

Foraging ecology of Olrog's Gull *Larus atlanticus* in Mar Chiquita Lagoon (Buenos Aires, Argentina): are there age-related differences?

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Summary

Olrog's Gull *Larus atlanticus* is an endemic species of the Atlantic coast of southern South America. It is one of six globally threatened gull species in the world, and is classified as Vulnerable. We studied age-related differences in the diet and foraging behaviour of this species in Mar Chiquita Lagoon during the non-breeding season. Diet was assessed by analysis of regurgitation casts, prey carcasses and direct observation, while foraging behaviour was quantified by focal observations. Grapsid crabs were by far the main prey in frequency of occurrence, followed by fish and snails. Some differences in diet were found between ages, particularly in spring when mature birds start to feed on the eggs of ovigerous females of the crab *Cyrtograpsus angulatus*. Foraging behaviour was similar between ages which is attributed to large resource availability, foraging strategies and social factors.

Introduction

Gulls (Laridae) are generalist seabirds that employ a wide variety of feeding tactics to exploit different habitats and prey types (Burger and Gochfeld 1996). In Buenos Aires Province, Argentina, Olrog's Gull *Larus atlanticus* has specialized feeding habits compared with other gull species, e.g. Kelp Gull *Larus dominicanus*, Brown-hooded Gull *L. maculipennis* and Grey-hooded Gull *L. cirrocephalus*. In previous studies, Olrog's Gulls have been reported to be a specialized predator on crabs (Escalante 1966, 1984, Spivak and Sánchez 1992, Yorio and Harris 1992, Burger and Gochfeld 1996), despite occasionally foraging on mussels *Mytilus* (Escalante 1966), fish (Olrog 1967), insects (Spivak and Sánchez 1992) and discarded offal from fishing vessels (Jehl and Rumboll 1976, Martínez *et al.* 2000).

Olrog's Gull is an endemic species of the Atlantic coast of southern South America. It breeds in estuaries south of Buenos Aires and Chubut Provinces. During the non-breeding period, they migrate northwards as far as southern Brazil (28°18'S, 52°48'W), and southwards to Puerto Deseado (45°02'S, 65°53'W) (Collar *et al.* 1994, Burger and Gochfeld 1996). Non-breeding birds are common from May to November in coastal areas in south-east Buenos Aires Province (Favero 1991, Narosky and Di Giacomo 1993, Bó *et al.* 1995). The most significant features of the population are: (1) a small number (< 2500) of breeding pairs; and

(2) a total of 11 colonies distributed along only 200 km of coastline (Burger and Gochfeld 1996, Yorio *et al.* 1998). The species is therefore classed as Vulnerable (Burger and Gochfeld 1996) and it is included in Appendix I of the Convention on Migratory Species (CMS 2000).

It has been suggested that the distribution of Olrog's Gull is restricted to estuarine environments with dense assemblages of grapsid crabs (Escalante 1966). This hypothesis was supported by dietary studies performed in Mar Chiquita Lagoon during winter and early spring (Spivak and Sánchez 1992). However, a recent study discussed the specialist or generalist role of Olrog's Gull on non-breeding grounds, reporting the scavenging behaviour of this species at Mar del Plata Harbour and its association with fishing operations (Martínez *et al.* 2000).

Age differences in foraging behaviour and feeding success have been reported in several seabirds including gulls *Larus* spp. (Verbeek 1977, Ingolfsson and Estrella 1978, Searcy 1978, Steele and Hockey 1995), Royal Tern *Sterna maxima* (Buckley and Buckley 1974), pelicans *Pelecanus* spp., frigatebirds *Fregata* spp. (Burger *et al.* 1980) and Neotropical Cormorant *Phalacrocorax olivaceus* (Morrison *et al.* 1978). In all cases adults had lower interfood interval (see Foraging behaviour below), higher foraging success, spent less time foraging for, obtaining and handling food items than juveniles, or exhibited a combination of these factors. These differences have been usually attributed to the difficulty of the tasks, or the difficulty in learning to recognize suitable food items, or both. These age-related differences have been cited as a cause for delayed maturity in seabirds, many species of which do not breed until their fourth year or later (Lack 1966).

This study was designed with the main objective of analysing the diet and foraging behaviour of Olrog's Gulls in Mar Chiquita Lagoon, with respect to changes through the non-breeding season and age-related differences between individuals. We hypothesized that due to differences in foraging behaviour between age classes, the foraging efficiency of adults is significantly higher than subadults, which in turn is higher than juveniles.

Study area and methods

Study area

The study area was located at Mar Chiquita Lagoon, Buenos Aires Province, Argentina (37°46'S, 57°27'W) (Figure 1). This area is a provincial reserve and was designated as a Biosphere Reserve by the MAB programme in 1996 (UNESCO). It is characterized by a 46 km² body of tidal brackish water on the coast, with mud flats bordered by *Spartina densiflora* grassland and inhabited by large numbers of intertidal crabs (Oliver *et al.* 1972). Five species of crab inhabit the study area: *Chasmagnathus granulata* and *Uca uruguayensis* are dominant in the upper littoral and are burrowing semi-terrestrial species; *Cyrtograpsus angulatus* inhabits predominantly the lower littoral and rocky seashores (Spivak *et al.* 1994). *Cyrtograpsus altimanus* and *Platyxanthus crenulatus* are euryhaline marine species that are found exclusively near the mouth of the lagoon. Other benthic organisms include stout razor clams *Tagelus plebeius* and the polychaete *Laeonereis pandoensis* (Olivier *et al.* 1972). Data were collected from May to September 1999.

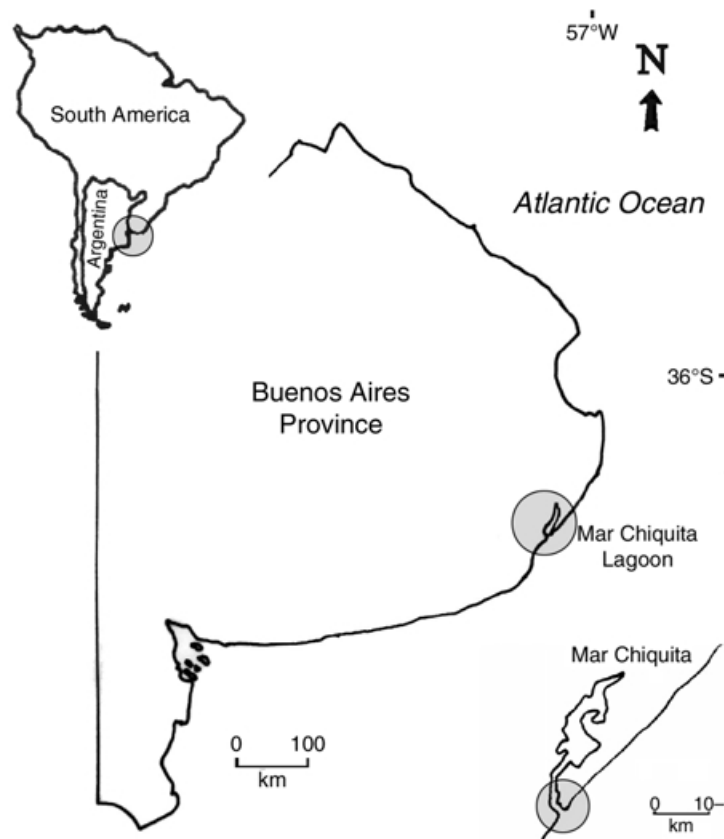


Figure 1. Study area at Mar Chiquita Lagoon ($37^{\circ}46'S$ $57^{\circ}27'W$), Buenos Aires Province, Argentina.

Diet

The diet of Olrog's Gull was assessed by the analysis of regurgitated pellets ($n = 363$), by direct observation of prey capture ($n = 449$) and from prey carcasses found on the shore ($n = 390$). Samples consisted of weekly collections of pellets in the middens and prey remains in different handling areas, as well as direct observations of foraging gulls.

In the laboratory, pellets were dried at ambient temperature ($20^{\circ}C$), dissected and the hard remains identified using a stereo microscope ($20\times$). The chelae and mandibles of prey were used as diagnostic elements (Spivak and Sánchez 1992). To identify these elements, we used reference material from our own collection of crabs taken in the study area. Crab species were identified by the different morphology of the mandibles while sex was determined by comparing the length and height of each chelae following regressions given by Spivak and Sánchez (1992). Crab size (as carapace width, CW) was estimated from specific linear regressions with mandible width (MW) following Spivak and Sánchez (1992). Mandibles were separated into right and left and the most abundant was consid-

ered to represent the total number of crabs present by species in each pellet. Prey carcasses were analysed in the same way as pellets.

In the case of crab captures during direct observations, species, sex, and relative sizes were distinguished as far as possible. Crab size was assessed in relation to bill length of the gull, categorized as small ($CW < 20$ mm), medium ($20 < CW < 40$ mm) or large ($CW > 40$ mm).

Foraging behaviour

Foraging behaviour of Olrog's Gull was quantified by focal observation (Altmann 1974), using a telescope (12–36×) and binoculars (10×). Different age classes were identified by plumage characteristics, grouping the individuals as "adult" (i.e. breeding birds of at least four years old), "subadults" (i.e. non-breeding individuals between two and three years old) and "juveniles" (i.e. individuals of one year old; see Harrison 1983). Observations of less than five minutes duration were excluded. Observations were recorded on a tape recorder and later transcribed in the laboratory.

The behavioural variables considered during sampling were: feeding method, prey handling time (food carrying included), movements between foraging areas (walking, swimming or flying), comfort behaviour (bathing and/or preening) and roosting (see Martin and Bateson 1994). Foraging time and location were also taken into account. Feeding methods considered were: surface seizing (SS), surface plunging (SP) (Ashmole 1971, Harper *et al.* 1985), and walking (W) (Favero *et al.* 1997). Intra- and interspecific interactions and their intensity (high, moderate or low) were recorded. The low-intensity interactions consisted of displays such as choking, aggressive upright postures, and long calls; moderate-intensity interactions included leaping at or jabbing at an opponent across a territorial boundary; high-intensity interactions included fights involving physical contact.

Capture attempts, prey captures and intake rates were estimated as the number of events observed in five minutes. Interfood interval (IFI) was also calculated as the time elapsed between first obtaining a food item and successfully obtaining a second food item, and was considered to be an index of foraging ability following Burger and Gochfeld (1983). The classical models of optimal foraging use the Holling's disc equation to estimate the amount of energy gained per unit time spent in handling (Charnov and Orians 1973). In order to correct the biases linked with the non-intake of captured prey, we used the equation modified by Meire and Ervynck (1993).

$$E/T = \frac{\sum E_i \lambda_i P_i}{1 + \sum \lambda_i (HP_i P_i + (1 - P_i) WH_i)}$$

where: E/T is the energy gained (wet tissue mass) per unit time; λ_i is the encounter rate for each age; P_i is the probability of intake for each age; E_i is the intake total of wet tissue mass; HP_i is the handling time (of intaken prey); and WH_i is the waste handling time (of non-intaken prey).

Encounter rates, probability of intake and handling time were obtained from

direct observations. Wet weight of prey was estimated using regressions between CW and wet weight (g) in Luppi *et al.* (1997).

Statistical analysis

Differences in crab size of each species eaten and the average IFI for each age-class were assessed using paired Student's *t*-tests. Comparisons of crab size distribution from pellets with that from other methodologies, prey type, sex and crab size, interactions and IFI distribution for each age, were analysed by chi-square tests (χ^2). Time budgets and rates for each age were compared by analysis of variance (ANOVA). Means are given ± 1 standard deviation. All methods follow Zar (1984) and Underwood (1997).

Results

Diet

All pellets ($n = 363$) had diagnostic prey remains. Crabs were by far the most frequent prey (Occurrence, $F\% = 100$), followed by fish ($F\% = 0.5$) and egg capsules of *Adelomedon* snails (each one containing several embryos, $F\% = 0.5$). The mean number of crabs per pellet was 3.2 ± 2.4 (range = 1–18, $n = 363$). The crab species identified were *Chasmagnathus granulata* (41%) and *Cyrtograpsus angulatus* (59%). Of *C. granulata*, 92% of those in pellets were males, while all *C. angulatus* were females.

The average size of crab prey was 28.4 ± 4.0 mm (range = 12–44 mm, $n = 1,435$). The average size of *C. angulatus* taken by gulls was significantly greater than that of *C. granulata* (27.6 mm ± 3.7 for *C. granulata* and 28.8 mm ± 4.1 for *C. angulatus*: $t_{1074} = 4.81$, $P < 0.001$). The modal size of *C. granulata* consumed was 24–27 mm and that of *C. angulatus* was 27–30 mm, being significantly different from that expected based on the size–frequency distribution of both prey species ($\chi^2_{10} = 28.5$, $P < 0.001$; Figure 2).

Of the 390 crabs found in handling areas, 86.1% were *C. granulata* (89.3% males), while 13.8% were *C. angulatus* (all females). The ratio between crab species in the diet differed significantly with sampling method ($\chi^2_1 = 304$, $P < 0.001$). However, the sex ratio was similar ($\chi^2_1 > 0.1$, $P > 0.5$).

Of the 449 prey captures recorded, 86.6% corresponded to crabs, 9% of which were dead when captured. Other items were identified as snail egg capsules (7%) and items with an anthropogenic source (i.e. fish bait, waste, etc. 6%). Of the crabs captured, 43% were identified to the species level, of which 54.4% were *C. angulatus* and 45.6% *C. granulata*. No significant difference was observed between the proportion of species obtained by direct observation and that by pellet analysis ($\chi^2_1 = 1.02$, $P > 0.1$). Adults gulls consumed significantly more female crabs than would be expected (87.0%, $\chi^2_1 = 27.65$, $P < 0.001$), while in subadults and juveniles the sex ratio of crabs taken did not differ significantly ($\chi^2_1 > 0.50$, $P > 0.5$ in both comparisons). Prey sizes observed were as follows: 32% small, 66% medium and 3% large crabs. No significant differences in the prey size consumed by adults, subadults and juveniles were observed ($\chi^2_4 = 2.8$, $P > 0.5$).

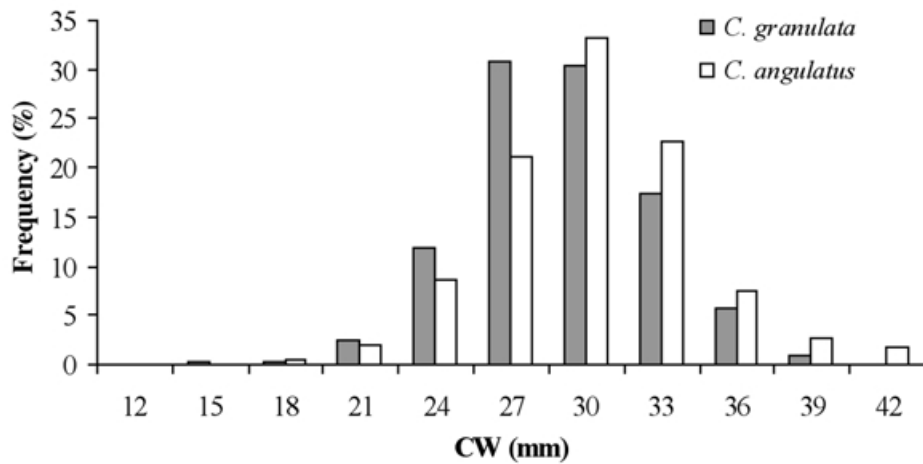


Figure 2. Size-frequency distribution of crab prey of Olrog's Gull at Mar Chiquita Lagoon, Buenos Aires, Argentina, 1999. CW = carapace width.

The importance by number of the prey types consumed was not significantly different between gull age classes ($\chi^2_6 = 10.23$, $P > 0.1$), with the exception of snail egg capsules, which were consumed at a higher proportion by juveniles (Table 1).

Foraging behaviour

The highest abundance recorded during the surveys was 110 birds, grouped in flocks of about 15 individuals. Half (50%) of them were juveniles. During the study, 222 focal observations of at least 5 minutes duration were made.

Overall, gulls spent 55% of the time searching for food, 8% attempting to capture prey, 11% in prey handling, 14% moving between foraging areas, 4% in comfort behaviour, and 8% in roosting. There were no significant differences in time budgets between different age classes ($F_{2, 1766} \leq 2.385$, $P > 0.1$ in all the comparisons). Foraging rates calculated were: 22.3 ± 21.2 capture attempts 5 min^{-1} , 1.7 ± 2.2 prey captures 5 min^{-1} and 0.9 ± 1.2 intakes 5 min^{-1} ($n = 222$). In

Table 1. Importance by number (in percentages) of prey items consumed by Olrog's Gull of each of three age-classes at Mar Chiquita Lagoon, Buenos Aires, Argentina, 1999

	Adults	Subadults	Juveniles
Live crabs	82.30	77.05	71.93
Dead crabs	6.22	9.84	7.02
Snails	5.26	6.01	15.79
Anthropogenic items ^a	6.22	7.10	5.26

^a Fisherman's bait, waste, etc.

all cases there were no significant differences between gull ages classes ($F_{2, 217} \leq 1.913$, $P > 0.15$ in all the comparisons) (Figure 3).

Mean biomass intake for Olrog's Gull was $42.6 \pm 53.2 \text{ g h}^{-1}$ (wet weight), and did not differ significantly between age classes ($F_{2, 118} = 1.48$, $P > 0.05$).

Gulls captured prey by three methods: walking (W) and surface seizing (SS) were the most frequent for all age classes (c. 50% for each), whereas surface plunging (SP) was used mostly by adults (2.7%) and never by juveniles. No significant differences were found between ages for W and SS ($F_{2, 219} > 0.74$, $P > 0.2$).

Searching time decreased by half between June and September in all ages (Figure 4A), while handling time increased fourfold from July to September in all ages (Figure 4B). No significant differences were found in searching or handling time between ages in each month ($F_{2, 218} = 0.044$, $P > 0.5$ for searching, $F_{2, 218} = 0.064$, $P > 0.5$ for handling).

Average IFI estimated for the species was 102.9 ± 62.7 seconds (range 9–246, $n = 87$). Mean IFIs did not differ significantly between ages ($t_{> 44} > 0.348$, $P > 0.30$). Significant differences were found in the comparison of these frequency distributions between adults with respect to subadults and juvenile ($\chi^2_4 = 6.63$, $P < 0.01$ and $\chi^2_4 = 6.51$, $P < 0.01$, respectively) (Figure 5).

The frequency of intraspecific interactions was 0.6 events per focal observation ($n = 134$). Most consisted of moderate-intensity interactions (60%) followed by low-intensity (36%) and high-intensity (4%). No significant dominance by any age class was apparent ($\chi^2_2 = 1.05$, $P > 0.5$), but a higher proportion of gull "losers" were juveniles. Only 1% of the interactions observed were interspecific, involving either Brown-hooded Gull *Larus maculipennis* or Chimango Caracara *Polyborus chimango*.

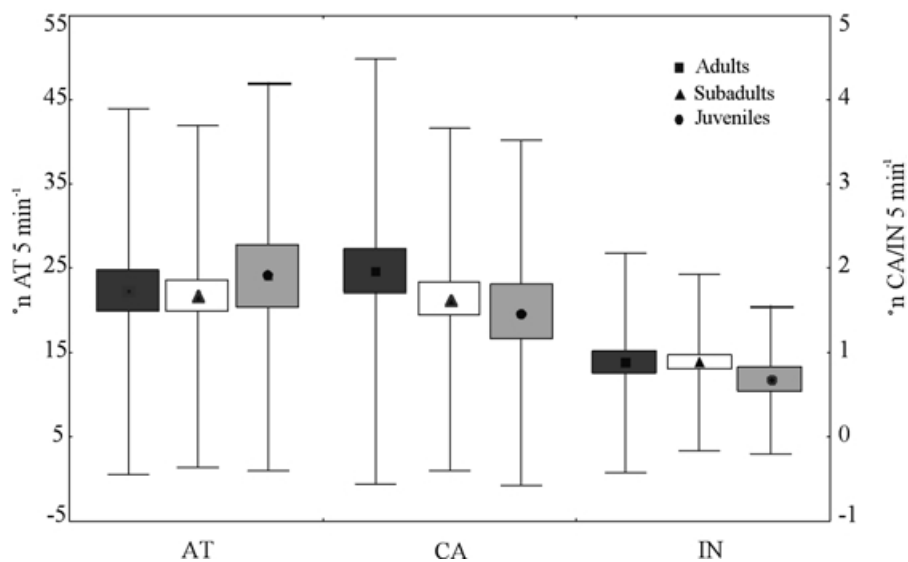


Figure 3. Attempts (AT), capture (CA) and intake (IN) rates for the different age-classes of Olrog's Gull at Mar Chiquita Lagoon, Buenos Aires, Argentina, 1999. Mean values (points) are given with standard errors (boxes) and standard deviations (whiskers).

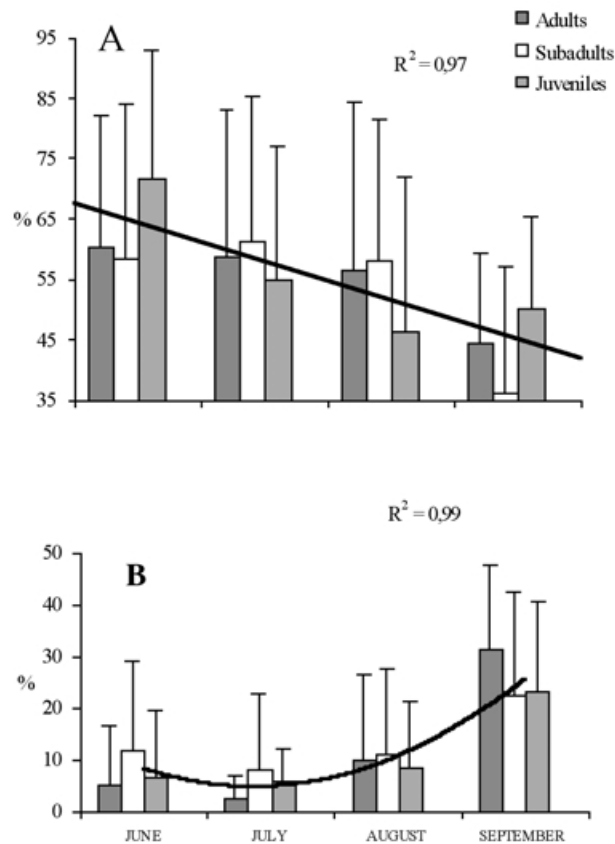


Figure 4. Searching time (A) and handling time (B) spent by the different age-classes of Olrog's Gull at Mar Chiquita Lagoon, Buenos Aires, Argentina, 1999. Trendlines are estimated for all individuals and were fitted with linear and squared models, respectively.

Discussion

The diet of Olrog's Gull in Mar Chiquita

Two grapsid crabs, *Chasmagnathus granulata* and *Cyrtograpsus angulatus*, constituted the bulk (in similar proportion) of the diet of Olrog's Gulls during the study period, as found in previous studies in the same area (Spivak and Sánchez 1992). However, unlike previous studies, we did not find any remains of the crab *Uca uruguayensis*, or of birds or insects in the samples, a fact that could be linked to differences in sampling period (i.e. insects were previously reported in the diet during late spring and our study period finished in September). The presence of *Adelomedon* snail eggshell remains is also previously reported for the species (Martínez *et al.* 2000).

It is potentially misleading to characterize a species as either a specialist or generalist forager without defining the resources being used, the temporal and spatial scales of the measurements made, and without presenting some measure of the degree of individual variation within the population studied (Recher 1990).

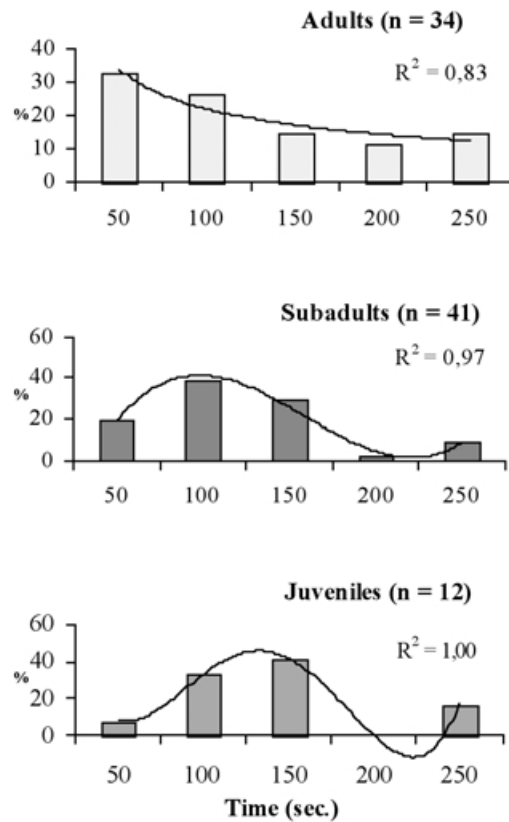


Figure 5. Interfood interval (IFI) frequency distributions for the different age-classes in Olrog's Gull at Mar Chiquita Lagoon, Buenos Aires, Argentina, 1999. Trendlines are fitted by polynomial models.

In agreement with the literature, our observations show that Olrog's Gull is a specialist forager during the non-breeding season at Mar Chiquita Lagoon (Escalante 1970, Spivak and Sánchez 1992). However, there is evidence of variation in diet in different parts of its range during both the breeding and non-breeding seasons. For example, during winter at Mar del Plata harbour, 30 km from Mar Chiquita Lagoon, the species foraged upon discarded offal from fishing vessels (Martínez *et al.* 2000). Therefore, Olrog's Gull could be considered a generalist forager in a broad sense, because of its foraging on a wide range of prey such as molluscs, fish, annelids and arthropods. However, in areas with high crab abundance, such as Mar Chiquita Lagoon, the species could be considered a specialist as suggested by Escalante (1970) and Spivak and Sánchez (1992).

Crabs in the diet

The sex ratio of crabs consumed estimated by pellet analysis was strongly biased towards females in *C. angulatus* (100%), and to males in *C. granulata* (92%). These results do not agree with those reported by Spivak and Sánchez (1992) who

found a female-biased consumption in both crab species, mostly in *C. granulata*. The sex ratio of crabs reported for the study area is strongly biased towards females in *C. angulatus* (5:1), and is even in *C. granulata* (Spivak *et al.* 1994). Thus, the sex ratio of *C. angulatus* consumed by gulls was in line with that of the crab population available. The strong differences observed in *C. granulata* could be linked with a higher predation risk of males of this species which spend more time outside or in the entrance of caves, while females prefer sheltered positions in the bottom of caves (T. Luppi 2000 pers. comm.).

The modal size of *C. angulatus* taken was higher than that of *C. granulata*, a fact that could be due to: (1) a greater availability of this crab size, (2) a higher cost-benefit pay-off, and/or (3) differences in the aggression of both crab species. With regard to the first hypothesis, the modal size of crabs consumed was in agreement with that reported for the sampling area (Spivak *et al.* 1994). Regarding the second possibility, it must be considered that *C. angulatus* has a weight-size ratio smaller than *C. granulata* (Luppi *et al.* 1997), thus gulls could maximize the energetic return per prey item by selecting larger crabs of the former species. The third hypothesis addresses the different anti-predator strategy of both crabs: while *C. granulata* defend their territories by attacking intruders or predators, *C. angulatus* usually escape by limb autotomy (E. Spivak 2000 pers. comm.). The anti-predator strategy of the former species makes handling *in situ* difficult, it being easier for gulls to take prey further inshore to be handled. This behaviour also explains the higher proportion of *C. granulata* (86%) in handling areas, suggesting also that gulls could have difficulty in handling large crabs of this species, avoiding the consumption of larger individuals in order to minimize the risk of injury.

Differences in diet between age-classes

Quantification of diet by direct observation allowed the identification of differences between age-classes. Some such differences could be allied with a higher predation experience of older birds since (1) adults consumed significantly more female crabs: the selection of this sex could be advantageous to predators since females are less aggressive and have smaller chelae than males, thus diminishing the costs of capture and/or risks of injuries; (2) juveniles consumed a higher proportion of snail eggshells, an abundant prey often stranded on the shore, therefore being much easier to capture and handle than crabs; (3) from mid-September onwards and coinciding with an increase in ovigerous (egg-bearing) *C. angulatus* females in the upper littoral of the lagoon, adults and subadults were seen capturing this prey in order to consume exclusively their eggs. At the same time as this change in diet of older birds, all gulls (including juveniles) changed foraging area, moving to the lagoon's mouth where these crabs were abundant.

Similarities in the foraging behaviour between age-classes

Many aspects of foraging behaviour change according to the age of seabirds; in general adults have a shorter IFI than juveniles, have higher foraging success, spend less time foraging, obtaining and handling prey, or have a combination of

these factors (see Burger 1987). In this study, the time budgets observed were similar for all ages. Between June and September there was no variation between ages in the time spent searching and handling. Searching time may have decreased because of the high *Cyrtograpsus* crab availability in the upper littoral; alternatively, handling time could have increased partly due to the more frequent carrying of prey to the shore.

No significant differences were found in attempts, capture rates or intake rates between age classes. Similarly, no significant difference between age classes in cost-benefit relationships estimated by using Holling's equation were found, perhaps due not only to prey and foraging characteristics, but also to gross estimation of prey size assessed by direct observation. Elsewhere, differences in foraging behaviour between age classes have been attributed to food availability or to difficulty of the task (Burger and Gochfeld 1983). Thus, the similarity found between age-classes in this study could be attributed to high crab availability in the lagoon (Olivier *et al.* 1972, Spivak *et al.* 1994), and/or to the fact that capture tactics used by gulls could be quickly learned by immature individuals. All ages used "easier" foraging methods, such as surface-seizing or walking, while more "difficult" tactics requiring high manoeuvrability, such as surface-plunging, were only used by adults and subadults.

Foraging inefficiency in juveniles can be attributed to different behavioural traits, including social factors such as aggression and dominance (Burger *et al.* 1980). There are several possible explanations for the paucity or scarcity of interactions between and among age-classes: (1) to decrease costs incurred (i.e. risk of injuries, Pierotti and Annett 1994), (2) the resources are not economically defendable (Krebs and Davies 1993) and/or (3) there are benefits acquired when individuals are in social groups (i.e. information sharing, Ward and Zahavi 1973). The low rate of interactions and the lack of dominance between ages could be linked to the high crab abundance and their wide distribution in the study area (Olivier *et al.* 1972, Spivak *et al.* 1994). To be in groups allows juveniles to achieve additional information from more experienced birds, reducing differences in foraging rate of adults (Ward and Zahavi 1973).

About 70% of the variance in the IFIs of different gull species was attributed to food type, species considered, age, foraging method and habitat (Burger 1987). The average IFI estimated in this study was more than twice that expected according to the literature. IFI values reported for crabs in the literature are about 40 ± 42 seconds, which also indicates higher variance (Burger 1988). Significant differences were found between age-classes in IFI frequency distributions, increasing by about 50 seconds from adults to subadult and juveniles.

Concluding remarks

We did not find substantial age-related differences in the foraging ecology, and particularly in the efficiency of Olrog's Gulls, thus not supporting the hypothesis formerly stated. The differences found in the IFI frequency distributions were in agreement with the literature. The lack of age-related differences could be due to resource features, especially the high availability and relatively easy handling of crabs. However, some differences found in diet were important. The ecological plasticity of Olrog's Gull revealed the ability of an individual to respond to

resource changes by shifting foraging behaviour (Greenberg 1990). The fact that adults and subadults foraged upon crab eggs (i.e. ovigerous females), suggests a higher plasticity of experienced individuals than naïve birds, and also a higher foraging efficiency since the high energy value of crabs' eggs is suspected. Different energetic needs of mature (i.e. reproductive) individuals through the year and pre-reproductive requirements may also be important. Future studies on diet and foraging ecology of Olrog's Gull in other areas and seasons will further our understanding of the species and allow better implementation of conservation measures for this threatened species.

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