

# Spatial and temporal patterns in the feeding behavior of a fiddler crab

Agustina di Virgilio · Pablo D. Ribeiro

Received: 26 July 2012 / Accepted: 17 December 2012 / Published online: 28 December 2012  
© Springer-Verlag Berlin Heidelberg 2012

**Abstract** Fiddler crabs consume the surficial microphytobenthos around their burrows during low tide. We studied the spatial and temporal feeding patterns in the species *Uca uruguayensis* by using sequences of digital pictures of feeding pellets accumulation. Data from 61 crabs, feeding without the interference of neighbors, were fitted to different models using Maximum Likelihood and Bayesian approaches. Initial feeding location was independent from the emergence location, and then, crabs continued holding a main feeding direction (clockwise or counterclockwise), suggesting a systematic mechanism that may avoid feeding over already processed sediment. Crabs used at least half of their potential feeding area, but these areas were heterogeneous. Both sexes developed similar feeding areas; however, females were faster and needed less time to feed than males, suggesting that males are time restricted. Our work also highlights the importance of incorporating other underlying mechanisms of the behavior of species into the study of feeding strategies.

## Introduction

The foraging theory framework allows us to propose the ways through which a determined species should behave in order to maximize energy intake (Hixon 1982; Schoener 1987; Hixon and Carpenter 1988), minimize the time employed in food acquisition (Hixon 1982; Hixon and Carpenter 1988), or assure the intake of determined proportions of multiple nutrients (Simpson et al. 2004). Classical foraging theories generally assume that foragers have some prior food distribution knowledge (MacArthur and Pianka 1966; Pyke et al. 1977; Krebs 1978; Hughes 1980; Pyke 1984); thus foragers are expected to respond to changes in food abundance and distribution, resulting in a non-random feeding (MacArthur and Pianka 1966; Sih 1982; Stanton 1982; Schoener 1983). However, the effect of time and mechanical constraints may hinder feeding during the moments of the highest food abundance (Ribeiro and Iribarne 2011). In addition, the ability to locate high-food quality patches or track changes in food availability, through time and space, may imply facing important costs. Under these circumstances, the species are unable to fully respond to changes in food abundance and distribution and are expected to forage uniformly or randomly in space (Zimmer-Faust 1987).

Fiddler crabs (genus *Uca*) are interesting organisms for exploring feeding strategies. These crabs inhabit salt marshes, mangroves, and sandy or muddy beaches where they dig individual burrows that maintain and defend them from wandering crabs (Crane 1975). Crabs feed on the surrounding sediment, and their feeding mechanism consists in lifting portions of superficial sediment to their mouth with their feeding chelae, ingesting the organic fraction (mostly microphytobenthos and bacteria) attached to sediment particles (Robertson and Newell 1982a, b) and

---

Communicated by M. G. Chapman.

---

A. di Virgilio (✉)  
Laboratorio Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue, Quintral 1250, R8400FRF, San Carlos de Bariloche, Río Negro, Argentina  
e-mail: agustinadivirgilio@yahoo.com.ar

P. D. Ribeiro  
Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET-Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

P. D. Ribeiro  
Grupo de Investigación y Educación en Temas Ambientales (GrIETA), Mar del Plata, Argentina

rejecting non-digestible material as feeding pellets which are deposited back on the surface. While feeding, crabs generally perform multiple radial paths starting each at the opening of the burrow and deposit a row of pellets, easily identifiable, along the path. Thus, the spatial and temporal patterns of pellets' accumulation may be used to describe the spatial and temporal patterns of crabs feeding activity.

There are two constraints with the potential effect on fiddler crabs foraging patterns which derive from particular characteristics in their behavior and environment. The first constraint may be given by the nature and distribution of food resource that is sparse within the surrounding sediment. Energetic and functional studies (Weissburg 1992, 1993; Weissburg and Derby 1995) suggest that fiddler crabs lack of a mechanism to assess food quality or are unable to track changes in time and space of food distribution. In this scenario, we expected that fiddler crabs feed randomly or systematically in space. The second constraint may arise from their need to stay close to their burrows. The burrow is a refuge during high tide, a shelter against predators, and a mating and molting site. Thus, to keep safe, as well as to be able to guard and defend their burrows from intruders, crabs should not stray too far from their burrows, which restrict the distance traveled while feeding. Under this last constraint, crabs would be expected to feed systematically and minimize the distance to their burrows by allocating the feeding effort in multiple and short feeding paths around their burrows (instead of a unique long path forcing crabs to stray far from their burrows).

As it is common to most deposit feeders, the food resource they consume is of low digestibility (Kristensen 1972) and generally considered of low quality (Valiela and Teal 1979; Rice 1982; Genoni 1985; Galván et al. 2008). Fiddler crabs may face a temporal restriction during feeding and could need to process large amounts of sediment to achieve the necessary nutrients (Lopez and Levinton 1987). Consequently, crabs may be expected to feed continuously up to the incoming flooding tide, but in order to extend feeding time, they should move further from their burrows to find food. In addition, during the low tide period, the microphytobenthos undergoes vertical migration within sediment (Boaden 1968; McIntyre and Eleftheriou 1968; Harris 1972; McLachlan et al. 1977; Dye 1978; Round 1979; Dye and Lasiak 1986), decreasing its availability to crabs. Therefore, crabs may have to trade off between increasing feeding effort, at the cost of increasing stray distance to their burrows, and a food abundance decrease due to microphytobenthos vertical migration. The resulting balance of feeding activity may be expressed by an exponential decay model (Weissburg 1992). In this context, it is possible that crabs stop feeding far before the flooding tide (de la Iglesia et al. 1994). Furthermore, this balance is likely to differ between sexes given that one of the male's

feeding claws loses its feeding function, developing an enlarged appendage involved in social contests (Salmon 1965; Crane 1975; Salmon et al. 1978; Christy 1980; Christy and Salmon 1984). Since males have lower handling rates, they would be expected to have larger feeding time compared to females.

Several works (e.g., Valiela et al. 1974; Caravello and Cameron 1987; Weissburg 1992; Weissburg and Derby 1995) have studied feeding characteristics of fiddler crabs. However, most of these works have been conducted under controlled laboratory conditions. In this work, we studied the spatial, temporal, and sex-specific feeding patterns of the fiddler crab *Uca uruguayensis* in the field. Given that fiddler crabs inhabit areas with highly variable densities (e.g., 10–200 individuals  $m^{-2}$ , Ribeiro et al. 2005), their feeding areas are likely to overlap (Wada 1993), leading to competition for food, resources, and space (Ydenberg et al. 1986; Giraldeau et al. 1994; Lair et al. 1994). The main aim of this work was to study feeding patterns of crabs when allowed to feed in the absence of direct competition with neighboring crabs over substrate surface. We achieved this aim by blocking the activity of neighboring crabs and examining the spatial and temporal development of feeding areas. Based on the data collected, we evaluated whether: (1) crabs initiated feeding at a fixed location and direction, and if these were determined by a burrow characteristic such as the access channel inclination, (2) crabs fed systematically in space and used the total area around their burrows in order to minimize the stray distance to burrows, (3) feeding time and feeding area size were related to sex and the quantity of crabs that the area can hold, and (4) whether the feeding activity of both sexes had different temporal dynamics due to sexual dimorphism.

## Methods

### Study site and species

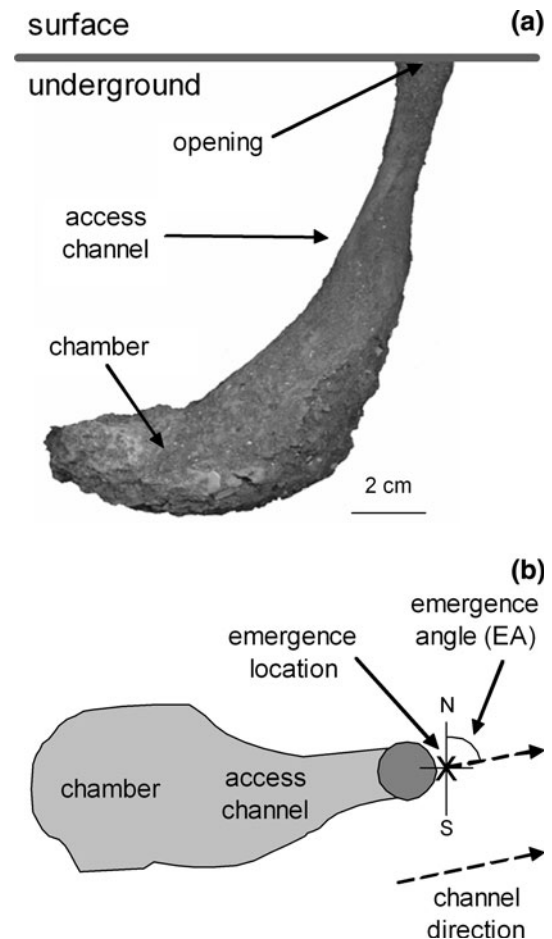
The study was conducted at the Mar Chiquita coastal lagoon (Argentina, 37°32'–37°45'S and 57°19'–57°26'W), a 46 km<sup>2</sup> body of brackish water affected by semidiurnal low-amplitude (<1.5 m) tides (Perillo et al. 1999). The fiddler crab *Uca uruguayensis* Nobili (up to 15 mm carapace width; Crane 1975) occurs in tidal flats of this lagoon above the mean high tide level, adjacent to the edge of cordgrass (*Spartina densiflora*) marshes (Bogazzi et al. 2001). Density of burrows in this area ranges from 10 to 30 crabs\*  $m^{-2}$  (Bogazzi et al. 2001). Fiddler crabs concentrate their mating activity from November to February (Bogazzi et al. 2001; Ribeiro et al. 2003). To minimize the effect of mating behavior on feeding activity, field work was conducted during the post-reproductive period (i.e., from

March to April) in 2009. Sampling was performed during days with diurnal low tides, in which the previous high tide covered the feeding areas. We observed different individuals each sampling day (i.e., the activity of each crab was not registered on different days).

#### Field work

Crabs emerge from their burrows during diurnal ebbing tides, generally 4 h before a low tide (Ribeiro et al. 2003), and plug their burrows before tide flow. This plugging is made with a cork of mud that crabs locate on the burrow opening until the next low tide. At the emergence time and before crabs initiated feeding, we randomly marked recently opened burrows (thereafter central burrows) using numbered sticks (one for each central burrow). We measured (1) access channel diameter (0.05 mm accuracy), (2) emergence angle respect to geographic coordinates (measured at the location around the entrance where individuals emerge from the underground burrow's chamber, Fig. 1), (3) number of neighboring burrows within a 60 cm radius area around central burrow (in preliminary observations, we found that feeding areas of crabs located outside a 60 cm radius area are unlikely to overlap with the feeding areas of central crabs), (4) distance between each neighboring burrow to central burrow (1 cm accuracy), and (5) carapace width (0.05 mm accuracy) of central crabs once they ended feeding. When central crabs were male, we also measured propodus length (0.05 mm accuracy) and registered the side of the enlarged claw. We sampled individuals which inhabit areas with densities ranging from 0 to 19 crabs  $m^{-2}$ . To avoid interference of neighboring crabs on feeding activity of central crabs, we temporarily blocked the opening of neighboring burrows (within a 60 cm radius area) by using spherical lead weights. This procedure prevented neighboring crabs' emergence and any potential overlap of feeding areas. Each blocking lead was covered with a shell found in the surrounding area (see Fig. 2b) to avoid any possible effect unnatural landmarks produced by leads.

Temporal dynamics of feeding areas formation of 36 females and 25 males was registered by taking digital pictures every 15–20 min, from the moment when crabs opened their burrows up to the moment when crabs ended their activity and closed their burrows (i.e., between 2 and 3 h after low tide). We used a Digital Camera (Nikon Coolpix E4300, ISO-100,  $2,048 \times 1,536$  pixels) mounted on a tripod which supported the camera 1 meter above central burrows. Tripod position was previously marked for all central burrows, which allowed us to locate the camera always in the same place. In each picture, a 20-cm rule and a compass were located within picture frame to provide a scale and a geographic orientation parameter (Fig. 2). The camera was triggered manually and we approached always

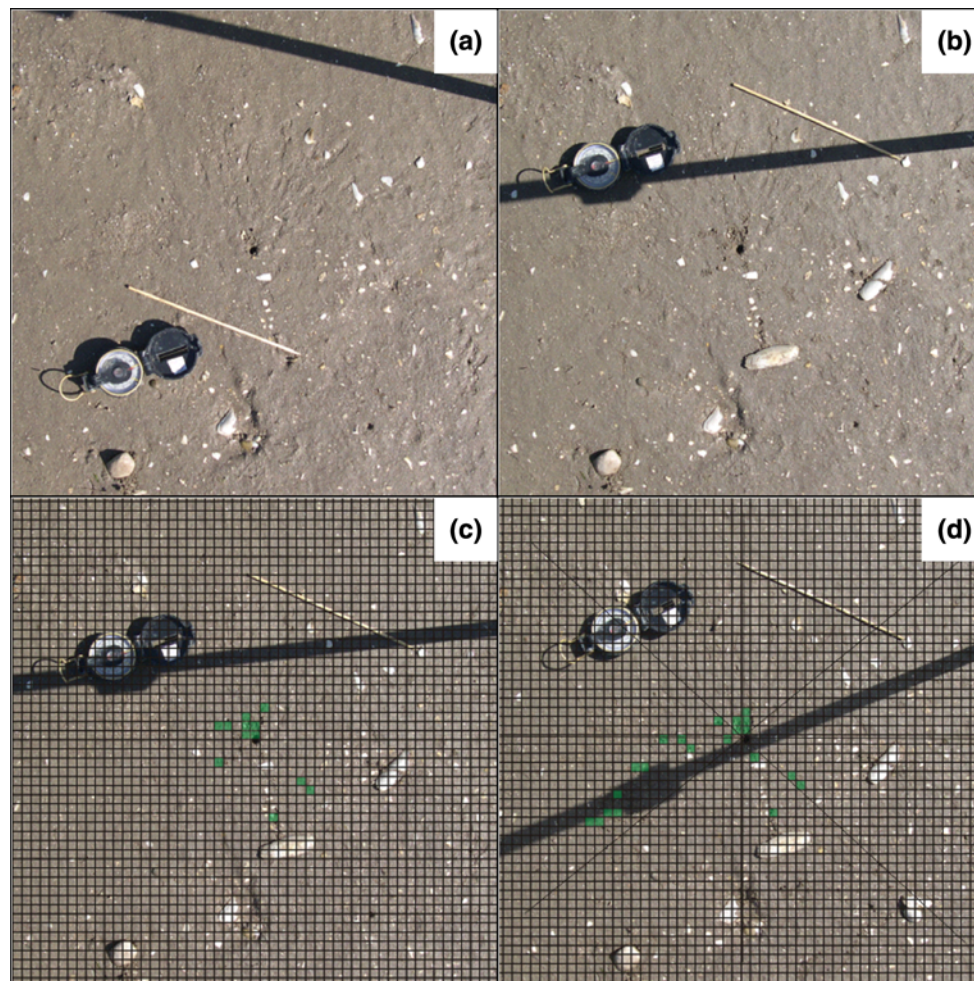


**Fig. 1** **a** A cast showing the underground structure of a burrow. **b** A schematic top view of a burrow. Only the burrow opening is visible from surface. The access channel vertical inclination leads crabs to emerge to surface at the location denoted with X. The projection of the channel direction vector on the surficial plane was used to measure the emergence angle (EA) in relation to geographic coordinates

from the same side to take each picture to minimize and standardize any possible effect of our sampling procedure on crabs' feeding movements. As a secondary effect, our methodology allowed us to detect the presence of new neighboring opened burrows and plug them (as we describe before) to prevent any superficial interference of feeding activity of central crabs by neighbors.

#### Pictures digital processing

To study feeding areas formation patterns, we divided each digital picture in 8 equal radial sectors circularly distributed around the burrow opening (see Fig. 2d). We drew a grid (cell size  $1 \text{ mm}^2$ ) in each picture to quantify the area used to feed in each sector. We marked each cell that had at least 50 % of the surface with feeding pellets and considered each as  $1 \text{ mm}^2$  of feeding area. The number of marked



**Fig. 2** A sequence of pictures showing the feeding activity of a central crab. A 20-cm rule and a compass were positioned in each picture to have a scale and a geographic orientation parameter. Neighbors' positions can be recognized by the presence of shells on

the surface. **a** Picture taken at the moment of burrow opening (time 0), **b** picture taken at 62 min, with some feeding activity, **c** picture b, but with a grid. Filled grid cells correspond to cells with feeding pellets, **d** picture taken at 86 min, with a grid and 8 sectors delimited

cells was used as an estimator of the area used to feed (see Fig. 2).

#### Calibration curve

A calibration curve was constructed to assess feeding area estimation accuracy. To construct this curve, we took pictures of known areas sketched with plasticine balls which emulated feeding pellets (i.e., 1–2 mm diameters). Pictures were processed following the same protocol described above. This procedure was repeated for a variable range of areas, and lineal relationship between real and estimated areas was used to adjust feeding areas estimation.

#### Feeding initial location

We analyzed the angular difference between emergence location and the feeding initial location to evaluate whether

feeding was initiated at the emergence location. Considering the burrow opening as a central point, we measured the emergence angle (EA) and the initial feeding angle (FA). For each crab, we used the mean angle of the sector where crab initiated feeding as an estimator of FA and calculated the minimal angular difference between EA and FA angles. We built 95 % confidence intervals to analyze the expected differences between EA and FA under two hypotheses: (1) feeding activity begins at a random position around the burrow and (2) feeding activity begins at the same sector of the EA. We evaluated whether the observed angular difference was included within the 95 % confidence intervals limits for each hypothesis.

#### Feeding movement direction

To assess whether crabs fed systematically in the space, we evaluated movement directions and changes in direction of

individuals while feeding. First, we inferred crabs movement direction, determining whether feeding area increased in clockwise (CD) or counterclockwise direction (AD) in consecutive pictures. In some cases, feeding area increase was observed at the same sector, and movement was classified as no displacement (ND). To evaluate switching frequency in movement direction, we registered the number of times a CD or an AD movement was followed by a movement of opposite direction for each crab. We constructed switching proportion frequency distribution, calculated mean switching proportion, and 95 % confidence limits using likelihood profile from a binomial distribution (Hilborn and Mangel 1997). To evaluate whether crabs had a main displacement direction, we calculated for each crab, proportions for each type of displacement ( $P_{CD}$ ,  $P_{AD}$  and  $P_{ND}$ ). We used a multinomial distribution to evaluate the likelihood (Edwards 1992) of the following models: (1) random displacement model (RDM) where, in average,  $P_{CD} = P_{AD}$ ; (2) general non-random displacement model (GNRDM), where a dominant feeding direction exists ( $P_{CD}$  differ to  $P_{AD}$ ) and is shared by all individuals (i.e., all crabs have the same values for  $P_{CD}$  and  $P_{AD}$ ), and (3) individual non-random displacement model (INRDM), where a dominant feeding direction exists but depends on each individual (i.e., modular difference between  $P_{CD}$  and  $P_{AD}$  keeps constant for all crabs). In all cases,  $P_{ND}$  value was left to fit freely and was used as an indicator uncertainty in displacement direction determination by using picture sectorization. Non-random models (i.e., GNRDM and INRDM) were confronted to random model (RDM) throughout likelihood ratio tests (LRT, Hilborn and Mangel 1997). We used Akaike information criterion (AIC; Hilborn and Mangel 1997) to confront between GNRDM and INRDM due to they were not nested models. We performed a similar procedure to determine whether feeding area development direction was influenced by (1) sex (i.e., different  $P_{CD}$  and  $P_{AD}$  values for males and females) and (2) by major chelae side in males (i.e., different  $P_{CD}$  and  $P_{AD}$  values for right- and left-handed individuals). Models were confronted using Likelihood Ratio Test (LRT; Hilborn and Mangel 1997).

#### Feeding area around the burrow

In order to minimize stray distance to their burrows, crabs may develop uniform feeding areas, which consist in similar sized feeding paths and even distributed proportions of processed sediment around their burrows. To evaluate whether crabs developed uniform feeding areas around their burrows, we first examined whether crabs devoted feeding in all sectors around their burrow; and secondly how crabs distributed their feeding activity in all sectors. For this aim, we used the last picture and counted the number of sectors with at least a 5 % of the total

feeding area. This 5 % threshold was obtained from preliminary analysis and represented the amount of feeding area which allowed us to determine the number of sectors used for feeding, avoiding an overestimation or underestimation of that variable. To evaluate how crabs distributed their feeding activity around their burrows, we calculated proportion of feeding area ( $P_f$ ) in each sector. To statistically evaluate feeding area spatial distribution, we estimated the likelihood of a multinomial distribution for the following models: (1) Uniform Area Model (Uniform), where each sector has the same  $P_f$ ; (2) Unimodal Area Model (Unimodal), where  $P_f$  of consecutive sectors increase or decrease gradually; and (3) Multimodal Area Model (Multimodal), where each sector has a different  $P_f$ , but without gradual variation between consecutive sectors. The Akaike information criterion (AIC; Hilborn and Mangel 1997) was used to select the model that better explains feeding area distribution around burrows. Finally, observed maximal distance with feeding signs was used to estimate the radius of the potential feeding area for each individual. We then calculated the proportion of the potential area that was used to feed.

#### Spatial and temporal characteristics of feeding areas, sex, and crabs density

We fitted lineal models (Neter et al. 1985) to evaluate relationship between maximum feeding area, maximum feeding distance, and total time spent feeding with local density and sex of crabs. Due to neighbor's burrows, plugging prevented any potential surficial interference between crabs; changes in feeding areas size in relation to local density of crabs could be linked to any other correlated variable, such as sediment characteristics (Ribeiro et al. 2005). This work was focused on adult crabs; however, we included carapace width as a covariable into the models. Data from maximum feeding area were root transformed to fit parametric assumptions.

#### Feeding dynamic

To explore whether females and males had different feeding dynamics, we fitted an exponential decay function for each sex (following Weissburg 1992) for modeling development of feeding areas along time and incorporated intra-individual variation (as a random effect). The exponential decay function was:

$$\text{Feeding Area}_{i,t} = \beta_{0,i} * (1 - e^{-(\beta_{1,i} * (t+p_i))}) + \varepsilon.$$

where  $\beta_0$  was maximum (asymptotic) feeding area,  $\beta_1$  was feeding area increment rate,  $t$  was feeding time,  $i$  represented each individual,  $p$  was a nuisance parameter which corrected the time elapsed from the first picture until

feeding initiation, and  $\varepsilon$  was the model's error term. We fitted this nonlinear mixed model employing a Bayesian approach with WinBUGS 1.4 (Bayesian Analysis Using Gibbs Sampler; Spiegelhalter et al. 1996). Bayesian framework uses Bayes' rule to compute from parameters prior distribution to posterior distributions using the data (See Bolker 2011; Matthiopoulos 2011). Prior probabilities are our previous beliefs about the study system (e.g., the structure of parameters distribution), and posterior distributions are the probabilities that our model (or hypothesis) be true given the information provided by our data. We fitted one model for each sex using Monte Carlo Markov-Chain (MCMC), which implements a Gibbs sampler to obtain samples from parameters posterior probabilities. We set vague (non-informative; see e.g., Bolker 2011) prior distributions for each parameter (i.e., a uniform distribution from 0 to 120 for  $p$ , and normal distributions with  $\mu = 0$  and  $\sigma^2 = 0.001$  for  $\beta_0$  and  $\beta_1$ ), ran three MCMC chains with 20,000 iterations each, and examined autocorrelations and convergence to stationary distributions in sample paths of the parameters to fit each model. 95 % credible intervals (higher posterior density—HPD interval) were calculated for parameters. To analyze inter-sexual differences, we calculated the overlap between posterior distributions of  $\beta_0$  and  $\beta_1$  estimated for both sexes.

## Results

### Calibration curve

Feeding areas estimation by counting cells with feeding pellets was very accurate. Relationship between real and estimated areas showed a  $R^2 = 0.93$  ( $p < 0.0001$ ;  $df = 53$ ). Estimated elevation and slope ( $\pm$ SE) were  $0.99 \pm 0.56$  and  $0.91 \pm 0.03 \text{ cm}^2$  respectively.

### General characteristics in spatial and temporal feeding patterns

Feeding areas mean size ( $\pm$ SE) was  $79.0 \pm 8.1 \text{ cm}^2$ , with feeding areas sizes ranging from 10.1 to  $411.6 \text{ cm}^2$ . Average time elapsed from burrow opening to the end of feeding activity ( $\pm$ SE) was 3 h and  $19.1 \pm 12.1$  min. The 50 % of crabs spent between 44.2 min and 1 h 42.2 min feeding. Distance traveled during feeding was, in average ( $\pm$ SE),  $19.3 \pm 1.1$  cm, and the 50 % of individuals traveled a distance between 13.9 and 24.5 cm.

### Feeding initial location

Our results showed that feeding initial location was not determined by access channel inclination. Observed mean angular difference between EA and FA (mean observed difference:  $89.47^\circ$ ; 95 % CI  $4.23^\circ$ ;  $172.96^\circ$ ) was not the one expected if crabs initiate feeding at the same sector where they emerged (mean expected difference:  $11.21^\circ$ ; 95 % CI  $0.530^\circ$ ;  $21.51^\circ$ ). On the other hand, observed mean angular difference between EA and FA was the one expected if feeding activity begins randomly around the burrow (mean expected difference:  $91.72^\circ$ ; 95 % CI  $5.37^\circ$ ;  $176.13^\circ$ ).

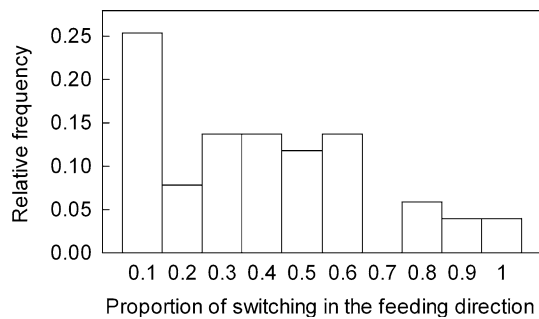
### Feeding movement direction

By pooling all individuals, AD and CD feeding movements proportions were not biased from 0.5 (mean proportion were 0.51 for AD and 0.49 for CD, with inter-quartile ranges from 0.27 to 0.76 and 0.24 to 0.70 respectively). However, according to the Likelihood Ratio Test (LRT) and Akaike information criterion (AIC), individual non-random displacement model (INRDM) was the one which better explained feeding directions from our model set (Table 1). Therefore, individuals fed over both directions

**Table 1** Negative log-likelihood values for feeding movement direction models: random displacement (RDM), general non-random displacement (GNRDM), and individual non-random displacement (INRDM)

Model	Neg. log-likelihood	LRT		$p$	AIC	Estimated proportions		
		$\chi^2$	$df$			PAD	PCD	PND
RDM	163.28		1	<b>0.007</b>		0.34	0.34	0.31
GNRDM	161.73	3.09	1	<b>0.001</b>	163.73	0.38	0.30	0.31
INRDM	145.46	35.63	1	<b>0.008</b>	147.46	0.47	0.22	0.31
Sex effect on INRDM	144.49	1.94	3	0.584				
Male Chelae-effect on INRDM								
Chelae side-dependent	57.35							
Chelae side-independent	58.13	1.56	3	0.668				

RDM and GNRDM were contrasted with Likelihood Ratio Test (LRT). GNRDM and INRDM models were contrasted using the Akaike information criterion (AIC). The effects of sex and side of males' enlarged chelae on variability observed in the INRDM model were evaluated throughout LRT.  $p$ -values highlighted in bold represent significant differences (i.e.,  $p < 0.05$ )

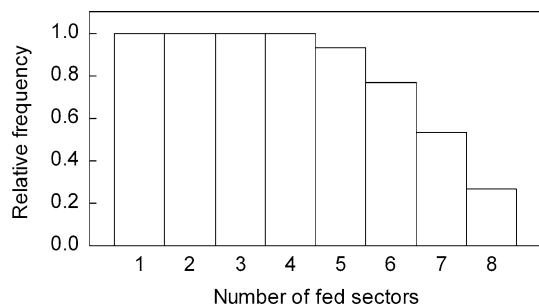


**Fig. 3** Relative frequency distribution for the proportion of times that crabs switched between clockwise and counter-clockwise feeding direction throughout their feeding activity

but maintained a main intra-individual feeding direction, which could suggest the development of a systematic feeding mechanism. Intra-individual differences in main feeding direction were not related to sex or handedness of males (Table 1). Even when crabs maintained a main feeding direction, individuals occasionally switched between directions (Fig. 3) with a mean switching rate = 0.29. The 95 % confidence limit (0.25; 0.35) did not include a switching rate = 0.5; thus, this results indicated that crabs switched between feeding directions less frequently than expected by chance.

#### Feeding area around the burrow

Analysis of how crabs developed their feeding areas around their burrows showed that all crabs used, at least, half of the circumference around their burrows (i.e., 4 sectors; Fig. 4) to feed and more than 50 % of crabs allocated their feeding activity, at least, at 7 sectors (Fig. 4). Mean potential feeding area ( $\pm$ SE) was  $140.33 \pm 14.52$  cm<sup>2</sup> and ranged from 4.10 to 448.01 cm<sup>2</sup>. The 64 % of crabs used at least the 50 % of their potential feeding areas. Although crabs fed, in general, all around their burrows, they did not develop circular or uniform feeding areas. Feeding area distribution around burrows was heterogeneous and, following AIC, this distribution was better explained by



**Fig. 4** Relative frequency distribution of the number of sectors used by crabs during feeding

**Table 2** Linear regression analysis statistics, which assess variation in total feeding area, total time spent feeding, and maximal feeding distance, in relation to explanatory variables (i.e., crabs density and sex)

	$r^2$	MSE	$F_{1,58}$	$p$
<b>Crabs density</b>				
Total feeding area	0.94	60.05	882.82	<b>&lt;0.001</b>
Total time spent feeding	0.13	67,875.00	8.49	<b>0.006</b>
Maximal feeding distance	0.04	162.03	2.12	0.143
<b>Sex</b>				
Total feeding area	0.94	0.003	0.05	0.496
Total time spent feeding	0.13	2,612.00	0.33	0.570
Maximal feeding distance	0.04	9.37	0.29	0.728

$p$ -values highlighted in bold represent significant differences (i.e.,  $p < 0.05$ )

Multimodal Area Model (AIC = 1,066.49) against Uniform and Unimodal Area models (AIC values: 2,775.39 and 1,660.58, respectively). Negative Log-Likelihood values for models were: Uniform = 2,775.39, Unimodal = 1,644.58, and Multimodal = 1,050.49.

Spatial and temporal characteristics of feeding areas, sex, and crabs density

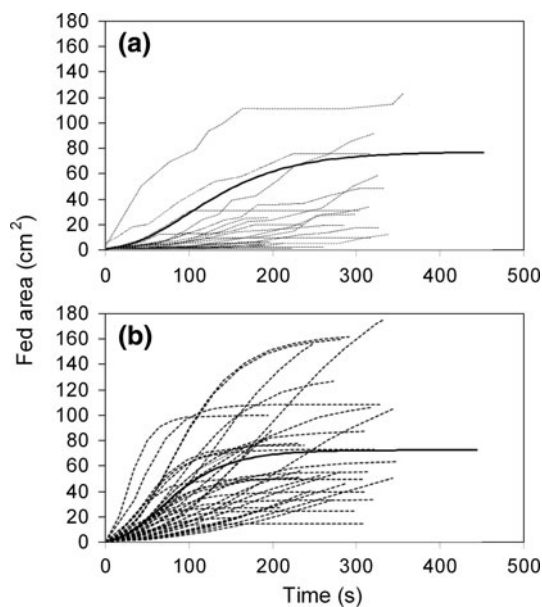
Results from density and sex effects on crabs feeding patterns in the absence of competitors on surface showed that only density affected the quantities of sediment processed by crabs and the time that individuals spent feeding. Total feeding area and total time spent feeding were positively related to crabs density (Table 2). Maximum feeding distance was not significantly related to crabs density (Table 2). None of the three variables analyzed in this study were related to sex (Table 2).

#### Feeding dynamic

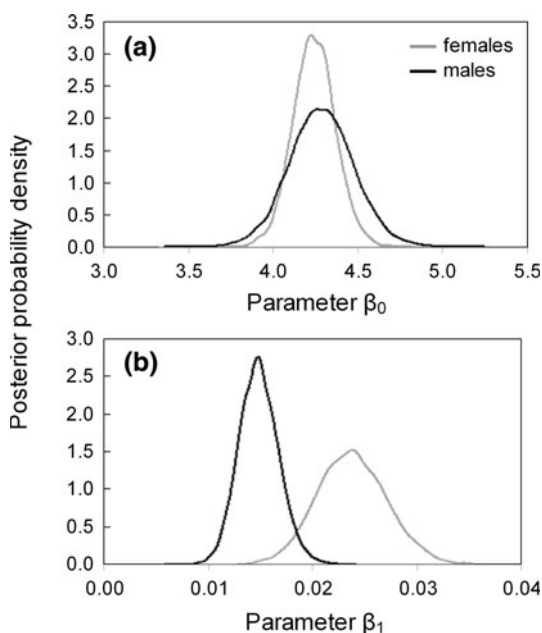
Exponential decay functions could explain feeding areas formation along crabs feeding period (Fig. 5). Feeding dynamics analysis showed that females and males developed areas of similar size (see Fig. 6). However, females were faster than males in developing their feeding areas (see Fig. 6). Parameters estimates for models and 95 % HPD intervals are shown in Table 3.

#### Discussion

In this work, we used an indirect technique to study animal feeding behavior in the field. By studying the particular accumulation of feeding pellets, we analyzed the spatial, temporal, and sex-specific feeding patterns of the fiddler



**Fig. 5** Exponential decay functions for females (a) and males (b), which explain feeding areas increase through time. *Soft lines* represent functions for individual crabs, and *solid line* represents mean decay function for all individuals



**Fig. 6** Posterior probability densities for **a**  $\beta_0$  and **b**  $\beta_1$  of females (gray lines) and males (black lines). The overlapped proportion between males' and females' parameters posterior distributions was 0.99 for  $\beta_0$  and 0.09 for  $\beta_1$  parameters

crab *Uca uruguayensis*. We found that crabs initiated feeding at a random position over the edge of the burrow opening and then maintained a main displacement direction, producing heterogeneous feeding areas around their burrows (i.e., consuming different proportion of sediment

**Table 3** Mean and 95 % HPD credible intervals for males' and females' parameters posterior distributions

Parameter	Mean	95 % HPD interval	
		Lower	Upper
Females			
$\beta_0$	4.27	4.01	4.51
$\beta_1$	0.02	0.02	0.03
Males			
$\beta_0$	4.33	3.92	4.69
$\beta_1$	0.01	0.01	0.02

in each sector). Males fed for longer time than females; however, the feeding areas of both sexes were of similar size. This sex difference in the feeding behavior may be the consequence of extreme sexual dimorphism of the genus *Uca* (Valiela et al. 1974; Weissburg 1993). However, up to the moment, there are no studies describing how sexual dimorphism may affect temporal dynamics of space used during feeding.

Contrary to the expected, the vertical inclination of the access channel, which determines the location where crabs emerge to the surface, did not establish the location where crabs initiated feeding. This inclination may be caused by the available space during the digging of a burrow. In fact, the architecture of burrows can be affected by lack of space and the presence of underground fossil shells (Ribeiro et al. 2005), and thus, the orientation of the access channel may not be necessarily related to food distribution (Zeil 1998; Layne et al. 2003a, b; Ribeiro et al. 2006). Moreover, the food resource of deposit feeders as fiddler crabs (i.e., Microphytobenthos, Lopez and Levinton 1987) can be patchily distributed over the intertidal soft sediments and varies over space and time as a consequence of several physical and biological factors (see McIntyre and Eleftheriou 1968; Reinsel and Rittschof 1995). Therefore, a possible lack of relationship between the emergence location and food distribution may lead crabs to initiate feeding at a different position than the one determined by the emergence location. However, we do not know whether the feeding initial location is or not related (i.e., random) to food abundance. In other Ocypodidae species (Zimmer-Faust 1987; Luschi et al. 1997), crabs were found to initiate the first feeding path at a random position and without the influence of factors such as landmarks (Young and Ambrose 1978; Langdon and Herrnkind 1985), sun position (Herrnkind 1968, 1983), magnetic north (Lohmann 1985), beach slope (Hamner et al. 1968; Young and Ambrose 1978), or food gradients (Anderson et al. 1997). Thus, even when orientation mechanisms are highly present and diverse within intertidal organisms (e.g., Hamner et al. 1968; Herrnkind 1968; Hyatt 1974; Young and



Ambrose 1978; Langdon and Herrnkind 1985; Lohmann 1985; Botton and Loveland 1987; Layne et al. 2003a, b), and given the low predictability of food abundance in time and space, it seems unlikely that there would be a mechanism determining the initial feeding location related to food abundance, concentration or quality.

Crabs frequently enter into their burrows, to avoid a predator (Bildstein et al. 1989; Koga et al. 1998, 2001), eliminate the possibility of losing their burrow due to intruders (Christy and Salmon 1984), or to obtain water under desiccation stress (Thurman 1998), among other reasons. In our sampling procedure, we approached the area to take photographs causing crabs to enter into their burrows which was a similar response as the one triggered by a predator. Thus, according to our results of the random feeding initiation, crabs should have resumed feeding by setting a new location and direction. Consequently, crabs should have not shown a main feeding direction. However, the examination of feeding movements showed that each individual had a main feeding direction throughout the entire feeding period. The main feeding direction was not influenced by sex or the side of the major chelae of males, which is congruent with the lack of handedness effect on mating and fighting ability (Jennions and Backwell 1996; Pratt et al. 2005). In addition, crabs switched their displacement direction less than the expected by chance; more than 25 % of individuals switched their feeding direction less than the 10 % of times when we disturbed them. This may indicate that crabs could have a mechanism to maintain a main direction in order to process sediment systematically, and thus decreasing the probabilities of reprocessing already consumed sediment. In other Ocypodidae species, crabs resume feeding next to the last feeding path (Luschi et al. 1997), by using cues from already processed substrates (as the presence of feeding pellets), visual landmarks, and information from the skylight polarization patterns (McIntyre and Eleftheriou 1968; Fielder 1970; Luschi et al. 1997). This suggests that a systematic mechanism of food consumption may be common in other deposit feeders or grazer intertidal species depending on the ability to predict or assess food patches, and the constraints imposed by the need to return or defend individual territories. For example, in order to reduce physical and biological stress, many chiton (see Hulings 1991) and limpet species (see Cook 1971) use individual scars from which they move in order to feed during low wave activity or predation risk. In a study comparing the feeding behavior of two limpet species (see Gray and Hodgson 1997), it was found that non-random feeding was associated with a high time constraint and the possible learning of highly predictable optimal feeding patches. In contrast, species that do not always defend a territory (e.g., *Cyrtograpsus angulatus*, Iribarne et al. 2003; Martinetto

et al. 2007) or not always return to the same homing place and whose time constraints are not high (e.g., *Patella granularis*, Gray and Hodgson 1997) may consume food while they move over the area, without a mechanism to resume feeding at the last location after a feeding interruption.

Fiddler crabs are highly dependent on their burrows, which are refuges against predators, water reservoirs during desiccation conditions, and mating sites (Crane 1975; Christy and Salmon 1984; Zimmer-Faust 1987). In contrast to many central place foragers that often carry food to their nests before its processing and consumption (Elliott 1988), fiddler crabs consume food while moving within the feeding area. However, their need to keep near to the burrows may shape the feeding strategy similarly to that of a central place forager. Classical foraging theories (Smith 1968; Covich 1976; Andersson 1978; Hixon 1980; Schoener 1983) assume that central place foragers optimize resource acquisition, developing circular or homogeneous foraging areas when food is evenly distributed or when individuals cannot detect food concentrations over determined thresholds. However, real foraging areas are generally more heterogeneous (Covich 1976), as a consequence of several factors, such as limited resources and changes in population density (Charnov 1976; Pyke et al. 1977; Stephens and Charnov 1982). Nevertheless, the feeding areas observed in this work were heterogeneously distributed around the burrows. Crabs fed in all sectors around the burrow, but contrary to what we expected whether crabs minimized the stray distance to burrows, crabs harvested different proportions of sediment in each sector. This result can be due to at least two, non-exclusive possible scenarios. First, although crabs may not be able to assess food quality at distance, they are able to respond to determined threshold levels of food concentration in the sediment they process (Zimmer-Faust 1987; Weissburg and Derby 1995). Thus, in contrast to species that may move toward a predictable food resource (e.g., *Siphonaria concinna*, Gray and Hodgson 1997), fiddler crabs may be unable to initiate feeding over high-quality food patches, but may be able to stop feeding when sediment is at a low food level (Zimmer-Faust 1987). It has been demonstrated in other deposit-feeding organisms, such as polichaete worms (Self and Jumars 1988; Kihslinger and Woodin 2000), that they can alter their feeding behavior in response to organic matter content by processing different proportions of sediment (Taghon and Jumars 1984; Jumars and Self 1986; Dade et al. 1990; Taghon and Greene 1990; Karrh and Miller 1994). Therefore, a departure feeding rule (Weissburg and Derby 1995) may shape the distribution of processed sediment according to the experienced food concentration. Second, we prevented neighbors to emerge and feed on the surface, but any type of interference from

underground that could alter the movement patterns of central foragers should not be discarded. Since crabs often inhabit high-density areas (Grimes et al. 1989; Spivak et al. 1991; Ribeiro et al. 2005), the development of different mechanisms for territorial delimitation and neighbors' position recognition could be possible (Grant 1968; Salmon and Atsaiades 1968; Horch and Salmon 1972; Popper et al. 2001).

Linear analyses showed that the maximum feeding area and time spent feeding were both related to local density of crabs, even when neighbors were prevented to emerge and feed. If crabs density was positively determined by sediment quality (i.e., more food in the sediment allowed the settlement of more crabs), a negative relationship would be expected between local density and feeding area. Considering that density partly increases with organic matter content in sediment (Ribeiro et al. 2005), individuals at high densities would be expected to develop smaller feeding areas. In addition, they would also employ less time feeding than crabs at low densities, because less sediment would be required to extract the same amount of food. However, our results showed the opposite, since size of feeding areas and time spent feeding increased with density. This result may be an outcome of the high competition with neighbors. At high densities, food resources may decrease faster throughout exploitative competition (Park 1957; but see Ribeiro and Iribarne 2011), and the presence of more neighbors could reduce available time for feeding due to interference (Park 1957; Miller 1967). In this context, the positive relationship between local densities of crabs, with time spent feeding and with size of the feeding area, suggests that crabs at high densities need larger areas and feed for longer periods to compensate for competition costs. In addition, the maximal feeding distance was not affected by sex and local density, suggesting that this characteristic may be controlled by additional factors such as perceived predation risk (Lima and Dill 1990; Pomeroy 2006), food abundance over determined thresholds, and several environmental factors (e.g., humidity, tides, temperature, and wind velocities) which were not accounted in this study. Nevertheless, our results provide information about how crabs feed without the direct effect of competitors on the surface, given that we prevented neighbors' emergence by blocking their burrows openings. It is interesting to note that as density increases, the chance of encounter between neighbors may also increase. Therefore, if the size of feeding areas increases with crab density, then the overlap degree between feeding areas may increase disproportionately. Future studies may explore whether crabs develop any specific mechanisms in order to avoid the overlap between feeding areas. As expected, the temporal dynamic of the formation of feeding areas could be expressed by an exponential decay model; thus feeding areas quickly increased at the beginning and

then flattened by the end of the feeding activity. Bayesian analysis showed some variability among individuals which may be caused by different requirements and trade-offs, affecting the time budgets of each individual (Werner and Gilliam 1984; McNamara and Houston 1986, 1994; Mangel and Ludwig 1992; Houston and Shine 1993). Despite this, a sex-specific temporal dynamic could be identified; feeding areas of females developed faster than those of males. A study in *Uca pugnax* analyzing the intake rate dynamic in relation to changes in food concentration (as it is being consumed) showed that females fed faster than males (Weissburg 1993). This sex-specific feeding rate may be a general pattern for all fiddler crab species, in which males lose one of the two initial feeding appendages to become a sexual signaling structure (Crane 1975). In contrast, females keep both feeding appendages and are able to handle more sediment per unit of time than males. Higher feeding rates in females may lead to a faster development of feeding areas compared to males. Furthermore, a sex-specific response to food concentration was found in *Uca pugnax*, where males ceased feeding at higher food concentrations than females (Weissburg and Derby 1995). Consequently, females could be able to consume more food per gram of sediment than males (Weissburg 1993). Therefore, if both sexes required the consumption of similar amounts of food, then females would be expected to form smaller feeding areas than males. However, we have not found differences in the size of feeding areas between sexes. Nevertheless, the sex-specific response to food concentration in *Uca pugilator* was given by the persistence of females feeding over decaying food concentration below those that stimulated male feeding (Weissburg and Derby 1995). In contrast, under field conditions, crabs avoid processing already processed sediment by moving to adjacent areas of fresh sediment, and where food concentration may be above the threshold required for both sexes (Zimmer-Faust 1987). However, in our study, females generally ceased feeding before males. In contrast, males generally finished feeding due to the upcoming tide or to sediment desiccation. Therefore, due to males feeding slower than females, it is likely that males lack enough time to form higher feeding areas compared to those developed by females. Thus, males would be energetically disadvantaged (Valiela et al. 1974; Crane 1975; Caravello and Cameron 1987; Weissburg 1993) requiring the development of compensatory strategies such as the defense of high-quality food areas (Murai et al. 1983; Caravello and Cameron 1987), or the development of sex-specific structures in the feeding appendages, allowing them to handle different amounts or size of sediment particles (Valiela et al. 1974; Colpo and Negreiros-Fransozo 2011).

In cases in which the species is unable to assess or predict the distribution of food resources, the expected

feeding strategy is to feed randomly or systematically (Hixon 1980; Schoener 1983; Zimmer-Faust 1987). The formation of feeding areas by the production of feeding paths radiating from burrows' openings, and the maintenance of a main feeding direction, evidence the systematic feeding behavior of fiddler crabs. Nevertheless, the systematic production of radial feeding paths may be also a consequence of the crabs' mechanism to orient and keep track their burrows location (see Layne et al. 2003a, b). Thus, the orientation mechanisms traits may impose additional restrictions on the type of displacements that crabs could perform during feeding. Finally, in order to increase our knowledge of how evolution shapes feeding strategies, it would be important to incorporate the characteristics and functioning of additional mechanisms controlling any aspects of the species behavior.

**Acknowledgments** This work was partially supported by a grant from Agencia Nacional de Promoción Científica y Tecnológica to P.D.R. (PICT 2007-01488). We thank Juan Manuel Morales for helping in statistical analysis.

## References

- Anderson ARA, Young IM, Sleeman BD, Griffiths BS, Robertson WM (1997) Nematode movement along a chemical gradient in a structurally heterogeneous environment, 1. Experiment. *Fundam Appl Nematol* 20:157–164
- Andersson M (1978) Optimal foraging area: size and allocation of search effort. *Theor Popul Biol* 13:397–409
- Bildstein KL, McDowell SG, Brisbin IL (1989) Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential vulnerability to avian predation. *Anim Behav* 37:133–139
- Boaden P (1968) Water movement—a dominant factor in interstitial ecology. *Sarsia* 34:125–136
- Bogazzi E, Iribarne O, Guerrero R, Spivak E (2001) Wind pattern may explain the southern limit of distribution of a southwestern Atlantic fiddler crab. [Un patrón de vientos puede explicar el límite sur de distribución del cangrejo violinista del Atlántico sudoccidental]. *J Shellfish Res* 20:353–360
- Bolker BM (2011) Ecological models and data in R. University Press, Princeton
- Botton ML, Loveland RE (1987) Orientation of the horseshoe crab, *Limulus polyphemus*, on a sandy beach. *Biol Bull* 173:289–298
- Caravello HE, Cameron GN (1987) The effects of sexual selection on the foraging behaviour of the Gulf Coast fiddler crab, *Uca panacea*. *Anim Behav* 35:1864–1874
- Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theor Popul Biol* 9:129–136
- Christy JH (1980) The mating system of the sand fiddler crab, *Uca pugilator*. Ph.D thesis, Cornell University
- Christy JH, Salmon M (1984) Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biol Rev* 59:483–509
- Colpo K, Negreiros-Fransozo M (2011) Sediment particle selection during feeding by four species of *Uca* (Brachyura, Ocypodidae). *Crustaceana* 84:5–6
- Cook SB (1971) A study of homing behavior in the limpet *Siphonaria alternata*. *Biol Bull* 141:449–457
- Covich AP (1976) Analyzing shapes of foraging areas: some ecological and economic theories. *Annu Rev Ecol Syst* 7:235–257
- Crane J (1975) Fiddler crabs of the world: Ocypodidae: genus *Uca*. Princeton University Press, Princeton
- Dade WB, Jumars PA, Penry DL (1990) Supply-side optimization: maximizing absorptive rates. In: RN H (ed) Behavioural mechanisms in food selection. Springer, Berlin, pp 531–555
- de la Iglesia HO, Rodríguez EM, Dezi RE (1994) Burrow plugging in the crab *Uca uruguayensis* and its synchronization with photoperiod and tides. *Physiol Behav* 55:913–919
- Dye A (1978) Diurnal vertical migrations of meiofauna in an estuarine sand flat. *Zool Afr* 13:201–205
- Dye A, Lasiak T (1986) Microbenthos, meiobenthos and fiddler crabs: trophic interactions in a tropical mangrove sediment. *Mar Ecol Prog Ser* 32:9–264
- Edwards A (1992) Likelihood. Johns Hopkins Ed. University Press, Baltimore
- Elliott PF (1988) Foraging behavior of a central-place forager: field tests of theoretical predictions. *Am Nat* 131:159–174
- Fielder D (1970) The feeding behaviour of the sand crab *Scopimera inflata* (Decapoda, Ocypodidae). *J Zool* 160:35–49
- Galván K, Fleegeer JW, Fry B (2008) Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna. *Mar Ecol Prog Ser* 359:37–49
- Genoni GP (1985) Food limitation in salt marsh fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae). *J Exp Mar Biol Ecol* 87:97–110
- Giraldeau LA, Kramer DL, Deslandes I, Lair H (1994) The effect of competitors and distance on central place foraging eastern chipmunks, *Tamias striatus*. *Anim Behav* 47:621–632
- Grant P (1968) Polyhedral territories of animal. *Am Nat* 102:75–80
- Gray D, Hodgson A (1997) Temporal variation in foraging behaviour of *Patella granularis* (Patellogastropoda) and *Siphonaria concinna* (Basommatophora) on a South African shore. *J Mollus Stud* 63:121–130
- Grimes BH, Huish MT, Kerby JH, Moran D (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic): summer and winter flounder, vol 82. U.S. Fish Wildlife Service Biological Report, US
- Hamner W, Smyth M, Mulford E (1968) Orientation of the sand-beach isopod *Tylos punctatus*. *Anim Behav* 16:405–409
- Harris RP (1972) Seasonal changes in population density and vertical distribution of harpacticoid copepods on an intertidal sand beach. *J Mar Biol Assoc UK* 52:493–505
- Herrnkind WF (1968) Adaptive visually-directed orientation in *Uca pugilator*. *Am Zool* 8:585–598
- Herrnkind WF (1983) Movement patterns and orientation. In: Vernberg Va (ed) The biology of Crustacea, vol 7. Academic Press, New York, pp 41–105
- Hilborn R, Mangel M (1997) The ecological detective: confronting models with data, vol 28. University Press, Princeton
- Hixon MA (1980) Food production and competitor density as the determinants of feeding territory size. *Am Nat* 115:510–530
- Hixon MA (1982) Energy maximizers and time minimizers: theory and reality. *Am Nat* 119:596–599
- Hixon MA, Carpenter FL (1988) Distinguishing energy maximizers from time minimizers: a comparative study of two hummingbird species. *Am Zool* 28:913–925
- Horch K, Salmon M (1972) Responses of the ghost crab, Ocypode, to acoustic stimuli. *Z Tierpsychol* 30:1–13
- Houston D, Shine R (1993) Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *J Anim Ecol* 62:737–748
- Hughes RN (1980) Optimal foraging theory in the marine context. *Oceanogr Mar Biol* 18:423–481

- Hulings N (1991) Activity patterns and homing of *Acanthopleura gemmata* (Blainville, 1825) (Mollusca: Polyplacophora) in the rocky intertidal of the Jordan Gulf of Aqaba. *Nautilus* 105:16–25
- Hyatt GW (1974) Behavioural evidence for light intensity discrimination by the fiddler crab, *Uca pugilator* (brachyura, ocyropodiidae). *Anim Behav* 22:796–801
- Iribarne O, Martinetto P, Schwindt E, Botto F, Bortolus A, Borboroglu PG (2003) Evidences of habitat displacement between two common soft-bottom SW Atlantic intertidal crabs. *J Exp Mar Biol Ecol* 296:167–182
- Jennions MD, Backwell PRY (1996) Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol J Linn Soc* 57:293–306
- Jumars P, Self R (1986) Gut-marker and gut-fullness methods for estimating field and laboratory effects of sediment transport on ingestion rates of deposit-feeders. *J Exp Mar Biol Ecol* 98:293–310
- Karrh RR, Miller DC (1994) Functional response of a surface-deposit feeder, *Saccoglossus kowalevskii*. *Limnol Oceanogr* 39:1455–1464
- Kihllinger RL, Woodin SA (2000) Food patches and a surface deposit feeding spionid polychaete. *Mar Ecol Prog Ser* 201:233–239
- Koga T, Backwell PRY, Jennions MD, Christy JH (1998) Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proc Roy Soc Lond B Biol* 265:1385–1390
- Koga T, Backwell PRY, Christy JH, Murai M, Kasuya E (2001) Male-biased predation of a fiddler crab. *Anim Behav* 62:201–207
- Krebs JR (1978) Optimal foraging: decision rules for predators. In: Krebs J, Davies N (eds) *Behavioural ecology: an evolutionary approach*. Blackwell Scientific Publishers, Oxford, pp 23–63
- Kristensen JH (1972) Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. *Mar Biol* 14:130–142
- Lair H, Kramer DL, Giraldeau LA (1994) Interference competition in central place foragers: the effect of imposed waiting on patch-use decisions of eastern chipmunks, *Tamias striatus*. *Behav Ecol* 5:237–244
- Langdon JW, Herrnkind W (1985) Visual shape discrimination in the fiddler crab, *Uca pugilator*. *Mar Freshw Behav Physiol* 11:315–325
- Layne JE, Barnes WJP, Duncan LMJ (2003a) Mechanisms of homing in the fiddler crab *Uca rapax* 1. Spatial and temporal characteristics of a system of small-scale navigation. *J Exp Biol* 206:4413–4423
- Layne JE, Barnes WJP, Duncan LMJ (2003b) Mechanisms of homing in the fiddler crab *Uca rapax* 2. Information sources and frame of reference for a path integration system. *J Exp Biol* 206:4425–4442
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Lohmann KJ (1985) Geomagnetic field detection by the western Atlantic spiny lobster, *Panulirus argus*. *Mar Freshw Behav Physiol* 12:1–7
- Lopez GR, Levinton JS (1987) Ecology of deposit-feeding animals in marine sediments. *Q Rev Biol* 62:235–260
- Luschi P, Seppia CD, Crosio E (1997) Orientation during short-range feeding in the crab *Dotilla wichmanni*. *J Comp Physiol A* 181:461–468
- MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *Am Nat* 100:603–609
- Mangel M, Ludwig D (1992) Definition and evaluation of the fitness of behavioral and developmental programs. *Annu Rev Ecol Syst* 23:507–536
- Martinetto P, Valiñas M, Palomo G, Iribarne O (2007) Negative interactions between two SW Atlantic intertidal crabs in soft-bottom habitats. *Mar Biol* 151:1479–1490
- Matthiopoulos J (2011) How to be a quantitative ecologist: the ‘A to R’ of green mathematics and statistics. Wiley, UK
- McIntyre A, Eleftheriou A (1968) The bottom fauna of a flatfish nursery ground. *J Mar Biol Assoc UK* 48:113–142
- McLachlan A, Winter P, Botha L (1977) Vertical and horizontal distribution of sub-littoral meiofauna in Algoa Bay, South Africa. *Mar Biol* 40:355–364
- McNamara JM, Houston AI (1986) The common currency for behavioral decisions. *Am Nat* 127:358–378
- McNamara JM, Houston AI (1994) The effect of a change in foraging options on intake rate and predation rate. *Am Nat* 144:978–1000
- Miller RS (1967) Pattern and process in competition. *Adv Ecol Res* 4:1–74
- Murai M, Goshima S, Nakasone Y (1983) Adaptive droving behavior observed in the fiddler crab *Uca vocans vocans*. *Mar Biol* 76:159–164
- Neter J, Kutner MH, Nachtsheim CJ, Wasserman W (1985) *Applied linear statistical models: Regression, analysis of variance, and experimental designs*, 4th edn. Richard D. Irwin, Inc, Homewood
- Park T (1957) Experimental studies of interspecies competition. III Relation of initial species proportion to competitive outcome in populations of *Tribolium*. *Physiol Zool* 30:22–40
- Perillo GME, Piccolo MC, Pino-Quivira M, Quivira P (1999) *Estuaries of South America: their geomorphology and dynamics*. Springer, Berlin
- Pomeroy AC (2006) Tradeoffs between food abundance and predation danger in spatial usage of a stopover site by western sandpipers, *Calidris mauri*. *Oikos* 112:629–637
- Popper AN, Salmon M, Horch KW (2001) Acoustic detection and communication by decapod crustaceans. *J Comp Physiol A* 187:83–89
- Pratt AE, McLain DK, Berry AS (2005) Variation in the boldness of courting sand fiddler crabs (*Uca pugilator*). *Ethology* 111:63–76
- Pyke GH (1984) Optimal foraging theory: a critical review. *Annu Rev Ecol Syst* 15:523–575
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Reinsel KA, Rittschof D (1995) Environmental regulation of foraging in the sand fiddler crab *Uca pugilator* (Bosc 1802). *J Exp Mar Biol Ecol* 187:269–287
- Ribeiro PD, Iribarne OO (2011) Coupling between microphytobenthic biomass and fiddler crab feeding. *J Exp Mar Biol Ecol* 407:147–154
- Ribeiro PD, Iribarne OO, Jaureguy L, Navarro D, Bogazzi E (2003) Variable sex-specific mortality due to shorebird predation on a fiddler crab. *Can J Zool* 81:1209–1221
- Ribeiro PD, Iribarne OO, Daleo P (2005) The relative importance of substratum characteristics and recruitment in determining the spatial distribution of the fiddler crab *Uca uruguayensis* Nobili. *J Exp Mar Biol Ecol* 314:99–111
- Ribeiro PD, Christy JH, Rissanen RJ, Kim TW (2006) Males are attracted by their own courtship signals. *Behav Ecol Sociobiol* 61:81–89
- Rice DL (1982) The detritus nitrogen problem: new observations and perspectives from organic geochemistry. *Mar Ecol Prog Ser* 9:153–162
- Robertson JR, Newell S (1982a) Experimental studies of particle ingestion by the sand fiddler crab *Uca pugilator* (Bosc). *J Exp Mar Biol Ecol* 59:1–21
- Robertson JR, Newell S (1982b) A study of particle ingestion by three fiddler crab species foraging on sandy sediments. *J Exp Mar Biol Ecol* 65:11–17
- Round F (1979) Occurrence and rhythmic behaviour of *Tropidoneis lepidoptera* in the epipelon of Barnstable Harbor, Massachusetts, USA. *Mar Biol* 54:215–217

- Salmon M (1965) Waving display and sound production in the courtship behavior of *Uca pugilator* with comparison to *Uca minax* and *Uca pugnax*. *Zoologica* 50:123–150
- Salmon M, Atsaiades SP (1968) Visual and acoustical signalling during courtship by fiddler crabs (genus *Uca*). *Am Zool* 8:623–639
- Salmon M, Hyatt G, McCarthy K, Costlow JD Jr (1978) Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. *Z Tierpsychol* 48:251–276
- Schoener TW (1983) Simple models of optimal feeding-territory size: a reconciliation. *Am Nat* 121:608–629
- Schoener TW (1987) Time budgets and territory size: some simultaneous optimization models for energy maximizers. *Am Zool* 27:259–291
- Self RFL, Jumars PA (1988) Cross-phyletic patterns of particle selection by deposit feeders. *J Mar Res* 46:119–143
- Sih A (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* 63:786–796
- Simpson SJ, Sibly RM, Lee KP, Behmer ST, Raubenheimer D (2004) Optimal foraging when regulating intake of multiple nutrients. *Anim Behav* 68:1299–1311
- Smith CC (1968) The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. *Ecol Monogr* 38:31–63
- Spiegelhalter D, Thomas A, Best N, Gilks W (1996) BUGS 0.5: Bayesian inference using Gibbs sampling manual (version ii). MRC Biostatistics Unit Institute of Public Health, Cambridge
- Spivak ED, Gavio MA, Navarro CE (1991) Life history and structure of the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita lagoon (Argentina). *Bull Mar Sci* 48:679–688
- Stanton ML (1982) Searching in a patchy environment: foodplant selection by *Colis philodice* eriphyle butterflies. *Ecology* 63:839–853
- Stephens DW, Charnov EL (1982) Optimal foraging: some simple stochastic models. *Behav Ecol Sociobiol* 10:251–263
- Taghon GL, Greene RR (1990) Effects of sediment-protein concentration on feeding and growth rates of *Abarenicola pacifica* Healy et Wells (Polychaeta: Arenicolidae). *J Exp Mar Biol Ecol* 136:197–216
- Taghon GL, Jumars PA (1984) Variable ingestion rate and its role in optimal foraging behavior of marine deposit feeders. *Ecology* 65:549–558
- Thurman CL (1998) Evaporative water loss, corporal temperature and the distribution of sympatric fiddler crabs (*Uca*) from South Texas. *Comp Biochem Phys A* 119:279–286
- Valiela I, Teal JM (1979) The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652–656
- Valiela I, Babiec DF, Atherton W, Seitzinger S, Krebs C (1974) Some consequences of sexual dimorphism: feeding in male and female fiddler crabs, *Uca pugnax* (Smith). *Biol Bull* 147:652–660
- Wada K (1993) Territorial behavior, and sizes of home range and territory, in relation to sex and body size in *Ilyoplax pusilla* (Crustacea: Brachyura: Ocypodidae). *Mar Biol* 115:47–52
- Weissburg M (1992) Functional analysis of fiddler crab foraging: sex-specific mechanics and constraints in *Uca pugnax* (Smith). *J Exp Mar Biol Ecol* 156:105–124
- Weissburg M (1993) Sex and the single forager: gender-specific energy maximization strategies in fiddler crabs. *Ecology* 74:280–291
- Weissburg M, Derby C (1995) Regulation of sex-specific feeding behavior in fiddler crabs: physiological properties of chemoreceptor neurons in claws and legs of males and females. *J Comp Physiol A* 176:513–526
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425
- Ydenberg R, Giraldeau L, Kramer D (1986) Interference competition, payoff asymmetries, and the social relationships of central place foragers. *Theor Popul Biol* 30:26–44
- Young DY, Ambrose HW (1978) Underwater orientation in the sand fiddler crab, *Uca pugilator*. *Biol Bull* 155:246–258
- Zeil J (1998) Homing in fiddler crabs (*Uca lactea annulipes* and *Uca vomeris*: Ocypodidae). *J Comp Physiol A* 183:367–377
- Zimmer-Faust RK (1987) Substrate selection and use by a deposit-feeding crab. *Ecology* 68:955–970