However, the scenario would potentially change if bird occurrences were higher than currently observed in nature. Here we used the model to explore whether bird predation becomes important if bird occurrences increase, and evaluated how likely it would be for the required bird occurrences to occur in nature.

To conduct this analysis, we used the empiric measures for *JDCR*, and assumed that a proportional change in bird occurrences would lead to a similar proportional change in *JDCR*. Thus, bird occurrences increased by a factor of *n* would lead to *JDCR* values increased by a factor of *n*. This assumption does not include the potential interference among birds as their occurrences increase. However, such effects would imply that bird predation effects are even lower than those found by our results, which makes the assumption reasonable in order to simplify the analysis. We called the *n*-times factor “bird load” and conducted similar Monte Carlo model estimations for a wide range of bird loads (1 to 20,000) and for different initial population crab densities.

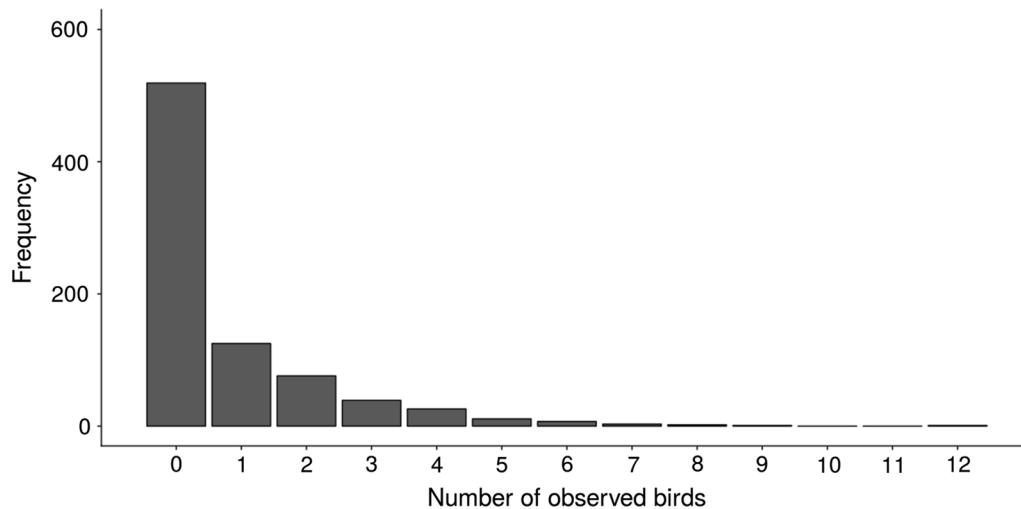


Fig. 1 Observed frequency distribution for the number of birds counted within an hourly census in a fiddler crab patch. Data shown is the pool of 810 hourly surveys on 15 different dates, 6 different fiddler crab patches, and 9 tidal states (from -4 to $+4$ h from low tide)

Contribution of bird predation to crab density changes

We evaluated whether bird predation may account for temporal changes in crab density. To do so, we used the data from density monitoring of three different fiddler crab patches and contrasted it to the density changes expected by the simulated bird predation model. The patches were monitored from August 2000 to May 2001 (on 10 different dates). Each month, at each patch, 10 randomly distributed 50×50 cm squares were dug (down to 0.4 m depth) to count all male and female fiddler crabs therein. We applied a similar Monte Carlo model estimation, in which the initial sex ratio and the proportion of ovigerous females corresponded to those obtained in the different field samples. The mean and 95% bootstrap confidence limit for the observed and expected density of crabs were calculated.

Results

Under natural bird occurrences (Fig. 1), the Joint Density Consumption Rates caused by the five bird species feeding together were generally low across all fiddler crab densities (Fig. 2). The Monte Carlo estimations indicate that the proportion of fiddler crabs consumed by birds decreases rapidly with fiddler crab population density. During one crab-bird interaction period, birds may not consume more than 10% of a fiddler crab population with initial densities above 0.02 crabs m^{-2} (Fig. 3a). Birds may not consume more than 0.03% of a fiddler crab population with initial densities of 10 crabs m^{-2} (Fig. 3b). For populations with very low densities (Fig. 4a), the population sex ratio at the end of the crab-bird interaction period may be strongly biased towards females. For

populations with initial densities above 1 crabs m^{-2} , the proportion of males still decreases (Fig. 4b); however, the magnitude of the change can be considered negligible (mean: $1.40 \cdot 10^{-5}$; 95% CL $1.04 \cdot 10^{-6}$, $9.22 \cdot 10^{-5}$).

Occurrence of birds and potential predation impact

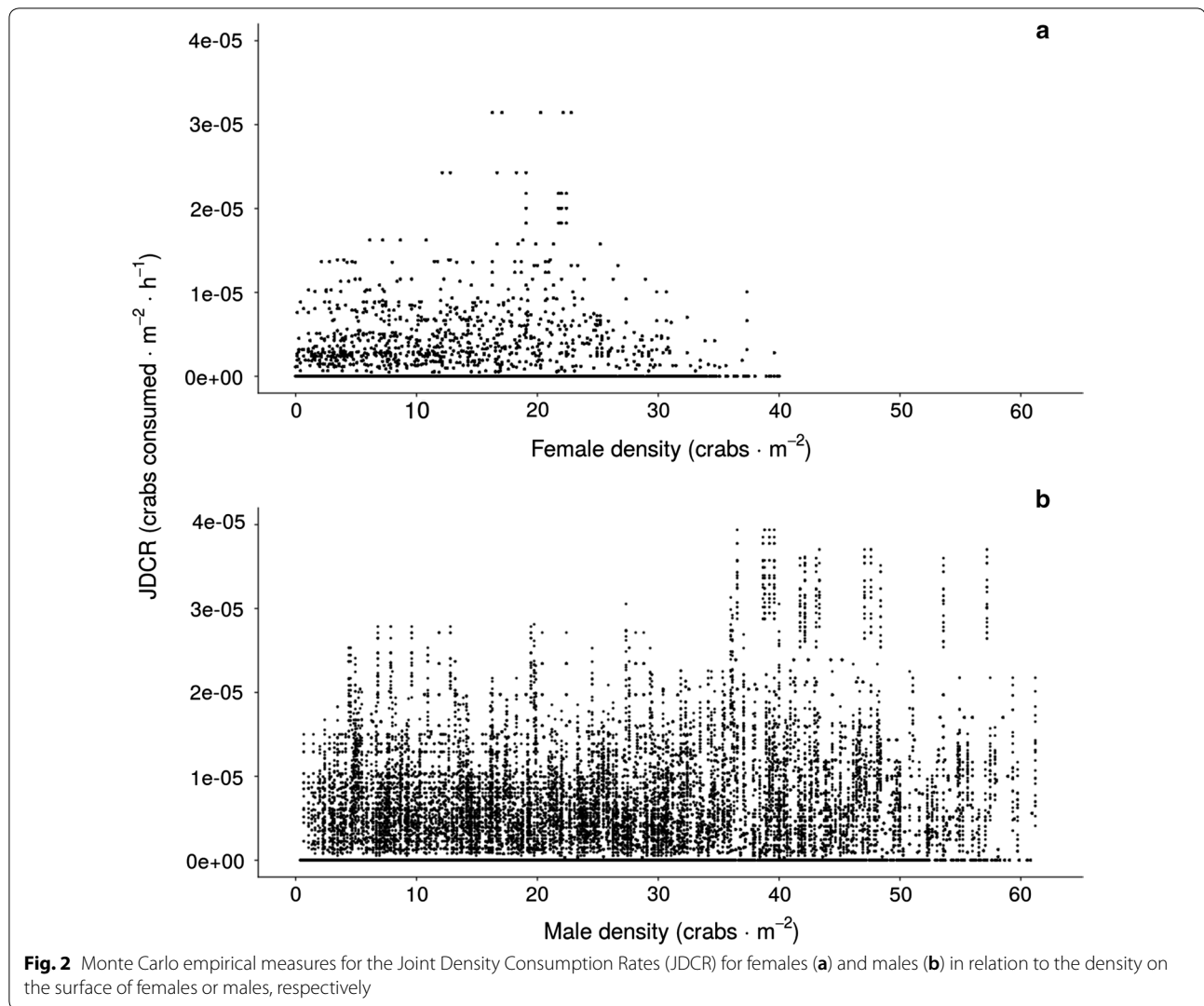
The analysis exploring the effect of the relative increase in the occurrence of birds on the proportion of fiddler crab populations consumed indicated that bird loads must be much higher than currently observed to achieve a significant consumption of a fiddler crab population. For example, bird load must be at least 3 orders of magnitude higher than currently observed to achieve the consumption of 25% of the population of crabs (Fig. 5).

Contribution of bird predation to crab density changes

The analysis applying the model to evaluate the expected densities of crabs after predation on the three monitored fiddler crab patches indicated that bird predation cannot account for temporal changes in crab density (Fig. 6). Especially during November and March, fiddler crab density undergoes significant temporal changes (both increases and decreases) which are beyond the values expected solely by the impact of predation.

Discussion

Predator-prey interactions have long been a topic of interest because the removal of individuals from a population can be viewed as a control mechanism on the prey populations [43–46]. Even though fiddler crabs are recognized to be an important food source for many wader and shorebird species worldwide [31–34,



47] studies estimating predation impacts at the scale of prey populations are rather scarce, even for other taxonomic groups (but see [48, 49]). However, most studies on fiddler crab predation focus on diet composition, time budgets and digestibility limitations of predators [33, 50, 51], and on the resulting size and sex-specific predation due to sexual dimorphism [52, 53] or to the size-specific spatial segregation of crabs across mudflat areas [54–56]. Few of them deal with the potential of prey choice segregation of different predator species while preying on different proportions of crab sizes and sexes [32, 34, 35]. However, except for some attempts to relate predation rates with bird densities and environmental stability of prey populations (e.g. [57, 58]), there have not been further studies aiming to estimate predation impacts. In the current study we formulated a simple model (based on real data) that conceived the decrease in a fiddler crab population as

the accumulation of daily decreases in the population density due to the joint consumption of 5 bird species.

The visual examination of empirical measures for JDCR in relation to the density of crabs on the surface suggests a density range for prey refuge [59–62] at low densities for both sexes and at high densities for females. The fact that the JDCR for females tends to decline at high densities may be associated to a differential increase in the vulnerability or conspicuity of males in relation to females. However, JDCR values for both sexes were generally low, and computer simulations found that birds may not consume more than 0.03% of a fiddler crab population with densities currently observed in nature. Consequently, the impact of predation can be considered negligible, with no significant effect on either population size or sex ratio due to sex-specific predation [34, 35].

Nevertheless, the model applies several simplifications [63, 64], and it should be analyzed whether its

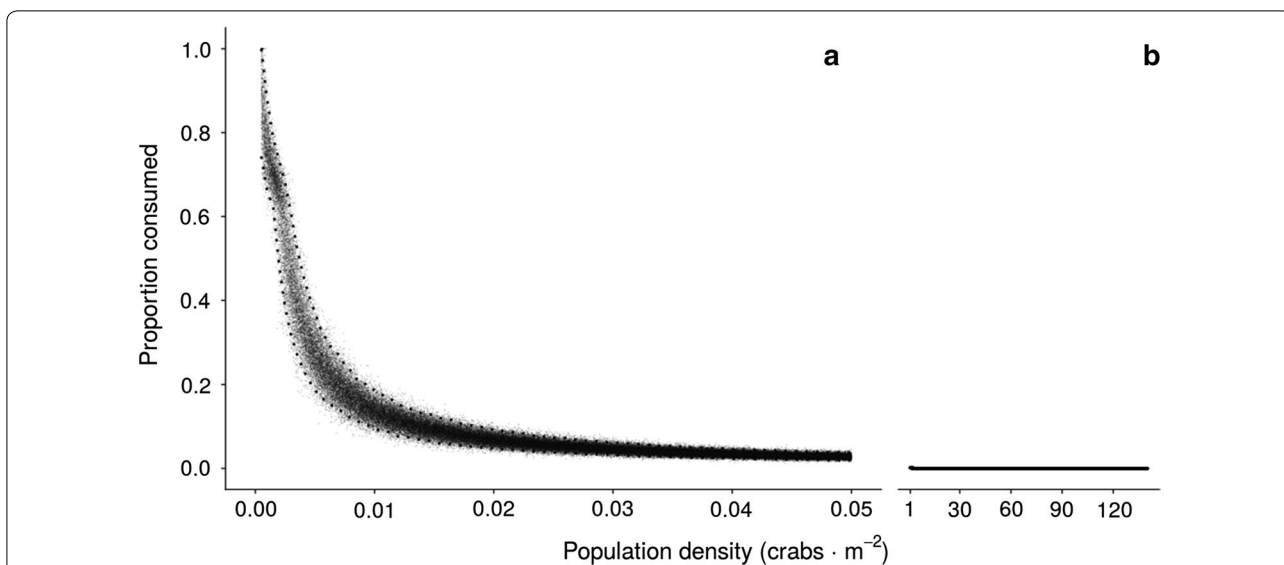


Fig. 3 Proportion of crabs consumed by birds resulting at the end of one crab-bird interaction period for **a** low initial population densities, and for **b** a wide range of initial population densities. Dotted curves delimit the 95% confidence limits for the proportion of crabs consumed

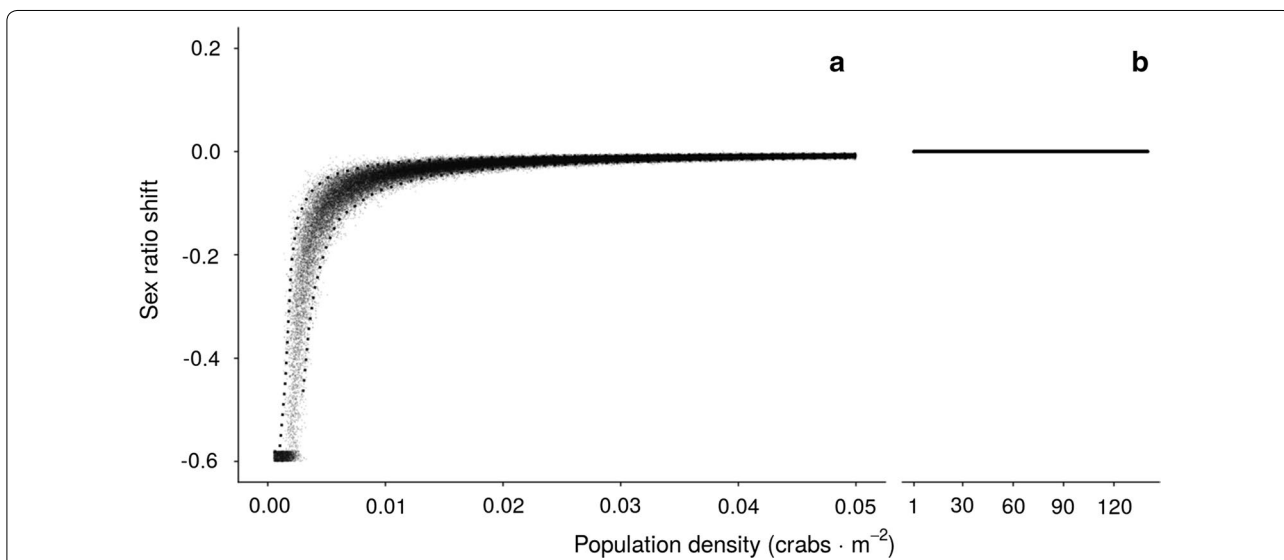
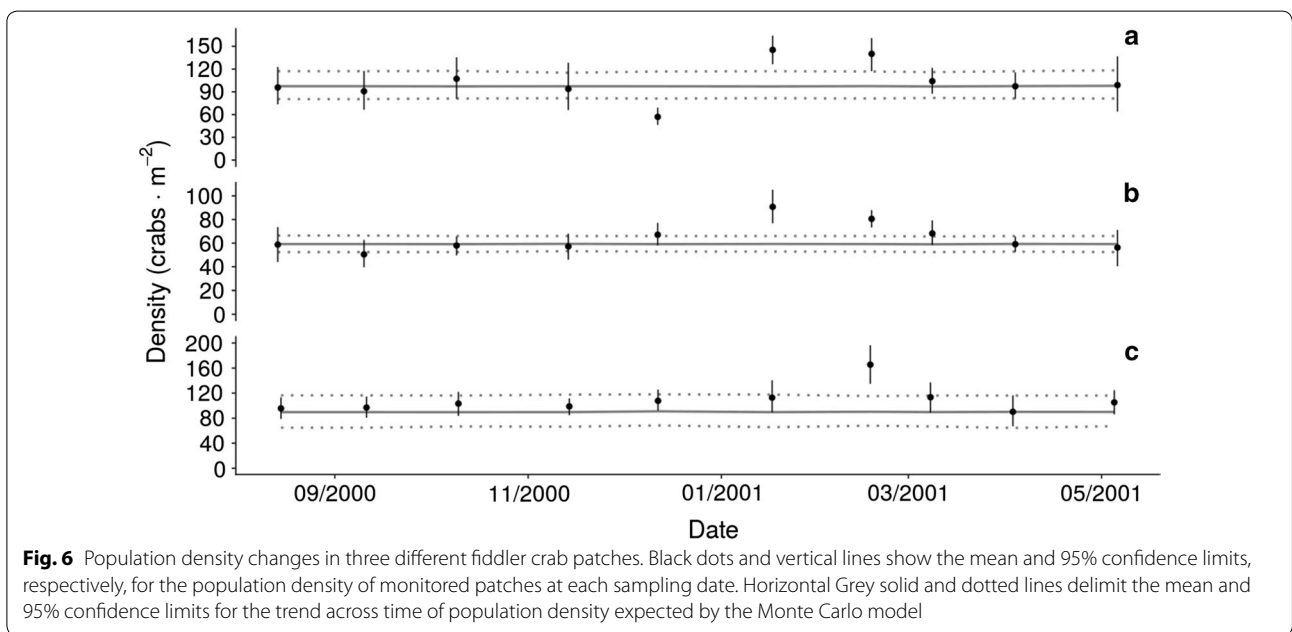
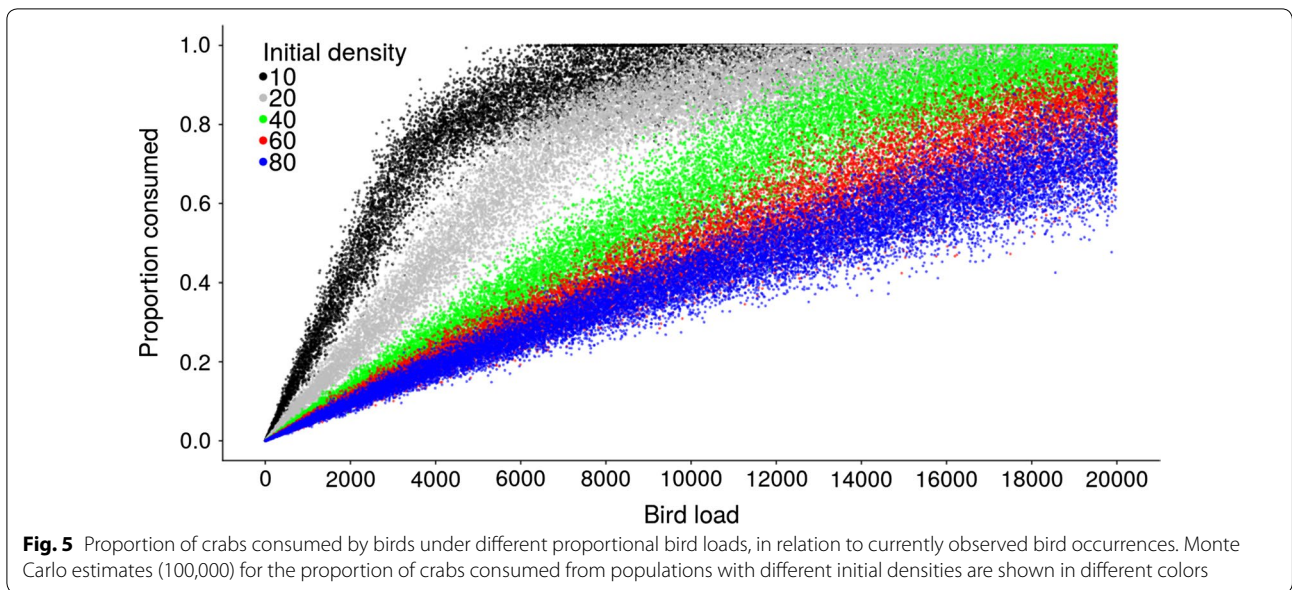


Fig. 4 Sex ratio shift due bird predation resulting at the end of one crab-bird interaction period for **a** low initial population densities, and for **b** a wide range of initial population densities. Dotted curves delimit the 95% confidence limits for the sex ratio shift

assumptions may obscure or limit the interpretation of results. First, the model does not formally specify the potential interference and/or correlations between the functional responses of each bird species [65–67]. Formulating an analytical functional response for each bird species would have made the structure of the model even more complex. However, during the process of computing the empirical measures for JDCR, the matrix of bird occurrences was kept unaltered without randomizing

between bird species. Therefore, when randomly selecting a census to apply bird occurrences, we used the joint information of the 5 bird species of the selected census. In addition, the feeding rates of each bird species and the information of the density of crabs active on the surface was obtained from the same patch and time as the selected census. As a consequence, any kind of negative (or positive) association between bird species and crab density on the surface was implicitly incorporated



by obtaining different estimations of JDCR associated with different densities of crabs on the surface. Finally, the model does not include the contribution of recruitment of new crabs or the loss due to natural mortality. Lifespan for the species *Leptuca uruguayensis* at temperate latitudes is 2 to 3 years (see [27]). Recruitment begins mainly as from December, but individuals rarely reach the adult size until the following spring [27]. However, a combination of different processes underlying crab population dynamics seems to be important during the

period from December to February when the density of crabs undergoes highly variable changes, both above and below the values expected according to our model (see Fig. 6). This supports the hypothesis that bird direct predation on the studied Southwestern Atlantic population of the fiddler crab *Leptuca uruguayensis* may be much less important than other processes such as crab competition, natural mortality, recruitment, molting, growth, spatial dispersion and mobility (e.g. [68, 69]), which are key to understanding the population dynamics of fiddler

crabs. In fact, for several fiddler crab species, population dynamics seem to be governed mainly by environmental conditions affecting physiological stress [70, 71], vegetation structure [72], sediment characteristics [36, 73], and processes contingent to the selection of settlement sites by the planktonic larvae [74], rather than by direct control by top predators [71, 75].

We also found that to achieve significant predation impacts, bird occurrences should be at least 3 orders of magnitude higher than those currently observed, a scenario which seems unrealistic. Similarly, under current bird occurrences and feeding rates, bird predation may not consume more than 10% of a crab population when crab densities are above 0.02 crabs m^{-2} . Crab densities for the study site were relatively stable over the years, and much higher than 0.02 crabs, sometimes reaching mean densities of up to 140 crabs m^{-2} [31, 36]. Even for an intermittent population such as those found further south from our study site at Mar Chiquita Coastal Lagoon (37°45'S, 57°19'W), the lowest crab densities registered where 1.1 crabs m^{-2} [76]. For those exceptionally low density values, and based on our model estimations, birds may not be able to consume more than 0.20% of the crab population.

Therefore, if we are only to evaluate the lethal effects of predation such as the removal of prey individuals from the population [45], birds do not currently constitute an important source of mortality for the studied fiddler crab populations (but see [77, 78]). However, there should be a broad variety of indirect effects that are worth evaluating, many of them probably being the outcome of past predation [59, 79]. It is generally accepted that predation may be part of the selective forces driving the evolution of morphological and behavioral strategies that enable preys to adjust their behavior according to perceived predation risk [80–82]. For example, the species *Leptuca beebei* can adjust the relative frequencies of different mating tactics depending on the level of the perceived predation risk [83], and males of the species *Leptuca terpsichores* take greater risks by traveling farther away from their burrows only if they are to court large females [84]. Similarly, the species *Gelasimus vomeris* exhibits different degrees of carapace colors in relation to perceived predation risk [85]. In addition, males of several fiddler crab species build mud structures that serve as landmarks that enable females to reduce predation risk while seeking mates [77, 78, 86, 87]. If we consider that the many antipredator strategies may cause a reduction in the efficiency and/or time available for feeding and reproduction [59, 79, 88–91], then maintaining such strategies may be costly under a scenario of apparently low predation pressure. In this vein, it can be alternatively

considered that predation impact is indeed low because fiddler crabs have evolved antipredator strategies, making them less vulnerable to direct predation [92–94]. To unravel this apparent circular dilemma, it would be interesting to conduct studies focusing on the relationships between what captured preys were and were not doing at the time of capture, as well as what non-captured preys were and were not doing at the time of escaping predators. Studies focusing on the mechanistic links between predator and prey tactics, as well as on the sensory and behavioral mechanism on which tactics are based, would enable exploration of predictions about changes in predation pressure in relation to either a relaxation or an increase in prey antipredator strategies. Furthermore, comparative studies on prey species with different underlying sensory capabilities and limitations to acquire and process information about risks to which they are exposed [95–97] would surely help to understand why so many contradictory conclusions are found when inquiring into the role of predation in the structure of soft bottom environments [7, 11–13, 17].

In conclusion, this study shows that predation caused by birds is not important for the Southwestern Atlantic populations of the fiddler crab *Leptuca uruguayensis*. Other potential predation impacts may be caused by some fish species or other co-occurring crabs such as the intertidal burrowing *Neohelice granulata* [98]. However, their predation impacts would probably be lower than those caused by birds because fiddler crabs plug their burrows during high tide, thus being unavailable to fishes, [40] and *N. granulata* have been documented to very occasionally capture and consume fiddler crabs [98]. Finally, this study may provide an example of how the combination of field observational data with computer simulation tools may enable exploration the probabilities of diverse scenarios that cannot easily be carried out experimentally on the scale of the system.

Abbreviations

JDCR: joint density consumption rate; SRS: sex ratio shift.

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Authors' contributions

All authors contributed to study conception, study design, field research, interpretation of findings, and commenting on manuscript drafts. PDR was responsible for data analysis and writing manuscript drafts. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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