

Age-related prey selectivity and foraging efficiency of Olrog's Gulls (*Larus atlanticus*) feeding on crabs in their non-breeding grounds

María Paula Berón^{A,B,D}, Germán O. García^{A,B}, Tomás Luppi^{A,C} and Marco Favero^{A,B}

^AConsejo Nacional de Investigaciones Científicas y Técnicas, Av. Rivadavia 1917, C1033AAJ, Ciudad Autónoma de Buenos Aires, Argentina.

^BVertebrados, Departamento Biología, Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ, Mar del Plata, Argentina.

^CInvertebrados, Departamento Biología, Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ, Mar del Plata, Argentina.

^DCorresponding author. Email: mpberon@mdp.edu.ar, mpb03@yahoo.com.ar

Abstract. Foraging ecology is an essential component of the life history of a species and a good understanding of foraging ecology is especially important for threatened species where prey populations may be adversely affected by anthropogenic processes. This study examines age-related prey selection and prey-handling efficiency of Olrog's Gulls (*Larus atlanticus*) during the non-breeding season at the Mar Chiquita Coastal Lagoon, Argentina. Foraging behaviour and diet were determined by focal observation and compared with the availability of prey within their foraging patches. All captured prey were crabs, with the Burrowing Crab (*Neohelice granulata*) more commonly taken than the Mud Crab (*Cyrtograpsus angulatus*). Gulls consumed small and medium-sized crabs in higher proportions than those available and consumed more male crabs. Juvenile Gulls had longer handling times than older birds. Handling times increased with size of crabs independently of the sex of prey. The handling efficiency of adults was significantly higher than that of subadults, which in turn was higher than that of juveniles. These differences between age-classes could be attributed to differential foraging skills and social subordination of juvenile Gulls. The reasons for avoidance of large crabs is not certain but might be because carapaces are not easily digested, there is a higher risk of injury, or capture of large crabs may result in more intense kleptoparasitic interactions, among others.

Additional keywords: Argentina, handling efficiency, predator–prey interactions.

Introduction

Foraging behaviour can be analysed in terms of costs and benefits to the forager (MacArthur and Pianka 1966). According to optimal foraging theory, organisms maximise net energy gain per unit of foraging time (Krebs and Davies 1993). Prey-size selectivity can be linked to the maximisation of the net energy gained per unit time (Bertness 1999) and size selectivity may change with the age and experience of foragers (O'Brien *et al.* 2005; Snellen *et al.* 2007). Age-related differences in foraging behaviour and foraging ability have been described in several species of seabirds, including gulls (e.g. McLean 1986; Steele and Hockey 1995). These differences have usually been attributed to learning of prey recognition and handling, and because older birds may be more competitive and dominate better foraging areas (Burger 1987; Bertellotti and Yorio 2000). Age-related differences in foraging behaviour and efficiency may be also linked to higher pre-reproductive or migratory requirements among adults (Limmer and Becker 2009).

Olrog's Gull (*Larus atlanticus*) is endemic to the Atlantic coast of southern South America and is currently listed as vulnerable (BirdLife International 2010). The estimated

population is 4000–5000 breeding pairs, with 14 breeding colonies in two areas of the Patagonian coast (Yorio *et al.* 2005). The species is considered to have a specialised diet, mostly foraging on crabs (Delhey *et al.* 2001; Herrera *et al.* 2005). However, in the non-breeding grounds, Olrog's Gulls of different age-classes may show a wider trophic spectrum (Copello and Favero 2001). In Mar Chiquita Coastal Lagoon, Argentina, Olrog's Gulls feed mainly on two species of varunid crab: the Mud Crab (*Cyrtograpsus angulatus*) and Burrowing Crab (*Neohelice chasmagnathus*) (Berón and Favero 2010).

Foraging ecology is an essential component of the life history of any species, and a good understanding of foraging is especially important for threatened species where their prey populations may be adversely affected by anthropogenic processes. Olrog's Gull and its prey face a range of threatening processes, including habitat degradation, pollutants, industrial and agricultural activities, human recreation in foraging areas and fishing (García Borboroglu and Yorio 2007; Berón and Favero 2009). This study examines age-related prey selectivity, handling time and the efficiency of Olrog's Gull foraging on varunid crabs.

Material and methods

The study was conducted between May and November in 2004–07, in the Mar Chiquita Coastal Lagoon, Buenos Aires Province, Argentina (37°40'S, 57°22'W), which is a UNESCO Man and the Biosphere (MAB) Programme world biosphere reserve (Reserva Mar Chiquita) and a Provincial Reserve). Olrog's Gulls breed in the south of Buenos Aires Province and Patagonia (Yorio *et al.* 2005). Mar Chiquita Reserve and other neighbouring coastal areas are used in the non-breeding period, from April to September. Although the abundance of juvenile Gulls is approximately constant throughout the year, subadult and adult Gulls show a peak in abundance during June–August and are absent in spring and summer (Berón *et al.* 2007).

Three crab species dominate the estuary, two semi-terrestrial burrowing species, the Burrowing Crab (*Neohelice granulata*) and the Fiddler Crab (*Uca uruguayensis*), occurring in the upper littoral, and the Mud Crab (*Cyrtograpsus angulatus*), which is mainly present in the lower littoral and on rocky seashores. *N. granulata* is the numerically dominant macro-invertebrate in this area, and this and *C. angulatus* (both Varunidae) are considered key species in 'cangrejal' (i.e. crab aggregations, from the Spanish, 'cangrejo' means crab) saltmarsh ecosystems, which are widespread along the warm-temperate south-western Atlantic coasts (Boschi 1964).

Foraging behaviour

Foraging behaviour was quantified by focal observations made on randomly selected individuals (Altmann 1974; Martin and Bateson 1994). Bushnell NatureView binoculars (magnification, 10×; lens diameter, 36 mm) and Nikon Spotting Scope (80/80 A telescope, magnification, 12×; lens diameter, 60 mm) were used to observe birds, and AIWA Voice Sensor Recording TP-M131 tape recorder was used to record observations. A total of 228 observations (from 228 samples) of singly foraging birds, with an average duration of 4.9 ± 2.1 (s.d.) min (range = 1.1–15.8 min). Observations began 10–15 min after observer's arrival and once the gull was habituated to the presence of the observer. During observations, focal individuals were ~10–30 m from the observer. Because the Gulls being studied were not marked, pseudo-replication was minimised by selecting, during a given day, individuals feeding in different foraging patches. The following were recorded:

- (1) age-class (determined after Harrison 1983) – juvenile (JU), which are 1 or 2 years old; subadults (SA), which are 3 years old; and adults, (AD), which are >4 years old and potential breeders (Harrison 1983);
- (2) number, type and size of captured prey (always crabs); and

- (3) handling time (the time spent in killing, cleaning and breaking prey into manageable portions and eating it (after Van de Kam *et al.* 2004).

Handling efficiency was estimated as the total consumed biomass (digestible dry weight (g); see 'Prey biomass' section below) per unit handling time (in min). Crab species were determined by shape and colour, and sex identified by the shape of claws and the abdomen, or pleon (clearly broader and rounded among females). Size (carapace width, CW) was estimated in relation to Gull bill-length (mean bill-length = 50.6, s.d. = 4.5 mm, $n = 27$; M. P. Berón, unpubl. data) and categorised as: 'small prey' ($CW \leq 15$ mm), 'medium' (15–25 mm), 'large' (25–35 mm) and 'very large' ($CW > 35$ mm).

Abundance of prey

Samples of the mudflat sediment were collected at the same time and foraging area in which observations of foraging were made. A total of 1411 *N. granulata* were collected during low spring tide using randomly distributed 0.25-m² quadrats and extracting all crabs to a depth of 0.50 m (crabs moved deep in their burrows owing to the mechanical disturbance). *C. angulatus* ($n = 446$) were collected during low tide on 10 transects (60 m long × 1 m wide) along the shoreline, in areas frequently used by foraging Olrog's Gulls. Collected specimens were measured and sexed in the field and then released alive. Body size of the crabs was measured as maximum carapace width (CW) to the nearest 0.1 mm with Vernier calipers. Crabs were then categorised as: small, medium, large and very large (as above). Taking into account the motility of crabs in the foraging patches and burrows, the estimated prey abundances were assumed to be a reliable indicator of crab availability for predators.

Prey biomass

Prey biomass (digestible dry weight, DDW (g)), assuming that all soft tissues (i.e. with the exception of the exoskeleton) were potentially digestible, was estimated by using regressions of wet weight (WW (g)) and carapace width (CW) from pre-existing data (Vertebrate Laboratory, Mar del Plata National University; see Table 1):

$$N. granulata: WW = 0.331 \times e^{0.1125 \times CW} \\ (R^2 = 0.966, n = 31); \quad DW = WW \times 0.28$$

$$C. angulatus: WW = 0.0465 \times e^{0.132 \times CW} \\ (R^2 = 0.814, n = 33); \quad DW = WW \times 0.30$$

Table 1. Mean biomass (digestible dry weight (g); mean \pm s.e.) calculated for female (F) and male (M) crabs

	Small (CW < 15 mm)		Medium (15 ≤ CW < 25 mm)		Large (25 ≤ CW < 35 mm)		Very large (CW ≥ 35 mm)	
	F	M	F	M	F	M	F	M
<i>N. granulata</i>	1.55 ± 0.07 (n = 4)	1.56 ± 0.04 (n = 4)	2.17 ± 0.12 (n = 5)	2.03 ± 0.04 (n = 5)	3.16 ± 0.10 (n = 4)	3.09 ± 0.07 (n = 4)	3.68 ± 0.0 (n = 3)	3.76 ± 0.21 (n = 2)
<i>C. angulatus</i>	0.10 ± 0.00 (n = 4)	0.10 ± 0.00 (n = 4)	0.26 ± 0.04 (n = 4)	0.23 ± 0.08 (n = 4)	0.76 ± 0.09 (n = 5)	0.65 ± 0.10 (n = 4)	2.25 ± 0.30 (n = 5)	3.91 ± 0.66 (n = 3)

Statistical analyses

Differences in the size of available and consumed prey were tested with *U*-test (*Z*). Selectivity of crab size was quantified by the Odds ratio (Fleiss 1973):

$$\text{Odds} = (P_{\text{ndiet}} - P_{\text{rhab}})/(P_{\text{nhab}} - P_{\text{rdiet}})$$

where P_{ndiet} is the proportion of size n in the diet; P_{rhab} is the proportion in the habitat (or available) of other size-classes; P_{nhab} is the proportion in the habitat (or available) of size class n ; and P_{rdiet} is the proportion in the diet of the rest of classes. Differences between males and females crabs available and consumed were tested with Chi-square tests.

To test the effect of different predictor variables on handling time and handling efficiency, we employed generalised linear models (GLM) with Gamma error structure and power (-1) link function (Crawley 2007). To analyse the effect of different factors on handling time and handling efficiency, we used GLM with Gull age and prey type as predictor variables and handling time and handling efficiency as response variables. These response variables were significantly correlated (Spearman rank correlation, $r_s = -0.55$, $n = 341$, $P < 0.001$). However, these variables were analysed separately given that responses were not comparable and in some cases differed, for example, while analysing the effect of prey size.

To analyse the effect of prey size on handling time and efficiency for Gulls of different age, we used GLM considering Gull age and prey size as explanatory variables and handling time and handling efficiency as response variables. Given the low number of prey categorised as 'very large', they were not included in the analysis. We assessed goodness-of-fit for models and estimated variance inflation factor (\hat{c}) as residual deviance divided by degrees of freedom (Burnham and Anderson 1998). All analyses were conducted using R software, Version 2.7.2 (R Development Core Team 2008).

Differences in capture rate were tested with Kruskal–Wallis one-way analysis of variance (ANOVA) and Dunn's Method for multiple comparisons. Unless stated otherwise, all summary statistics are presented as untransformed means \pm one standard deviation. All methods follow Zar (1999) and Underwood (1997) unless otherwise specified.

Results

All prey seen to be caught were crabs ($n = 341$ items) and 93% caught were eaten. Of those eaten, 69% were *N. granulata* and the rest *C. angulatus*. The size of available *N. granulata* and *C. angulatus* was 25.2 ± 6.6 and 23.9 ± 5.7 mm respectively. The size of crabs eaten was significantly different from that expected based on the frequency distribution of sizes of available prey (*N. granulata* modal size = large, $\chi^2_3 = 183.72$, $P < 0.001$; *C. angulatus* modal size = medium, $\chi^2_3 = 472.18$, $P < 0.001$). The Odds ratio showed that Gulls ate small and medium *N. granulata* in larger proportions than available: small crabs were eaten in significantly larger proportions by juvenile and adult Gulls, and medium crabs consumed in significantly larger proportions by juvenile and subadult Gulls ($Z > 2.49$, d.f. = 1410, $P < 0.001$ in all cases); and that adult and subadult Gulls avoided eating large crabs ($Z > 2.49$, d.f. = 1410, $P < 0.05$ in both cases). Very large crabs were rarely eaten (<5% occurrence) by adult and subadult

Gulls and were never eaten by juveniles (Fig. 1a–c). As with *N. granulata*, juvenile Gulls ate small *C. angulatus* in larger proportions than available ($Z = 4.797$, d.f. = 286, $P < 0.001$), but avoided medium-sized crabs ($Z = 2.299$, d.f. = 286, $P < 0.05$) (Fig. 1d–f).

The average prey density in foraging patches was 17.73 ± 2.54 crabs m^{-2} for *N. granulata* and 7.45 ± 1.95 crabs m^{-2} for *C. angulatus*. The sex-ratio of available crabs was approximately even for both species of crab. However, there was a significant bias towards the consumption of male crabs by Gulls of all age-classes (for all age-classes pooled: 2.6:1 for *N. granulata*, $\chi^2_1 = 31.61$, $P < 0.001$; 2.2:1 for *C. angulatus*, $\chi^2_1 = 13.69$, $P < 0.001$). These biases towards the consumption of male crabs were also observed when analysing the sex-ratio of prey taken by adult, subadult and juvenile Gulls (2.5:1, 2.1:1 and 2.5:1 respectively for *N. granulata* ($n = 234$), $P < 0.001$ for all comparisons; 2.3:1, 1.8:1, 3.6:1 respectively for *C. angulatus* ($n = 107$), $P < 0.05$ for all comparisons except for subadults where $P > 0.05$).

Capture rates by adult Gulls (0.41 ± 0.34 crab min^{-1}) were higher than those of subadult (0.35 ± 0.26 crab min^{-1}) and juvenile Gulls (0.32 ± 0.18 crab min^{-1}), although the differences were not significant (Kruskal–Wallis $H_2 = 0.725$, $P = 0.696$). Handling times differed significantly between age-classes, being longer for younger birds (GLM: $t_{\text{JU-SA}} = 8.45$, $P < 0.001$; $t_{\text{JU-AD}} = 12.2$, $P < 0.001$; $t_{\text{SA-AD}} = 2.82$, $P < 0.01$). The parameter estimate was between 1.6 and 1.2 times shorter when Gulls were adults and subadults respectively compared with juveniles (Table 2). Handling time was not affected by species of crab (Table 2), but it was significantly affected by size of prey, increasing with the size of captured crabs (Table 3). Handling times were significantly shorter with small prey compared with other prey categories (GLM: $t_{\text{small-medium}} = 3.65$, $P < 0.001$; $t_{\text{small-large}} = 4.13$, $P < 0.001$; $t_{\text{medium-large}} = 1.01$, $P = 0.31$). We found the same pattern when analysing the effect of prey size on handling time within each age-class of Gull (Tables 3 and 4). Handling time for a given prey size was related to the age of Gulls, becoming shorter with increasing age. When Gulls captured small prey we found differences in handling time only between juveniles compared with adults and subadults. However, when Gulls captured medium and large prey we found differences between all ages (Table 4, Fig. 2).

Handling efficiency was influenced by age, being lower in juveniles than in subadults and adults, and lower in subadults than adults (GLM: $t_{\text{JU-SA}} = 5.90$, $P < 0.001$; $t_{\text{JU-AD}} = 9.41$, $P < 0.001$; $t_{\text{SA-AD}} = -2.73$, $P < 0.005$; Table 2). The parameter estimate was between 1.3 and 0.9 times higher in adults and subadults, respectively, compared with juveniles. Handling efficiency was higher when Gulls fed on *N. granulata* than when feeding on *C. angulatus* (Table 2). Handling efficiency was differed significantly with size of prey, being lower for small and medium prey than for large prey (GLM: $t_{\text{small-medium}} = 0.41$, $P = 0.68$; $t_{\text{small-large}} = 2.61$, $P < 0.005$; $t_{\text{medium-large}} = 2.63$, $P < 0.005$). However, there was no effect of prey size on handling efficiency within each age-class (Tables 3, 4). Conversely, handling efficiency for a particular prey size was affected by the age of Gulls. For all prey size-classes we found differences in handling efficiency between juveniles and adults, and between juveniles and subadults, but not between subadults and adults (Table 4, Fig. 2).

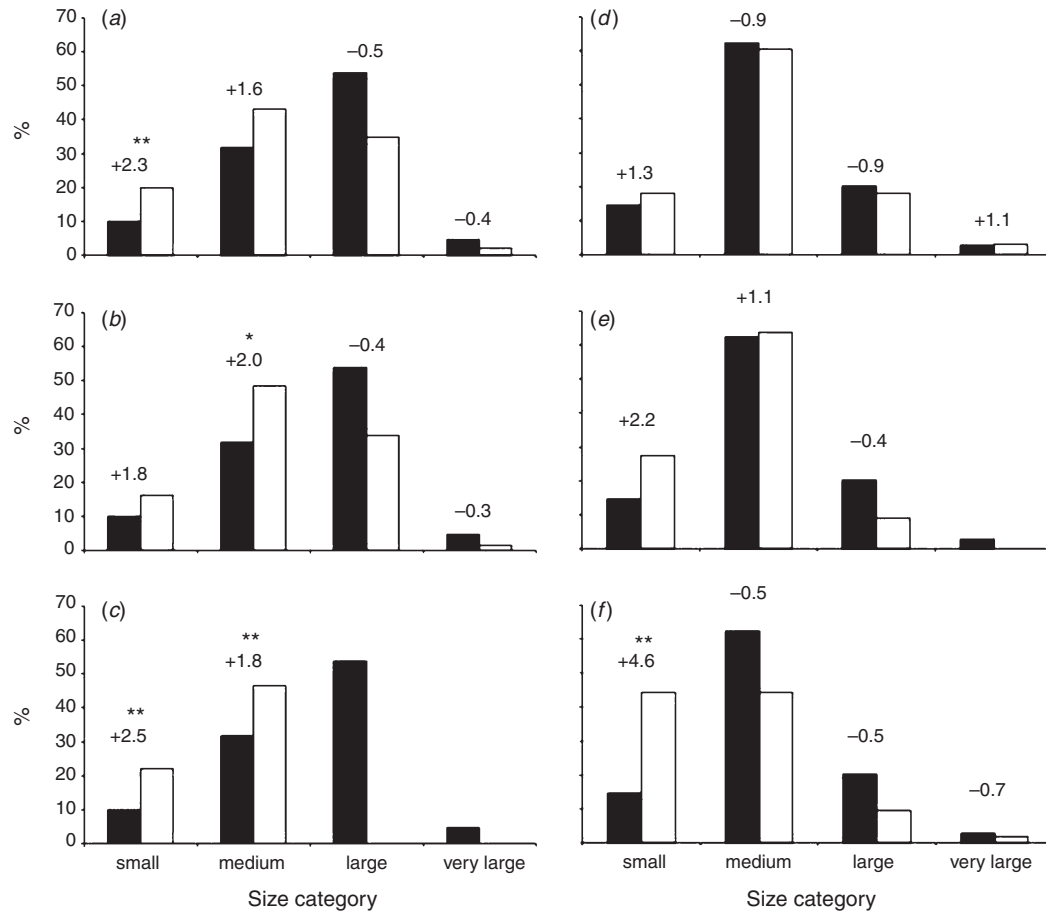


Fig. 1. Size distribution of available (black) and eaten (open bars) (*a–c*) *N. granulata* and (*d–f*) *C. angulatus* taken by adult (*a, d*), subadult (*b, e*) and juvenile (*c, f*) Olrog's Gulls. Odds ratios are shown on top of the bars; asterisks above these values indicate significant differences between groups (*U*-test *Z*, * *P* < 0.05, ** *P* < 0.001).

Table 2. Generalised linear models describing the effect of different explanatory variables on handling time and efficiency in Olrog's Gulls

Explanatory variable	Categories	Estimated handling time (\pm s.e.)	<i>P</i>	Estimated handling efficiency (\pm s.e.)	<i>P</i>
Intercept		-1.34 ± 0.19	0.00	0.82 ± 0.12	0.00
Age	Juvenile				
	Subadult	-1.22 ± 0.14	0.00	0.91 ± 0.15	0.00
	Adult	-1.62 ± 0.13	0.00	1.33 ± 0.14	0.00
Prey type	<i>C. angulatus</i>				
	<i>N. granulata</i>	0.05 ± 0.22	0.82	1.92 ± 0.13	0.00

Discussion

Two varunid crabs comprised the diet of Olrog's Gulls at Mar Chiquita Coastal Lagoon, which is consistent with results of previous studies in the same area describing the dietary composition of the species (Spivak and Sánchez 1992; Copello and Favero 2001). The crab *N. granulata* was taken and consumed more than *C. angulatus*, corresponding with the relative availability of these prey species in the study area. The consumption of small and medium crabs, particularly *N. granulata*, in larger proportions than available in the study area might result from

greater vulnerability of smaller crabs to predation (see Spivak and Sánchez 1992) or the avoidance of large and very large crabs owing to the crabs anti-predatory mechanisms and that the capture of large and more aggressive male crabs can increase the risk of injury to predators (Bildstein *et al.* 1989; Koga *et al.* 2001; Van de Kam *et al.* 2004; M. P. Berón, pers. obs.). Large crabs might also be avoided for a number of other reasons not considered in the present study, such as poor digestibility of carapaces (Stienen *et al.* 2008) or increased risk or intensity of kleptoparasitism (Gochfeld and Burger 1981; Bertellotti and

Table 3. Generalised linear models describing the effect of size of crabs on handling time and handling efficiency in juvenile, subadult and adult Olrog's Gulls

Explanatory variable	Categories	Estimated handling time (\pm s.e.)	<i>P</i>	Estimate handling efficiency (\pm s.e.)	<i>P</i>
Intercept		-1.91 \pm 0.15	0.00	3.80 \pm 0.28	0.00
Age, Prey size	Juvenile, Small				
	Juvenile, Medium	0.92 \pm 0.27	0.00	-0.17 \pm 0.29	0.56
	Juvenile, Large	1.23 \pm 0.22	0.00	0.32 \pm 0.35	0.36
	Subadult, Small				
	Subadult, Medium	0.80 \pm 0.25	0.00	0.06 \pm 0.40	0.86
	Subadult, Large	0.78 \pm 0.28	0.00	0.49 \pm 0.44	0.27
	Adult, Small				
	Adult, Medium	0.74 \pm 0.22	0.00	-0.08 \pm 0.33	0.80
	Adult, Large	0.71 \pm 0.24	0.00	0.29 \pm 0.36	0.42

Table 4. Effect of size of crabs and age of Olrog's Gull on handling time and handling efficiency
JU, juvenile; SA, subadult; AD, adult; S, small; M, medium; L, large

Variable	Category	Comparison	Handling time		Handling efficiency	
			<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
Age	Juvenile (JU)	S v. M	4.71	0.00	-5.82	0.56
		S v. L	5.44	0.00	0.92	0.36
		M v. L	1.47	0.14	1.51	0.13
	Subadult (SA)	S v. M	3.11	0.00	0.16	0.86
		S v. L	2.74	0.00	1.11	0.27
		M v. L	0.11	0.91	1.22	0.22
	Adult (AD)	S v. M	3.41	0.00	-0.45	0.80
		S v. L	2.97	0.00	0.80	0.42
		M v. L	0.18	0.85	1.28	0.20
Prey size	Small (S)	JU v. SA	3.79	0.00	2.14	0.03
		JU v. AD	5.97	0.00	-4.13	0.00
		SA v. AD	1.40	0.15	-1.39	0.16
	Medium (M)	JU v. SA	6.30	0.00	4.02	0.00
		JU v. AD	9.51	0.00	-6.09	0.00
		SA v. AD	2.67	0.01	-1.70	0.09
	Large (L)	JU v. SA	6.47	0.00	2.70	0.00
		JU v. AD	8.69	0.00	-4.17	0.00
		SA v. AD	2.06	0.03	-1.14	0.25

Yorio 2000; García *et al.* 2008), but further study is required to examine such factors.

Irrespective of age, Olrog's Gulls ate more male crabs than female crabs. Preliminary data on the behaviour of the crab *N. granulata* show that males defend the entrance to their burrows more frequently than females (ratio of males to females defending burrows: 2.2 : 1 for small crabs ($n=67$); 1.8 : 1 for medium-sized crabs ($n=135$); 16.0 : 1 for large crabs ($n=68$); M. P. Berón, unpubl. data). The higher levels of burrow defence combined with the higher motility of male crabs (TL unpubl. data) may be linked to a higher risk of predation in male crabs. This is consistent with studies of other species of crabs in which males with enlarged claws and which are usually more active than females are more conspicuous to predators (Bildstein *et al.* 1989; Magnhagen 1991).

In this study, handling times increased with the size of crabs, with larger crabs presumably more difficult to capture and handle. Handling times also varied with the age of Gulls, with adult Gulls more efficient at handling prey than younger birds, irrespective of

the size of prey (Papakostas *et al.* 2005; Gomez *et al.* 2009). Handling efficiency was also higher when eating *N. granulata* than *C. angulatus*. Because handling time was not influenced by the species of crab taken, differences in handling efficiency may be explained by the differences in biomass between the two species of crab. However, preliminary data indicate that the energy content of both species of crab is similar (*N. granulata*: 21.06 \pm 2.43 kJ g⁻¹ dry weight, $n=8$; *C. angulatus*: 20.57 \pm 3.60 kJ g⁻¹ dry weight, $n=7$; García *et al.* 2008; M. P. Berón, unpubl. data), so there is unlikely to be a significant effect of differential profitability of prey.

The handling efficiency of adults was significantly greater than that of subadults, which in turn was greater than that of juveniles. In earlier studies in the same area, juveniles were generally socially subordinate to adults in the selection of foraging sites and showed fewer skills in capturing and handling crabs (Copello and Favero 2001; Berón *et al.* 2007). These age-related differences in foraging efficiency may be linked to differences in individual experience and social interactions

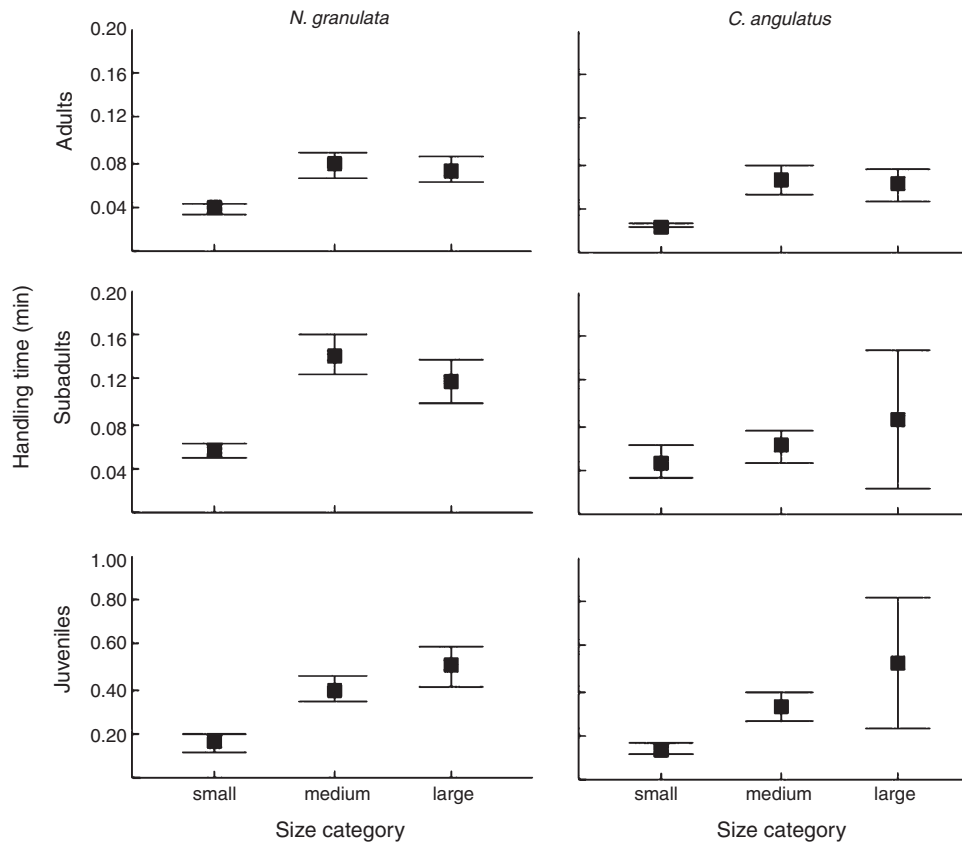


Fig. 2. Handling times of *N. granulata* and *C. angulatus* of different sizes eaten by Olrog's Gulls of different age-classes. Average values (dots) are shown along with standard errors (whiskers). Note different y-axis in juveniles compared with the other graphs.

(Snellen *et al.* 2007). Juveniles might compensate for lower foraging success either by foraging for longer periods, by selecting different sizes and types of prey, by using alternative capture methods, or by stealing food (Bertellotti and Yorio 2000). For example, in earlier studies in the area, juvenile Olrog's Gulls used more food resources of anthropogenic origin than did adults (Berón *et al.* 2007). These differences in the trophic spectrum between age-classes could be partly attributed to differential foraging skills and social subordination of juveniles in the preferred foraging sites where crabs are more abundant.

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