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Authors: Suárez, Nicolás, Retana, María Valeria, and Yorio, Pablo

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Effect of Feeding Technique and Prey Characteristics on the Feeding Rate of Olrog's Gulls (*Larus atlanticus*)

Nicolás Suárez[1,*], María Valeria Retana[1] and Pablo Yorio[1,2]

[1]Centro Nacional Patagónico (CONICET), Boulevard Brown 2915, U9120ACD, Puerto Madryn, Chubut, Argentina

[2]Wildlife Conservation Society, Amenábar 1595, P 2, Of. 19, C1426AKC, Ciudad de Buenos Aires, Argentina

[*]Corresponding author; E-mail: suarez@cenpat.edu.ar

Abstract.—The Olrog's Gull (*Larus atlanticus*) is a species that feeds almost exclusively on intertidal crabs. The influence of feeding technique, food source, and habitat characteristics on the feeding rate of breeding individuals was examined at Bahía San Blas, Argentina, from September to December 2007. Olrog's Gulls used four feeding techniques, with more prey captured by pecking than by peck-digging, head submergence, or up-ending. Olrog's Gulls fed throughout the tidal cycle using different intertidal zones when they were exposed and covered by water. However, feeding techniques used in exposed intertidal areas (pecking and peck-digging) resulted in significantly higher feeding rates. Feeding rate increased with average prey density and was higher when feeding in structured environments, characterized by the presence of rocks or oysters and high densities of the intertidal crab *Cyrtograpsus altimanus*. The burrowing crab *Neohelice granulata* is the main component of the Olrog's Gull diet during most of the breeding cycle. Although average density of *N. granulata* in feeding patches was lower than that of *C. altimanus*, body size of the former was significantly larger and energy density of individuals higher, resulting in a higher energy profitability of unstructured habitats. Prey switching toward *C. altimanus* during the young chick stage observed in previous studies may result from the need to feed chicks with smaller prey. *Received 24 June 2013, accepted 26 December 2013.*

Key words.—Argentina, Bahía San Blas protected area, crabs, feeding behavior, intertidal crabs, *Larus atlanticus*, Olrog's Gull.

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Intertidal areas are important feeding habitats for many waterbirds (Burger 1984; Piersma *et al.* 1993). The use of intertidal feeding grounds by birds is predominantly determined by the distribution and abundance of prey (Goss-Custard 1970; Yates *et al.* 1993; Ribeiro *et al.* 2004; Rose and Nol 2010), which in turn is affected by the physical characteristics of the environment (Yates *et al.* 1993; Danufsky and Colwell 2003). Food resources along intertidal areas are relatively predictable and generally available at regular intervals depending on the tidal cycle. For birds that depend on these resources, tidal state is an important factor determining their local distribution and behavior because tides can cover foraging habitats and alter food availability (Burger *et al.* 1977; Warnock *et al.* 2002; Ribeiro *et al.* 2004; Ellis *et al.* 2005). Tidal cycles can therefore make birds alter feeding techniques, select different prey, or use different habitats (Curtis and Thompson 1985; McNeil *et al.* 1992; Withers and Chapman 1993; De Vlas *et al.* 1996). These changes may influence the rate at which birds obtain their prey and thus directly affect their fitness.

Several gull species depend on intertidal resources at least during part of their annual cycle (Burger and Gochfeld 1996), and their plasticity and generalist feeding behavior allows them to use a wide variety of feeding methods (Burger 1988). Olrog's Gull (*Larus atlanticus*) is an endemic species of the southwestern Atlantic coast that only breeds in Argentina (Yorio *et al.* 1999) and is considered globally vulnerable (Birdlife International 2013). During the breeding season, Olrog's Gulls prey almost exclusively on intertidal crabs (Delhey *et al.* 2001; Herrera *et al.* 2005; Suárez *et al.* 2012) and thus are highly dependent on intertidal environments. Like other gulls, Olrog's Gulls use a variety of feeding techniques, such as pecking, head submergence, and surface plunging, allowing capture of prey both in exposed and covered intertidal areas (Martinez *et al.* 2000; Copello and Favero 2001; Gatto *et al.* 2008), and studies during the non-breeding season have revealed differences in feeding techniques (Copello and Favero 2001) and capture rates (Berón *et al.* 2011) among different age-classes. However, little is known

about how feeding rate is related to feeding technique, feeding habitat or prey type, size, and density in this and other gull species. Our objective was to describe the feeding behavior of Olrog's Gulls breeding at the Bahía San Blas protected area, Argentina, and examine how feeding rate relates to factors such as feeding technique, food source, and habitat characteristics.

METHODS

Our study was conducted in the southwestern sector of the Bahía San Blas protected area in Buenos Aires Province, Argentina (Fig. 1). This sector is used as foraging grounds by Olrog's Gulls nesting at Islote Arroyo Jabalí Oeste (40° 32' 42.20" S, 62° 17' 23.48" W) (Suárez *et al.* 2012). Colony size during the study year was estimated at 508 nests (N. Suárez, unpubl. data). The coastal sector is 16 km long and is characterized by extensive mudflats and marshes of *Spartina* spp. and *Salicornia ambigua*, with crab beds consisting of *Neohelice granulata*, *Cyrtograpsus altimanus*, and *C. angulatus* (Zalba *et al.* 2008). These are intertidal crabs common in southwest Atlantic coastal and estuarine areas (Iribarne *et al.* 2003). *C. altimanus* is mostly found in structured environments, while *N. granulata* is found in marshes characterized by muddy substrates with *Spartina* spp. and *C. angulatus* in sectors dominated by muddy substrates (Iribarne *et al.* 2003; Isacch *et al.* 2006; Suárez *et al.* 2012). Olrog's Gulls in our study area feed almost exclusively (99% of total prey biomass) on the three crab species, primarily *N. granulata* and *C. altimanus*, with a differential contribution of each species depending on the stage of the breeding cycle (Suárez *et al.* 2011). *N.*

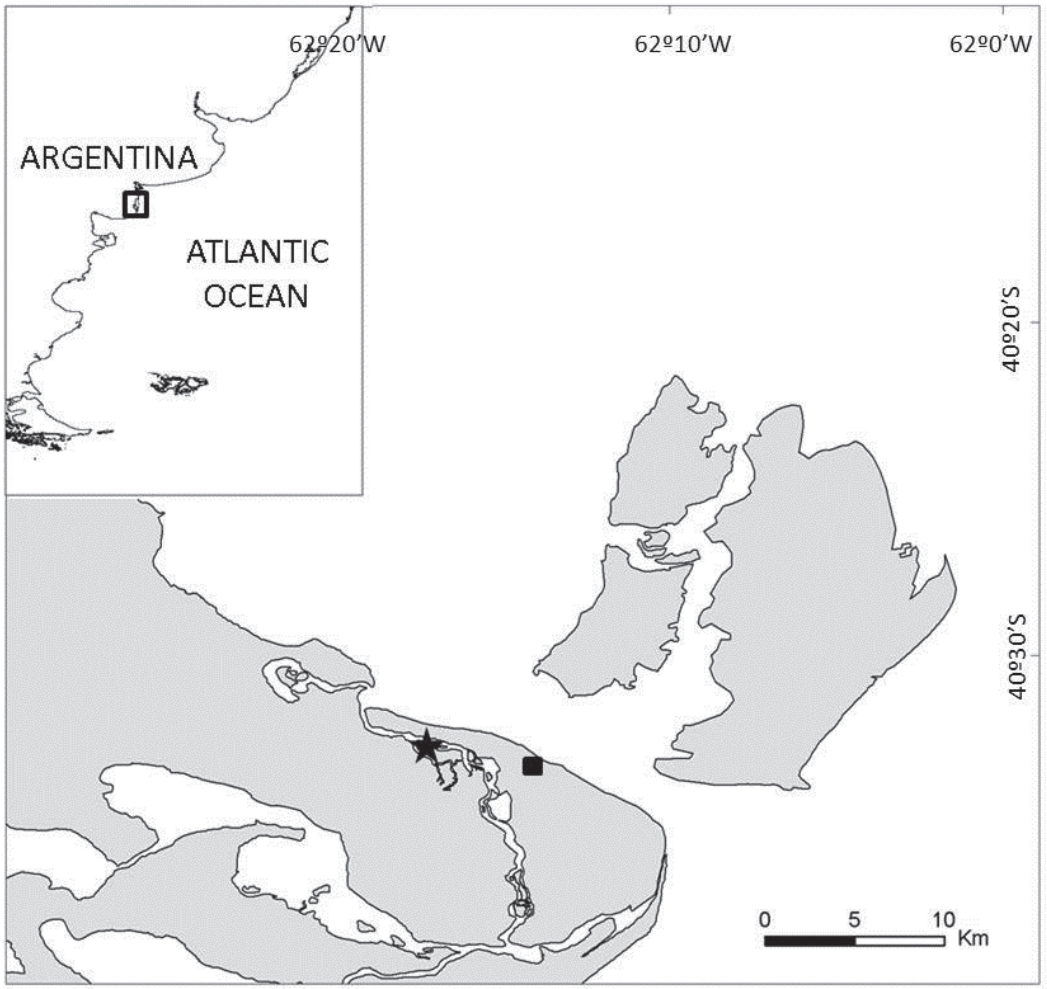

Figure 1. The study area showing the location of the Olrog's Gull (*Larus atlanticus*) colony (star) and the town of San Blas (square).

granulata is the primary prey of Olrog's Gulls during incubation, *C. altimanus* is the dominant prey during the young chick stage, and both contribute similarly during the older chick stage (Suárez *et al.* 2011). In our study area, Olrog's Gulls initiate laying in late September, eggs start hatching in late October, and chicks start fledging in early December (Suárez *et al.* 2011).

The behavior of Olrog's Gulls while feeding was studied using focal individual observations (Altmann 1974; Martin and Bateson 1994). Observations were made on feeding adult individuals distributed throughout the entire coastal area used for foraging (Suárez *et al.* 2012). From eight to 15 focal individuals were selected randomly and observed daily from an estimated distance of 50 m. Each feeding Olrog's Gull was filmed for 5 min using a digital camcorder (Sony Handycam SR68, with 60X optical), and recordings were then analyzed in the lab to obtain feeding technique and feeding rate. Feeding rate was defined as the number of prey captured per minute (all captured prey were ingested). Sampling was conducted from 13 September to 8 December 2007; observations were distributed between 08:00 and 21:00 hr and encompassed different stages of the tidal cycle as well as habitat characteristics. Observations began no sooner than 5 min after a focal bird was selected to minimize possible bias due to behavioral changes resulting from an observer's approach.

In the field, a focal Olrog's Gull's feeding technique and habitat were recorded for each 5-min feeding observation period. Feeding techniques were categorized following the definitions of Gatto *et al.* (2008): 1) pecking (P): prey capture from the substrate's surface by striking with the beak while walking; 2) peck-digging (PD): prey capture by dipping the beak in soft substrate; 3) head submergence (HS): prey capture by dipping the head underwater while swimming; and 4) up-ending (UE): prey capture by submerging the head, neck, and upper body, with tail raised in the air. Birds generally displayed only one feeding technique, switching feeding technique in less than 2% of observation periods. Sites where Olrog's Gulls fed were categorized as either structured (habitats with some structure, such as rocks or Pacific oysters (*Crassostrea gigas*), along the substrate that served as shelter for crabs) or unstructured (habitats without such structural components), and were divided into three classes of intertidal zoning: 1) upper; 2) middle; and 3) lower. Intertidal zones were defined as the upper, middle, and lower third of the elevation gradient for each study site considered. In addition, the state of the tide for each record was noted and assigned to one of three categories: high, medium, and low, with high and low tides determined as 2 hr before and after the higher and lower tides, respectively.

We recorded a total of 417 5-min feeding observations that were distributed similarly between the two habitat categories (structured habitat: 214 records, 51.32%; unstructured habitat: 203 records, 48.68%). Observations were also similarly distributed among the three tidal states considered (28.53, 34.29, and 37.17% at high, medium, and low tides, respectively). The breeding cycle was divided into three stages: incubation, young chicks (< 15 days of age), and old chicks (> 15 days of age). Young and old chicks were distinguished by size and the degree of plumage development.

At the end of each observation period, the density and size of the main prey of Olrog's Gulls (the crabs *N. granulata*, *C. altimanus*, and *C. angulatus*; Suárez *et al.* 2011) were assessed in the specific sites where gulls were observed feeding by randomly placing 1-m^2 quadrats (mean number of quadrats per site = 5.55 ± 3.33; Range = 3-12; n = 2,299) throughout the area used by the focal individual (Iribarne *et al.* 1997). In each quadrat, the number of burrows or individual crabs was counted, prey species were identified, and a random subsample of crabs was collected to assess prey size (Spivak and Sánchez 1992). Crab densities from quadrats corresponding to the same feeding site were averaged for comparisons among habitat and intertidal zoning categories. No significant differences were found between the three stages of the breeding cycle with respect to the frequency of occurrence and numerical importance, density or size of crabs in Olrog's Gull potential feeding areas (Suárez *et al.* 2011).

For each feeding patch, total energy available (KJ/m^2) was estimated using the density and size of the crabs present. The energy density of each prey item was estimated using its wet weight (WW) in grams and the species energy content from Ciancio *et al.* (2013; 3.73 KJ/gWW *N. granulata*, 3.04 KJ/gWW *C. altimanus*, and 3.33 KJ/gWW *C. angulatus*). The wet weight (WW) of the three species of crabs was estimated using the following regressions and carapace widths (CW (mm)) obtained from quadrat sampling:

C. altimanus: Ln (WW) = 2.657 * Ln (CW) - 6.716
C. angulatus: Ln (WW) = 2.647 * Ln (CW) - 6.676
N. granulata: Ln (WW) = 2.991 * Ln (CW) - 7.561

Finally, the total energy available in the feeding patch was obtained by pooling the energy densities calculated for all crab prey in that quadrat.

To identify the characteristics of the food patch that best explained feeding rate, we analyzed its relationship with the above mentioned variables using Nonlinear (Categorical) Principal Component Analysis of habitat type (structured habitat and unstructured habitat), average density of each crab species, average total crab density (the three species pooled), average crab size (the three species pooled), available energy in the feeding patch, intertidal zone (upper, middle, and lower), and stage of the breeding cycle (incubation, young chicks, old chicks) for each of the 417 recorded feeding observations. This method assigns numerical values to the categories of each variable, and aims to reduce the original set of categorical and numerical variables to a smaller set of factors that represent most of the information contained in the original variables. In addition, a graph was constructed with the centroids of each analyzed variable, considering the different categories of each categorical variable to interpret the contributions of these categories to each component. Regressions were then constructed between the feeding

rate and the values (scores) of the axes obtained from the Principal Component Analysis to determine the synthetic variable that best explains feeding rate. Non-parametric Kruskal-Wallis tests analyzed differences in capture rate in relation to the feeding technique used followed by Dunn's Test for multiple comparisons (Zar 1994). Means are reported ± 1 SD.

RESULTS

Factors Affecting Feeding Techniques

Olrog's Gulls fed in the intertidal zone throughout the tidal cycle, either in exposed areas or in flooded areas, and all crabs were consumed where they were captured. Olrog's Gulls used four feeding techniques, with prey capture occurring more frequently by pecking than through the remaining three techniques ($\chi^2_3 = 11.0$, $P = 0.011$, $n = 417$; Contrasts: $\chi^2_{HS\text{-}PD} = 3.2$, $P = 0.21$; $\chi^2_{HS\text{-}P} = 9.4$, $P = 0.009$; $\chi^2_{HS\text{-}UE} = 22.1$, $P < 0.001$; $\chi^2_{PD\text{-}P} = 13.6$, $P = 0.001$; $\chi^2_{PD\text{-}UE} = 15.4$, $P < 0.001$; $\chi^2_{P\text{-}UE} = 31.2$, $P < 0.001$). Pecking techniques were used more at low tide (57.4%, $\chi^2_3 = 16.1$, $P < 0.001$, $n = 417$) and head submergence more at high tide (50.3%, $\chi^2_3 = 9.1$, $P = 0.011$, $n = 417$) (Fig. 2).

Intertidal areas were used differently depending on tidal state. At high tide when intertidal areas were flooded, 79% of feeding observations were in the upper intertidal and 21% in the middle intertidal zone. During medium tides, observations were split between the middle and upper intertidal zones (54.5 and 44.1%, respectively), with < 2% of records in the lower intertidal zone. At low tide, Olrog's Gulls increased their use of the lower intertidal (12.9%), but mostly used the middle intertidal (52.2%) and higher intertidal zones (34.9%).

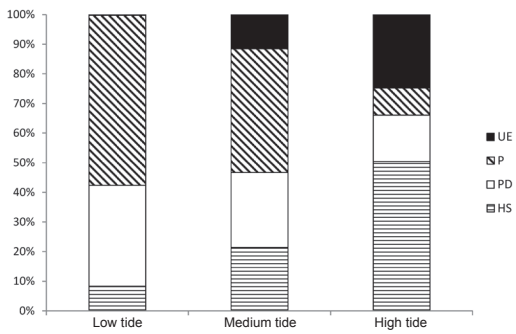

Figure 2. Use of different feeding methods by Olrog's Gulls at high, medium and low tides in Bahia San Blas, Argentina (P: 'pecking', PD: 'peck-digging', HS: 'head submergence' and UE: 'up-ending').

Factors Affecting Feeding Rates

Prey density (the three crab species pooled) was significantly higher in the middle intertidal zone (mean = 59 ± 16 individuals/m^2, $n = 169$) than the upper intertidal (mean = 42 ± 18 individuals/m^2, $n = 143$) and lower intertidal zones (mean = 21 ± 13 crabs/m^2, $n = 105$) (Kruskal-Wallis test: $H_2 = 79.6$, $P < 0.001$, $n = 417$; Contrasts: $Q_{LOW\text{-}MID} = 27.4$, $P < 0.001$; $Q_{LOW\text{-}UPP} = 42.3$, $P < 0.001$; $Q_{MID\text{-}UPP} = 6.7$, $P = 0.035$). Densities and body size of the two main crab species in our study area differed; density of *N. granulata* at the feeding patches was significantly lower than that of *C. altimanus* (29.1 ± 28.2 individuals/m^2 vs. 20.3 ± 27.1 individuals/m^2, $n = 417$; F-test: $F_{1,416} = 173.3$, $P < 0.001$), whereas *N. granulata* (mean = 25.7 ± 4.2 mm, Range = 16-31 mm, $n = 2,314$) were significantly larger than *C. altimanus* (14.3 ± 8.4 mm, Range = 10-22 mm, $n = 1,839$) (F-test: $F_{1,1838} = 136.4$, $P < 0.001$). The energy available in feeding patches was higher in unstructured than structured habitats (2,451 and 976 KJ/m^2, respectively, Mann-Whitney U-test: $U = 6.9$, $P < 0.001$).

Feeding rates differed with feeding technique. Olrog's Gulls fed at higher rates when pecking (0.78 ± 0.15 crabs/min, $n = 161$) and peck-digging (0.74 ± 0.14 crabs/min, $n = 108$) in exposed intertidal areas than when using the head submergence (0.59 ± 0.16 crabs/min, $n = 100$) and up-ending (0.53 ± 0.09 crabs/min, $n = 48$) methods (Kruskal-Wallis test: $H_3 = 375.6$, $P < 0.001$, $n = 417$; Dunn's: $Q_{PD\text{-}HS} = 4.2$, $P = 0.041$; $Q_{PD\text{-}P} = 0.4$, $P = 0.53$; $Q_{PD\text{-}UE} = 5.2$, $P = 0.022$; $Q_{HS,P} = 5.4$, $P = 0.02$; $Q_{HS\text{-}UE} = 0.8$, $P = 0.369$; $Q_{P\text{-}UE} = 3.9$, $P = 0.041$).

The Nonlinear Principal Component Analysis generated two components that together explained 71.94% of the total variation in the original data (Table 1). The first principal component (PC1) explained

Table 1. Factor loadings and total and cumulative percent variance explained for Principal Component Analysis of habitat and prey resource variables measured in 417 feeding records of Olrog's Gull breeding in Isla Arroyo Jabalí Oeste, Argentina. Factor loadings with absolute values > 0.4 are shown in bold.

	Principal Components	
Variable	1	**2**
Habitat type	**0.84**	0.11
Intertidal zone	0.04	**0.58**
Cyrtograpsus altimanus density	**-0.82**	0.19
Cyrtograpsus angulatus density	**0.61**	0.33
Neohelice granulata density	**0.64**	0.21
Average size (mm)	-0.11	**0.58**
Total crab density	**-0.73**	-0.15
Patch energy density (KJ/m^2)	**0.49**	0.15
Breeding stage	0.31	0.16
Percentage total variance	51.15 %	19.79 %
Cumulative variance	51.15 %	71.94 %

51.15% of the total variation and was represented by the habitat type, average density of each crab species, average total crab density, and available energy in the feeding patch. Positive factor loadings included *C. angulatus* and *N. granulata* average densities, habitat variables, and available energy in the feeding patch; negative factor loadings included *C. altimanus* average density and average total crab density. The second principal component (PC2) accounted for 19.79% of the variance and was represented by the intertidal zones used and average crab size; both factor loadings were positive. The graphical representation of the category centroids of each categorical variable and the numeric variables shows that both habitat types contribute in the opposite direction to the first axis (negatively and positively for the structured and unstructured habitats, respectively). The intertidal categories used by Olrog's Gulls were distributed along the second axis, with a positive contribution by the upper intertidal and a negative contribution by the middle and lower intertidal zones (Fig. 3). Only the first component showed a significant negative association with the feeding rate (PC1, r = -0.85, $P < 0.001$). Therefore, the variables that dominated this axis with negative contributions (density of *C. altimanus* and average total crab density) and the structured habitat category were the variables that best explained the increase in the feeding rate of Olrog's Gulls (Fig. 3). Feeding rates in structured habitats (0.76 ± 0.17 crabs/min, n = 214) were significantly higher (Mann-Whitney test: U = 6.0, $P < 0.001$) than in unstructured habitats (0.51 ± 0.19 crabs/min, n = 203).

DISCUSSION

Olrog's Gulls in our study fed throughout the tidal cycle using different intertidal zones when they were exposed and covered by water. This use of different intertidal habitats appears to be related to the species' flexibility in use of feeding techniques. Olrog's Gulls fed either by capturing crabs by pecking or peck-digging on exposed intertidal areas or by head submergence or up-ending in shallow waters. The four feeding techniques used by Olrog's Gulls in our study have already been described at their breeding grounds to the north and south of the study area (Delhey *et al.* 2001; Gatto *et al.* 2008) and at their wintering grounds (Copello and Favero 2001). The use of surface plunging, reported in low frequencies in other studies (Martinez *et al.* 2000; Copello and Favero 2001; Delhey *et al.* 2001), was not observed in our study. The frequency of use of each feeding technique was clearly determined by water presence, as reported for Black-headed Gulls (*L. ridibundus*) (Curtis and Thompson 1985).

Our results show that feeding rates of Olrog's Gulls differed with the feeding technique used, being higher when feeding by peck-digging in exposed intertidal areas. When using this technique, Olrog's Gulls walk along the shore scanning for prey, which must be much easier when intertidal areas are exposed. It could be argued that, at least for *N. granulata*, individual activity is higher when habitats are covered by water, which would increase their vulnerability to predators (Luppi *et al.* 2012). Nonetheless, a greater difficulty in prey detection due to reduced visibility in turbid waters or water movement forced by wind or tidal action could explain the lower feeding rate when foraging in areas covered

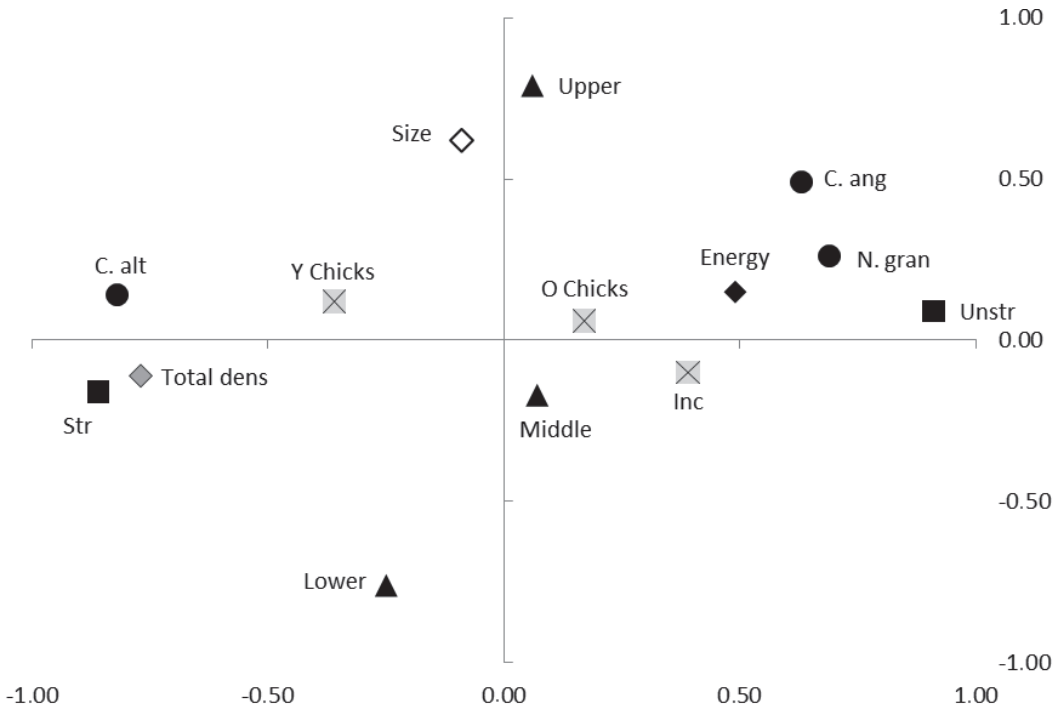

Figure 3. Contribution and distribution of the variance of habitat and food resource variables, represented as centroids, in the identified two principal components. Variable description and abbreviations are: pc1 = principal component 1; pc2 = principal component 2; Str = structured habitat; Unstr = unstructured habitat; Average density of each crab species: C. alt = *Cyrtograpsus altimanus*, C. ang = *Cyrtograpsus angulatus* and N. gran = *Neohelice granulata*; Total dens = average total crab density; Size = average crab size; Energy = energy in feeding patch; Intertidal zone: Upper, Middle and Lower; Breeding stage: Inc = Incubation, Y Chicks = Young Chicks, O Chicks = Old Chicks.

by water (Evans 1979). Delhey *et al.* (2001) reported that, when capturing prey under water, Olrog's Gulls sometimes kept their head submerged for several seconds, and suggested that gulls may detect prey by touch. Future studies should explore the relationship between the feeding technique used and the sensory mechanisms of prey detection so as to better understand its implication for Olrog's Gull foraging success. Thus, despite their flexibility in the use of intertidal habitats as a result of alternative feeding techniques, the observed differences in feeding rate suggest the existence of foraging limitations imposed by the tide cycle.

Our results also show that feeding rate varied according to different factors related to food resource and foraging habitat characteristics. Feeding rate increased with average prey density, as reported in other studies of intertidal waterbirds (e.g., Goss-Custard 1984; Kalejta and Hockey 1994; Yates *et al.* 2000). Feeding rates were also higher in structured environments characterized by the presence of rocks or oysters than in environments with muddy substrates and crab burrows. Crab survival could increase with the use of shelters and deep burrows (Zwarts 1988; Morrier and McNeil 1991; Good 1992; Dumas and Witman 1993), and it has been observed that prey retreating into burrows may result in a reduced feeding rate in some shorebird species (Yates *et al.* 2000; Goss-Custard *et al.* 2006). In our study area, observations suggest that crab capture would be more difficult in burrow habitats than in structured environments because crabs can hide in deeper shelters (N. Suárez, pers. obs). The burrowing crab *N. granulata* in the study area, and also to a large extent *C. angulatus*, live in burrows that may be up to 40 cm deep (N. Suárez, unpubl. data) where they could quickly retreat when detecting the pres-

ence of an Olrog's Gull. Moreover, *N. granulata* individuals are generally near or inside their burrows at low tide (Luppi *et al.* 2012), favoring a rapid retreat down their burrows when approached by a potential predator. In contrast, *C. altimanus* individuals generally seek shelter in crevices or under rocks when disturbed (N. Suárez, pers. obs), but can still be available to Olrog's Gulls. Differences in escape behaviors, crypticity, and defensive capabilities have been shown to influence the differential vulnerability of three crab species to Herring Gull (*L. argentatus*) and Great Black-backed Gull (*L. marinus*) predation in New England, USA (Ellis *et al.* 2012). Given the relatively small size of crabs preyed upon by Olrog's Gulls at Bahía San Blas, it is unlikely that crab defense behavior is an important factor affecting Olrog's Gull prey selection, but the effects of differences in escape behavior and coloration among prey species deserve further investigation.

Despite the higher feeding rate in structured habitats with high densities of *C. altimanus*, the burrowing crab *N. granulata* was the main component of the Olrog's Gull diet during the incubation period and to a large extent during the late chick stage in the study area (Suárez *et al.* 2011). However, although average density of *N. granulata* in feeding patches was lower than that of *C. altimanus*, body size of the former was significantly larger and energy density of individuals is higher (Ciancio *et al.* 2013), resulting in a higher energy profitability of unstructured habitats. Prey switching toward *C. altimanus* particularly during the young chick stage appears to result from the need to feed chicks with smaller prey (Suárez *et al.* 2011). In this context of differences in prey density and profitability driven by habitat characteristics and restrictions imposed by the breeding cycle, future studies should assess the Olrog's Gull feeding behavior in greater detail, analyzing the energy gain per unit of foraging time to adequately understand the relationship between feeding decisions and foraging efficiency.

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Literature Cited

Altman, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49: 227-267.

Berón, M. P., G. O. Gacía, T. Luppi and M. Favero. 2011. Age-related prey selectivity and foraging efficiency of Olrog's Gulls (*Larus atlanticus*) feeding on crabs in their non-breeding grounds. Emu 111: 172-178.

BirdLife International. 2013. Species fact sheet: *Larus atlanticus*. Birdlife International, Cambridge, U.K. http://www.birdlife.org/datazone/speciesfactsheet.php?id=3210, accessed 10 May 2013.

Burger, J. 1984. Abiotic factors affecting migrant shorebirds. Pages 1-72 *in* Behavior of Marine Animals, vol. 6. Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York, New York.

Burger, J. 1988. Foraging behavior in gulls: differences in method, prey and habitat. Colonial Waterbirds 11: 9-23.

Burger, J. and M. Gochfeld. 1996. Family Laridae (gulls). Pages 572-623 *in* Handbook of the Birds of the World, vol. 3: Hoatzin to Auks (J. del Hoyo., A. Elliot and J. Sargatal, Eds.). Lynx Edicions. Barcelona, Spain.

Burger, J., L. Niles and K. E. Clark. 1997. Importance of beach, mudflat and marsh habitats to migrant shorebirds on Delaware Bay. Biological Conservation 79: 283-292.

Burger, J., M. A. Howe, D. C. Hahn and J. Chase. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94: 743-758.

Ciancio, J., N. Suárez and P. Yorio. 2013. Energy density empirical predictor models for three coastal crab species in the Southwestern Atlantic Ocean. Journal of Crustacean Biology 33: 667-671.

Copello, S. and M. Favero. 2001. Foraging ecology of Olrog's Gull *Larus atlanticus* in Mar Chiquita Lagoon (Buenos Aires, Argentina): are there age-related differences? Bird Conservation International 11: 175-188.

Curtis, D. J. and D. B. A. Thompson. 1985. Spacing and foraging behaviour of Black-headed Gulls *Larus ridibundus* in an estuary. Ornis Scandinavica 16: 245-252.

Danufsky, T. and M. A. Colwell. 2003. Winter shorebird communities and tidal flat characteristics at Humboldt Bay, California. Condor 105: 117-129.

De Vlas, S. E. J., J. Bunskoeke, B. J. Ens and J. B. Hulscher. 1996. Tidal changes in the choice of *Nereis diversicolor* or *Macoma balthica* as main prey species in the diet of the Oystercatcher *Haematopus ostralegus*. Ardea 84A: 105-116.

Delhey, J. K. V., M. Carrete and M. M. Martínez. 2001. Diet and feeding behavior of Olrog's gull *Larus atlanticus* in Bahía Blanca, Argentina. Ardea 89: 319-389.

Dumas, J. V. and J. D. Witman. 1993. Predation by Herring Gulls (*Larus argentatus* Coues) on two rocky intertidal crab species [*Carcinus maenas* (L.) & *Cancer irroratus* Say]. Journal of Experimental Marine Biology and Ecology 169: 89-101.

Ellis, J. C., K. E. Allen, M. S. Rome and M. J. Shulman. 2012. Choosing among mobile prey species: why do gulls prefer a rare subtidal crab over a highly abundant intertidal one? Journal of Experimental Marine Biology and Ecology 416-417: 84-91.

Ellis, J. C., W. Chen, B. O'Keefe, M. J. Shulman and J. D. Witman. 2005. Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 324: 31-43.

Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. Pages 357-366 *in* Cyclic Phenomena in Marine Plants and Animals (E. Naylor and R. G. Hartnall, Eds.). Pergamon Press, Oxford, U.K.

Gatto, A., F. Quintana and P. Yorio. 2008. Feeding behavior and habitat use in a waterbird assemblage at a marine wetland in coastal Patagonia, Argentina. Waterbirds 31: 463-471.

Good, T. P. 1992. Experimental assessment of gull predation on the Jonah crab *Cancer borealis* (Stimpson) in New England rocky intertidal and shallow subtidal zones. Journal of Experimental Marine Biology and Ecology 157: 275-284.

Goss-Custard, D. 1970. The responses of Redshank (*Tringa tetanus* (L.)) to spatial variations in the density of their prey. Journal of Animal Ecology 39: 91-113.

Goss-Custard, J. D. 1984. Intake rates and food supply in migrating and wintering shorebirds. Pages 233-277 *in* Behavior of Marine Animals, vol. 6. Shorebirds: Migration and Foraging Behavior (J. Burger and B. L. Olla, Eds.). Plenum Press, New York, New York.

Goss-Custard, J. D., A. D. West, M. G. Yates, R. W. Caldow, R. A. Stillman, L. Bardsley, J. Castilla, M. Castro, V. Dierschke, S. E. Durell, G. Eichhorn, B. J. Ens, K. M. Exo, P. U. Udayangani-Fernando, P. N. Ferns, P. A. Hockey, J. A. Gill, I. Johnstone, B. Kalejta-Summers, J. A. Masero, F. Moreira, R. V. Nagarajan, I. P. Owens, C. Pacheco, A. Perez-Hurtado, D. Rogers, G. Scheiffarth, H. Sitters, W. J. Sutherland, P. Triplet, D. H. Worrall, Y. Zharikov, L. Zwarts and R. A. Pettifor. 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biological Reviews 81: 501-529.

Herrera, G., G. Punta and P. Yorio. 2005. Diet specialization of the threatened Olrog's gull *Larus atlanticus* during the breeding season at Golfo San Jorge, Argentina. Bird Conservation International 15: 89-97.

Iribarne, O., A. Bortolus and F. Botto. 1997. Between-habitat differences in burrow characteristics and trophic modes in the south western Atlantic burrowing crab *Chasmagnathus granulata*. Marine Ecology Progress Series 155: 137-145.

Iribarne, O., P. Martinetto, E. Schwindt, F. Botto, A. Bortolus and P. Garcia Borboroglu. 2003. Evidences of habitat displacement between two common soft-bottom SW Atlantic intertidal crabs. Journal of Experimental Marine Biology and Ecology 296: 167-182.

Isacch, J. P., C. F. Pérez and O. Iribarne. 2006. Bird species composition and diversity at middle Argentinean coast of La Plata river. Ornitologia Neotropical 17: 419-432.

Kalejta, B. and P. A. R. Hockey. 1994. Distribution of shorebirds at the Berg River estuary, South Africa, in relation to foraging modes, food supply and environmental features. Ibis 136: 233-239.

Luppi, T., C. Bas, A. Méndez Casariego, M. Albano, J. Lancia, M. Kittlein, A. Rosenthal, N. Farías, E. Spivak and O. Iribarne. 2012. The influence of habitat, season and tidal regime in the activity of the intertidal crab *Neohelice* (=*Chasmagnathus*) *granulata*. Helgoland Marine Research 67: 1-15.

Martin, P. and P. Bateson. 1994. Measuring behaviour: an introductory guide, 2nd ed. Cambridge University Press, Cambridge, U.K.

Martinez, M. M., J. P. Isacch and M. Rojas. 2000. Olrog's Gull *Larus atlanticus*: specialist or generalist?. Bird Conservation International 10: 89-92.

McNeil, R., P. Drapeau and J. D.Goss-Custard. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biological Reviews 67: 381-419.

Morrier, A. and R. McNeil. 1991. Time-activity budget of Wilson's and Semipalmated plovers in a tropical environment. Wilson Bulletin 103: 598-620.

Piersma, T., P. De Goeij and I. Tulp. 1993. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. Netherlands Journal of Sea Research 31: 503-512.

Ribeiro, P. D., O. O. Iribarne, D. Navarro and L. Jaureguy. 2004. Environmental heterogeneity, spatial segregation of prey, and the utilization of southwest Atlantic mudflats by migratory shorebirds. Ibis 146: 672-682.

Rose, M. and E. Nol. 2010. Foraging behavior of nonbreeding Semipalmated Plovers. Waterbirds 33: 59-69.

Spivak, E. and N. Sánchez. 1992. Prey selection by *Larus belcheri atlanticus* in Mar Chiquita lagoon, Buenos Aires, Argentina: a possible explanation for its discontinuous distribution. Revista Chilena de Historia Natural 65: 209-220.

Suárez, N., M. V. Retana and P. Yorio. 2011. Seasonal changes in diet and prey selection in the threatened Olrog's gull *Larus atlanticus* breeding in Patagonia, Argentina. Ardeola 58: 35-47.

Suárez, N., M. V. Retana and P. Yorio. 2012. Spatial patterns in the use of foraging areas and its relationship with prey resources in the threatened Olrog's gull (*Larus atlanticus*). Journal of Ornithology 153: 861-871.

Warnock, N., C. Elphick and M. A. Rubega. 2002. Shorebirds in the marine environment. Pages 581-615 *in* Biology of Marine Birds (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.

Withers, K. and B. R. Chapman. 1993. Seasonal abundance and habitat use of shorebirds on an Oso Bay mudflat, Corpus Christi Texas. Journal of Field Ornithology 64: 382-392.

Yates, M. G., R. A. Stillman and J. D. Goss-Custard. 2000. Contrasting interference functions and foraging dispersion in two species of shorebirds (Charadrii). Journal of Animal Ecology 69: 314-322.

Yates, M. G., A. R. Jones, J. D. Goss-Custard and S. McGrorty. 1993. Satellite imagery to monitor ecological change in estuarine systems: example of the Wash, England. Pages 56-60 *in* Waterfowl and Wetland Conservation in the 1990s: a Global Perspective (Proceedings of the International Waterbird and Wetlands Research Bureau Symposium, St. Petersburg Beach, Florida, USA) (M. Moser, R. C. Prentice and J. Van Vessem, Eds.). International Waterfowl Research Bureau Special Publication 26, Slimbridge, U.K.

Yorio, P., E. Frere, P. Gandini and W. Conway. 1999. Status and conservation of seabirds breeding in Argentina. Bird Conservation International 9: 299-314.

Zalba, S. M., A. J. Nebbia and S. M. Fiori. 2008. Propuesta de Plan de Manejo de la Reserva Natural de Uso Múltiple Bahía San Blas. Universidad Nacional del Sur, Bahía Blanca, Argentina. (in Spanish).

Zar, J. H. 1994. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Zwarts, L. 1988. Numbers and distribution of coastal waders in Guinea-Bissau. Ardea 76: 42-55.