J Ornithol (2008) 149:31–39
DOI 10.1007/s10336-007-0208-3

ORIGINAL ARTICLE

# Habitat utilisation, feeding tactics and age related feeding efficiency in the Caspian Gull *Larus cachinnans*

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Received: 27 October 2006 / Revised: 19 July 2007 / Accepted: 23 July 2007 / Published online: 21 August 2007


**Abstract** The feeding behaviour of the Caspian Gull *Larus cachinnans* was analysed in southern Poland in 2001. During the pre-breeding period, most birds foraged on a refuse dump and some foraged in a river valley. During incubation, similar numbers of birds foraged on fishponds, gravel pits and the refuse dump. During the chick-rearing period, fishponds were the most important foraging grounds. The foraging success of three main foraging tactics was analysed: digging on refuse, fishing and kleptoparasitism. We found that digging success was higher in juveniles than in immature or adult birds. However, older birds moved and ate more items per unit of time than juveniles, which indicates that older birds improved their energy gain simply by a higher speed of searching. The opposite was found for fishing success. As juvenile birds made fewer attempts than immature or adult birds, fishing success was higher in adults. Adults and immature birds interrupted more attacks than juveniles, which indicates that older birds were better able to assess the probability of fish catching than juveniles. Kleptoparasitism was observed almost exclusively on the refuse dump during the pre-breeding period. Young birds kleptoparasitised more frequently than adults, but they had a lower rate of success. However, the lower success in young birds was due to victim choice, rather than differences in flight skills. Young birds kleptoparasitised Black-headed Gulls *Larus ridibundus* and Jackdaws *Corvus monedula* more frequently than adults, but none of the attacks towards these species was successful. Generally, Caspian Gulls kleptoparasitised conspecifics more often than expected from species frequency. Only attacks towards conspecifics yielded any success.

**Keywords** Optimal foraging · Maturation · Feeding success · Kleptoparasitism

Communicated by P.-H. Becker.

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## Introduction

Among birds, populations of many gull species have grown and expanded into new areas (Snow and Perrins 1998). The most important factor responsible for these changes is the availability of anthropogenic food sources: trawler discards and refuse dumps (Spaans 1971; Gonzáles-Solís et al. 1997; Bertellotti and Yorio 2000). These food sources have improved breeding success, body condition and likely winter survival as well (Spaans 1971; Kihlman and Larsson 1974; Hüppop and Wurm 2000). Gulls are opportunistic feeders, utilising various sources of food, but it is also known that fish may greatly enhance breeding success (Pierotti 1982; Murphy et al. 1984; Sydeman et al. 1991; Annett and Pierotti 1999). Fish are easily digestible and contain many microelements, e.g. calcium, necessary for chick development and adult birds should switch to fish diet during the chick-rearing period (Murphy et al. 1984; Hillström et al. 1994; Annett and Pierotti 1999). Therefore, it can be inferred that fish should be favoured food item during the breeding season, especially the chick-rearing stage. It has also been suggested that fish availability may constitute the key factor responsible for successful colonisation of inland areas by several gull species (Hüppop and Hüppop 1999; Skórka et al. 2005). However, the relative importance of fish and refuse is little known. Optimal foraging theory predicts that, when preferred food becomes abundant, animals should then be more selective and ignore other food items regardless of their abundance (Stephens and Krebs 1986). Therefore, if the distances between food patches and breeding grounds are similar, the shift in foraging habitat utilisation should be visible—the birds should start to forage in the habitat guaranteeing the availability of the favoured food.

Young birds are usually less efficient foragers than adults (Greig et al. 1983; Burger 1987; Wunderle 1991). These differences in skills may have very important consequences: young birds have lower survival rates under extreme winter conditions, especially when they must compete with older birds (Orians 1969; Wunderle 1991). This pattern has been found true in a variety of gull species (Burger 1987). It is known that foraging tactics consist of many components, such as, e.g., food searching, assessment, pursuit and handling that may differ in costs (energy loss, predation risk, etc.; see Kramer 2001). For example, food searching by one tactic may involve flying (high energetic cost) and by another only walking (low energetic cost) (Sturkie 1976; Norberg 1990; Bryant 1997; Wuczynski 2005). Consequently a very important question arises. How do young birds improve their foraging success during maturation using different foraging tactics in order to become as efficient as adults? Optimal foraging theory predicts that the rate of food item capture should decrease with increasing difficulty of the task (Burger 1987). Therefore, if the costs of foraging by one tactic are low and benefits high then young birds should improve their foraging success simply via a higher rate of food searching. However, if the foraging costs of the second tactic are high and benefits relatively low, we would expect that improvement in foraging success over the years should be achieved by real improvement in skills, as a simple increase in the speed of food searching may not be profitable due to the high energy loss of failure.

In this paper, we present new data on the foraging behaviour of the Caspian Gull *Larus cachinnans* in southern Poland. First, we describe the patterns of utilisation of foraging habitat during consecutive season stages, and the foraging tactics involved. We expected that birds would adjust their preferred habitats according to fish availability and would forage in habitats that guarantee fish availability especially during the chick-rearing period. Second, age-related differences in the foraging success of different tactics were examined. We were interested in whether improvement of foraging success of birds during maturation is achieved in the same way using foraging tactics differing in energetic cost. We compare two tactics differing in foraging costs (digging in refuse and fishing) that were used by birds at the same time. Foraging success during digging in the refuse dump (low cost of foraging) was expected to improve over years simply by increasing the speed of digging. In contrast, foraging success during fishing (high cost of foraging) should be enhanced by improvement of skills, not through a higher rate of diving. Third, the kleptoparasitism was also investigated as a tactic often used by gulls. We expected young birds to have a lower success of kleptoparasitim than adults and that gulls should kleptoparasite mainly smaller and more abundant species.

## Methods

### The study species

The Caspian Gull is a large gull with a mean ± SD body mass of 1,080 ± 146 g ($n$ = 30 individuals; data from the studied population). The original breeding range of the species is the Black Sea and Mediterranean Sea basins. In the 1980s, the population size of the species increased and range expansion into the north followed, mainly along river valleys (Jonsson 1998). In southern Poland, the first breeding attempts were noted at the beginning of the 1990s, and since then the population has grown to over 250 pairs (Faber et al. 2001; Skórka et al. 2005).

### Study area

The studied area was located in Tarnów (130,000 inhabitants—SE Poland) and adjacent areas. The largest breeding colony of this species in Poland was located on sedimentation basins of the Nitrogen Works in Tarnów (Fig. 1). In 2001, 177 breeding pairs were noted there (Skórka et al. 2005). The most important foraging areas neighbouring the colony were a refuse dump in Tarnów located 5 km east, fishponds (two complexes, 3 km east and 4.5 km west from the colony), and gravel pits (~700 ha) in the valleys of the Dunajec and Biała rivers (Fig. 1). The refuse tip deposits 125 tonnes of refuse daily without visible year-round variation. The fishponds and gravel-pits are sunken or frozen between November and March. In April, after ice and snow has thawed, fish become available to birds and, moreover, ponds are stocked with young fish in April.

### Data sampling

The study was carried out during 2001. Initial observations were performed in 1999 and 2000, but here we present data only from 2001.

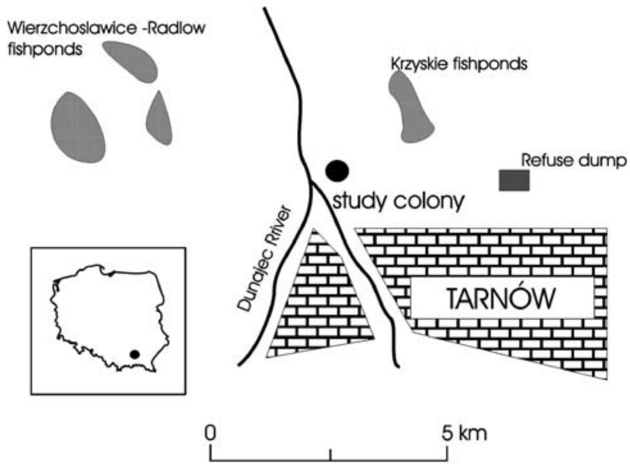


**Fig. 1** Map of the study area of the Caspian Gull *Larus cachinnans* in south-eastern Poland

Utilisation of foraging habitats by birds

To quantify the utilisation of feeding habitats by birds during the course of the season all foraging birds were counted in a radius of 5 km from the breeding colony. Birds were counted from the end of February to the beginning of June in three main habitat types: (1) a refuse dump, (2) fishponds and gravel-pits, and (3) river valleys. The season was divided into three parts: pre-incubation period (March), incubation period (April) and chick-rearing period (May–June). Six counts were performed during each of the periods at c. 2-day intervals. We counted all birds foraging at each habitat type. Previous studies had revealed that birds appear on the breeding ground in December, then their numbers increase and by the beginning of February most birds are present in the colony area (unpublished data).

Feeding behaviour

Three of the most commonly used methods of foraging were investigated: digging (on the refuse dump), fishing (in fishponds) and kleptoparasitism (on the refuse dump). All observations aimed to find individual differences between juvenile, immature and adult birds. Juveniles are defined as all birds in their first winter or first summer plumage, immature birds were all individuals in second and third winter or summer plumage (see Jonsson 1998 for details).

*Digging*

Digging behaviour was observed during 4 days on the refuse dump in April 2001. We observed birds from the top of the refuse dump, which enabled good visibility of all birds foraging at the bottom and those resting outside the refuse. We used 15× binoculars. Selected birds were observed for as long as possible. Birds foraging on the refuse dump generally searched for refuse and moved/pecked different items to find edible ones. The number of items eaten by the individual and the number of items moved in the period of time was noted. An observation ended when the bird flew away, was lost from sight, kleptoparasitised (or was a victim of a kleptoparasite) or when it found a large food item (which usually resulted in that bird leaving the foraging place). We managed to receive analysable sample sizes for 59 individuals comprising 390 min in total (mean time of observation of one individual ± SD was 374 ± 153 s, range 138–820 s).

*Fishing*

We observed fishing behaviour simultaneously with digging (on the same four surveys) during the incubation period (April). The observations were carried out on fishponds in Tarnów and Stawy w Lasach Radłowskich. These were the main foraging habitats during the breeding period. On fishponds and gravel-pits, most of the individuals flew actively above the water surface and dived for fish. During fishing, several types of flight are involved, including hovering, with high energy cost. Caspian Gulls fly over the water surface, hover, and frequently dive for fish. Frequent dives inevitably involve taking off after each attempt, including unsuccessful ones. This may introduce high additional costs besides flying and hovering.

Birds were also observed a few times swimming and searching for prey (probably insects) in shallow water with offshore vegetation, and three times we observed birds hunting Coot *Fulica atra* and Moorhen *Gallinula chloropus* chicks.

The number of successful and unsuccessful dives was noted, as well as the number of interrupted attacks (when the bird did not make contact with water or did so only with its bill). After catching a fish, some birds stayed on the water for handling and eating the prey and this period of time was excluded from the calculations. In other cases, observations were interrupted when the bird flew away or was lost from sight. We noted the behaviour of 45 individuals during 934 min of observations (mean time of observation of one individual ± SD was 1,118 ± 507 s, range 440–2,700 s).

*Kleptoparasitism*

This phenomenon was studied in January 2001 on the refuse dump and during the incubation period on fishponds. However, during the latter period we noted only two cases of this behaviour and so only the results from our January observations on the refuse dump are presented. We noted all cases of kleptoparasitism, measured their duration, the birds' ages and type of victim. Kleptoparasites usually flew quickly just behind the victim with prey, screaming loudly and trying to steal the prey directly from the host's bill or trying to force the victim to drop the prey. To analyse whether the Caspian Gull targeted the more abundant species, we assessed the abundance of Caspian Gull and other species foraging on the refuse dump. Caspian Gull were counted directly and other species were counted in randomly selected sectors of the refuse dump and then related to the total area where birds foraged. We pooled data for juvenile and immature Caspian Gulls, referred to in the following description as young birds. We observed 48 individuals during 2 days in January (307 min of observation in total). Some birds could be individually recognised by plumage characteristics, and about 10% of the birds in our population were tagged with colour rings. The ringed birds were also used to assess bias caused by possible pseudoreplication. Out of randomly chosen birds whose behaviour had been observed on the refuse dump, eight were ringed and none was selected again. Similarly, during observation on fishponds, out of four ringed birds none was selected twice. Therefore, our sampling protocol was correct and pseudoreplication is likely to be insignificant.

### Diet

The size of food items consumed by birds was assessed during observations of the three feeding tactics. We classified food items according to three size categories in relation to bill length (mean 6 cm; Faber et al. 2001): small: <10 cm; medium: 10–15 cm; large: >15 cm. In the case of fishing, we included 12 additional Caspian Gulls besides those for which behaviour was described in order to enlarge the sample size; additionally, the available data were pooled for individual birds. Pooling of the data did not confound the results as it was found that the repeatability of the size of food items carried by adults to nests was low (<0.2) and statistically insignificant (unpublished data) (see Leger and Didrichsons 1994 and Shealer et al. 1997 for discussion). We also observed (but were unable to measure directly) individual birds consuming food items of various sizes while foraging on refuse as well as fishing on ponds.

### Statistics

To control for differences in bird number per count among the season stages and test changes in pattern of habitat utilisation, we used two-way ANOVA (an interaction season stage × habitat type was of main interest). One-way ANOVA (with Tukey's test for unequal samples) was used to find differences among ages in foraging efficiency in the cases of digging and fishing. We used arcsin transformations for proportions when necessary. To test if the Caspian Gull preferred specific species during kleptoparasitic attacks, we compared the frequencies of attacks toward different species with the relative abundance of the species on the refuse tip. The *G*-test was used to compare the proportion of successful kleptoparasitic attacks in young and adult birds as well as to compare young birds to adults in frequency of attacks towards victims holding different food sizes. The same test was used to test if the size of food items eaten by birds differed in age classes in the analysed foraging tactics. The *t*-test was used to test for differences in duration of kleptoparsitic attacks between young and adult gulls.

## Results

### Foraging habitats

The mean number of foraging adults noted per count equalled 51.7 ± 12.6 (mean ± SD), 45.5 ± 6.0, 47.0 ± 12.5 for pre-breeding, incubation and chick-rearing periods, respectively, and did not differ significantly among periods (two-way ANOVA: $F_{2,45} = 0.6$, n.s.). However, in the analysis we found significant interaction among season stage and habitat (two-way ANOVA: $F_{2,45} = 39.925$, $P < 0.001$) which indicates that birds differentially utilised foraging habitat types during consecutive season stages. Therefore, we split up the analysis by season stages and performed one-way ANOVA tests. During the pre-breeding period most birds foraged on the refuse dump (ANOVA: $F_{2,15} = 35.904$, $P < 0.001$; Fig. 2). In the incubation period, birds started foraging on fishponds and gravel pits which resulted in similar mean number of birds noted in three types of habitat (ANOVA: $F_{2,15} = 1.897$, n.s.; Fig. 2). During the chick-rearing period, fishponds were the main foraging habitats and the refuse dump was used only by a small number of birds (ANOVA: $F_{2,15} = 35.147$, $P < 0.001$; Fig. 2). During all three periods, only the river valley was utilised by a consistent number of birds.

### Digging success

We found that older birds moved more items per 1 min than younger ones (ANOVA: $F_{2,56} = 24.801$, $P < 0.0001$; Fig. 3a). The number of items consumed per minute was higher in adults and immature birds than in juvenile birds (ANOVA: $F_{2,56} = 5.010$, $P = 0.01$; Fig. 3b; Tukey test: $P < 0.01$, immature birds and adults did not differ between

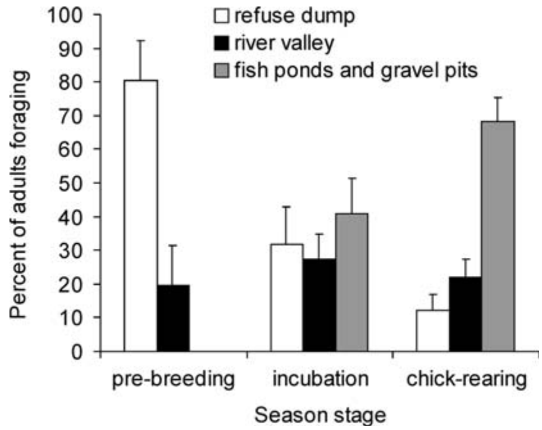


**Fig. 2** Mean (with 95% confidence interval) number of adult Caspian Gulls foraging on refuse, river valleys and fishponds in consecutive season stages

each other). Surprisingly, foraging success (number of items eaten divided by all attempts) was higher in juvenile birds than in immature and adult birds (ANOVA: $F_{2,56} = 18.219$, $P < 0.0001$; with Tukey's test: $P < 0.02$ and 0.001, respectively; Fig. 3c). Tukey's test also showed that digging success did not differ between immature and adult birds. Handling time did not differ among ages (ANOVA: $F_{2,56} = 0.901$, $P = 0.412$; Fig. 3d).

Modal category of size of food items eaten by birds was medium (10–15 cm) and there was no differences among ages ($G_4 = 2.318$, n.s., $n = 121$ food items).

### Fishing success

We found significant differences in the rate of attempts of fish catching (ANOVA: $F_{2,42} = 8.532$, $P < 0.001$; Fig. 4a). Tukey's tests showed that adult and immature birds made significantly more attempts per 5 min than juveniles ($P < 0.01$ and 0.05, respectively). Older birds interrupted more attacks than immature and juvenile birds (ANOVA: $F_{2,42} = 26.614$, $P < 0.0001$; with Tukey's test, $P < 0.05$ and 0.001, respectively; Fig. 4b). Simultaneously, adult birds had a higher rate of successful dives (interrupted attempts excluded) than immature and juvenile ones (ANOVA: $F_{2,42} = 13.654$, $P < 0.0001$; with Tukey's test, $P < 0.01$ and 0.001, respectively; Fig. 4c). Similarly, the percent of successful dives was significantly higher in adult birds than in immature and juvenile birds (ANOVA: $F_{2,42} = 28.498$, $P < 0.0001$; with Tukey's test, $P < 0.001$ and 0.001, respectively; Fig. 4d). Handling time was longer in young birds than in adults (ANOVA: $F_{2,42} = 3.482$, $P < 0.05$; with Tukey's test, $P < 0.05$; Fig. 4e).

Modal category of size of food items eaten by birds was medium (10–15 cm) and there was no differences among ages ($G_4 = 3.794$ n.s., $n = 136$ food items).

### Kleptoparasitism

A total of 48 cases of kleptoparasitism were noted. Caspian Gulls kleptoparasitised three species: conspecifics, Black-headed Gulls *Larus ridibundus* and Jackdaws *Corvus monedula* (Table 1). We found that Caspian Gulls kleptoparasitised conspecifics more frequently than should be expected from species frequency ($G_2 = 81.171$, $P < 0.0001$; Table 1). Mainly single birds attacked, with only two cases in which two attackers were involved. We observed 30 attacks (63%) by young birds and 18 (37%) by adults. The frequency of attacks performed by young birds was higher than expected from the number of young and adult gulls present at the refuse dump ($G_2 = 4.830$, $P < 0.03$). The duration of attacks was rather short (range 3–20 s) and differed between young birds and adults (mean ± SD for young birds: 10.4 ± 4.6 s; for adults: 6.9 ± 3.0 s; *t*-test, $t_{41} = 2.520$, $P < 0.02$). Among the 28 attacks performed by single young birds, 9 (32%) were successful, while among the 18 attacks performed by adults, 11 (61%) were successful. This difference was significant ($G_1 = 3.654$, $P = 0.05$). However, when attacks towards other species were excluded (all of which were unsuccessful), there was no significant difference in kleptoparasitic success between young and adult birds ($G_1 = 1.370$, n.s.). In this case, among the 17 attacks performed by young birds, 9 (53%) were successful, and among the 15 attacks by adults, 11 (73%) were successful. The young birds attacked other species more frequently (11 attacks of 30) than adults (3 attacks of 18). However, these differences appeared to be statistically insignificant ($G_1 = 2.230$, n.s.).

Young birds did not differ from adults in selection of victims as far as food size carried by the victim is concerned ($G_2 = 1.899$, n.s., $n = 34$ food items; analyses performed only for the Caspian Gull), but Caspian Gulls that were kleptoparasitised carried larger food items than the food items usually found during digging ($G_2 = 20.390$, $P < 0.001$, $n = 34$ items for kleptoparasitism and $n = 121$ food items found during digging). Additionally, there was no effect of the size of food items carried by the victim on the success of the kleptoparsite ($G_2 = 0.524$, n.s., $n = 34$ food items) most likely due to small sample size.

## Discussion

### Habitat utilisation

Clear shifts were noted in foraging habitat utilisation by adult Caspian Gulls as the breeding season progressed and new food sources gradually appeared. As bird numbers stabilised by the end of February, those changes in habitat use could not be linked with, e.g., increased competition

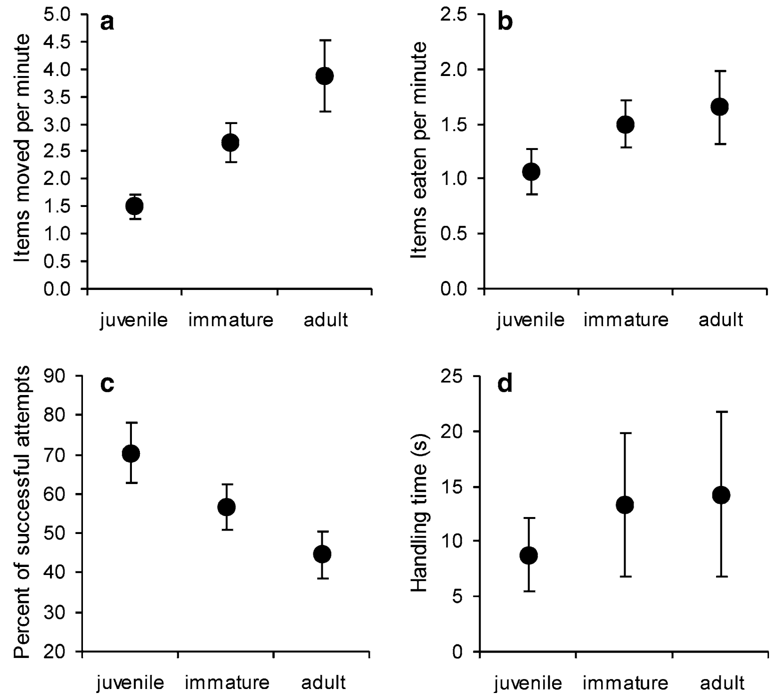


**Fig. 3** The efficiency of digging on refuse in the Caspian Gull: **a** number of items moved per minute, **b** number of items eaten per minute, **c** per cent of successful attempts, **d** handling time. Means and 95% confidence intervals are shown. Sample sizes for juvenile, immature and adult birds were 19, 15 and 25 individuals, respectively

for preferred sites due to more breeding birds arriving in the area (if the number of gulls increased the competition for food could also rise and some individuals would be forced to change their foraging habitat). The same changes in habitat utilisation were observed in other years based on our irregular counts. Very similar patterns were also found true for young birds, though their highly variable abundance (peaking in April), rendered exact analysis and inference impossible.

In our study, the distances between the colony, fish ponds and refuse tip were similar and this enabled us to assess the importance of the two food resources. The availability of fish during the breeding period is probably of primary importance for the Caspian Gull. During the breeding period, birds foraged mainly on fishponds and gravel pits, despite refuse still being available on the refuse dump. Refuse is typically highly energetic and makes for good provisions during winter. However, during the breeding period birds need food items rich in microelements, especially calcium, which may be in short supply for large gulls in inland habitats (Hüppop and Hüppop 1999; Tilgar et al. 1999). Fish are the appropriate food in this case, and it was shown that pairs which fed their chicks with fish had higher breeding success than pairs which fed their chicks with refuse or other food (Pierotti 1982, 1987; Murphy et al. 1984; Sydeman et al. 1991; Annett and Pierotti 1999). An alternative hypothesis explaining observed shifts in foraging habitat utilisation posits that, if fish availability is very high during the chick rearing stage, it may be more profitable for parents to forage in fish ponds rather than on the refuse tip because they can obtain food more rapidly. However, our data do not support this as the distances between the colony and refuse tip and fish ponds were similar (Fig. 1) and short compared to other gull species, in which gulls travelled several kilometres on average to find food. The rate of food item capturing was over eight times higher during digging (7.5 food items per 5 min) than during fishing (0.9 food items per 5 min). Furthermore, the size of food captured by adults during digging and fishing did not differ ($G_2 = 2.412$, n.s., $n = 106$ food items) and the duration of the foraging trip was shorter when birds carried refuse to the nest (82.5 ± 31.9 min) than when birds brought fish (126.4 ± 48.8 min, $t_{25} = 2.531$, $P < 0.05$; P. Skórka, unpublished data). Moreover, refuse and fish were comparable in energy terms. In our study, most birds at refuse tip ate pieces of chicken (100–150 kcal/100 g), pork (200–500 kcal/100 g), beef (100–200 kcal/100 g), pie (270–400 kcal/100 g) and bread (150–200 kcal/100 g) whereas fresh-water fish contain on average 100–150 kcal/100 g. This, however, only strengthens our conclusion that fish are a favourable food during the breeding period.

It has been shown that fish availability may facilitate inland colonisation by large gulls (Hüppop and Hüppop 1999) and our results provide important insights into the possible mechanisms of expansion and colonisation of southern Poland by the Caspian Gull. Rich food resources during winter (refuse dumps, fishery discards) probably improve winter survival (Spaans 1971; Kihlman and Larson 1974; Kilpi and Ost 1998; Pons and Migot 1995;

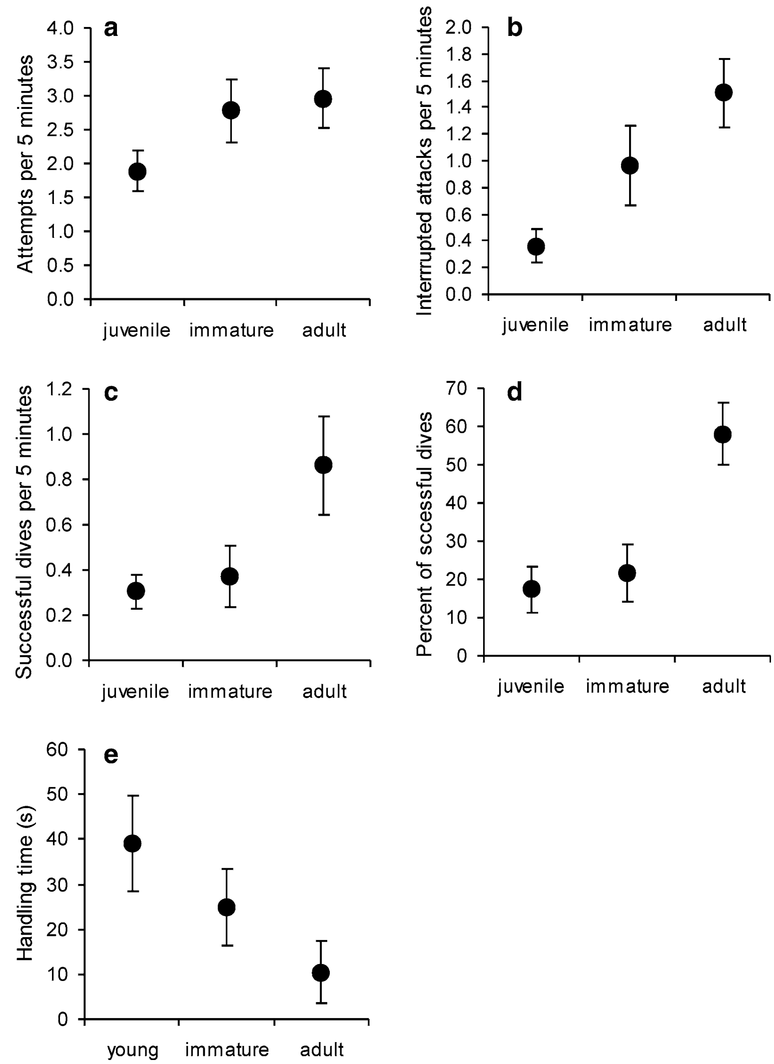


**Fig. 4** The efficiency of fishing in the Caspian Gull: **a** number of attempts per 5 min, **b** number of interrupted attacks, **c** number of successful dives per 5 min, **d** per cent of successful dives, **e** handling time. Means and 95% confidence intervals are shown. Sample sizes for juvenile, immature and adult birds were 14, 11 and 20 individuals, respectively

**Table 1** Average numbers of Caspian Gulls, Black-headed Gulls and Jackdaws present on the Tarnów refuse dump in January 2001

| Species | Abundance (individuals) | Number of kleptoparasitic attacks |
|---|---|---|
| Caspian Gull[a] | ~250 | 34 |
| Black-headed Gull | ~1,000 | 9 |
| Jackdaw | ~600 | 5 |

Observed frequencies of kleptoparasitism towards the species are also shown

[a] Adult: ~150, young: ~100

Hüppop and Wurm 2000), while the presence of rich fishponds during the breeding period guarantee high breeding success, which was noted in our population (Skórka et al. 2005). Fishponds are shallow and often densely stocked with fish that can be easily caught by the gulls.

## Age related differences in foraging skills

Our hypothesis about differences in foraging skills between young and adult birds relative to the cost of foraging tactic was partially confirmed. When birds foraged on the refuse dump the foraging success of adults (expressed as the proportion of successful attempts) was lower than in juvenile birds. However, adult birds moved more items and found more food in the end. Thus, the higher intake rate of food by adult birds in this case resulted solely from a higher speed of searching, but not from improvement of skills (taken as the percentage of successful attempts). Walking and digging are of low energy cost, therefore improvement of foraging skills is of lesser importance and young birds should rather increase their speed of searching. Similarly in the case of fishing, adult birds made more attempts during diving than juvenile birds and the rate of successful dives was higher in adult birds. Flight in general is costly, even more when animals frequently land and take off (Sturkie 1976; Norberg 1990; Chai and Dudley 1995; Bryant 1997). Therefore, natural selection should favour birds that improve their skills during fishing by the ability to assess the chances of success of attack. This was confirmed by our data, as adult birds interrupted more attacks and had a higher proportion of successful dives. However, our results also indicate that, as in digging, in fishing birds also improve their rate of food finding over the years. Thus, fishing is a tactic where birds improve general skills as they mature.

Our results are generally similar to the results of other studies (MacLean 1986; Burger 1987; Wunderle 1991; Bertellotti and Yorio 2000; Willson and Marston 2002). However, in the case of digging they differ significantly as most authors studying foraging success on refuse dumps found that young birds also improved their foraging success during maturation (Greig et al. 1983; Burger 1987). Greig et al. (1983) found that although adult birds had a higher rate of food pecking than young birds, their foraging success (ratio of number of items consumed to number of pecks) was also higher. In the case of diving, MacLean (1986) found that adult birds had a higher rate of diving than young birds. Adults made also fewer mistakes and therefore had higher foraging success, as in our study. The only difference was that in MacLean's (1986) study adult birds interrupted fewer attacks than younger birds.

## Kleptoparasitism

Only two cases of kleptoparasitism were noted during the incubation period, which may result from a lower density of birds at this time than during the pre-breeding period. Both the lower incidence of this phenomenon during the pre-breeding period and the fact that young birds kleptoparasitised more frequently than adults indicate that kleptoparasitism occurs mainly during food shortage (Brockman and Barnard 1979; Oro 1996).

Our results indicate that kleptoparasitic success depends primarily on appropriate victim selection. Surprisingly, Caspian Gulls kleptoparasitised other Caspian Gulls more frequently than smaller species. Other authors have suggested that larger species are better competitors and are able to effectively force smaller species to regurgitate food items (Brockman and Barnard 1979). However, smaller species can be quick and may be able to outmanoeuvre larger species (Willson and Marston 2002), as was probably the case in our study. The Caspian Gull is probably too large compared to the Black-headed Gull or Corvids and it is not as highly skilled during flight as these smaller species. None of the attacks towards Black-headed Gulls or Jackdaws was successful. The success of kleptoparasitism for young birds was lower than in adults, probably because young birds kleptoparasitised Black-headed Gulls and Jackdaws more frequently than adults. However, young birds had apparently inferior flight skills, as the duration of their attacks was longer than in adults (an alternative possibility is that adult birds decide more rapidly to suspend an attack as soon as the probability of success decreases). In contrast, Bellebaum (2005) found in the Herring Gull *Larus argentatus* (related to the Caspian Gull), that every kleptoparasitic/aggressive attack towards Black-headed Gulls was successful. However, all attacks observed by Bellebaum (2005) were on the ground, whereas in our study most of attacks resulted in aerial pursuits. This may explain the discrepancy between Bellebaum (2005) and our study.

We found that birds carrying larger food items were more prone to kleptoparasitic attack than birds carrying smaller items. This confirms the idea that food items must be large enough to compensate energy expenditure during attack (Brockman and Barnard 1979; Thompson 1986). Likewise, such large items are difficult to handle, making them easier to steal.

## Conclusions

Our findings highlight the importance of fish for inland breeding by large gulls. Availability of fish during the breeding period together with access to refuse, which seems to be particularly important during winter, are probably the key factors responsible for successful colonisation of inland reservoirs by the Caspian Gull. This is an example of successful species exploiting human-related activity and environment.

Feeding is crucial activity influencing directly fitness. Young birds are less efficient foragers than adults. Our results show the significance of cost of the foraging tactic on the way in which young birds improve their skills during maturation. If costs of the foraging tactic are low and benefits high, the young birds improve only speed of searching over years. That is because possible failures do not contain high (energetic) costs. However, if the foraging tactic involves high cost of failure the young birds improve all skills and not only speed of searching. Moreover, our analysis of kleptoparasitism demonstrates that foraging success may be related to appropriate choice of victim kind, probably independently from other foraging skills.

**Acknowledgements** We thank M. Woyciechowski, M. Cichon, J. Rutkowska, H. Szentgyorgi, M. Witek, R. Martyka and other people from Fajt Klap for discussion and helpful comments. We also thank two anonymous referees for their valuable comments. Peter Nelson made linguistic corrections. P.S. was a beneficiary of the Grant for Young Scientist of The Foundation for Polish Science.

## References


Annett CA, Pierotti R (1999) Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. Ecology 80:288–297

Bellebaum J (2005) Between the Herring Gull *Larus argentatus* and the bulldozer: black-headed Gull *Larus ridibundus* feeding sites on a refuse dump. Ornis Fenn 82:166–171

Bertellotti M, Yorio P (2000) Age-related feeding behaviour and foraging efficiency in Kelp Gulls *Larus dominicanus* attending coastal trawlers in Argentina. Ardea 88:207–214

Brockman HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487–514

Bryant DM (1997) Energy expenditure in wild birds. Proc Nutr Soc 56:1025–1039

Burger J (1987) Foraging efficiency in gulls: a congeneric comparison of age differences in efficiency and age of maturity. Stud Avian Biol 10:83–90

Chai P, Dudley R (1995) Limits to vertebrate locomotor energetic suggested by hummingbirds hovering in heliox. Nature 377:722–725

Faber M, Betleja J, Malczyk P, Gwiazda R (2001) Mixed colonies of large white-headed gulls in southern Poland. Br Birds 94:529–534

Gonzáles-Solís J, Oro D, Jover L, Ruiz X, Pedrocchi V (1997) Trophic niche width and overlap of two sympatric gulls in the southwestern Mediterranean. Oecologia 112:75–80

Greig SA, Coulson JC, Monaghan P (1983) Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). Anim Behav 31:1237–1243

Hillström L, Kipi M, Lindström K (1994) Diet of Herring Gull *Larus argentatus* during chick rearing in the Gulf of Finland. Ornis Fenn 71:95–101

Hüppop O, Hüppop K (1999) The food of breeding Herring Gulls *Larus argentatus* at the lower river Elbe: does fish availability limit inland colonisation? Atl Seabirds 1:27–42

Hüppop O, Wurm S (2000) Effects of winter fishery activities on resting numbers, food and body condition of large gulls *Larus argentatus* and *L. marinus* in the south-eastern North Sea. Mar Ecol Prog Ser 194:241–247

Jonsson L (1998) Yellow-legged Gulls and yellow-legged Herring Gulls in the Baltic. Alula 3:74–100

Kihlman J, Larsson L (1974) On the importance of refuse dumps as a food source for wintering Herring Gulls *Larus argentatus* Pont. Ornis Scand 5:63–70

Kilpi M, Ost M (1998) Reduced availability of refuse and breeding output in a herring gull (*Larus argentatus*) colony. Ann Zool Fenn 35:37–42

Kramer DL (2001) Foraging behavior. In: Fox CW, Roff DA, Fairbairn DJ (eds) Evolutionary ecology: concepts and case studies. Oxford University Press, New York, pp 232–246

Leger DW, Didrichsons IA (1994) An assessment of data pooling and some alternatives. Anim Behav 48:823–832

MacLean AAE (1986) Age-specific foraging ability and the evolution of deferred breeding in three species of gulls. Wilson Bull 98:267–279

Murphy EC, Day RH, Oakley KL, Hoover AA (1984) Dietary changes and poor reproductive performance in glaucous-winged gulls. Auk 101:532–541

Norberg UM (1990) Vertebrate flight. Springer, Berlin Heidelberg New York

Orians GH (1969) Age and hunting success in the brown pelican (*Pelecans occidentalis*). Anim Behav 17:316–319

Oro D (1996) Interspecific kleptoparasitism in Audouin's Gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. Ibis 138:218–221

Pierotti R (1982) Habitat selection and its effects on reproductive output in the herring gull in Newfoundland. Ecology 63:854–868

Pierotti R (1987) Behavioral consequences of habitat selection in the Herring Gull. Stud Avian Biol 10:119–128

Pons J-M, Migot P (1995) Life—history strategy of the Herring Gull: changes in survival and fecundity in a population subjected to various feeding conditions. J Anim Ecol 64:592–599

Shealer DA, Floyd T, Burger J (1997) Host choice and success of gulls and terns kleptoparasitizing brown pelicans. Anim Behav 53:655–665

Skórka P, Wójcik JD, Martyka R (2005) Colonization and population growth of Yellow-legged Gull *Larus cachinnans* in south-eastern Poland: causes and influence on native species. Ibis 147:471–482

Snow DW, Perrins CM (1998) The birds of the Western Palearctic, vol 1. Oxford University Press, New York

Spaans AL (1971) On the feeding ecology of the Herring Gull *Larus argentatus* Pont in the northern part of the Netherlands. Ardea 59:73–188

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ

Sturkie PD (1976) Avian physiology. Springer, New York Heidelberg Berlin

Sydeman WJ, Penniman JF, Penniman TM, Pyle P, Ainley DG (1991) Breeding performance in the western gull: effect of parental age, timing of breeding and year in relation to food availability. J Anim Ecol 60:135–149

Tilgar V, Mänd R, Levitis A (1999) Breeding in calcium-poor habitats: are there any extra costs? Acta Ornithol 34:215–218

Thompson DBA (1986) The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. Anim Behav 34:1189–1205

Willson MF, Marston BH (2002) Fishing success of gulls at southeast Alaska smelt run. J Field Ornithol 73:91–96

Wuczynski A (2005) Habitat use and hunting behaviour of Common Buzzards *Buteo buteo* wintering in south-western Poland. Acta Ornithol 40:147–154

Wunderle JM (1991) Age-specific foraging proficiency in birds. Curr Ornithol 8:273–324