AGE-RELATED FEEDING BEHAVIOUR AND FORAGING EFFICIENCY IN KELP GULLS *LARUS DOMINICANUS* ATTENDING COASTAL TRAWLERS IN ARGENTINA

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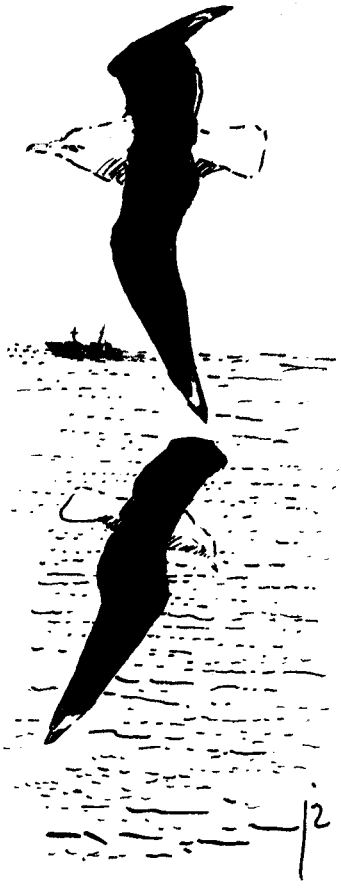

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We studied age-related differences in feeding behaviour and foraging success of Kelp Gulls *Larus dominicanus* feeding on fishery discards at trawl vessels in northern Patagonia, Argentina. Kelp Gulls consumed fish by direct capture and intraspecific kleptoparasitism. Direct capture rate increased significantly with age. Juveniles dropped a higher proportion of handled fish than older birds. Intraspecific kleptoparasitism involved gulls of all age-classes and was recorded in all hauls. The percentage of successful attempts was similar among different age-classes. However, juveniles and immatures attempted to steal prey more frequently and therefore obtained more prey than expected. The proportion in which each feeding method (direct capture and kleptoparasitism) contributed to overall fish consumption varied significantly among age-classes. Juveniles obtained most of the food through kleptoparasitism (72%), while immature, subadult and adults consumed prey mostly through direct capture (77, 91 and 92%, respectively). Using both feeding methods, Kelp Gulls swallowed 87.6% of the discarded fish that they handled. However the percentage of fish swallowed over total handled fish were different among age-classes (juveniles 45.5%, immatures 70.8%, subadults 83.3%, adults 94.8%). Kleptoparasitism may be used as an alternative strategy to compensate the lower efficiency of young birds.

Key-words: *Larus dominicanus* - age related feeding efficiency - fishery waste - scavenging - kleptoparasitism

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INTRODUCTION

In many seabird species, younger individuals have a lower foraging success and often show different feeding strategies than adult birds (Orians 1969; Morrison *et al.* 1978; McLean 1986; Burger 1987). Juveniles are generally less efficient in their selection of feeding sites and show less skill when capturing and handling prey (review in Wunderle 1991). These age differences in foraging proficiency have been attributed to differences in individual experience (Greig *et al.* 1983; Wunderle 1991) and it has been argued that juveniles may compensate lower feeding success by foraging for longer periods, by selecting different sizes and types of prey, by using alternative capture methods, or by robbing food from other individuals (Wunderle 1991). Opportunistic species such

as gulls (*Larus spp.*) use kleptoparasitism both inter-and intra-specifically as a way to obtain food (Hulsman 1976; Greig *et al.* 1983; Hockey *et al.* 1989) increasing this behaviour during periods of food shortage (Oro & Martinez-Vilalta 1994). Moreover, younger gulls may also increase kleptoparasitic attacks as a way to compensate the lower foraging efficiency (Verbeek 1977; Wunderle 1991).

Kelp Gulls *Larus dominicanus* along the Argentine coast are generalist foragers that feed mostly on intertidal invertebrates and fish, and taking advantage of artificial food sources such as refuse tips and fisheries discards (Giaccardi *et al.* 1997; Yorio *et al.* 1998; Bertellotti & Yorio 1999). In northern Patagonia, it is one of the main seabird species associated to coastal fisheries (Yorio & Caille 1999), and displacements, aggressions and kleptoparasitism among individuals of different age-classes are commonly observed while they are feeding on discards (Yorio & Caille 1999; Bertellotti 1998). In this paper we analyse the foraging behaviour of Kelp Gulls using fishery discards at trawl vessels in northern Patagonia, Argentina. We quantify age-related differences in feeding methods, foraging efficiency and feeding success as kleptoparasite.

STUDY AREA AND METHODS

Between November 1996 and May 1997, observations were conducted onboard coastal trawlers operating in Golfo San Matías, Río Negro, Argentina. These trawlers are 19-24 m long and tow bottomtrawls at 2-3 nautical miles h^{-1}. Trawls last between one and three hours and the main target is Argentine Hake *Merluccius hubbsi*. These trawlers fish in general within 30 km of shore and fishing trips last between three and six days (3-4 hauls per day). Fish captured by trawlers are sorted on deck and both non-commercial sizes and bycatch are discarded overboard.

Kelp Gull feeding behaviour was studied on 14 days (56 hauls). Counts of gulls associated with these vessels were made from the top deck, every 30 minutes throughout the entire fishing operation (237 counts in total; mean ± SD 16.9 ± 4.3 counts day^{-1}). Gulls were aged on the basis of plumage characteristics, using four age classes: juveniles (first year), immatures (between one and two years), subadults (between two and three years), and adults (fully-grown and adult plumage; Bo *et al.* 1995). The maximum number of gulls attending the ship at each haul was assessed and the mean maximum number of gulls per fishing day was calculated afterwards. A fishing day was defined as a daylight period in which at least one haul was made.

Prey consumption was studied through the experimental discarding of fish that was taken randomly from the discard-fraction of each catch. Fish species were selected on the basis of their frequency of occurrence and abundance in the discards, using data obtained during the fishing season of 1995-1996 by the On-board Observer Program (Patagonian Coastal Zone Management Plan). A total of 23 fish species were discarded, with Argentine Hake, Longtail Hake *Macruronus magellanicus*, Flounders *Paralicthys isosceles* and *Xystreurys rasile*, Skate *Raja flavirostris* and Brazilian Codling *Urophycis brasiliensis* being the most numerous species. Another three species, which were common in the discards during the present study (Butterfish *Stromateus brasiliensis*, Blackbelly Rosefish *Helicolenus dactylopterus*, and Sea Salmon *Pseudopercis semifasciata*), were frequently included in the discard experiments. The nine fish species selected represented more than 85% of the total discarded biomass in 1995-1996 (G. Caille, pers. comm.). Fish were identified and measured (total length in cm) and experimentally discarded singly at 10 s intervals from the stern while the vessel trawled for the next catch. In each case, it was recorded if the fish was taken, swallowed, robbed or dropped by a gull. All gulls handling discarded fish were aged.

To evaluate the frequency of kleptoparasitism during experimental discards we recorded the success or failure of each robbing attempt, and the age of the kleptoparasite. We considered a robbing attempt as such when a Kelp Gull made a

clear movement towards another gull with prey in its beak. An attempt was considered as a successful attack when the kleptoparasite obtained prey from the other, even if this prey was only partially taken. We calculated a foraging success index (S.I.; see Camphuysen 1994) on the basis of mean numbers of Kelp Gulls present at vessels and the total numbers of consumed discards by each age-class (null hypothesis is that birds of all age-classes have an equal likelihood of obtaining discards). We used parametric statistics when possible, after testing homogeneity of variance by means of Barlett-test. We used ANOVA and post hoc comparisons using Tukey test. Means are given ± 1 SD. Differences among observed and expected frequencies were tested using χ^2 goodness of fit. *G*-test was used for the analysis of frequencies.

RESULTS

Kelp Gulls were present at all hauls, with a mean maximum number per day (± SD) of 299.2 ± 73.38 individuals (n = 14). All age-classes were represented in all counts, but adults numerically predominated always (juveniles 5.7%, immatures 8.1%, subadults 8.3%, and adults 77.9%). This proportion was similar on all days of study (G_{39} = 19.8, P = 0.99). During experimental discarding, Kelp Gulls of all age-classes fed mostly by direct capture (plunge diving, and to a lesser extent by surface seizing) and by kleptoparasitism. Juveniles consumed 12.9% of the fish they handled, while immatures and subadults consumed 54.6 and 76.0% of their prey, respectively. Adults had the highest success rates, with 87.1% consumed of the fish they handled. The consumption rates are significantly different between age groups (G_3 = 386.9, $P < 0.001$, n = 1915).

Table 1. Number of dropped items for each Kelp Gull age-class feeding on experimentally discarded fish at coastal trawlers in Golfo San Matías (number of handled fish in parentheses).

	Fish dropped (n)			
Age class	Observed	Expected	% dropped	n
Juveniles	72	13.6	54.5	132
Immatures	63	19.3	29.2	216
Subadults	32	19.6	16.7	192
Adults	71	185.5	5.2	1375

During experimental discards, Kelp Gulls dropped 12.4% of the handled fish (n = 1915). Juveniles dropped a much higher proportion of the fish they handled, while adults dropped the least (G_3 = 262.9, $P < 0.001$; Table 1). Younger gulls dropped more fish than expected according to their relative abundance around vessels (χ^2_3 = 428.7, $P < 0.001$; n = 238). Also the size of fish handled differed among age-classes (ANOVA $F_{3,1911}$ = 33.1, $P < 0.001$, all Tukey-test contrasts, $P < 0.001$), except between adults and subadults (Tukey-test, P = 0.99). Fish picked up by immatures and juveniles was on average larger in younger than older birds (Table 2). The mean size of fish consumed by direct capture, however, was similar among age-classes (ANOVA $F_{3,1474}$ = 2.3, P = 0.07, Table 2), indicating that immatures were less capable of selecting fish of suitable size by eye. Each age-class consumed Argentine Hake

Table 2. Mean length (± SD) of fish handled and swallowed by Kelp Gulls during experimental discarding at trawl vessels in Golfo San Matías. Sample sizes in parentheses.

Age-class	Fish handled (cm)	n	Fish swallowed (cm)	n
Juveniles	31.9 ± 8.2	134	22.4 ± 4.3	17
Immatures	28.0 ± 6.3	214	25.7 ± 5.0	118
Subadults	26.2 ± 5.8	192	25.9 ± 5.5	146
Adults	26.0 ± 5.5	1375	25.5 ± 5.1	1197

Table 3. Frequencies observed and expected (in parentheses) of the main fish species taken by direct capture for each Kelp Gull age-class feeding on experimentally discarded fish at coastal trawlers in Golfo San Matías. Expected number of each fish species were calculated using the relative abundance of Kelp Gull age-classes around vessels.

Age-classes	Argentine Hake	Brazilian codling	Longtail Hake
Juveniles	11 (58.5)	6 (15.8)	0 (6.0)
Immatures	85 (83.0)	19 (22.4)	11 (8.5)
Subadults	90 (84.6)	34 (22.9)	8 (8.7)
Adults	839 (798.9)	218 (215.9)	86 (81.8)
χ^2	41.0	12.1	7.0
P	< 0.001	< 0.01	n.s.

Table 4. Observed and expected numbers of robbing attempts for each Kelp Gull age-class foraging on experimentally discarded fish at coastal trawlers in Golfo San Matías.

Age of kleptoparasite	Robbing attempts		Number of fish stolen	
	Observed	Expected	Observed	Expected
Juveniles	94	25.7	43	11.4
Immatures	84	36.5	35	16.1
Subadults	36	37.1	14	16.4
Adults	236	350.7	107	155.1
Total	450	450	199	199

Table 5. Observed and expected numbers of fish consumed by each Kelp Gull age-class foraging on experimentally discarded fish at coastal trawlers in Golfo San Matías.

Age-class	Number of fish consumed		Success index
	Observed	Expected	
Juveniles	60	96	0.63
Immatures	153	136	1.13
Subadults	160	138	1.16
Adults	1304	1307	1.00
Total	1677	1677	

and Brazilian Codling in different proportions to what was expected according to their relative abundance around vessels, while they consumed Longtail Hake as expected (Table 3). Juveniles consumed less Argentine Hake than expected, while the rest took prey as predicted from their numerical abundance at the trawler. Similarly, juveniles and subadults consumed less Brazilian

clear movement towards another gull with prey in its beak. An attempt was considered as a successful attack when the kleptoparasite obtained prey from the other, even if this prey was only partially taken. We calculated a foraging success index (S.I.; see Camphuysen 1994) on the basis of mean numbers of Kelp Gulls present at vessels and the total numbers of consumed discards by each age-class (null hypothesis is that birds of all age-classes have an equal likelihood of obtaining discards). We used parametric statistics when possible, after testing homogeneity of variance by means of Barlett-test. We used ANOVA and post hoc comparisons using Tukey test. Means are given ± 1 SD. Differences among observed and expected frequencies were tested using χ^2 goodness of fit. *G*-test was used for the analysis of frequencies.

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Codling than expected (Table 3). These three fish species comprised 95% of consumed discarded items. The sample size was too small to warrant an analysis of other discarded species.

Fish obtained by kleptoparasitism

Intraspecific kleptoparasitism involved gulls of all age-classes and was recorded in all hauls, mostly during haulback and discarding activities. During experimental discarding of fish, Kelp Gulls attempted to steal fish from other gulls in 450 (23.5%) of 1915 cases. Gulls were successful in 44.2% of those attempts, with no differences between age-classes (G_3 = 0.85, P = 0.83; juveniles 45.7%, immatures 41.7%, subadults 38.9%, adults 45.3%). However, significant differences were found in the number of robbing attempts (χ^2_3 = 281.2, $P < 0.001$) and the number of discarded fish taken through kleptoparasitism (χ^2_3 = 125.5, $P < 0.001$) by each age-class from what could be expected according to their relative frequency at vessels. Juveniles and immatures attempted to steal prey more frequently and obtained more prey than expected, while the opposite was observed in adult gulls (Table 4). The size of successfully stolen fish was similar among all age classes (Kruskal-Wallis test: H_3 = 6.9, P = 0.07).

Overall consumption of fish by different age-classes

The proportion in which direct capture and kleptoparasitism contributed to the overall fish consumption varied significantly among age-classes (G_3 = 150.6, $P < 0.001$). Juveniles obtained most of the food through kleptoparasitism (71.7%), while subadults and adults consumed prey mostly through direct capture (immatures: 77.1%; subadults: 91.2%; adults: 91.8%). The numbers of total fish consumed by each age-classes were significantly different from expectation based on their relative abundance at the trawlers (χ^2_3 = 18.9, $P < 0.001$) (Table 5), with juveniles showing the lowest feeding efficiency (S.I. = 0.7; Table 5). Using both feeding methods, Kelp Gulls swallowed 87.6% of the discarded fish that they handled (n = 1915), being different the relative overall foraging success among age-classes (juveniles 45.5%; immatures 70.8%; subadults 83.3%; adults 94.8%; G_3 =262.9, $P <$ 0.001).

DISCUSSION

Several studies have shown that foraging efficiency increases markedly with age in many gull species (Verbeek 1977; Greig *et al.* 1983; Burger 1987; Furness *et al.* 1988), including the Kelp Gull (Hockey *et al.* 1989), and as expected, during the controlled discarding experiments, juvenile Kelp Gulls were less successful than older age-classes in obtaining prey by direct capture. Kelp Gulls foraging at trawl vessels obtain discards mostly using a method that requires considerable skill, such as plunge diving. Most young seabirds may require of a period of learning and practice to develop the necessary skills for prey capture (Wunderle 1991).

When foraging on discards in the present study, younger Kelp Gulls not only obtained less prey by direct capture than adults but also dropped more items. A higher rate of prey dropping in juveniles has been also reported for several gull species (Burger 1981; Burger & Gochfeld 1981; McLean 1986). Higher dropping rate may be due to both the lack of handling skills and the choice of larger prey. Young Kelp Gulls have been found in other studies to be less efficient at handling their prey (Hockey & Steele 1990). Limited handling abilities should result in the selection of smaller prey than those taken by adult birds, and this has been observed in several bird taxa (Wunderle 1991). However, discarded fish handled during our study was larger for younger gulls. Although more profitable in terms of energy gained, larger discards are more difficult to handle (Wunderle 1991), and are more likely to be stolen by Kelp Gulls through intraspecific kleptoparasitism (Bertellotti & Yorio, unpubl. data).

The success rate of kleptoparasitic attacks was high (> 40%), similar to that reported by Oro & Martínez-Vilalta (1994) for the Yellow-legged

Gull *Larus michahellis*. Attacks involved individuals of all age-classes, and young Kelp Gulls attempted to steal fish more often than adults. Similar results, where the frequency of kleptoparasitic attempts decreased with age, were reported for Kelp Gulls feeding on Sand Mussels *Mesodesma donacium* in Chile (Hockey *et al.* 1989) and on natural and artificial food sources in South Africa (Steele & Hockey 1995). Several other studies have shown age-related differences in the use of piracy. Burger (1981) showed that Herring Gull *Larus argentatus* juveniles were more likely to attempt piracy, while Verbeek (1977) reports that immatures of the same species stole much more of their food from other gulls. However, Burger & Gochfeld (1981) found that adult Herring and Ring-billed Gulls (*L. delawarensis*) engaged in kleptoparasitism more often than young individuals.

Previous studies on kleptoparasitism by gulls have found that adults are in general more successful when stealing prey (Burger & Gochfeld 1979, 1981; Hockey & Steele 1990; Gómez-Tejedor & De Lope 1995). However, the present study showed that all age-classes had a similar robbing success. Lack of differences in success may be partly explained by the foraging conditions observed at trawl vessels, which are different to those observed in other studies, where kleptoparasitism demands more complex feeding techniques. When feeding on experimental discarded fish, Kelp Gulls stole by snatching prey from the victim usually at a close range, and therefore did not need the variety of skills required when victims have to be chased (Wunderle 1991).

The proportions in which each feeding method (direct capture and kleptoparasitism) contributed to total intake varied among age-classes. While adult, and to a lesser degree subadult birds, fed mainly by direct capture of prey, most of the fish consumed by juveniles were obtained through intraspecific kleptoparasitism. Juveniles obtained 72% of their prey by kleptoparasitism while adults stole only 8%. Similar results were obtained for Kelp Gulls in coastal Chile (Hockey *et al.* 1989) where the percentage of food obtained through robbing was higher in juvenile than immature and adult birds. The use of kleptoparasitism by juvenile Kelp Gulls foraging on discards appears to compensate the low success attained by direct capture, since juveniles increased their foraging success through the use of this feeding method. This agrees with the hypothesis that kleptoparasitism may be used as an alternative strategy to compensate the lower efficiency of young birds (Verbeek 1977; Wunderle 1991). However, although the use of kleptoparasitism may have increased overall foraging success in juvenile gulls, this was anyway less than half than that of older age-classes.

Competition among birds feeding on discards around fishing vessels can be intense, mainly due to the high density of feeding individuals and the limited time available before items sink. This study shows that adult Kelp Gulls are more successful in capturing discarded fish than the rest of age-classes. Of the nine experimentally discarded fish, Argentine Hake and Brazilian Codling were the most preferred species (Bertellotti 1998). However, juvenile gulls consumed less discards of these two species than adult birds. Age related differences in foraging might be due to the lower skill of young birds and/or to adult dominance. As a result of adult dominance, younger birds are often displaced form best feeding sites, are prevented from taking prey, or are more likely to be victims of kleptoparasitism (Wunderle 1991). Adult Kelp Gulls are often observed displacing young gulls while foraging on discarded waste (Bertellotti, unpublished data) and juveniles are hosts more frequently than older birds (Bertellotti & Yorio, unpubl.data). Whatever the mechanisms involved, adult birds appear to have a competitive advantage over juvenile Kelp Gulls. This may have implications on the dynamics of Kelp Gull populations using fishery waste, as different age classes are being affected differently by the availability of this supplementary food source.

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SAMENVATTING

Bij veel vogels hebben onvolwassen individuen een geringer foerageersucces dan hun oudere soortgenoten. Dit is het resultaat van een combinatie van factoren, waaronder een gebrek aan ervaring bij het uitzoeken van de voedselgebieden en een geringere vaardigheid bij het vangen en verwerken van prooien. Jonge zeevogels foerageren daarom vaak langduriger dan oudere exemplaren; ook zoeken zij vaak andere prooien uit. Ook de vangtechnieken van onvolwassen zeevogels wijken dikwijls af van die van oudere soortgenoten. Voor de Argentijnse kust benut de Kelpmeeuw *Larus dominicanus* het rijke voedselaanbod bij commerciële treilers voor de kust; het is de talrijkste zeevogel die daar profiteert van overboord gezette ondermaatse vis. De korte perioden van rijk voedselaanbod achter dergelijke schepen na afloop van elke vistrek leidt elke keer weer tot een geweldig spektakel van elkaar beconcurrerende zeevogels. In dit artikel wordt beschreven welke verschillen er bestaan in het foerageersucces en gedrag tussen meeuwen van verschillende leeftijdsklassen: juveniele (eerste jaar), onvolwassen (1-2 jaar), subadulte (2-3 jaar) en volwassen (volgroeid en uitgekleurd)vogels. Van alle door Kelpmeeuwen opgepikte prooien werd uiteindelijk 87,6% succesvol geconsumeerd. Volwassen vogels waren aanzienlijk handiger in het oppikken van vis dan juveniele vogels en deze lieten eenmaal opgepikte vis ook veel vaker weer vallen dan de oudere dieren. Meeuwen van alle leeftijdscategorieën probeerden elkaar te beroven; het foerageersucces (% succesvolle pogingen) was echter voor alle groepen min of meer gelijk. Juveniele en onvolwassen Kelpmeeuwen bemachtigden echter aanmerkelijk meer vis als kleptoparasiet dan oudere vogels, doordat zij deze strategie veel vaker toepasten. Juveniele Kelpmeeuwen bemachtigden 72% van hun voedsel door andere meeuwen te beroven, terwijl onvolwassen, subadulte en adulte meeuwen respectievelijk 77%, 91% en 92% van hun voedsel zelf uit het water oppikten. Dat jonge Kelpmeeuwen veel vaker overgingen tot kleptoparasitair gedrag, wordt gezien als een poging om hun gebrekkige vaardigheden bij het 'normaal' foerageren te compenseren. Het foerageersucces (aantal geconsumeerde vissen (%) van het totaal aantal vissen dat op enigerlei wijze was verkregen achter het schip) was bij juveniele vogels laag (45.5%), in vergelijking met onvolwassen (70,8%), subadulte (83,3%) en adulte (94,8%) Kelpmeeuwen. De grotere neiging tot kleptoparasitisme bij juveniele vogels leidt dus niet tot een gelijkwaardige consumptie in vergelijking met oudere soortgenoten. (CJC)

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