

## Diet composition of the Caspian Gull (*Larus cachinnans*) in inland Poland: effects of breeding area, breeding stage and sympatric breeding with the Herring Gull (*Larus argentatus*)

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The food composition in breeding colonies of large gulls (mainly Caspian Gull *Larus cachinnans*) was investigated at three sites representing recently-colonized inland habitats in Poland: a gravel pit, an unregulated river and a reservoir. No differences were found in the diet of sympatrically-breeding Caspian and Herring Gulls (*L. argentatus*) that consisted mainly of fish: 57–82% of discarded food items and 71–94% of prey items detected in pellets were fish. The fish diet consisted of 6–14 species, depending on locality. At the gravel pit and at the river where fish ponds were located near the breeding colonies, Carp (*Cyprinus carpio*) was the dominant fish species in the diet, whereas at the reservoir, Roach (*Rutilus rutilus*) predominated. The size of fish caught by these gulls was relatively similar at all sites, median length being 14.8 cm at the river, 15.6 cm at the gravel pit and 17.0 cm at the reservoir. The proportion of species but not the size of fish differed significantly between egg-laying/incubation and chick-rearing periods at the gravel pit. These results highlight the importance of fish food for large gulls during the breeding season in recently-colonized inland habitats. We suggest that easily accessible foraging areas, such as fish ponds, crucially affect the food composition of these gulls. Such food opportunism could favor rapid colonization of inland habitats.



## 1. Introduction

The food composition of Herring, Caspian and Yellow-legged Gulls (*Larus argentatus*, *L. cachinnans* and *L. michahellis*, respectively) has been intensively studied in coastal regions (Cramp & Simmons 1983, Hillström *et al.* 1994, González-Solis *et al.* 1997a, González-Solis *et al.* 1997b, Duhem *et al.* 2003a, Duhem *et al.* 2003b, Kubetzki & Garthe 2003) but infrequently inland (Vermeer 1973, Ewins *et al.* 1994, Belant *et al.* 1998, Gwiazda 2004, Skórka *et al.* 2005). The proportion of fish in the diet of these gulls appears high in coastal areas and largely consists of dead fish provided by humans at harbours and fishing vessels (González-Solis *et al.* 1997a, Oro *et al.* 1997, González-Solis 2003). Fish availability may thus be a key factor in the successful colonisation of inland areas by these gulls (Hüppop & Hüppop 1999, Skórka *et al.* 2005). Fish are the most important food for Caspian Gulls breeding in south-eastern Poland (Skórka *et al.* 2005, Skórka & Wójcik 2008). Hüppop and Hüppop (1999) suggested that the inland breeding distribution of large gulls in Central Europe is limited by the availability of fish during the breeding season rather than by the availability of food at refuse sites.

The focal species of this paper, the Caspian Gull, has been breeding in central Poland since the early 1980s (Bukaciński *et al.* 1989) and in southern Poland since 1992 (Tomiałojć & Stawarczyk 2003). This species has increased rapidly in Poland, reaching a total of 480 breeding pairs throughout Poland in 2004 (Neubauer *et al.* 2006) and approximately 800 pairs in 2007 (G. Neubauer, M. Zagalska-Neubauer & J. Betleja, unpubl. data). The inland areas of Poland are the contact zone between the Caspian Gull and Yellow-legged Gull, another species expanding from south-eastern and southern Europe, and the Herring Gull, which is expanding from the Baltic Sea (Neubauer *et al.* 2006). A small population of Herring Gulls has been breeding in northern Poland since 1968, mostly on natural lakes, and Yellow-legged Gulls have rarely bred at a few isolated sites (Neubauer *et al.* 2006).

The wide range of habitats occupied by these gulls in Poland provide an opportunity to test whether the species composition, foraging habitat and breeding stage of gull colonies influence the

diet composition of large gulls inhabiting inland areas. The sizes and species of fish in the diet of large gulls in inland habitats have thus far been little studied (see Gwiazda 2004, Skórka *et al.* 2005). Dietary shifts during the breeding stages have been reported for many gull species (e.g., Spaans *et al.* 1994, Bukacińska *et al.* 1996, Bertellotti & Yorio 1999, Duhem *et al.* 2003b, Skórka *et al.* 2005). However, the size and species composition of fish eaten by large gulls during laying, incubation and chick-rearing periods are sufficiently understood (Spaans 1971, Spaans *et al.* 1994).

To fill this knowledge gap the following questions are addressed by studying three inland colonies of large gulls. (1) What is the relative importance of fish in the diet of Caspian Gulls? (2) Which fish species are caught by Caspian and Herring gulls? (3) How large are the fish caught by these gulls? (4) Do the species and/or size of fish consumed by Caspian Gulls differ between the incubation and chick-rearing stages? (5) Do the diets of Caspian and Herring Gulls differ? Sympatric, breeding large gull species might forage on different prey that maximizes the fitness-related benefit according to the optimal foraging theory. Moreover, according to the ecological niche theory, the diet ('food niche') of gull species – that are relatively similar in size and structure but partly occur at the same sites – might be different.

## 2. Material and methods

### 2.1. Study areas

The study was carried out at four breeding sites in Poland, representing three inland habitat types (Fig. 1). Four study colonies of large gulls (of which two were combined in the analysis; see below) were selected for study in the vicinity of Vistula, which is a large and unregulated lowland river. One colony was located on an island within a large gravel pit in Jankowice (Gravel pit; 52 ha in area; 50°02'N, 19°26'E), two others were on islands of the middle reaches of the Vistula River near Kozienice and Zastów Karczmiski (Vistula 1 and 2, pooled in the analysis; 51°37' N, 20°40' E and 51°17' N, 21°52' E, respectively), and the fourth was on a man-made dam at a reservoir in Włocławek (Reservoir; ca. 7,000 ha in area,



Fig. 1. Locations of the study sites along with the dominant species of large gulls.

52°39' N, 19°08' E; Table 1). The gravel pit, the reservoir and nearby garbage dumps were considered suboptimal for gull foraging, whereas the river and nearby fish ponds were considered optimal foraging sites (Table 1).

## 2.2. Species composition in the colonies

All nests in the studied colonies were marked by a numbered wooden stick. Adult gulls in colonies were visually identified to the species level using telescopes. Identification of each bird was based on a combination of diagnostic features in colouration of bare parts and in wing-tip patterns. Both parents bringing food to a given nest were identi-

fied at the species level whenever possible. The gravel pit and the two Vistula colonies were dominated by Caspian Gulls and with only occasional Herring Gulls, whereas the reservoir hosted a mixed Caspian and Herring Gull colony where the latter was dominant. Food samples from eight Herring Gull and ten Caspian Gull pairs were collected there.

## 2.3. Diet analysis

Food samples (here, freshly regurgitated pellets and fresh food remains) were collected at all colonies during the breeding period, i.e., from mid April to early June, as close to the studied nests as

Table 1. Breeding populations, and the potential foraging areas of Caspian and Herring Gulls at four inland sites in Poland. The two Vistula sites were pooled for analysis. The colony size is given in breeding pairs for 2003 and 2004 (years separated by a slash line); ? = not known; na = not applicable.

Location	Jankowice	Kozenice	Zastów	Wrocław
Habitat type	Gravel pit	Vistula river 1	Vistula river 2	Reservoir
Breeding pairs 2003 / 2004	104 / 119	5 / 3	? / ca. 240	157 / 149
Distance to (km)				
– Gravel pit	0	na	na	na
– Reservoir	na	na	na	0
– River	0.5	0	0	0.4
– Fish ponds	1.5	5.5	10.5	na
– Rubbish dump	11	10	7–9	12

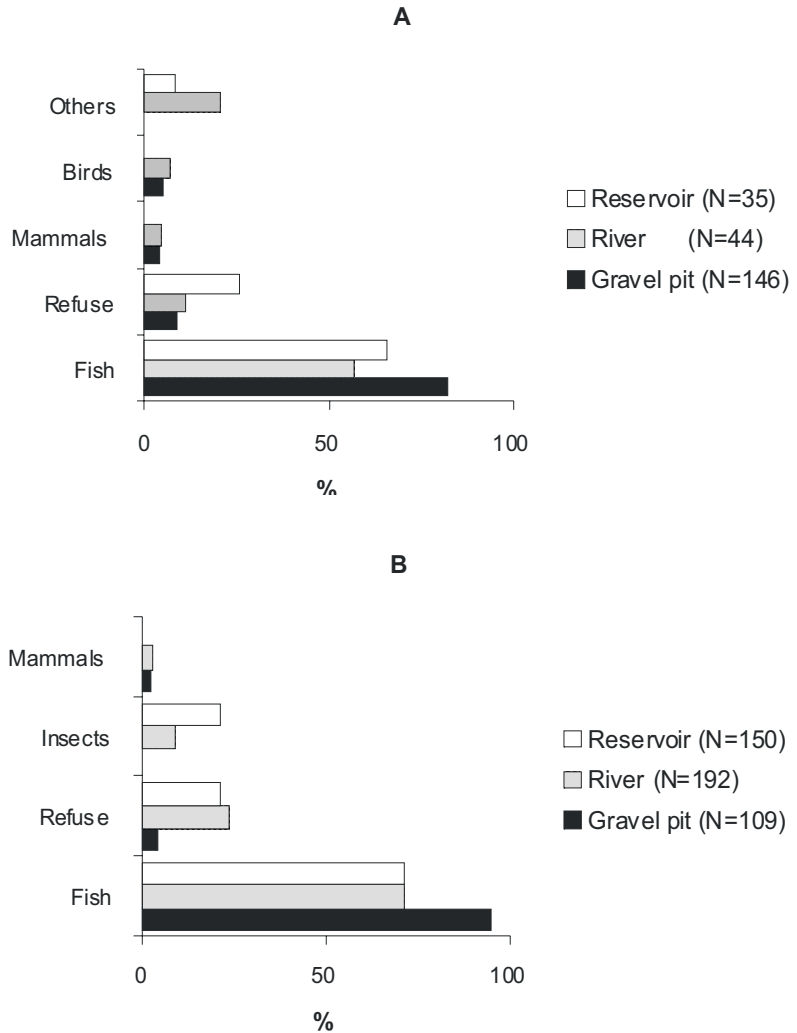


Fig. 2. Frequency of particular food types in (A) dropped food remains and (B) pellets of large gulls breeding at three inland habitat types.  $N$  = number of prey items examined.

possible so as to make sure fish remains and pellets could be linked to these particular nests. Only confirmed Caspian Gull nests along with respective food samples are considered below except for the reservoir colony with samples for both species.

The colonies were usually monitored at intervals of 1 to 3 days at the gravel pit and at the reservoir, and slightly less frequently at the two Vistula colonies. If more than one pellet was recorded for a given nest at a given sampling date, the average content of these pellets was calculated to standardize the diet-composition measures to pellet/pair for each collecting visit. Prey items found in the pellets, and fresh food remains, were identified to the lowest taxonomic level possible, using a binocular microscope. The number of pellets containing a

specific kind of food (mammals, birds, fish, insects, plants and refuse) was determined and the fraction of different food types in each colony was calculated as an average of all prey items collected. In the colonies of the gravel pit and the reservoir, the breeding status of each nest (egg laying, incubation and chick rearing), from which pellets and food remains were collected, was noted. Breeding status was not evaluated at the two Vistula colonies.

Whenever fish remains (e.g., otoliths, pharyngeal bones and chewing pads) were found in the studied pellets, the number of fish individuals was determined by assuming that any detected left- and right-hand-side bones of a given species always belonged to the same individual. The length of the

Table 2. Fish species composition (% of all recorded fish) in the diet of large gulls in the studied habitats in 2003–2004, based largely on pellet analysis. The two sites at the Vistula river are combined. Species recorded only in food remains other than pellets are marked with +.

Species	Scientific name	Gravel pit	Vistula 1–2	Reservoir
Common Carp	<i>Cyprinus carpio</i>	56.2	60.8	6.8
Grass Carp	<i>Ctenopharyngodon idella</i>	–	2.8	–
Gibel Carp	<i>Carassius auratus gibelio</i>	15.9	5.6	1.7
Roach	<i>Rutilus rutilus</i>	11.3	16.1	64.3
White Bream	<i>Abramis bjoerkna</i>	1.3	2.8	13.6
Common Bream	<i>A. brama</i>	0.7	–	11.9
White Bream × Roach	<i>A. bjoerkna</i> × <i>R. rutilus</i>	–	0.7	–
Chub	<i>Leuciscus cephalus</i>	8.6	6.3	–
Ide	<i>L. idus</i>	–	0.7	–
Vimba	<i>Vimba vimba</i>	–	0.7	–
Bleak	<i>Alburnus alburnus</i>	+	–	–
Nase	<i>Chondrostoma nasus</i>	4.6	–	–
Barbel	<i>Barbus barbus</i>	–	0.7	–
Spotted Barbel	<i>B. carpaticus</i>	+	–	–
Tench	<i>Tinca tinca</i>	+	–	–
Perch	<i>Perca fluviatilis</i>	0.7	–	–
Ruffe	<i>Gymnocephalus cernuus</i>	0.7	–	–
Pike	<i>Esox lucius</i>	+	1.4	1.7
Brown Bullhead	<i>Ictalurus nebulosus</i>	+	1.4	–
Total number of fish		151	143	59

pharyngeal bones of cyprinids (in mm) was measured and used to estimate fish body length (in cm) based on the equations given by Horoszewicz (1960). Fresh prey items, dropped by the gulls, were identified, and undigested fish were measured, in the field.

The frequency of different food items and fish species was compared between the three sites (gravel pit, river [two colonies pooled; see above] and reservoir) and among breeding stages (evaluated only for the gravel-pit and reservoir colonies) using a Fisher test, indicated by  $F^2$  statistic. Here, average measures for each of the compared sites were used as “samples” (test result  $df = 1$ ). The length of fish caught by the studied gulls was examined using the Kruskal-Wallis test (Sokal & Rohlf 1995). As with Fisher test, average measures for each of the compared sites were used as “samples”. The analyses were done using STATISTICA 8 software.

### 3. Results

The data consisted of 109 pellets and 146 discarded food items that were collected and exam-

ined from the gravel pit, 192 pellets and 44 food items from the two Vistula colonies pooled, and 150 pellets and 35 food items from the reservoir. Fish were the most frequently detected prey at all sites in both years, followed by refuse (Fig. 2). Carp (*Cyprinus carpio*) and Roach (*Rutilus rutilus*) were the main fish species detected (Table 2). Differences in fish-species composition in the diet of Caspian Gulls at the gravel pit between egg laying/incubation and chick rearing periods suggest a change of foraging sites during the breeding season. According to the data collected, the diet between Caspian and Herring Gulls were similar; hence, they may compete for food.

#### 3.1. Variation among sites in the Caspian Gull diet

The pellets and discarded food items consisted of small mammals, small birds, birds' eggs, fish, crustaceans, molluscs, insects, spiders, plants (grasses), seeds and refuse (mostly meat remains). However, different items were represented at different frequencies among the four sites. Fish con-

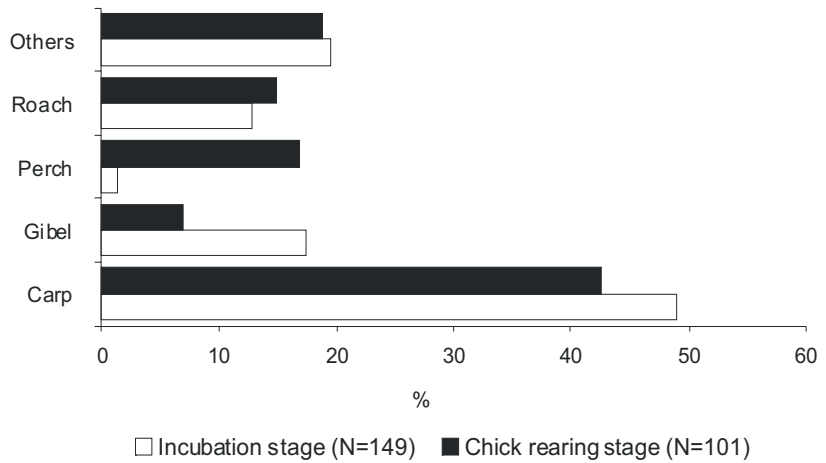


Fig. 3. Proportion of selected fish species as prey of Caspian Gulls in the gravel pit colony during incubation and chick-rearing periods.  $N$  = number of fish recorded.

stituted 82% of food items ( $N = 146$ ) found in the gravel pit, 57% ( $N = 44$ ) at the two Vistula sites, and 66% ( $N = 35$ ) at the reservoir (Fig. 2a). Fish were found in 94% of pellets at the gravel pit ( $N = 109$ ), 71% of pellets at the Vistula sites ( $N = 192$ ) and 71% at the reservoir ( $N = 150$ ; Fig. 2b). Various refuse items represented 9%–26% of the discarded food items and comprised between 5% and 23% of the food items recovered from the pellets. The proportion of pellets containing fish was higher at the gravel pit than at the two Vistula sites or at the reservoir ( $F^2 = 0.109$ ,  $p < 0.0001$  and  $F^2 = 0.103$ ,  $p < 0.0001$ , respectively). Moreover, the proportion of fish in the pellets was higher at the gravel pit than at the reservoir ( $F^2 = 0.137$ ,  $p < 0.0007$ ).

### 3.2. Fish species and size in the Caspian Gull diet

Pellets with fish remains contained 1–4 different species, altogether making up eighteen fish species recorded in the studied colonies. Carp was the most frequently encountered fish at the gravel pit and the two Vistula sites while roach dominated at the reservoir (Table 2). The samples collected at the gravel pit included 14 fish species, 11 fish species (and possibly one hybrid) were found at the two Vistula sites, and six were recorded at the reservoir (Table 2). The frequency of Carp was higher at the gravel pit and the Vistula sites than at the reservoir ( $F^2 = 0.203$ ,  $p < 0.0001$  and  $F^2 = 0.244$ ,  $p < 0.0001$ , respectively). Rheophilous fish

were recorded at the gravel pit and the Vistula sites; these included Chub (*Leuciscus cephalus*), Ide (*Leuciscus idus*), Nase (*Chondrostoma nasus*), Vimba (*Vimba vimba*), Barbel (*Barbus barbus*) and Spotted Barbel (*Barbus carpaticus*). The frequencies of Roach and White Bream (*Abramis bjoerkna*) were significantly higher at the reservoir than at the gravel pit ( $F^2 = 0.295$ ,  $p < 0.001$  and  $F^2 = 0.067$ ,  $p = 0.007$ , respectively) or at the Vistula sites ( $F^2 = 0.229$ ,  $p < 0.001$  and  $F^2 = 0.043$ ,  $p = 0.006$ , respectively).

Fish size ranged between 6 and 40 cm, and was marginally higher at the reservoir than at the other sites ( $H = 4.97$ ,  $df = 2$ ,  $p = 0.08$ ). The median length of fish was 15.6 cm (quartiles 13.2 and 18.1;  $N = 145$ ) at the gravel pit, 14.8 cm (quartiles 12.6 and 17.3;  $N = 44$ ) at the Vistula sites and 17.0 cm (quartiles 14.6 and 19.0;  $N = 34$ ) at the reservoir.

### 3.3. Diet during egg laying/incubation and chick-rearing in the Caspian Gull

The proportion of pellets containing fish remains was similar during chick rearing and egg laying/incubation stages at the gravel pit ( $F^2 = 0.004$ ,  $p = 0.43$ ) and at the reservoir ( $F^2 = 0.003$ ,  $p = 0.76$ ). However, fish-species specific differences were found at the gravel pit between chick-rearing and egg laying/incubation periods: the proportion of Perch (*Perca fluviatilis*) was higher and that of Gibel Carp (*Carassius auratus gibelio*) was lower during chick-rearing than during egg-laying/incubation period ( $F^2 = 0.082$ ,  $p < 0.001$  and  $F^2 =$

0.023,  $p < 0.02$ , respectively; Fig. 3). However, Roach and White Bream did not show significant differences between the two breeding stages ( $F^2 = 0.016, p = 0.523$  and  $F^2 = 0.005, p = 0.680$ , respectively). Moreover, at the gravel pit there were no differences in the size of fish caught during egg laying/incubation and chick rearing (respective median lengths 17.5 and 19.3 cm;  $H = 0.23, df = 2, p = 0.63$ ).

### 3.4. Diet of Caspian and Herring Gulls at the reservoir colony

The proportion of fish found in pellets did not differ between Caspian and Herring Gulls ( $F^2 = 0.002, p = 1.0$ ). Roach was the most numerous fish prey for both species. Moreover, the proportion of refuse in the pellets did not differ between the two gull species ( $F^2 = 0.002, p = 1.0$ ).

## 4. Discussion

### 4.1. The diet of large gulls is determined by local conditions

Our investigations suggest that the locality (habitat) of the breeding colony was the key factor determining the diet of large gulls breeding in inland sites in Poland. Fish were the most numerous prey items in the diet at all study sites, which is in accordance with other studies on Herring, Caspian and Yellow-legged Gulls, showing that fish constitute 70–90% of prey items in the diet (Hillström *et al.* 1994, Fox *et al.* 1990, Hüppop & Hüppop 1999, Vercrujssse *et al.* 2002, Skórka & Wójcik 2008). Hillström *et al.* (1994) concluded that Herring Gulls foraged mostly on fish, even if other types of food were available. However, in breeding Yellow-legged Gulls in the south-western Mediterranean region, birds mainly feed on refuse dumps, and fish are most frequently used when birds can utilize fishing vessels and harbours (González-Solis *et al.* 1997b). Our results showed that Caspian and Herring Gulls breeding inland in Poland are generally fish eaters. Furthermore, the similarity in samples collected at the reservoir, with a mixed-species colony, suggests that the food niches of Caspian and Herring Gulls overlap.

### 4.2. Fish species and size in the diet of large gulls at inland habitats

Pellet data can provide a quantitative index of diet composition (Barrett *et al.* 2007). The variation in food composition at different locations suggests that birds foraged in different habitats. The higher proportion of fish and larger number of Carp in the diet of Caspian Gulls breeding at the gravel pit probably reflects the close proximity of the fish ponds, where these fish constitute an easy prey. The high density of fish and low water level of these ponds make foraging energetically less costly and increase the foraging success. Carp was reported as being the most numerous fish species found at the nests of Caspian Gulls in the Tarnów colony in south-eastern Poland (Skórka *et al.* 2005).

The proportion of Carp at the Vistula sites, reported here, was high despite the 5–10 km distance to the nearest fish ponds. Carp do occur in very low densities (0.04%) in the ichthyofauna at the middle reaches of the Vistula River, where Bleak (*Alburnus alburnus*) and Roach are the dominant fish species (Wiśniewolski *et al.* 2001). The occurrence of Carp in the diet suggests that foraging at fish ponds, where Carp constitute an easy prey, may be beneficial over foraging at the river despite the need to travel longer distances. Carp may also be more attractive as a prey, owing to its higher biomass:length relationship: a Carp of 20 cm is >30% heavier than a Roach of the same length, based on formulae given by Dirksen *et al.* (1995). Skórka *et al.* (2005) showed that fishery management may be a key factor contributing to the high breeding success of Caspian Gulls in southern Poland.

The occurrence of Nase, Chub or Spotted Barbel in the diet, on the other hand, showed that the studied gulls also catch fish at the river. Moreover, at the reservoir, the diet of the studied gulls was dominated by Roach and Perch (26.1% and 28.3%, respectively), and these fish species indeed constitute the majority of the fish population at that site (Wiśniewolski *et al.* 2001). Roach occur at similar habitats as Perch do, but was more frequently found in the diet of the studied gulls. Large gulls forage on several fish species and optimize their foraging strategy to gain maximal energetic benefits. Optimization of energy load may be

achieved through selecting larger fish, because these generally contain more energy per item and per gram (Montevecchi & Piatt 1984).

Generally, data on the size distribution of fish caught by gulls are scarce. In the studied inland habitats of Poland, Caspian and Herring Gulls caught relatively large fish, which might indicate an optimal prey size or a high availability of this specific size class. In another study in the upper River Vistula valley, large gulls and Cormorants (*Phalacrocorax carbo*) preyed upon fish of similar size (mainly 14–26 cm in length; Gwiazda 2004). Skórka *et al.* (2005) showed that the mean length of fish recovered at Caspian Gull nests in south-eastern Poland was 14.5 cm for eaten and 16.1 cm for discarded fish. Perhaps such large items have been more often found dead or in bad condition, compared to smaller items, being readily available to foraging gulls.

#### 4.3. Diet preferences of Caspian Gulls at different breeding stages

Food composition of large gulls can vary during the breeding season, and diet changes can be explained by food availability but also by nestlings' requirements. Chick food normally differs from the food eaten by adults, and the diet of adults may reflect changing demands through the breeding period (Spaans 1971, Pierotti & Annett 1991). Moreover, younger chicks of Yellow-legged Gulls in Spain tend to be consistently provisioned with smaller prey (Ramos *et al.* 2009).

The proportion of fish in the diet of Caspian Gulls at Tarnów, southern Poland, was greater during chick rearing than incubation (Skórka *et al.* 2005). This colony was situated ca. 5 km from fish ponds, which potentially represent an important foraging area for Caspian Gulls during the chick-rearing period (Skórka & Wójcik 2008). Ludynia *et al.* (2005) showed that breeding Kelp Gulls (*Larus dominicanus*) at Coquimbo, Chile, had a higher proportion of fish in the diet than non-breeding birds that fed on a wider range of organisms and on refuse.

Also other studies suggest that adult birds switch to a fish-dominated diet during the chick-

rearing stage (Hillström *et al.* 1994, Annett & Pierotti 1999), probably because fish are readily digestible and contain nutrients necessary for chick development. Moreno *et al.* (2010) showed that chicks of Yellow-legged Gulls in Spain were fed with a high percentage of fish. Differences in the proportion of fish species caught by Caspian Gulls at the gravel pit during egg laying/incubation vs. chick rearing stages may reflect a changing availability of Perch and Gibel Carp at foraging sites of these gulls.

The present study indicated no major differences in the size of caught fish between egg laying/incubation and the chick rearing stages. Foraging large gulls may need to take all accessible fish of reasonable size because they require more food for chicks during this period. Fish remains found at breeding colonies do not properly reflect chick diet (Barrett *et al.* 2007). Pedrocchi *et al.* (1996) found differences in diet between chicks and adults of Audouin's Gull (*Larus audouinii*) on the Chafarinas Islands, Spain. In that study, the amount of fish fed to young and their size increased with chick age. Likewise, Gilliland *et al.* (2004) showed that the diet composition Great Black-backed Gull (*Larus marinus*) chicks changed with age.

Fish appeared important food for Caspian and Herring Gulls breeding at inland habitats in Poland. The diet, reflecting their foraging niche, was similar for the two species according to samples collected at the same site. Fish species consumed by Caspian Gulls differed between inland sites, but the size of fish caught was similar between the study sites, and it was large at all sites and breeding stages. The Central European population of the Caspian Gull will probably continue to expand, with consequent increasing fish consumption at fish farms and likely more frequent conflicts with human interests.

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## Aroharmalokin ravinto sisämaaympäristöissä Puolassa: ravinnonhankinta-alueen, pesimävaiheen ja sekapesinnän vaikutukset

Suurten lokiin (pääosin aroharmalokin *Larus cachinnans*) ravinnon koostumusta pesimäkolonioissa tutkittiin Puolassa kolmessa paikassa, jotka kaikki ovat lokiin hiljattain asuttamia: soranottoalue, säännöstelemätön joki sekä tekojärvi. Samassa koloniassa pesineiden aroharmaa- ja harmalokin (*Larus argentatus*) ravinto oli samantaista ja koostui pääasiassa kalasta: 57–82 % syömättömistä ja 71–94 % oksennuspalloista löydettyistä ravintopartikkeleista oli kalaa. Kalaravinto koostui 6–14 kalalajista pesimäpaikasta riippuen. Soranottoalueella ja joella, missä kummassakin oli kalankasvatusalaita kolonioiden lähellä, karppi oli ravinnossa yleisin kalalaji, kun taas tekojärvelä särki oli yleisin.

Lokiin saalistamat kalat olivat samaa kokoluokkaa kaikissa kolonioissa: keskipituus 14,8 cm joella, 15,6 cm soranottoalueella ja 17,0 cm tekojärvellä. Yhdessä koloniassa kalojen lajikooste (muttei kalojen koko) vaihteli merkittävästi muninta- ja haudontajakson sekä pesäpoikasvaiheiden välillä. Tulokset heijastavat kalaravinnon merkitystä suurille lokilajeille eri pesintävaiheissa hiljattain asutetuissa sisämaakolonioissa. Helpot ravinnonhankinta-alueet, kuten kalankasvatusalaita, voivat suuresti vaikuttaa näiden lokiin ravinnon koostumukseen. Tällainen ravinnonhankintaoppportunismi voi edesauttaa sisämaaympäristöjen asuttamista.

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