THE FOOD OF BREEDING HERRING GULLS *LARUS ARGENTATUS* AT THE LOWER RIVER ELBE: DOES FISH AVAILABILITY LIMIT INLAND COLONISATION?

HET VOEDSEL VAN ZILVERMEEUWEN AAN DE RIVIER DE ELBE: VIS-AANBOD BEPERKEND VOOR KOLONISATIE IN HET BINNENLAND?

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In a Herring Gull Larus argentatus *colony on an island in the lower river Elbe, northern Germany, diet during the breeding season was investigated. Fish was found in 79% of all pellets, followed by crustaceans (39%, presumably Mitten Crabs* Eriocheir sinensis *only) and human refuse (10%). Overall, 77% of all pellets only contained fish and/or crab, suggesting that feeding was predominantly at the river bank near the colony. Of (potential) food remains other than pellets, 46% were fish, 19% gull eggs, 17% crustaceans, 10% small birds and 8% human refuse. The strong tidal rhythm of the adults' attendance at the colony coincides with fishery activities at the river banks and supports their dependence on unwanted bycatches from fisheries. From this and other studies, there is strong evidence to suggest that the inland breeding distribution of Herring Gulls is limited by the availability of fish during the breeding season rather than by the availability of human refuse or by the lack of breeding habitats.*

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INTRODUCTION

The Herring Gull *Larus argentatus* increased considerably in numbers and established many new colonies both in Europe and in North America during the 20th century until the middle of the 1970s. It is generally accepted that extended human activities, typical of improved standards of living, the Herring Gull's broad ability to exploit these activities and a decline in persecution, are the main reasons for the increase and spread (Goethe 1982; Cramp & Simmons 1983; Vauk & Prüter 1987; Lloyd *et al.* 1991, Burger & Gochfeld 1996).

Herring Gulls colonised inland areas mainly from about 1950, mainly moorlands (in Great Britain and Scandinavia), islands in freshwater lakes or rivers, and roofs of buildings (Ludwig 1966; Goethe 1982; Cramp & Simmons 1983; Vauk & Prüter 1987; Lloyd *et al.* 1991; Burger & Gochfeld 1996; Hagemeijer & Blair 1997). Vauk & Prüter (1987), Lloyd *et al.* (1991) and others assumed that the increasing amounts of human refuse enabled the colonisation of inland areas by (marine) gulls. However, although this food source is still available in large amounts and heavily used by gulls throughout the year all over Europe (e.g. Horton *et al.* 1983; Vauk & Prüter 1987), most inland colonies of the Herring Gull remain very small, and settlements generally last for a few years. Possible reasons are: the low nutritional value of human refuse for egg formation and chick growth (Pierotti & Annett 1987, 1991), low availability of alternative food, or the lack of suitable nesting habitats.

We evaluated whether food choice or food availability might explain why the breeding of Herring Gulls is almost exclusively restricted to coastal areas. To do this, we studied the diet and the activity rhythms of a relatively large inland breeding colony in northern Germany. Our results combined with those from other inland colonies in Europe and North America allow testing of the hypothesis that food other than refuse limits the inland breeding of this gull species.

MATERIALS AND METHODS

The study was carried out in a breeding colony of Herring Gulls on a small artificial island in the river Elbe near the island of Lühesand (53°35'N, 9°36'E), 18 km downstream of Hamburg, Germany. This part of the river Elbe, 80 km from its mouth (following the stream, 68 km as the crow flies), is still under strong tidal influence (tidal range *c.* 3 m) but already totally limnic. The artificial island measures 540 m by 75 m and, during our research, was part of a restricted access military area.

The island of Lühesand has been occupied by single Herring Gull pairs from 1952. Later, numbers increased from around 1965 to a maximum of 88 pairs in 1975. In 1976-77, the colony relocated to the small military island. In 1983 and 1985, 57 and 22 breeding pairs, respectively, were found here. From 1990 onwards, numbers increased up to 142 breeding pairs in 1994 (Mitschke 1996).

In spring and summer 1983 and 1985, a total of 192 pellets and 48 other (potential) food remains were collected in the breeding colony. They were taken from the region of the colony exclusively colonised by Herring Gulls in order to exclude the possibility of collecting pellets from Great Black-backed Gulls *Larus marinus* that rest on the island, and from Common Gulls *Larus*

canus, which nest in large numbers in another part of the island. Food remains could be identified immediately, whereas pellets had to be dissected after air-drying. The identification of fish species resulted from pharyngeal teeth (cyprinids) and scales, following Brauer (1909), Grote *et al.* (1909) and Nitsche & Hein (1909), and using self-collected material for comparison (scales, otoliths and bones). Crustaceans could be identified with the help of reference specimens from the collection of the Zoological Institute and Zoological Museum of the University of Hamburg, mainly by the morphology of carapace and claws; molluscs were identified according to Stresemann (1976). Almost all other items (human refuse, earthworms, birds, mammals, plants, etc.) were easily identified.

All results were grouped into three periods according to Hüppop (1987): pre-incubation (till 12 May), incubation (13 May to 10 June), and chick-rearing (11 June onwards). All figures relating to percentages give the number of pellets (or other food remains) in which the respective food category was found. Because more than one food category may be found in one pellet, the total of the percentages may be greater than 100. Frequencies of occurrences in the pellets and in other food remains, respectively, were compared using the G-test (likelihood ratio test) for goodness of fit for all cases with total $n > 5$.

In order to discover if colony attendance showed diurnal or tidal periodicity, all adult Herring Gulls present in the whole colony were counted every hour during daylight, on several days from 5 to 27 May 1985 and from 29 April to 2 May 1986. Reliable counts later in the breeding season were impossible since the vegetation had grown too high. Circular-linear regression techniques (Batschelet 1981) were used for statistical testing of these counts. To enable this, the average tidal cycle (12.38 h, former German Hydrographic Institute) was transformed into angular values.

RESULTS

Fish was the dominant food type throughout the whole breeding period (Table 1). On average it was found in 79% of all pellets, followed by crustaceans (39%, presumably Mitten Crabs *Eriocheir sinensis* only) and human refuse (10%). Although plant material was found in 22% of all pellets and single (gull) feathers in 22%, these two groups are assumed to have been swallowed incidentally, with only four exceptions: cereals were found in three pellets, and the remains of tomato in one (see Appendix). On average, 46% of all (possible) food remains other than pellets were fish, 19% were gull eggs, 17% crustaceans, 10% small birds (including gull chicks) and 8% human refuse (Table 1). On a species level, the fish species mostly taken were cyprinids (identified as *Leuciscus idus, Rutilus rutilus, Abramis brama, Blicca bjoerkna*) and Eel *An-*

Table 1. Frequency of pellet contents and (potential) food remains of a Herring Gull colony at the lower river Elbe. Periods: 1 = pre-incubation, 2 = incubation, 3 = chick rearing.

Tabel 1. De inhoud van braakballen (n, %) en (potentiële) voedselresten in een zilvermeeuwkolonie aan de rivier de Elbe. 1= voorafgaande aan het broeden, 2= tijdens het broeden, 3= nesten met jongen.

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
small mammals	0	0	2 (3%)	2 (1%)	0	0	0	0
birds	0	1 (1%)	3 (5%)	4 (2%)	0	1	4	5
eggs	0	3 (3%)	0	3 (2%)	0	2	7	9
feathers	0	24 (21%)	18 (27%)	42 (22%)	0	0	0	0
fish	10 (83%)	88 (77%)	53 (80%)	151 (79%)	1	19	2	22
crustaceans	5 (42%)	38 (33%)	31 (47%)	74 (39%)	0	3	5	8
other invertebr.	0	9 (8%)	0	9 (5%)	0	0	0	0
plant material	1 (8%)	27 (24%)	14 (21%)	42 (22%)	0	0	0	0
refuse	0	12 (11%)	8 (7%)	20 (10%)	0	1	3	4
other	1 (8%)	3 (3%)	3 (5%)	7 (4%)	0	0	0	0
n =	12	114	66	192	1	26	21	48

guilla anguilla. Nevertheless, many fish remains could not be identified to species level (see Appendix). The spectrum of fish species parallels well with the abundance and accessibility of the fish (see Discussion) at the lower river Elbe (Peters *et al.* 1986; Diercking & Wehrmann 1991; Gaumert & Kämmereit 1993; Gaumert 1995).

Throughout the breeding season, there were virtually no changes in the proportion of pellets containing fish and crustaceans (Table 1), whereas there was a significant increase in the proportion of pellets containing feathers (G-test, $P < 0.05$). Therefore, all further interpretations of the pellet contents are based on the combined data from the whole breeding season. With respect to (potential) food remains other than pellets, the proportion of fish dropped significantly from the breeding to the chick rearing period ($P < 0.001$), while the proportion of gull eggs increased significantly ($P < 0.05$).

The number of adults present on the island showed a strong tidal rhythm, whereas time of day had a smaller effect. Although time of day is sig-

nificantly correlated with the number present ($r^2 = 0.18$, $P < 0.001$), it explains less than 18% of the variance in the number of adults present in the colony. In contrast, a circular-linear regression revealed that the tidal cycle explained 73% of the variance (Fig. 1). The residuals of this regression further correlate significantly with the time of day and they explain 40% of the variance in numbers (Fig. 2). Hence it is not surprising that tidal cycle and daytime together explain 84% of the variance ($r^2 = 0.84$, $P < 0.001$).

DISCUSSION

The results of food studies in seabirds may heavily be influenced by the method adopted. Pellet analyses can be biased towards hard and larger parts and hence other prey may be under-represented (Duffy & Jackson 1986). Some food, e.g. eggs minus the shell or meat without bones or packing material, will rarely leave detectable remains in pellets. The importance of (potential) food remains found close to a nest is also difficult to evaluate. They may reliably reflect the true spectrum of food items consumed by adults. On the other hand, these food remains may reflect objects too large to be swallowed by the chicks (see discussion e.g. in Duffy & Jackson 1986 and Becker *et al.* 1987) or objects that are rejected by both chicks and adults due to their unpalatability or for other reasons. Nevertheless, our analysis of pellet contents and the analysis of other food remains found show both the same relative importance of the different food classes (with the exception of eggs). Although grass and other plant material may reflect the consumption of earthworms and leather-jackets (Tipulidae), we did not find remains of these animals. Furthermore, in our study Herring Gulls were rarely seen foraging on grassland or arable land. However, grass and other plant material may help pellet formation (Nogales *et al.* 1995).

Table 2. Pellet contents at a Herring Gull colony at the lower river Elbe arranged according to super-categories.
Tabel 2. Braakbalinhoud van Zilvermeeuwen aan de rivier de Elbe, onderverdeeld naar enkele 'super-categoriën'.

super-category	frequency (n, %)	
homogeneous fish	89	46.4%
homogeneous crustaceans	22	11.5%
fish and crustaceans	36	18.8%
homogeneous refuse	8	4.2%
fish, crustaceans and refuse	12	6.3%
other homogeneous	4	2.1%
other heterogeneous	21	10.9%
total number of pellets	192	100%

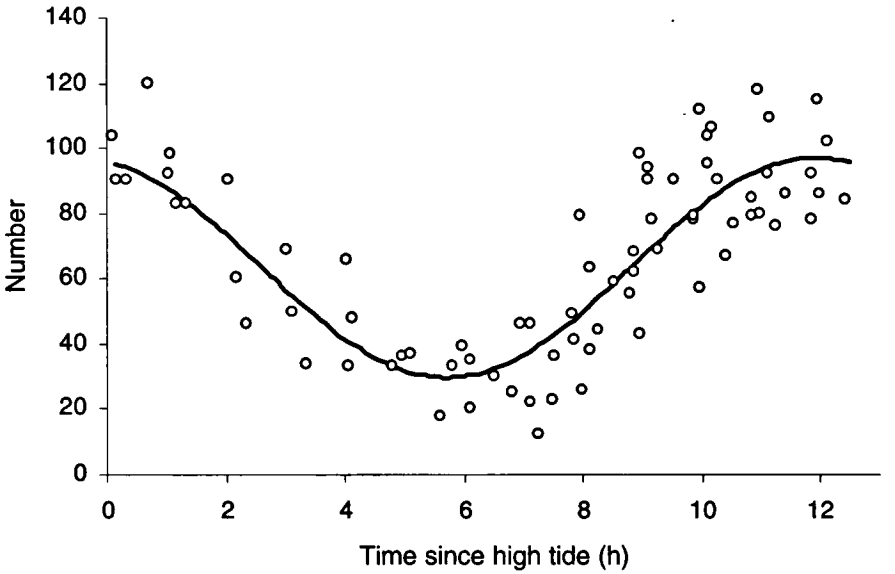

Figure 1. Number of adult Herring Gulls present in the colony at the lower river Elbe during the pre-incubation and early incubation period (29 April to 27 May) in relation to tidal cycle. Low tide = high tide + 5 h 13 min. To calculate a circular regression, the time after high tide was transformed to angular values. y = 63.4 + 33.7 cos (t + 0.250), r^2 = 0.73, P < 0.001, t = time (in radians) since high tide = time since high tide (in hours) x 12.38 h^{-1} x 2Π

Figuur 1. Aantal volwassen Zilvermeeuwen op de kolonie in het begin van de broedtijd (29 april-27 mei) in relatie tot de getijdecyclus. Laagwater = hoogwater + 5 uur en 13 minuten.

Under these assumptions, our pellet analysis allows quantitative conclusions about *where* the gulls preferably foraged. Pellets containing only fish and/or crustaceans indicate foraging at the river. Those containing only human refuse indicate foraging at refuse tips. Hence, all pellets were regrouped according to these super-categories (Table 2). Of all 192 pellets, 147 (77%) contained exclusively fish and/or crab, whereas not more than 8 pellets (4%) were exclusively refuse pellets, and 12 (6%) contained refuse mixed with fish and/or crustaceans. These findings support our observations that the Herring Gulls breeding near Lühesand feed predominantly at the river banks near the colony and add human refuse or other food items to their diet only to a small extent. At least two refuse tips (Ketzendorf and Neu Wulmstorf, nearly 20 km

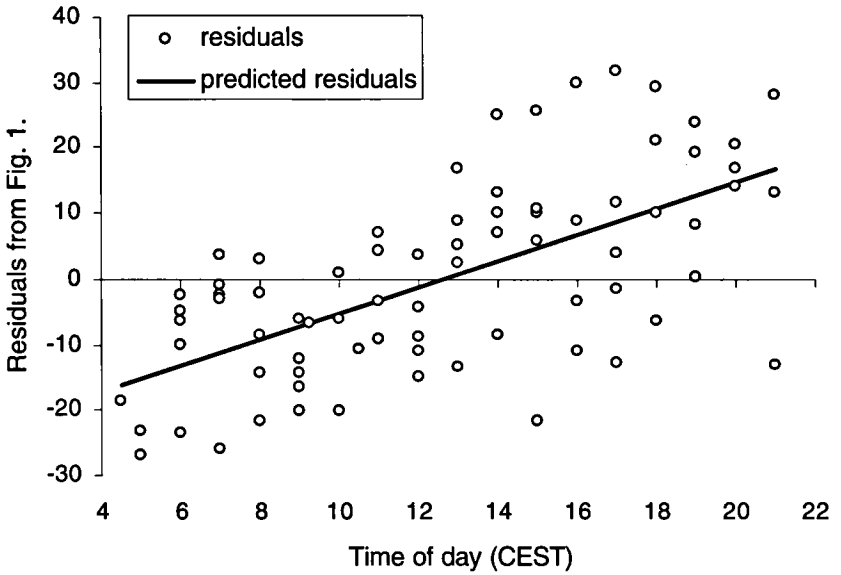

Figure 2. Number of adult Herring Gulls present in the colony at the lower river Elbe during the pre-incubation and early incubation period (29 April to 27 May) as residuals from figure 1 in relation to time of day (Central European Summer Time; GMT + 2), y = 1.99 x - 25.2, r^2= 0.40, P < 0.0001.

Figuur 2. Aantal volwassen Zilvermeeuwen op de kolonie in het begin van de broedtijd (29 april-27 mei) als residu van Fig. 1 in relatie tot de tijd van de dag (Midden-europese Zomertijd; GMT +2).

south-east of the colony; K. Burdorf pers. comm.) were well within the usual feeding range (e.g. Bergman 1951: 35 km; Focke 1959: 35 km; Andersson 1970: 28 km; Spaans 1971: 35 km; Sibly & McCleery 1983: > 30 km).

However, even at the river bank, foraging is based to a large extent on human activities. The strong tidal rhythm of the Herring Gulls at the colony near Lühesand supports the assumption that the gulls feed predominantly at the river bank and explains their access to the aquatic food there. Fishermen empty their fish traps around low tide and then discard unwanted bycatch such as cyprinids, Mitten Crabs and undersized Eel on the tidal flats, where the Herring Gulls can easily feed on these items. Further, low tides render cyprinids that spawn in the bank areas (Diercking & Wehrmann 1991; Gaumert & Kämmereit 1993) and Mitten Crabs migrating up the river (Peters & Panning 1933) accessible to the gulls. The well known tidal influence on coastal Herring Gull foraging activities

(e.g. Drent 1970; Spaans 1971; Verbeek 1977; Galusha & Amlaner 1978) is maintained at the (inland) colony near Lühesand, but it can be assumed that the reasons are different. Natural availability of prey items at the coast versus predominantly anthropogenic availability of food at the river Elbe.

The influence of daytime on the presence of the gulls at the colony can easily be interpreted by hunger. Many birds were seen leaving the colony during the morning twilight before the first count was possible (Hüppop 1987). This corroborates McCleery & Sibly (1986) who found no nocturnal feeding activity of Herring Gulls during the incubation period.

The decrease of fish found in the (potential) food remains in the colony might reflect a higher demand for fish in the chick rearing period (eaten fish cannot be found!). In other breeding colonies of the Herring Gull, increases in

Table 3. Diet composition of inland Herring Gulls. Figures give percentages in pellets, stomachs or prey remains containing the respective categories. A= fish, B= refuse, C= insects, D= other invertebrates, E= mammals, F= birds, G= plants, H= other

Tabel 3. Voedselsamenstelling van Zilvermeeuwen in het binnenland. Weergegeven zijn percentages in braakballen, magen of andere voedselresten. A= vis, B= afval, C= insekten, D= andere ongewervelden, E= zoogdieren, F= vogels, G= plantaardig materiaal, H= overigen.

Locality	period	meth	A	B	C	D	E	F	G	H	ref[5]
Maine, USA	Jun-Sep	S[1]	77	8					8	7	1
Maine, USA	Jun-Jul	S	76	16	8						2
Michigan, USA	breeding	S,R[2]	>85	2	+	1	+	>4		4	3
Järnlunden, S	breeding	P	74	21	37	11	1	2	36	8	4
Manitoba, Can	May-Jun	P	94		+	+	6		2		5
Connecticut, USA	?	S,R	100								6
Gr Lake Plön, D	Apr-May	S	75-87	13-31	34	7	<1			86	7
Hohe Schaar, D	Apr-Jul	P[3]	88	3		17		1		1	8
Mühlenb. Loch, D	Jun-Aug	P[3]	92	2		26					8
Lake Ontario, Can	Apr-Jun	P	58		32		19	11		11	9
Lake Huron, Can	Apr-Jul	P	22	9	3		27	12	18	2	10
Lake Erie, USA	May-Jul	P	98	1	1	1	1	1	8	<1	11
		R	74	17	1	5	<1	7	2	<1	11
		S[4]	79	11	3	20	1		13	2	11
Great Lakes, Can/USA	winter-early spring	P	56	19		7	19	11	21		12
Lühesand, D	May-Jul	P	79	10		44		2	22	28	13

[1]P= pellet, S= stomach contents, R= prey remains, += present; [2]percentages based on number of items detected, excluding insects; [3]Herring Gull and Common Gull mixed; [4]boli from chicks; [5]1= Mendall (1939), 2 = Vik (1963), 3 = Ludwig (1966), 4 = Andersson (1970), 5 = Vermeer (1973), 6 = Tolonen (1976), 7 = Demuth (1983), 8 = Gruner (1986), 9 = Fox *et al.* (1990), 10 = Allan in Fox *et al.* (1990), 11 = Belant *et al.* (1993), 12 = Ewins *et al.* (1994), 13 = this study.

the proportion of fish consumed were found throughout the breeding season (e.g. Spaans 1971; Vermeer 1973; Fox *et al.* 1990; Noordhuis & Spaans 1992). The increased proportion of eggs in the food remains in the chick-rearing period can be explained by high predation and cannibalism rates by the gulls late in the season (see Discussion in Burger 1984).

The Herring Gull has a very broad food spectrum with large local and seasonal differences. In marine areas, both in Europe and in North America, crustaceans, molluscs, echinoderms, fish and human refuse form the bulk of the food. Where fish is easily available, it may become the most important food category (Goethe 1982 and 1991; Cramp & Simmons 1983; Vauk & Prüter 1987; Pierotti & Good 1994; Burger & Gochfeld 1996). Marine Herring Gulls obtain molluscs and crabs mainly from intertidal areas. Since these are usually not available to inland breeders, it is not surprising that in almost all inland breeding Herring Gulls studied so far, fish is the most important food category (Table 3). However, Herring Gulls are relatively inefficient when foraging on healthy fish in open water (e.g. Goethe 1982; Koop 1990). Hence, fish can only become an important food source where they are concentrated in shallow water, as can be the case in spawning areas (Vermeer 1973; Sjöberg 1989; Fox *et al.* 1990), or where they are available as discards from fisheries (pers. obs.; Nepszy in Ewins *et al.* 1994). The latter is not surprising since Herring Gulls are well-known as scavengers, profiting from human fishing activities at sea or in harbours (Goethe 1982; Hüppop *et al.* 1994; Burger & Gochfeld 1996).

The opportunistic Herring Gull can also successfully exploit other anthropogenic food resources such as refuse. The improved standard of living of men in combination with regular refuse collection and deposition has been interpreted to affect not only the Herring Gull's general increase in numbers and enlargement of its distribution area, but in particular the increased use of inland habitats in the 20th century during the non-breeding season (e.g. Horton *et al.* 1983; SOVON 1987; Vauk & Prüter 1987; Goethe 1991; Arbeitsgruppe Möwen 1996). In some cases, the availability of refuse is assumed to enhance, or even to be essential for, reproductive success (Kadlec & Drury 1968; Hunt 1972; Sibley & McCleery 1983; Pons 1992; 1994). However, the numbers of Herring Gulls breeding inland are still very small (Teixeira 1979; Meltofte & Fjeldså 1989; Monaghan 1993; Bauer & Berthold 1996). Is the occurrence of human refuse really important for the inland breeding distribution of Herring Gulls?

In all inland colonies of Herring Gulls studied so far, fish was found in 22 to 100% of the stomachs or pellets, which is on average much more than in marine conspecifics. However, only 0 to 31% of the stomachs or pellets contained refuse (Table 3). Indeed, even the closure of a refuse tip at Great Lake Plön, one of the largest lakes in northern Germany, could not check the growth of the colony (Berndt 1980; Koop in Busche & Berndt 1996). The proportion of

stomachs of Herring Gulls, killed for population management, containing refuse decreased from 31% to 13% after the closure, whereas the proportion of stomachs with fish increased slightly from 75% to 87% (Demuth 1983).

There is some evidence that, at least in marine areas, foraging in natural habitats is preferred to foraging on refuse tips. The latter are mainly visited when access to natural food sources is restricted e.g. during high waters (Spaans 1971; Kihlman & Larsson 1974; Greig *et al.* 1986). Niebuhr (1983) observed that females in the pre-laying period prefer mussels, which provide calcium for egg-shell formation, whereas males feed on refuse. In fact, despite the higher energetic value of refuse, mussel specialists produce more offspring, being larger at all developmental stages compared with refuse specialists (Pierotti & Annett 1987). Black Tern *Chlidonias niger* chicks exclusively fed on insects may die due to calcium deficiency (Beintema *et al.* 1997). In our and other studies (Chudzik *et al.* 1994; Nogales *et al.* 1995) fish bones which are calcium-rich, may substitute for mussel shells. Pairs that switch to a fish diet at the time of hatching have lower chick mortality (Pierotti & Annett 1987; Bukacinska *et al.* 1996). The ability of chicks to digest fish bones in the early phase of growth implies that fish might be an important source of calcium (Spaans 1971). However, Spaans (1971) also found that chicks from broods fed on refuse as well as marine food grew faster than chicks not supplied with refuse. Hence, natural food, such as mussels, crabs and fish, which are rich in protein and calcium, seems to be essential for a high reproductive success, which can be improved even more by high energetic refuse.

Outside the breeding season, however, the availability of human refuse determines to a great extent the inland distribution of Herring Gulls (Monaghan 1980; Goethe 1991; Arbeitsgruppe Möwen 1996). Then, refuse may be an important food and act as an alternative when natural food is unavailable. This could increase life expectancy (Pierotti & Annett 1987) and possibly lifetime reproduction.

The suggestion that the inland breeding distribution of the Herring Gull is limited by the lack of breeding habitats cannot easily be supported. In contrast to the Herring Gull, there exist several very large inland colonies of the Common Gull (Bauer & Berthold 1996; Hagemeijer & Blair 1997), and the inland total of about 6000 pairs in Germany is still increasing (Witt 1976; Koop in Busche & Berndt 1986; Meyer & Sudmann 1996; Mlody 1996; K. Witt pers. comm.). Since Herring Gulls and Common Gulls often nest close together both in coastal and in inland colonies (e.g. Hüppop & Hüppop 1995; Koop in Busche & Berndt 1996; Mitschke 1996; Südbeck & Hälterlein 1997), there are no reasons to assume a lack of inland breeding habitats for Herring Gulls. Correspondingly, Chudzik *et al.* (1994) suggested that food rather than the

availability of breeding habitats limit Herring Gull numbers throughout the Great Lakes of North America.

In conclusion, the food spectrum of Herring Gulls of almost all inland colonies investigated is relatively similar and almost exclusively dominated by fish (Table 3). Further, all larger inland colonies in both Europe and North America (Pierotti & Good 1994; Hagemeijer & Blair 1997) seem to be confined to areas with a sufficient natural or anthropogenic supply of fish (Vermeer 1973; Fox *et al.* 1990; Chudzik *et al.* 1994). For some inland breeding Herring Gulls, e.g. for those in colonies in Brandenburg (eastern Germany, 75-77 pairs in 1995, Haupt & Kaminski 1995) their diet is not known nor whether they have access to fish (H. Haupt pers. comm.), but there is strong evidence that the inland breeding distribution of Herring Gulls is generally limited by the availability of fish during the breeding season rather than by the availability of human refuse or by the lack of breeding habitats.

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SAMENVATTING

Zilvermeeuwen zijn deze eeuw zowel in Noord-Amerika als in Europa sterk in aantal toegenomen en tot aan het midden van de jaren zeventig ontstonden talloze nieuwe kolonies. Over het algemeen werd verondersteld dat deze meeuw zich succesvol had aangepast aan de mens en dat de toename vooral een afspiegeling was van onze verhoogde levensstandaard. Behalve dat de Zilvermeeuw profiteerde van nieuwe, door de mens veroorzaakte voedselbronnen (bijvoorbeeld vuilnisbelten, visafval), was ook de verminderde bestrijding van meeuwen een belangrijke voorwaarde voor het succes. Sinds de jaren vijftig werden ook steeds meer vestigingen van Zilvermeeuwen in het binnenland aangetroffen. Vooral deze vestigingen zouden tot stand zijn gekomen door de talrijke (open) vuilnisbelten in West Europa. Toch waren deze meeuwen maar weinig succesvol. Ofschoon dergelijke voedselbronnen nog steeds volop aanwezig zijn, werden dergelijke nieuwe vestigingen dikwijls al snel weer verlaten en het broedsucces bleef vaak gering. Verklaringen voor deze teleurstellende resultaten werden vooral gezocht in de geringe voedingswaarde van menselijk afval in vergelijking met meer natuurlijke prooien, een beperkte toegankelijkheid van alternatieve voedselbronnen en een gebrek aan geschikte nestplaatsen in het binnenland. In dit artikel wordt onderzocht of de voedselbeschikbaarheid verklaart waarom Zilvermeeuwen toch vooral kustgebonden vogels zijn. Hiertoe werd het dieet van Zilvermeeuwen op één van de grootste kolonies in het binnenland (Lühesand, rivier de Elbe, West Duitsland; 53°35'NB, 9°36'OL) onderzocht en vergeleken met gegevens uit de literatuur.

Visresten werden aangetroffen in 79% van alle onderzochte braakballen. Andere veelvoorkomende prooisoorten waren crustacea (39%; waarschijnlijk uitsluitend de Chinese Wolhandkrab *Eriocheir sinensis*) en menselijk vuilnis (10%). In totaal bevatte 77% van alle braakballen uitsluitend vis- of krabbenresten, waaruit kon worden afgeleid dat deze meeuwen vooral op de rivier voedsel zochten. Andere belangrijke voedselresten in de kolonie, naast de prooiresten

die in braakballen gevonden zijn, waren vis (46%), meeuweneieren (19%), crustacea (17%), kleine vogels (10%) en vuilnis (8%). Op de kolonie werd een duidelijk verband gevonden tussen het foerageergedrag van de meeuwen en het getij, waaruit kon worden afgeleid dat de Zilvermeeuwen hun gedrag voor een belangrijk deel hadden afgestemd op de visserijactiviteiten op de rivier de Elbe, profiterend van de overboord gezette visresten en krabben. Uit de gepresenteerde gegevens, in vergelijking met materiaal uit de literatuur, blijkt dat het succes van Zilvermeeuwen in het binnenland in hoge mate afhangt van de beschikbaarheid van vis in de kuikenfase. De beschikbaarheid van vuilnis en het aanbod van geschikte nestplaatsen lijken aanmerkelijk minder van belang te zijn.

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Appendix. Absolute occurrence of food items found in pellets and (potential) food remains in a Herring Gull colony at the lower river Elbe. Periods: 1 = pre-incubation, 2 = incubation, 3 = chick rearing.

Appendix. De precieze inhoud van braakballen (n) en (potentiële) voedselresten in een zilvermeeuwkolonie aan de rivier de Elbe. 1= voorafgaande aan het broeden, 2= tijdens het broeden, 3= nesten met jongen.

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
unident. small mammal	0	0	2	2	0	0	0	0
chick *Larus argentatus*	0	0	0	0	0	0	1	1
chick *L. canus*	0	0	0	0	0	0	2	2
Alauda arvensis	0	0	1	1	0	1	1	2
unident. small bird	0	1	2	3	0	0	0	0
Anguilla anguilla	0	2	0	2	1	7	2	10
Osmerus eperlanus	0	0	0	0	0	2	0	2
Abramis brama	1	8	4	13	0	3	0	3
Blicca bjoerkna	0	8	3	11	0	1	0	1
Leuciscus idus	2	13	6	21	0	0	0	0
Rutilus rutilus	3	10	5	18	0	1	0	1
unident. cyprinid	1	12	6	19	0	0	0	0
Gymnocephalus cernua	0	0	0	0	0	1	0	1
unident. perch	0	4	0	4	0	0	0	0
Platichthys flesus	0	1	0	1	0	4	0	4
unident. fish	3	40	31	74	0	0	0	0
unident. beetle	0	3	0	3	0	0	0	0
diptera larvae	0	2	0	2	0	0	0	0
Eriocheir sinensis	5	28	27	60	0	3	5	8
unident. crustacean	0	10	4	14	0	0	0	0
unident. snail	0	1	0	1	0	0	0	0
Succinea putris (terr. snail)	0	2	0	2	0	0	0	0

Type of food	pellets				food remains			
	1	2	3	total	1	2	3	total
unident. earthworm	0	1	0	1	0	0	0	0
tomato	0	1	0	1	0	0	0	0
thorn	0	1	0	1	0	0	0	0
cereal	0	3	0	3	0	0	0	0
grass or other plant material	1	23	14	38	0	0	0	0
bone	0	10	2	12	0	0	2	2
sausage remains	0	5	1	6	0	0	0	0
rind (of bacon)	0	0	0	0	0	0	1	1
thread	0	2	0	2	0	0	0	0
glass	0	5	0	5	0	0	0	0
plastic material	0	8	0	8	0	1	0	1
paper	0	2	2	4	0	0	0	0
tin foil	0	3	3	6	0	0	0	0
metal particle	0	1	0	1	0	0	0	0
pin	0	1	0	1	0	0	0	0
button	0	1	0	1	0	0	0	0
unident. refuse	0	2	2	4	0	0	0	0
human hair	0	0	1	1	0	0	0	0
feather	0	24	18	42	0	0	0	0
egg	0	3	0	3	0	2	7	9
gravel	1	3	2	6	0	0	0	0
total number of pellets/ prey items investigated	12	114	66	192	1	26	21	48