Food and foraging in five European *Larus* gulls in the breeding season: a comparative review

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This review compares the feeding habits of five species of *Larus* gulls in NW Europe, where these species are mostly sympatric. *L. marinus* mainly eats fish, and feeds more on birds than the other species. *L. argentatus* feeds on refuse, fish offal, marine invertebrates and sometimes also takes earthworms and grain on fields. *L. fuscus* mostly eats fish, which may be caught or taken at fishing boats; it also forages on fields, and takes refuse (though to a lesser extent than *argentatus). L. canus* feeds mainly on terrestrial food (earthworms, insects, grain, refuse), sometimes also on fish and marine invertebrates. *L. ridibundus* largely feeds on insects; it also takes earthworms and refuse.

Size differences among the five *Larus* gulls are probably partly responsible for the differences in diet, the largest and most powerful species taking relatively large prey, the smallest taking small prey (mostly invertebrates).

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Introduction

Knowledge of the food and foraging ecology of a species is essential for an understanding of other aspects of its biology. For example, both habitat selection and social organization are related to the type and exploitation of food (e.g. Crook 1965, Lack 1968). A comparison of diets and foraging is also important in studies of interspecific competition.

In this review, I compare the feeding habits of five European *Larus* gulls during the breeding season. The species are the Great Black-backed Gull *L. marinus,* Herring Gull *L. argentatus,* Lesser Black-backed Gull *L. fuscus,* Common Gull *L. canus,* and Black-headed Gull *L. ridibundus.* In an analysis of differences in the social organization (colonial tendency) of these species along the coast of SW Sweden (Götmark 1982), I suggested that the degree of coloniality was related to foraging ecology. Since relevant data for all five species are not available from SW Sweden or any other local part of Europe, I have reviewed their feeding habits in a larger geographical area: NW Europe. The results are presented here, together with some new data on the food choice of *argentatus* and *fuscus,* collected in SW Sweden in 1983.

Material and methods

The review is restricted to the breeding season (unless otherwise stated) and the literature published in the past 40—50 years. The sites mentioned in the text and the species investigated at these sites are indicated in Fig. 1. Short notes on food choice and feeding behaviour were usually ignored, and I favoured studies that compare the diet of several gull species in one area. Rare food items (occurrence in less than about 5 % of pellets or stomachs) are usually not mentioned. Detailed descriptions of foraging methods and lists of food items are given in Cramp & Simmons (1983) and Glutz & Bauer (1982), and will not be repeated here. My aim is rather to present a fairly detailed review of comprehensive and quantitative studies of the feeding habits of the gulls.

It is often difficult to obtain an accurate picture of the diet of a bird species. Several authors have concluded that two or more methods should be used, since different methods may give different results. In studies where two methods were used, the weights of different food types gave a different picture of the diet from that yielded by frequencies based on the total number of food items (Creutz 1963, Pearson 1968). In most studies, the frequencies refer to the number of samples (e.g. stomachs) in which a particular food type was present, and then the result may differ only slightly from that obtained by using weights or volumes (Spaans 1971, Mudge & Ferns 1982, but see Fordham 1970 and Hanssen 1982a, b). Most workers on gulls have examined the frequencies, but not the volumes or weights, of the different kinds of food in the samples; comparisons between species thus have to be based on frequencies (unless otherwise stated, numerical values in the text refer to frequencies).

One difficulty is that soft, easily digested items may be overlooked in analyses of faeces, pellets or stomachs. For example, oligochaetes and polychaetes may not be detected, unless the presence of chaetae are checked (e.g. Andersson 1970). Collaring of chicks (e.g. Creutz 1963, Bianki 1977, Hanssen 1982a, b), or examination of the food in the gullet or the proventriculus (such food can be obtained by forcing chicks to regurgitate; see Hunt 1972), seem to be useful methods of analysing the diet. Both Spaans (1971:134) and Hanssen (1982a) concluded that regurgitations did not give a biased pic-

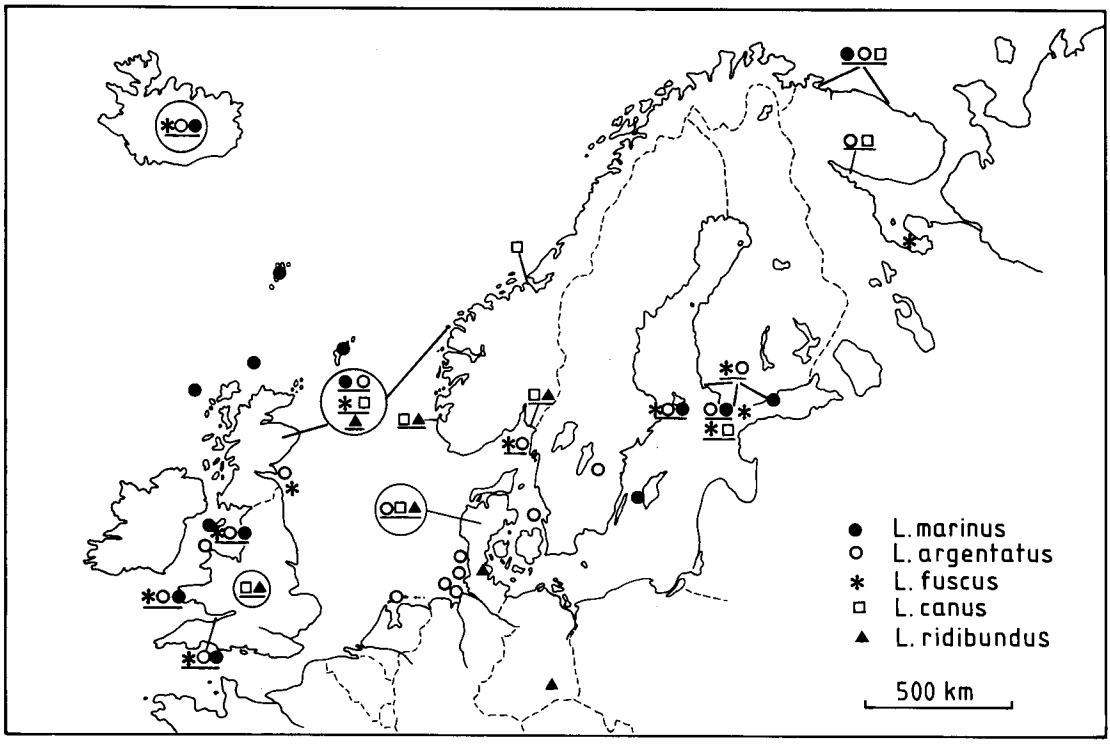

Fig. 1. Study areas in northwestern Europe included in the review and mentioned in the text. In each area, the species investigated is indicated; in cases where comparative data for two or more species have been published from a single area, the symbols are underlined. Encircled symbols indicate studies covering a larger geographical area (usually a country, or part of a country).

ture of the food eaten; however, chicks of *marinus* seem to regurgitate fish more easily than ducklings (Å. Andersson, pers. comm.). In some studies, the diet of chicks has been shown to differ from that of adults (see below). Possibly, such a difference exists only in the case of small chicks (cf. Mudge & Ferns 1982:499).

Results

Great Black-backed Gull L. marinus

On Skomer and Skokholm (England), 228 stomachs collected in March-July contained birds and eggs (19 %; mainly shearwaters), fish (14 %; probably obtained through human activities), beetles (11 %), refuse (7 %), or were empty (28 %). Food remains (n=420) collected at nests of *marinus* consisted of birds (53 %; mainly shearwaters), fish (21 %), rabbits (15 %) and refuse (7 %; mainly meat bones) (Harris 1965; calculated from his Tables 4 and 5). On the Calf of Man, Zelenka (1960) noted that rats (besides fish) were an important prey. Verbeek (1979) analysed 133 gullet samples from chicks at Walney Island; of these, 56 % contained fish, 2 % gull chicks, 1 % refuse, while 41 % were empty. In 103 pellets, he found fish (92 %), refuse (21 %), crabs (18 %), gull chicks (12 %) and shellfish (7 %). Much of the food was obtained by stealing from other gulls. Mudge & Ferns (1982) examined 11 chick regurgitations from the Bristol Channel and found fish (in 4 regurgitations), Herring Gull chicks (3), refuse (at least 1) and marine invertebrates (2).

On Dun, St. Kilda (Scotland), 40 pairs fed almost entirely on Puffins *Fratercula arctica* from April-July in several years (Harris 1980). The Puffins were caught in flight in front of the colony. In a preliminary note, Beaman (1978) stated that although *marinus* largely feeds on birds at some sites, at several larger colonies in Scotland it feeds mainly on shoals of Sandeels *Ammodytes* spp., and to a lesser extent on fish offal obtained at fishing boats (see also Evans 1975). The gulls caught Sandeels by brief plunge-dives from a sitting position on the water. Solitary pairs took more seabirds than did colonial pairs.

Fish was the major prey in pellets collected at a colony in SE Sweden in two years (73 % and 82 %, n=158 and 246) (Hjernquist 1980). Eggs (11 %, 4 %) and birds (6 %, 7 %) were less important as food. In Finland, fish and birds (mainly small ducklings) seem to be important

food (Nordberg 1950, Lemmetyinen 1963, Bergman et al. 1940, Bergman 1965). Lemmetyinen found remains of young birds (in 56 % of 34 pellets), fish (41 %), and *Mytilus* (9 %). Nordberg examined 109 pellets from two nests and noted only fish (52 %) and birds (49 %; mainly ducklings), while Bergman et al. found birds in 38 % of 102 pellets. Ingolfsson (1976) analysed the diet of Icelandic *marinus* over two whole years; fish predominated, while mussels, birds and plants were less important food. The fish was mainly Sandeels and Capelins *Mallotus villosus,* which were taken in spring and summer. In the area where most data were collected, Sandeels and Capelins occurred in 62 % of 208 stomachs; also taken were fish offal (10 %), mussels (18 %), plants (33 %) and birds (14 %; this figure was considered too low, because there were no samples from June, when Eider *Somateria mollissima* ducklings are common).

Hunt & Hunt (1973) studied habitat partitioning by foraging gulls in Scotland and W Norway in "July and August" 1970 (at least in August, all species must have had fledged young). *L. marinus* (n=137 foragers) occurred mainly at dumps and waste effluents, to a lesser extent also on "mud" and "water" (birds plunge-diving or feeding on the water surface). Many birds were eating carrion, "ranging from fish to seal carcasses".

Belopol'skii (1961) analysed 357 stomachs from islands off the Murman coast, Barents Sea. Fish was noted in 73 % of all stomachs, while plants (43 %), molluscs (29 %), crustaceans (13 %) and birds (12 %) were less frequent. The proportion of fish in the diet increased during the breeding season.

In SW Sweden, the Garfish *Belone belone* is one common food source, at least in the inner archipelago (Pehrsson 1967, pers. obs.). Predation on Eider ducklings occurs, especially when the broods are disturbed by people (Åhlund, Götmark & Nordmalm, in prep.).

Herring Gull L. argentatus

More work has been done on the diet of *argentatus* than of the other species. Fairly extensive reviews are provided by Harris (1965), Spaans (1971) and Cramp & Simmons (1983), and I will treat only the more comprehensive works and some studies not summarized before. Comparative studies of *argentatus* and *fuscus* are reviewed in the section on *fuscus*.

On Skomer and Skokholm, 60 stomachs collected in March-July contained fish (17 %; most probably from a fish dock), earthworms (17 %), insects (12 %; mainly beetles), grass (10 %), refuse (10 %), or were empty (27 %). Two-thirds of 3208 pellets and food remains from Skomer consisted of human waste (meat bones, waste fish), while nearly 25 % consisted of marine invertebrates. At another site, in Anglesey, 53 stomachs collected in March-May contained insects (19 %; mainly beetles), earthworms (15 %), grass (19 %), waste grain (11 %), marine invertebrates (15 %) and refuse (13 %) (Harris 1965; calculated from his Tables 1, 2 and 3). A few years later in Anglesey, the feeding habits were similar (Threlfall 1968).

In 1975—77, Sibley & McCleery (1983) studied the foraging ecology of *argentatus* at Walney Island. Counts of birds at different feeding sites revealed that the major food sources were "earthworms and terrestrial invertebrates obtained mainly on pasture fields within an hour of sunrise, domestic waste obtained mainly on refuse tips from 8.30 to 16.30 h on weekdays and 8.30 to 11.30 h on Saturday mornings, *Mytilus edulis* and *Carcinus maenas* obtained mainly when the height of water was below 1.9 m below O.D., and *Asterias rubens* obtained mainly when the height of water was below 3.1 m below O.D." (p. 51). On the Isle of May (Scotland), Parsons (1971) found that a few adults in a large colony were specialized cannibals, eating chicks of other pairs.

On the islands Terschelling and Vlieland in the Netherlands (Spaans 1971), chick regurgitations collected during several years contained mainly fish [72 % by frequency (from his Table 19), 68 % by weight (Table 20)], garbage (25 %, 21 %) and marine invertebrates (19 %, 10 %). Of the fish, Clupeidae, Gadidae and flat-fish were most common; most or all of the two last-named were taken as offal from the commercial fishery. The human contribution (fish offal, garbage) to the total chick food in four different years amounted to 34—61 % (frequency) or 48—58 % (weight). The food eaten by adults (examined from pellets and stomachs) differed from that of chicks, and consisted mainly of marine invertebrates (crabs, mussels, starfish) from the littoral or sublittoral zones.

In the German Bight, Vauk & Löhmer (1969) collected 153 pellets in a colony in early August; 70 % of these consisted entirely (and 17 % partially) of *Carcinus maenas*. Other food was mussels (10 %), fish (8 %) and waste (7 %). On Sylt, Hartwig & Söhl (1975, 1979) examined 922 pellets from June 1969 to May 1970. In the breeding season (April-July), marine invertebrates (mainly *Mytilus, Cardium* and *Carcinus)* from the Wadden Sea predominated (78—96 %), while refuse (39—61 %) and fish (22—49 %) were less common food (Hartwig & Söhl 1979; Figure 2). On an island in the estuary of Weser-Elbe, 262 pellets from resting birds contained mainly *Mytilus* (53 %), *Carcinus* (48 %), *Cardium* (40 %) and

Macoma (11 %) in June and July (Weitfeld 1977; Table 3). Thus, it appears that marine invertebrates are especially important as food for *argentatus* in the German Bight (see also Meijering 1954, Goethe 1956, Ehlert 1957, 1961, Focke 1959, Glutz & Bauer 1982). On Heligoland, on the other hand, food obtained through man's activities (especially fish) is taken more often (Löhmer & Vauk 1969, 1970). In the breeding season (~ 75 stomachs), fish made up 48 % of 61 food items; polychaetes, crustaceans and insects 33 %, and waste 12 % (Löhmer & Vauk 1970). Eighty-five per cent of the food was considered to have been obtained with the aid of man.

Spärck (1944, 1951; figures from 1944) summarized data from 905 stomachs collected in all months of the year in Denmark. The most common food was human waste (in 32 % of stomachs), mussels (26 %), fish (21 %; mainly *Gadus morhua),* crabs (11 %) and starfish (11 %).

Birds in a colony in a Swedish lake fed primarily on freshwater fish (in 74 % of 537 pellets from two years), the most important species being Perch *Perca fluviatilis,* Roach *Rutilus rutilus* and Pike *Esox lucius* (Andersson 1970). It was not clear how the gulls obtained the fish. Other food sources were waste grain (28 %), refuse (21 %), insects (37 %) and earthworms (10 %). The occurrence of fish and refuse increased during the chick period, while the occurrence of grain decreased.

In a large colony in S Sweden, Andersson (1968) collected 567 stomachs from chicks and 1990 pellets during three years. The pellets (collected in April-July) contained refuse (51 %), insects (34 %), earthworms (33 %), grain (26 %), plants (26 %), fish (15 %) and mussels (9 %). In the chick stomachs, there were mainly refuse (50 % of the food by volume), fish (21 %) and earthworms (19 %). The chicks were fed mainly with earthworms in the morning (also in the evening) and fish at mid-day, while the importance of refuse increased steadily through the day. Grain and mussels were taken mainly in April and May. Refuse became increasingly important as the chicks grew larger. The foraging range was estimated to be usually about 30 km, and maximally 60 km. In an earlier study of the same colony (Otterlind 1948), the birds did not feed on grain or earthworms and ate less refuse; instead, they took more fish and mussels.

Hunt & Hunt (1973) observed foraging *argentatus* (n=2373), mainly at dumps (24 %) and at effluents (24 %), but also on mud flats (13 %), mussel banks (13 %), rocks (12 %) and water (13 %). Few birds visited fields. Ingolfsson (1968) compared the feeding ecology of five *Larus* gulls in Iceland and concluded that *argentatus* "takes most of its food from the intertidal zone of the seashore". Belopol'skii (1961) analysed 515 stomachs from the Murman coast, and found much fish (52 %), plants (47 %) and molluscs (42 %), besides crustaceans (12 %), birds (10 %) and insects (8 %). As in *marinus,* the occurrence of fish increased during the breeding season.

In Kandalaksha Bay, White Sea, Bianki (1977) analysed 1706 droppings, and some stomachs of adults. Summed over three years, the major food sources were molluscs (31 %), berries (27 %), fish (14 %) and rodents (7 %). The diet of adults differed from that of chicks; as in the Netherlands, nestlings were fed mainly with fish (43 %, mostly Three-spined Sticklebacks *Gasterosteus aculeatus;* 88 regurgitation and collaring samples), besides fish eggs (17 %), birds (10 %), insects (8 %) and echinoderms (6 %).

Lesser Black-backed Gull L. fuscus

Harris (1965) examined 55 stomachs from Skomer and Skokholm and found fish (29 %; seldom taken as waste), beetles (29 %), plants (20 %), earthworms (11 %) and waste grain (7 %). In a later (1969—70) comparison of the feeding habits of *fuscus* and *argentatus* on Skokholm, Davis (1974) found that chicks and adults of *argentatus* ate fish waste (at least 6 % of 318 regurgitations), other waste and garbage (38 %), fish "thought to have been caught by the gulls" (25 %) and earthworms and "soil organisms" (25 %). Chicks of *fuscus* were fed mostly with fish (73—82 %) and earthworms; waste made up only 3—4 % of the food. Many birds caught fish in the open sea (Davis 1973 cited from Cramp & Simmons 1983).

On Walney Island, males of *fuscus* fed their females with fish (52 %; n=83 observations), "shore food" (25 %) and garbage (23 %). Males of *argentatus* fed their females less with fish (30 %, n=30), and more with shore food (37 %) and garbage (33 %) (Brown 1967). In the same colony, Verbeek (1977a) compared the feeding sites used by the two species. He found that *fuscus* fed frequently at sea (observed at fishing boats), in cities and in fields; *argentatus* fed more on dumps, in fish markets, harbours and intertidal areas. On the Farne Islands, Pearson (1968) analysed 68 regurgitations of adults and chicks of *fuscus.* Fish (Ammodytidae, Clupeidae and Gadidae) accounted for 74 % of all food items (77 % by weight), earthworms 19 % (3 %) and offal 5 % (19 %). The fish was probably taken at sea, either alive or at fishing boats. The foraging range of the gulls was estimated at about 45 km.

Mudge & Ferns (1982) analysed the diet of *argentatus* and *fuscus* breeding in or near heavily industrialized areas in the Bristol Channel (332

chick regurgitations collected in 3 years). Chicks of *argentatus* were mainly fed with food from refuse tips (69 % by volume); *fuscus* chicks ate slightly less refuse (47 %) and more food from littoral and inshore areas (20 %; 3—7 % in *argentatus)*. Food from fields was taken to the same extent by the two species. Chicks of *fuscus* ate slightly more fish (12 %; 7—9 % in *argentatus),* "rather little of which appeared to have originated from refuse tips" (p. 502).

In the archipelago of SW Finland, fish (87 %), *Mytilus edulis* (18 %) and refuse (7 %) were the most common items in 299 pellets (Lemmetyinen 1963). *L. argentatus* took more refuse (33 %) and less fish (60 %), but the sample was small (15 pellets). Goethe (1975) also found that fish, particularly Roach and Perch, was the major food in pellets in this area. Since *fuscus* has been observed diving in the same manner as terns, Goethe argued that the fish was obtained by plunge-diving. In three areas in S Finland, the proportion of birds (ducklings) in pellets was low in both *fuscus* (1 %; n=1262) and *argentatus* (3 %; n=292) (Bergman et al. 1940). Near Åland, SW Finland, 479 pellets from 12 pairs of *fuscus* contained much Roach and Perch, besides other fish, refuse, ducklings (13 %) and some mammals (Nordberg 1950). In the same area, 527 pellets from 8 pairs of *argentatus* consisted mainly of fish, *Mytilus,* refuse and birds (30 %; in this study, the high frequencies of birds were partly due to inclusion of specialized foragers).

Hunt & Hunt (1973) observed very few *fuscus,* but noted that this species predominated among gulls observed behind fishing boats in Norway. On Iceland, Gudmundsson (1955) observed that *fuscus* foraged more on fields than did the other species (it then bred mainly in inland areas). Ingolfsson (1968) concluded that *fuscus* "takes beetles to a larger extent than the other (large gull) species". In Onega Bay, White Sea, the birds had eaten berries (in 83 % of 60 droppings), insects (43 %), fish (35 %) and molluscs (23 %) in July 1962 (Bianki 1977).

To examine differences in the feeding habits of *argentatus* and *fuscus* on the coast of SW Sweden, I collected a total of 145 droppings at Ärholmen, Väderöarna (58°35'N, 11°05'E) on 23 June 1983. About 125 pairs of *fuscus* and 100 pairs of *argentatus* nested on this island, which lies 11 km from the mainland. For each species, I arbitrarily chose three sites (each of about 2 m^2) within the colony and carefully collected all faeces there. The droppings were examined under a stereo microscope with up to 50x magnification, and specialists on various groups were consulted to identify the food remains.

Statistical tests with droppings as sample units could not be used: since the faeces were probably produced by relatively few individuals, such tests would inflate the sample size (Siegel 1956). However, within the species there were no apparent differences between the three sample sites (Table 1) so the estimates of differences between the two species seem reliable.

Fish remains were much more frequent in droppings from *fuscus* than in those from *argentatus,* while the reverse applied to remains of *Mytilus*

Table 1. Frequency of occurrence of different food in faeces from Lesser Black-backed Gulls and Herring Gulls nesting on Ärholmen, SW Sweden.

Food	Species and site in colony							
	Lesser Black-backed Gull				Herring Gull			
	A	B	C	A+B+C	A	B [1]	C [2]	A+B+C
Fish	22	23	24	69 (92 %)	13	13	10	36 (51 %)
Mytilus edulis	—	1	—	1 (1 %)	17	16	19	52 (74 %)
Littorina sp.	—	—	—	—	—	1	2	3 (4 %)
Crustaceans [3]	—	3	2	5 (7 %)	5	—	3	8 (11 %)
Starfish	—	—	—	—	2	—	—	2 (3 %)
Earthworms [4]	1	4	4	9 (12 %)	5	1	5	11 (16 %)
Insects [5]	13	9	10	32 (43 %)	6	2	6	14 (20 %)
Egg-shells	—	—	2	2 (3 %)	—	—	—	—
Waste grain	2	—	1	3 (4 %)	3	1	3	7 (10 %)
Grass	1	3	2	6 (8 %)	2	1	4	7 (10 %)
No. of droppings examined	22	27	26	75	29	20	21	70

1) Also remains of *Balanus* sp. in one dropping.
2) Also one small unidentified bone in one dropping.
3) Mainly *Carcinus maenas.*
4) Identified from presence of chaetae (these droppings also contained soil).
5) Mainly beetles.

Table 2. Frequency of occurrence and size (length) of different fish species in droppings from *L. fuscus* (species of fish determined from otoliths). [1]

Species	Frequency	Size (mm)
Herring *Clupea harengus*	1	
Sandeel *Ammodytes* sp.	1	42—50
American plaice *Hippoglossoides platessoides*	2	100—155
Unidentified flat-fish	1	
Gadidae	11	
Poutassou *Micromesistius poutassou*	2	195—310
Four-bearded rockling *Onos cimbrius*	1	110
Saithe *Pollachius virens*	4	<50
Unidentified Gadidae [2]	4	<50
Unidentified fish	1	
Total no. of droppings with otoliths	17	

[1] Determination and size estimates made by Tero Härkönen, Tjärnö Marine Biological Station. Size could not be estimated in all cases, because sometimes only fragments of otoliths were found. Only otoliths from one species of fish were present in each dropping.

[2] *Pollachius virens, P. pollachius, Micromesistius poutassou* or, possibly *Gadus morhua.*

(Table 1). Furthermore, insects were more common in droppings from *fuscus* than from *argentatus*. For the other food items, there were only minor differences between the two species. Otoliths from fish were found in 17 droppings from *fuscus,* and from these the species and size of the consumed fish could be determined (Table 2). Flat-fish (18 %) and especially *Gadidae* (65 %) predominated in the droppings. The larger fish (>100 mm; Table 2) were presumably taken as offal at fishing boats, but the small *Gadidae* (<50 mm) are too small to be caught in any fishing tackle (T. Härkönen, pers. comm.), and were therefore probably taken by the gulls themselves. In droppings from *argentatus,* I found only one otolith, from the Goldsinny *Ctenolabrus rupestris.* Pellets were rare in the colonies: two, consisting of fish, were found in the *fuscus* colony, and one, consisting of fish and a meat bone, was found in the *argentatus* colony.

In conclusion, the differences in the feeding habits of *fuscus* and *argentatus* observed at Ärholmen in SW Sweden are in agreement with those found in other parts of NW Europe, though food from refuse tips seemed to be of minor importance for *argentatus* at Ärholmen. Although the frequency of earthworms was about equal in the faeces from the two species, *fuscus* generally seems to feed on fields more often than does *argentatus* in SW Sweden (pers. obs.). In fields near the coast, *fuscus* always greatly outnumbers *argentatus* (J. Uddén, pers. comm.), even though the two species are about equally abundant in the neighbouring archipelago (Götmark 1982).

Common Gull L. canus

In England, Vernon (1972) concluded that *canus* takes much of its food on farmland (earthworms, insects, grain), but that it also frequents shores and sometimes also urban habitats. Spärck (1944, 1951) analysed 2865 stomachs from Denmark, collected in all months of the year, and noted insects (50 %), offal (25 %), plants (25 %), earthworms (16 %), fish (10 %) and molluscs/crustaceans (10 %).

In Norway, Bakke (1970, 1972) collected 277 (1970) and 68 (1972) stomachs in April-October. In 1970 (an inland colony close to the coast), he found mainly insects (56 %; principally beetles), plants and grain (74 %), fish (22 %), marine molluscs (14 %; mainly *Mytilus edulis),* waste (19 %), earthworms (8 %) and mink fodder (17 %; obtained from farms nearby). The occurrence of insects increased during the breeding season, while the occurrence of grain decreased. At another site in 1972 (no birds collected in July), there were more insects (85 %), plants and corn (93 %) and earthworms (26 %), and less fish (2 %) and molluscs (10 %).

In an archipelago in SE Norway, Hanssen (1982a, b) studied the gull's use of foraging habitats and collected food samples from the gullet of the chicks (1980, n=19; 1981, n=37). Summed over both years, the major food sources were waste (mainly bread) (in 27 % of samples, 32 % by dry weight), earthworms (52 %, 37 %), plants (50 %, 12 %), crustaceans (14 %, 6 %), adult insects (29 %, 3 %) and larvae and pupae of insects (12 %, 2 %). Remains of (large) fish (10 %, 5 %) occurred only in 1980. Only gulls nesting in the outer archipelago fed on marine invertebrates. The main foraging grounds were mud flats (containing 29 % of 4757 foragers), fields (29 %), river and waste effluents (22 %), and rocky shores (12 %). The utilization of fields increased during the breeding season.

Of 2642 foragers, Hunt & Hunt (1973) recorded many on fields (75 %), and some on water (15 %) and mud (6 %). In 76 pellets collected in SW Finland in the first half of June, Lemmetyinen (1963) noted grain (43 %), *Mytilus* (39 %) and fish (17 %). In 221 stomachs, Belopol'skii (1961) found fish (40 %), insects (44 %), plants (63 %), molluscs (17 %) and crustaceans (10 %). The frequency of insects and fish increased slightly during the breeding season. The stomachs of nestlings and newly fledged birds (n=49) contained mainly fish (49 %), while the stomachs of adults (n=158)

contained less fish (20 %) and more molluscs, crustaceans, insects and berries (a similar but less marked difference was found in *marinus* and *argentatus)*.

In Kandalaksha Bay, 577 droppings collected in two years contained fish (mainly *Gasterosteus aculeatus)* and fish eggs (28 %), molluscs (22 %), berries (17 %) and polycheates (8 %); 76 stomachs contained fish and their eggs (31 %), Eel grass *Zostera marina* (17 %), molluscs (13 %), polycheates (12 %), berries (11 %) and insects (10 %) (Bianki 1977). The frequency of fish increased during the breeding season.

Black-headed Gull L. ridibundus

In England, *ridibundus* frequently foraged on low-lying and poorly drained farmland, whereas *canus* preferred drier, better drained soils (Vernon 1972). *L. ridibundus* was more abundant than *canus* in urban areas and preferred mud flats, while *canus* foraged more on sandy shores. Flight-feeding on insects over water and land also seems to be more common in *ridibundus* than in *canus* (Vernon 1972, pers. obs.).

At an inland colony in E Germany, Creutz (1963; see also Schlegel 1977) collected 490 food samples (stomachs from adults, gullets from chicks, and pellets) during two years. Of 7228 food items, 80 % were insects and 15 % earthworms, the remaining mainly fish and rodents. In the gullets, insects accounted for 79 % of 5234 items (14 % by weight), earthworms 18 % (46 %) and freshwater fish 1 % (20 %). The foraging range of the colony was considered to be less than 30 km. In W Germany, in a colony near the Baltic, Hartwig and Müller-Jensen (1980) collected 630 pellets during two years. Food from fields occurred in 80 % of the pellets [these contained plants (47 %), insects (40 %, mainly beetles) and rodents (17 %)]. Also taken by the gulls were refuse from meat-processing factories (42 %), household garbage (21 %) and food from the firth/sea (13 %; mostly fish, *Balanus* and *Cardium)*. The foraging range of the colony was estimated at 5—20 km. On the island Wangerooge (German Bight), Lorch et al. (1982) examined 41 stomachs of chicks and found plants (64 %), insects (42 %), fish (31 %), mussels (28 %) and shrimps (8 %).

In Denmark, Spärck (1944, 1951) found insects (in 60 % of 3378 stomachs from all months), earthworms (20 %), fish (14 %), molluscs/crustaceans (16 %), plants (13 %) and offal (25 %). Bakke (1972) collected 20 stomachs (June, 8; July, 10; October, 2) in SW Norway and noted only mink fodder (95 %), plants and grain (55 %) and insects (40 %).

Hanssen (1982a, b) studied the foraging ecology of *ridibundus* in the same area as he studied *canus* (37 gullet samples in 1980, 34 in 1981). Summed over both years, the major food sources were waste (mainly bread) (in 18 % of samples, 22 % by dry weight), earthworms (22 %, 13 %), plants (31 %, 1 %), fish (10 %, 18 %), adult chironomids (32 %, 11 %), other adult insects (44 %, 10 %) and larvae and pupae of insects (25 %, 15 %). Small chicks were mainly fed with insects, while larger ones received more waste and fish. Earthworms were mostly taken before midday, insects, fish and waste mainly later in the day. The main foraging grounds were mud flats (52 % of 12213 foragers), refuse dumps (17 %), feeding stations for ducks (12 %) and freshwater ponds (11 %). However, most of the gulls foraging on mud flats were probably non-breeders or migrants. In Scotland and W Norway, Hunt and Hunt (1973) recorded most of the foragers (n=3232) on mud (62 %); the remaining occurred on water (12 %), fields (12 %), at effluents (9 %), rocks (3 %) or in the air (3 %).

In SW Sweden, the feeding habits of *canus* and *ridibundus* are probably much the same as in Hanssen's (1982a, b) study area, since it is adjacent to the coast of SW Sweden and the habitat is similar. For example, in SW Sweden *ridibundus* and especially *canus* (which is the most abundant species) are often seen foraging on fields near their coastal breeding sites (pers. obs.).

Conclusions and discussion

The present review does not permit precise conclusions regarding the proportions of different food items taken by the gull species. The feeding habits of a gull population are influenced by the relative availability of different types of food near the breeding site, the time of year and time of day, and perhaps also individual specialization (e.g. Nordberg 1950, Parsons 1971, Davis 1975, Morris and Black 1980). Nevertheless, general differences have been noted in the feeding habits of the gulls, and as the differences are similar in several areas of NW Europe, they are probably real.

For *marinus,* fish (provided by human activities, or in some areas caught) is clearly important food. Birds may also be important food, although not everywhere; in all areas, however, *marinus* takes more birds than the other species *(argentatus* occasionally feeds on birds, but the occurrence in the food samples rarely exceeds more than a few per cent). To a lesser extent, *marinus* also feeds on marine invertebrates, mammals and refuse. Carcasses of birds and mammals seem to be taken

more often by *marinus* than by the other gulls (e.g. Hope Jones 1980, Hewson 1981).

L. argentatus feeds on food supplied by man (refuse from dumps, fish offal from harbours and fishing boats) to a larger extent than any of the other species. Another important food item is marine invertebrates, such as crabs *(Carcinus)* and mussels *(Cardium, Mytilus).* Some populations also take earthworms in fields. In a colony in S Sweden (Andersson 1968), the diet shifted over a period of 18 years (1947—65) from mainly fish and *Mytilus* to refuse and earthworms. During that time the colony increased from 3000 to 8000 pairs (Andersson 1968). Since the breeding success for pairs feeding on refuse seems to be higher than for pairs feeding on natural food (Spaans 1971:141, 170, Davis 1974), the increase of this colony may partly be due to the shift to refuse.

L. fuscus often feeds on fish out at sea (the fish may be taken alive or obtained at fishing boats), and also takes earthworms, insects and grain on fields. Refuse tips are visited less often by *fuscus* than by *argentatus.* Verbeek (1977b) found that *argentatus* was more efficient than *fuscus* in obtaining refuse from the ground at a tip; *fuscus* fed there almost solely by kleptoparasitizing *argentatus* in the air.

The two smaller gulls consume much more terrestrial food than do the larger gulls. This might be expected, as both species often nest inland (especially *ridibundus).* It seems, however, that they mostly feed on terrestrial food even when nesting along the coast (see above). *L. canus* thus takes less fish than the larger gulls (Kandalaksha Bay seems to be an exception), and feeds more on insects, earthworms and grain (mainly in May); such food is generally obtained in fields and pastures. In some areas, waste from inhabited areas is important food. *L. ridibundus* seems to feed even more on insects than does *canus* (e.g. Spärck 1944, 1951, Hanssen 1982a, b); other common food items are earthworms and waste from dumps and inhabited areas. Fish is taken less frequently than in the other species.

These general differences between the gull species are confirmed in those few studies which compare the feeding habits of several of the species in one area (Spärck 1951, Belopol'skii 1961, Lemmetyinen 1963, Harris 1965, Hunt & Hunt 1973, Davis 1973, Verbeek 1977a, Hanssen 1982a, b, see also Ingolfsson 1968, 1976). For example, Belopol'skii (1961) found that *marinus* fed more on fish and birds than did *argentatus* and *canus; argentatus* ate more molluscs than the other two species; and *canus* fed more on insects and plants than did the others. Mudge & Ferns (1982) found no significant differences in food choice between *fuscus* and *argentatus* in the Bristol Channel, and emphasized the similarities in the diet. In other areas, however, the differences between these two species appear to be clear-cut (e.g. Davis 1973, Verbeek 1977a, Lemmetyinen 1963, present study).

In all species (perhaps less so in *marinus),* grass or other plants often occur in the food samples. Most workers believe that these items are consumed incidentally with other food, such as earthworms (e.g. Harris 1965, Spaans 1971, Vernon 1972, Hanssen 1982a, b, but see Threlfall 1968). Waste grain, however, appears to be readily taken by several of the gull species.

In SW Sweden, *marinus* nests in single pairs or small colonies, *argentatus* and *canus* in colonies of intermediate size, and *fuscus* and especially *ridibundus* in large colonies (Götmark 1982). Partly on the basis of the evidence reviewed here, I suggested that the colonial tendency tends to be strong when the foraging range is wide and the food sources unpredictable. The differences in food choice between *argentatus* and *fuscus* at Ärholmen in SW Sweden support this suggestion, since the species with the smallest colonies *(argentatus)* fed largely on mussels, probably obtained from predictable sites near the colony, and the species with the largest colonies *(fuscus)* fed more on fish, probably obtained far from the colony (presumably taken alive or at fishing boats, i.e. at unpredictable sites). However, further studies are needed to measure foraging range and predictability of food more exactly for these and the other three *Larus* gulls.

Mudge & Ferns (1982) stated that *fuscus* tends to feed at tips farther from the colonies than does *argentatus,* and Sibly & McCleery (1983) found that the proportion of *fuscus* at tips increased with distance from a mixed colony of *argentatus* and *fuscus* at Walney Island. These authors suggested that *fuscus* was displaced from tips near the breeding sites by the larger, dominant *argentatus.*

Some of the differences in the feeding habits of the gulls are apparently related to body size; the larger the species, the larger the prey. For example, it is mainly the two largest species *(argentatus* and *marinus)* that take birds; *marinus* easily swallows eider ducklings and catches large garfish by plunge-diving (pers. obs.). The two smaller species *(canus* and especially *ridibundus)* feed more on small prey, such as insects. The diet of *L. minutus,* the smallest European gull, consists almost entirely of insects in the breeding season (Cramp & Simmons 1983). *L. fuscus* feeds more on fish and less on shellfish than does *argentatus,* and this may also be related to body size or other aspects of the morphology. Verbeek (1977a) showed that *fuscus* has a smaller wing loading than *argentatus,* which should make *fuscus* better adapted for long foraging flights. The intertidal feeding habits of *argentatus* were suggested to have preadapted this species to feed on refuse.

The size differences between the gulls, which are linked with differences in feeding habits, may reduce potential competition for food and facilitate coexistence, as has been suggested for other closely related birds (e.g. Newton 1967, Lack 1971). At present, the gull species seem to be fairly well separated in foraging ecology, and extensive overlap in food choice and foraging habitat seems to occur mainly when there is a super-abundance of prey of intermediate size. For example, all species except *marinus* sometimes feed on earthworms in fields, and all three larger species at times feed on shoals of small fish, such as *Ammodytes* and *Clupea*.

Long-term studies of the feeding habits of gull populations are rare, but would be useful, since they could document changes in the diet (e.g. Andersson 1968) and are of potential interest in the study of population dynamics. For instance, in Scandinavia both the diet and population size of *argentatus* may be affected by the present covering or closure of many previously open refuse tips (Møller 1981:134, pers. obs.).

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Selostus: **Viiden eurooppalaisen lokkilajin pesimäaikaisesta ravinnosta ja ruokailusta**

Katsauksessa vertaillaan pääosassa Luoteis-Eurooppaa sympatrisesti pesivien viiden lokkilajin ravintoa ja ruokailua. Merilokki syö enimmäkseen kalaa ja muita lokkeja enemmän merilintujen poikasia. Harmaalokki syö kala- ja muuta jätettä, merellisiä selkärangattomia sekä joskus pelloilta kastematoja ja viljaakin. Selkälokki käyttää ravinnokseen itse saalistamaansa tai kalastusaluksilta ryövättyä kalaa. Se ruokailee myös pelloilla ja jätteillä joskin harmaalokkia vähemmän. Kalalokin ravinto on pääosin peräisin maalta (matoja, hyönteisiä, viljaa, jätteitä) mutta siihen kuuluu myös kalaa ja veden selkärangattomia. Naurulokki syö hyönteisten ohella matoja ja jätteitä.

Suurimmat lokkilajit syövät keskimäärin suurempia saaliseläimiä kuin pienimmät, joten lajin ruumiin koko ja ravintokohteiden koko näyttävät riippuvan toisistaan.

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