BREEDING LESSER BLACK-BACKED GULLS *LARUS GRAELLSII* AND HERRING GULLS *LARUS ARGENTATUS*: COEXISTENCE OR COMPETITION?

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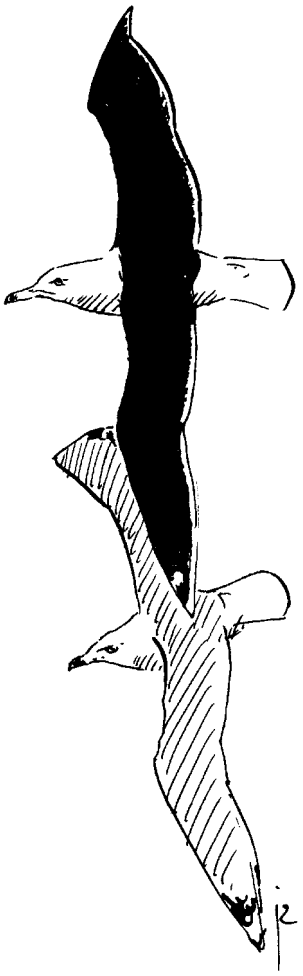

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While Lesser Black-backed Gull *Larus graellsii* numbers increase substantially at the German North Sea coast since the late 1980s, Herring Gull *Larus argentatus* numbers have been roughly stable since the mid-1980s. In order to investigate whether a different ecology might explain the current trends, we studied diet, colony attendance, reproductive output and aggressive behaviour in a mixed-colony on Amrum, southeastern North Sea, in 1994 and 1995. During incubation Lesser Black-backed Gulls fed mainly upon crustaceans and molluscs which were taken from the intertidal zone. During chick-rearing, they took mainly crustaceans and fish which were gathered mostly as trawler discards. The main food of Herring Gulls throughout the reproductive season were molluscs and crustaceans which were obtained from the intertidal zone. Numbers of Lesser Black-backed Gulls in the colony mainly varied with season and time of day, those of Herring Gulls with tide and season. Numbers of Herring Gulls commuting to the open sea roughly equalled those commuting to the Wadden Sea. Lesser Black-backed Gulls generally flew to the open sea but hardly towards the Wadden Sea. Nest attendance was significantly higher in Lesser Black-backed Gulls than in Herring Gulls during the chick-rearing period. Hatching success and fledging success tended to be higher in Lesser Black-backed Gulls. Lesser Black-backed Gulls won interspecific aggressive interactions significantly more often than Herring Gulls in the chick-rearing period. Our study indicates that Lesser Black-backed Gulls currently enjoy a few ecological advantages compared with Herring Gulls, particularly because they feed on food of apparently higher quality. We conclude that Lesser Black-backed Gulls have filled an empty niche rather than have outcompeted Herring Gulls during the past decades.

Key words: *Larus graellsii* - *Larus argentatus* - seabirds - population trend - diet - colony attendance - reproduction - aggression - competition - niche

**Larus graellsii*, formerly known as *Larus fuscus*

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INTRODUCTION

The closely-related Lesser Black-backed Gull *Larus graellsii* and Herring Gull *Larus argentatus* breed sympatrically in many areas, including the southern North Sea (Hagemeijer & Blair 1998). Although both Lesser Black-backed and Herring Gulls showed obvious increases in population sizes at the German North Sea coast after 1945, they differ quite remarkably in time and degree of their increase (Fig. 1). Herring Gull numbers increased despite so-called 'population regulation meas-

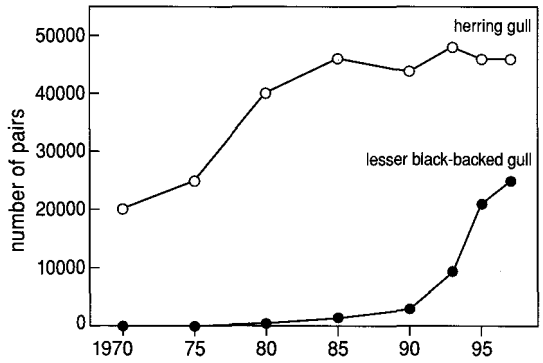

Fig. 1. Population development of Lesser Black-backed and Herring Gull in Germany. Data were taken or estimated from the following sources: Behm-Berkelmann & Heckenroth (1991), Hälterlein (1986, 1996), Hälterlein & Behm-Berkelmann (1991), Südbeck & Hälterlein (1995, 1997) and Thiessen (1986).

ures' (e.g. Thiessen 1986; Hälterlein 1996) until the mid-1980s, with a particular strong increase in the late 1970s. Since 1985 numbers have been stable. Lesser Black-backed Gulls bred in very low numbers until the 1970s. A slight increase in the early 1980s was followed by an exponential increase which still occurs today. The Herring Gull population has more than doubled since 1970 while that of Lesser Black-backed Gulls has increased by a factor of over 200. Lesser Black-backed Gulls started to increase at a time when Herring Gull numbers had already reached a plateau (Fig. 1).

Since comparative data on the foraging and breeding ecology of both species in the southeastern North Sea have become available only recently, it is not possible to investigate why the populations have developed so differently. These recent studies in the southern North Sea indicate that the two species show considerable differences, in their ecology, at least nowadays (Noordhuis & Spaans 1992; Camphuysen 1995). Lesser Black-backed Gulls are widely distributed at sea and forage often far from the colonies (Camphuysen 1995; Garthe *et al.* 1995). They extensively use discards from fishing trawlers, but pelagic fish in the open sea seem to be their target food (Spaans *et al.* 1994; Camphuysen 1995). On the contrary, Herring Gulls are much more restricted to the coastal zone, especially to the tidal flats of the Wadden Sea where they mainly prey upon invertebrates during the breeding season (Spaans 1971). Herring Gulls therefore tend to forage much closer to the colonies, but also use fishery waste from nearshore fisheries (Camphuysen 1995; Garthe 1997).

In this paper we examined possible causes for these differences by studying diet, colony attendance, aggressive interactions and reproductive output in a mixed breeding colony. We subsequently discuss how the differences in population trends can be interpreted with respect to competition.

METHODS

This study was carried out in the nature reserve 'Amrum-Odde' on the island Amrum (54°40'N, 8°21'E) in the years 1994 and 1995. Amrum is located between the open North Sea and the Wadden Sea, some 25 km from the mainland coast of Schleswig-Holstein (northern Germany). Observations were designed to cover all parts of the tidal cycle, time of day during daylight and seasons as completely as possible. Results are usually presented separately for the incubation and the chick-rearing periods.

Diet was analysed on the basis of pellets. About 20 pellets of both species were collected in 1994 on: 14, 21 and 28 May, 6, 13, 20, 22 and 27 June, 5, 11, 19, 25 and 28 July (n = 268 for Lesser Black-backed Gulls, n = 259 for Herring Gulls). We tried to avoid local biases from specialised individuals by covering large parts of the colonies rather than single nests. Samples could be attributed to the two species relatively easily, because the species bred often in single-species groups within the whole colony.

The diet was determined to the lowest possible taxon. Results are presented both by taxonomic order and by the food source. For the latter, food items were assigned to their presumed origin, derived from classifications in Garthe (1993),

Kubetzki (1997) and from personal observations near the breeding colonies. Some prey items could be assigned to more than one category, in which cases the most probable category was chosen: all molluscs, Shore Crabs *Carcinus maenas*, Brown Shrimps *Crangon crangon*, echinoderms and chicks of Eider Ducks *Somateria mollissima* were assumed to be taken in the intertidal zone which includes tidal flats and beaches. Swimming crabs *Liocarcinus* spec., clupeids, Garfish *Belone belone* and Mackerels *Scomber scombrus* were probably taken at sea (pelagic zone). Hermit Crabs *Eupagurus bernhardus*, gadids, gurnards, Scads *Trachurus trachurus*, flatfish, Hooknoses *Agonus cataphractus* and dragonets *Callionymus* spec. were asssumed to be taken as fishery waste behind fishing vessels, while insects, eggs, birds other than Eider Duck chicks, mammals, cereals, fruits, other plant material and garbage were assigned to terrestrial sources.

In order to study how the two species utilise either the open sea or the Wadden Sea and to assess how important abiotic factors possibly influence colony attendance, two types of counts were performed. First, all birds present in one dune valley (at or close to the nest) in the sub-colony Odde were counted every 30 min for up to four hours per day on 25 days from May to July 1994. These data were then linked with the independent variables season (entered as Julian day), tidal stage, time of day, wind direction and wind speed in stepwise multiple regression analysis. The variables tidal stage, time of day and wind direction had to be sine and cosine transformed before further calculations because of their periodic nature (Batschelet 1981). Only significant variables ($P < 0.05$) are given in the text. Wind data are considered important because wind may influence foraging possibilities. Wind data from List (Island of Sylt, 37 km north of the colony) were kindly provided by the 'Deutscher Wetterdienst'. Second, gulls leaving for, or returning to, the colony were counted by passage counts near the sub-colony Odde on 23 days from May to July in 1994. Counts were conducted separately on the western (gulls leaving from, or returning to, the open sea) and eastern (gulls leaving for, or returning to, the Wadden Sea) edges of the colony. Counts were carried out continuously for up to 4 hours per day, the data being grouped into 15 min-intervals.

In order to assess how much time parents spent foraging and how much time the chicks were (un)attended and therefore vulnerable to predation, nest attendance was monitored in 1994 in five randomly selected breeding pairs of each species. The same breeding pairs were watched by scan-sampling (Altmann 1974) every five min for up to four hours per day on 25 days in total during the whole breeding cycle (n = 743 to 918 scans for each pair in total, depending on breeding phenology).

Reproductive success was assessed for both species in 1995. Nest sites were selected so that they could be checked by eye, binoculars and telescope and were subsequently marked. We tried to follow the fate of the known chicks over the reproductive period. Data were only taken from those nest sites where chicks could be assigned to parents with certainly. In the study plot, vegetation tended to be higher at the nest sites of Lesser Black-backed Gulls than at the nest sites of Herring Gulls so that reproductive performance may have been slightly underestimated in the former.

In order to study whether one species may be dominant over the other at the breeding sites, interspecific interactions were quantified in a particular dune valley in the sub-colony Odde in 1995. Four types of aggressive interactions (walking-towards counterpart, flying-towards counterpart, grass-pulling, fighting) were distinguished. These aggressive interactions between species were noticed during 140.5 hours of observations on 38 days from May to July. The whole dune valley was scanned for interactions in order to avoid biases due to the position of the birds.

RESULTS

There was a substantial dietary change from invertebrates towards fish between incubation and

Table 1. Frequency of occurrence of different prey items in pellets of Lesser Black-backed Gull and Herring Gull. The data give the percentage of pellets in which the respective items were found. For the most important prey categories, differences between periods and species were tested by the g-test: for molluscs and fish differences between periods were statistically significant for both species, as were the differences between species.

	Lesser Black-backed Gull		Herring Gull	
	incubation period	chick-rearing period	incubation period	chick-rearing period
no. pellets	103	165	80	179
molluscs	48	7	75	48
Cerastoderma spp.	38	4	64	30
Macoma spp.	4	1	6	4
Mytilus edulis	15	2	23	16
crustaceans	49	52	35	45
Carcinus maenas	24	22	28	27
Liocarcinus spp.	24	29	9	23
Eupagurus bernhardus	7	4	8	3
insects	-	1	-	-
echinoderms	-	1	-	1
fish	15	51	4	2
gadids	4	21	1	1
Whiting *Merlangius merlangus*	1	7	-	-
Cod *Gadus morhua*	1	2	-	-
Bib *Trisopterus luscus*	1	1	-	-
Haddock *Melanogr. aeglefinus*	-	1	-	-
Saithe *Pollachius virens*	-	1	-	-
not identified to species	3	15	1	1
clupeids	-	3	-	-
Herring *Clupea harengus*	-	1	-	-
not identified to species	-	2	-	-
Garfish *Belone belone*	2	5	-	-
gurnards	3	10	-	-
Mackerel *Scomber scombrus*	-	1	-	-
Scad *Trachurus trachurus*	2	3	1	1
dragonets	1	3	-	-
Hooknose *Agonus cataphractus*	-	1	-	-
flatfish	8	7	1	-
Dab *Limanda limanda*	4	2	-	-
not identified to species	4	5	1	-
not identified	1	3	-	1
birds/eggs	-	2	-	9
mammals	-	1	-	1
cereals	1	-	-	-
fruits	-	1	-	1
other plant material	1	2	1	1
garbage	2	1	-	-

Table 2. Origin of the diet of all pellets from Lesser Black-backed Gull and Herring Gull. Values are given as frequency of occurrence (in %). Differences between periods and species were tested by the g-test. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *n.s.* = not significant

	Lesser Black-backed Gull			Herring Gull				
	incubation period	chick-rearing period	diff. betw. periods	incubation period	chick-rearing period	diff. betw. periods	diff. betw. species incub.	chick-r.
no. pellets	103	165		80	179			
intertidal zone	69	28	***	93	76	***	***	***
open sea (pelagic)	26-27	38-39	*	9	23	**	**	**
discard	19-20	45-47	***	11	4	n.s.	n.s.	***
terrestrial	3	7	n.s.	1	8	*	n.s.	n.s.

chick-rearing in Lesser Black-backed Gulls, whereas the frequencies of occurrence of the dietary components remained relatively constant in Herring Gulls (Table 1). Lesser Black-backed Gulls took prey from all three marine habitats. Herring Gulls mainly utilised food from the intertidal zone in both periods (Table 2).

Numbers of adult Lesser Black-backed Gulls present in the colony varied between 47 and 234 (mean ± SD, 116 ± 34, $n = 209$), those of Herring Gulls between 60 and 212 (120 ± 35). In the Lesser Black-backed Gull (stepwise multiple regression model: $n = 209$, $P < 0.001$), numbers present in the colony decreased significantly throughout the breeding season and reached highest values around noon (Fig. 2). 47% of the variance (adjusted $R^2_{4,208}$) in the numbers of Lesser Black-backed Gull could be explained by the date. Time of day explained further 11% of the residuals, wind direction another 2%.

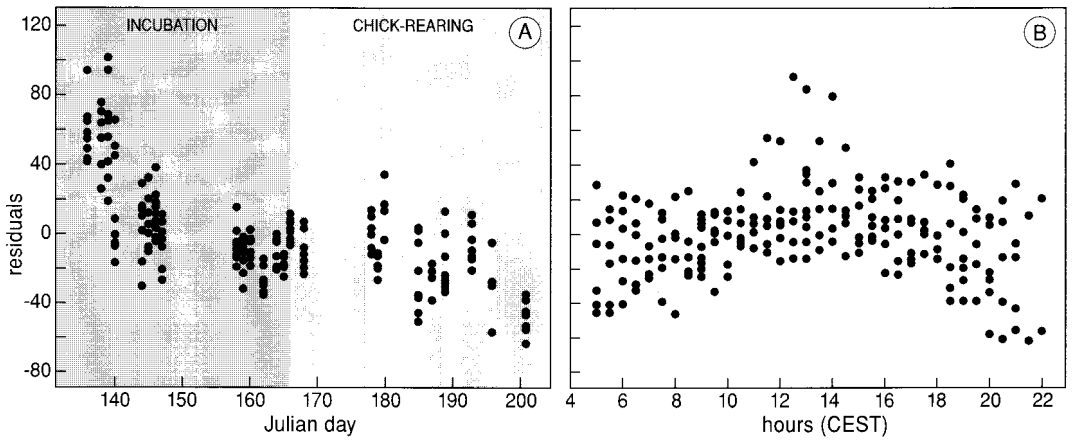

Fig. 2. Presence of adult Lesser Black-backed Gulls in the colony expressed as residuals of multiple regressions with the two most important significant independent variables; (A) in relation to season (as Julian day; corrected for the influence of time of day and wind direction), (B) in relation to time of day (corrected for the influence of Julian day and wind direction).

Table 3. Mean numbers (± SE) of gulls returning to the colony per 15 min period from the open sea and from the Wadden Sea, respectively. Levene's test for equality of variances revealed significantly different variances in all cases ($P < 0.05$). Hence, a t-test for unequal variances was applied. n = number of counts.

Incubation period	offshore (n)	Wadden Sea (n)	t-value
Lesser Black-b. Gull	5.94 ± 0.48 (105)	1.00 ± 0.14 (80)	9.83 ($P < 0.001$)
Herring Gull	4.63 ± 0.35 (105)	4.54 ± 0.77 (64)	0.10 ($P = 0.920$)
Chick-rearing period	**offshore (n)**	**Wadden Sea (n)**	**t-value**
Lesser Black-b. Gull	13.51 ± 0.87 (72)	1.56 ± 0.16 (110)	13.6 ($P < 0.001$)
Herring Gull	11.18 ± 1.13 (72)	10.19 ± 0.61 (126)	0.78 ($P = 0.439$)

In the Herring Gull (stepwise multiple regression model: $n = 209$, $P < 0.001$), the tidal stage had the strongest influence (explaining 44% of the variance in numbers; Fig. 3). Lowest numbers were observed around low tide, highest shortly prior to high tide. The next important factor was Julian day, explaining a further 12% of the variance. The influence of both wind direction (further 5%) and wind speed (further 2%) was small but still significant. Both in the incubation period and in the chick rearing period, Lesser Black-backed Gulls performed foraging trips significantly more often to the open sea than into the Wadden Sea (Table 3). The ratio increased from sixfold in the incubation period to almost ninefold in the chick rearing period. In contrast, no differences in the numbers of birds commuting from the Wadden Sea and from offshore areas, respectively, were detected in the Herring Gull.

Nest attendance time did not differ between

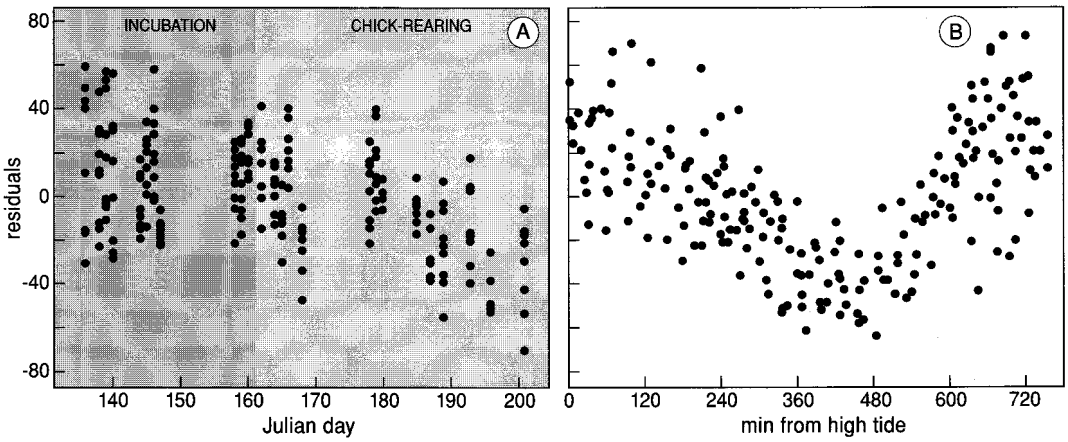

Fig. 3. Presence of adult Herring Gulls in the colony expressed as residuals of multiple regressions with the two most important significant independent variables; (A) in relation to Julian day (corrected for the influence of tidal stage, wind direction and wind speed), (B) in relation to tidal stage (corrected for the influence of Julian day, wind direction and wind speed).

Lesser Black-backed Gulls (99.6% of total time) and Herring Gulls (99.6%) during incubation (χ^2_1 = 0.02, n.s.). It was, however, significantly longer in Lesser Black-backed Gulls (92.0%) during the chick-rearing period than in Herring Gulls (68.0%; χ^2_1 = 60.26, $P < 0.001$). Hatching success was 2.3 chicks pair^{-1} (n = 24 nests) for Lesser Black-backed Gulls and 2.2 chicks pair^{-1} (n = 17) for Herring Gulls. Fledging success was 1.8 (n = 12) and 1.1 chicks pair^{-1} (n = 14), respectively. However, neither hatching (U = 190.5, P = 0.697) nor fledging success (U = 55.0, P = 0.116) differed significantly between Lesser Black-backed Gulls and Herring Gulls (Mann-Whitney U-test).

Lesser Black-backed Gulls won significantly more interspecific interactions than did Herring Gulls in the chick-rearing period (148 versus 60 occasions, respectively; χ^2_1 = 37.23, $P < 0.001$), while there was no significant difference in the incubation period (21 versus 18 occasions, respectively; χ^2_1 = 0.24, n.s.). Herring Gulls intruded significantly more often into Lesser Black-backed Gull territories than vice versa (128 versus 89 occasions, respectively; χ^2_1 = 7.01, $P <$ 0.01).

DISCUSSION

It was shown in the introduction that the populations of Lesser Black-backed and Herring Gulls have developed differently (Fig. 1). But what does this mean with respect to the reasons for these trends? Are the two species subject to interspecific competition?

We found evidence that important aspects of the foraging habits differ remarkably between the two species. Lesser Black-backed Gulls chiefly fed on prey at the open sea. In contrast, Herring Gull foraging was strongly influenced by the tide. These birds fed predominantly in the intertidal zone, and their main prey were molluscs and crustaceans. Differences were also apparent in the breeding ecology where nest attendance patterns showed that Herring Gull chicks were much less attended by their parents than were Lesser Black-backed Gull chicks. Lesser Black-backed Gulls won significantly more aggressive interactions with Herring Gulls than *vice versa* in the chick-rearing phase, although the Lesser Black-backed Gull is about 16% lighter and 2% smaller in body length (Cramp & Simmons 1983). In general, larger-sized birds have a competitive advantage in interspecific interactions (Burger & Shisler 1978; Burger 1983; Garthe & Hüppop 1998). In addition, Lesser Black-backed Gulls drove some Herring Gulls out of their territories even when they returned to the breeding colony after Herring Gulls had already established territories (Dominique Wölke pers. observ.).

There are several topics which suggest that Lesser Black-backed Gulls fare better than Herring Gulls. Lesser Black-backed Gulls fed much more upon fish and much less upon intertidal invertebrates than Herring Gulls. This may affect reproductive performance since the different food items differ e.g. in energy, protein, calcium and amino-acids contents (Cummins & Wuycheck 1971; Sidwell 1981). Lesser Black-backed Gulls in The Netherlands which fed regularly on land were at a disadvantage compared with conspecifics which went almost exclusively to the open sea (Spaans *et al.* 1994). In Dutch Herring Gulls, Bukacińska *et al.* (1996) found that successful pairs took more fish and chicks than unsuccessful pairs. However, at least in this species, invertebrates such as mussels or crabs can warrant a high reproductive output, too (Pierotti & Annett 1990, this study). Hence, the influence of the different food choice on the reproductive performance of the two species on Amrum might have been fairly small. Herring Gulls employed much more time in finding suitable food as shown by the nest attendance patterns. Poor nest attendance has been interpreted as a sign of either low parental quality (Morris 1987) or insufficient food availability (Cairns 1987; Bukacińska *et al.* 1996). Even if both cases were not valid, lower chick attendance in Herring Gulls than in Lesser Black-backed Gulls make them much more vulnerable to predation (e.g. Morris & Black 1980). Lesser Black-backed Gulls are more successful in inter-

specific aggressive interactions. This can lead to higher predation rates of Herring Gull offspring as well as to losses in preferred breeding sites but interspecific interaction rates were generally not very high and other evidence is rather circumstantial. Lesser Black-backed Gulls tended to have better reproductive performance. Despite this, the fledging success of Herring Gulls on Amrum is high, that of Lesser Black-backed Gulls very high if compared to other study areas (Bezzel 1985).

The sudden increase of Lesser Black-backed Gulls occurred when Herring Gull numbers had already stagnated. Apparent disadvantages of the latter can only have led to the relaxation and stop of the population increase if Herring Gulls were behaving differently in previous decades. This is not supported by dietary analyses in the German Bight as marine invertebrates from the intertidal zone, particularly molluscs and crustaceans, have formed more or less consistently the bulk of the diet over the second half of this century, even if the proportion of fish appears to have been slightly larger in the 1960s and 1970s than nowadays (Vauk & Prüter 1987; Goethe 1991). As both species have similar success and kleptoparasitic performance when foraging at fishing vessels (Camphuysen 1994; Garthe & Hüppop 1998), Camphuysen (1995) concluded that there is no evidence that Lesser Black-backed Gulls have outcompeted Herring Gulls at fishing vessels.

We conclude that the interspecific differences in feeding ecology, aggressive behaviour and reproductive traits could well have influenced the different population trends of the two gull species. In the longer term, Lesser Black-backed Gulls appear to have filled an empty niche rather than have outcompeted Herring Gulls. Thus, our findings nicely fit the 'competitive exclusion principle' that states that complete competitors cannot exist (Hardin 1960; Wiens 1989). The two species of gulls are able to coexist because they have quite different foraging strategies, and hence avoid competition for food, and they have slightly different nesting habitats (e.g. Harris 1964; Calladine 1997).

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SAMENVATTING

Terwijl de aantallen broedende Kleine Mantelmeeuwen *Larus graellsii* langs de Duitse Waddenkust sinds de jaren tachtig exponentieel toenemen, zijn de aantallen Zilvermeeuwen *Larus argentatus* min of meer gelijk gebleven. Om te onderzoeken of er relaties zijn te vinden tussen enkele ecologische eigenschappen van de

twee soorten en de verschillen in aantalsontwikkeling, worden in dit artikel gegevens over voedselkeuze, aanwezigheid in de kolonie, broedsucces en agressief gedrag besproken die in een gemengde broedkolonie in 1994 en 1995 op het Noordfriese eiland Amrum werden verzameld. Tijdens het bebroeden van de eieren aten Kleine Mantelmeeuwen voornamelijk schaal- en schelpdieren, die op het wad werden verzameld. In de jongentijd aten ze voornamelijk schaaldieren en vis, die op de Noordzee als visafval bij trawlers werden gevonden. Het voedsel van de Zilvermeeuwen bestond uit schelp- en schaaldieren, die voornamelijk op het wad werden verzameld. De aantallen Kleine Mantelmeeuwen in de kolonie waren het grootst in het begin van het broedseizoen en midden op de dag. De aanwezigheid van Zilvermeeuwen nam ook in de loop van het broedseizoen af, maar waren steeds het talrijkst tijdens hoogwater. Zilvermeeuwen gingen vanuit de kolonie zowel de Noordzee als de Waddenzee op. Vrijwel alle Kleine Mantelmeeuwen vlogen vanuit de kolonie naar de Noordzee. In de jongentijd spendeerden Kleine Mantelmeeuwen meer tijd bij het nest dan Zilvermeeuwen, en hun broedsucces was dan ook hoger (zij het statistisch niet significant). Kleine Mantelmeeuwen wonnen het meestal in gevechten met Zilvermeeuwen. Dat de aantallen Kleine Mantelmeeuwen toenemen, terwijl die van Zilvermeeuwen gelijk blijven lijkt te kunnen worden verklaard doordat de kwaliteit van het mantelmeeuwenvoedsel momenteel hoger is. De auteurs achten het niet waarschijnlijk dat Kleine Mantelmeeuw de Zilvermeeuwen er door concurrentie zouden uitdrukken. (TP)

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