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Interspecific differences in foraging preferences, breeding performance and demography in herring (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) at a mixed colony

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Abstract

Herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus* breeding at Walney Island, Cumbria, the largest breeding colony of the two species in the UK, have recently shown very different population trends. The former has declined sharply, whereas numbers of the latter have been maintained for several years. Here we compare aspects of the feeding and breeding ecology of the two species in order to examine whether or not this suggests explanations for their different population trends. Comparison of the ratio of the two species in flight lines leading to different feeding sites and their diet composition showed that the lesser black-backed gulls fed more at sea and the herring gulls fed more in the intertidal zone. Urban resources were used by both these species. These differences have been consistent over the last three decades. Susceptibility to death from botulism at the breeding colony was the same for the two species. The availability of the intertidal zone for foraging appears to have declined in recent years, and this may have had a more negative impact on the herring gull. However, the breeding success of the two species remains relatively high. This study suggests that differences in foraging behaviour and food availability during the breeding season are unlikely to be responsible for the marked differences in demographic trends in the two species. Changes in local food availability during the winter would be expected to have more effect on the resident herring gull. This work highlights the need for more detailed studies of the ecology of both species during the breeding season and in winter in regions showing differing patterns of population change.

Introduction

For seasonally breeding birds, the pattern of food availability is an important environmental factor, influencing annual productivity, survival and thereby population dynamics. Where two closely related species breed sympatrically, they often show different foraging preferences, which can involve differences in prey size or type, or foraging habitat (Witt *et al.*, 1981; Mudge & Ferns, 1982; Pierotti & Annett, 1991; Chudzik, Graham & Morris, 1994; Bukacińska, Bukaciński & Spaans, 1996; González-Solís *et al.*, 1997*a*; Garthe *et al.*, 1999; Kubetzki & Garthe, 2003). Consequently, changes in local food availability may affect the two species in different ways, giving rise to differential patterns of population change.

The herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* both increased dramatically in numbers during the 20th century (Snow & Perrins, 1998; Calladine, 2004; Madden & Newton, 2004). As generalist and opportunistic feeders, they appear to have benefited from increased protection from human exploitation as well as from improved food availability through fishery discards and refuse tips (Furness & Monaghan, 1987). In the UK, the numbers of both herring and lesser black-backed gulls peaked in the early 1970s, since when a substantial decline has occurred in herring gull numbers at many breeding colonies (Madden & Newton, 2004). The largest colony of the two species in the UK is located at South Walney, Cumbria (Fig. 1). As with other UK colonies, numbers peaked at Walney in 1974, each species reaching an estimated 23 500 breeding pairs. Since then, the herring gull population at Walney has declined sharply (Madden & Newton, 2004). Interestingly, although the two species are closely related and have similar ecologies, the lesser black-backed gull has not shown the same declines (Fig. 2). At South Walney, *c.* 4400 pairs of herring gulls and 18 600 pairs of lesser black-backed gulls were recorded breeding in 2002 (Kim & Monaghan, 2005). It has been suggested that culling, botulism and effects of decreased food availability could be involved (Malling-Olsen & Larsson, 2003; Mitchell *et al.*, 2004), but supporting data for any of these possibilities are scarce.

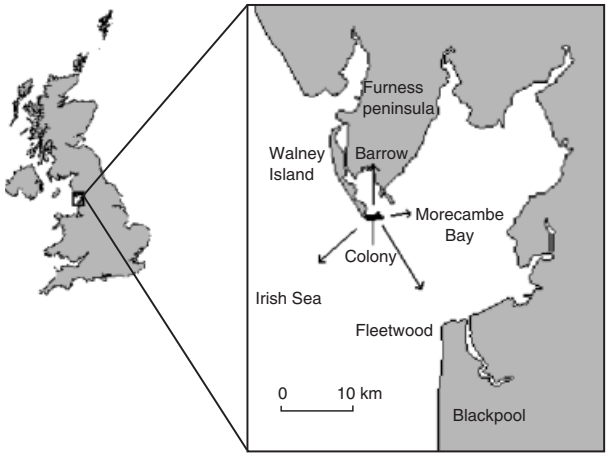

Figure 1 Location of the South Walney gull colony in northern England and the main flight lines of herring *Larus argentatus* and lesser black-backed gulls *Larus fuscus* around the colony.

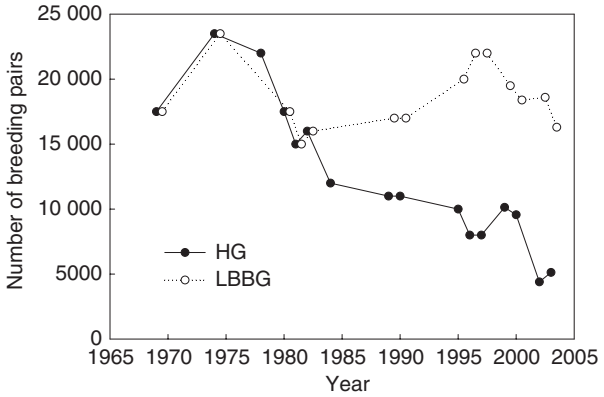

Figure 2 Changes in the breeding population of herring *Larus argentatus* and lesser black-backed gulls *Larus fuscus* at the South Walney colony. The counts were organized by the following. 1969: MacRoberts & MacRoberts (1972); 1974: Verbeek (1977); 1978, 1982, 1984: Dean (1991); 1980: Sibly & McCleery (1983); 1981, 1989–2003: Cumbria Wildlife Trust (unpubl. data). In most years, the total number of nests of the two species combined was counted during the incubation period; the number of each species was estimated from a ratio of the two obtained by direct counts of numbers of each breeding in selected areas of the colony.

In the present study, we focused on the breeding season, in order to ascertain whether or not there is any evidence of marked differences in food availability for the two species, and how diet and breeding performance compare with data collected when the populations of both species were expanding, and that of the herring gull was much larger than it is now. We examined the breeding performance, foraging behaviour, diet and colony-based mortality from apparent botulism during the breeding season in herring and lesser black-backed gulls breeding at Walney in 2002 and 2003 to assess the extent to which the differential action of these factors could explain the difference in the population trends observed for the two species. We compared the dietary and feeding behaviour data during the breeding season with earlier studies of the foraging preferences of the two species at the Walney colony in the early 1970s (Shaffer, 1971; Verbeek, 1977). At that time, the lesser black-backed gulls fed mainly at sea, in the surrounding fields and in local city areas. The herring gulls fed more on intertidal animals, and scavenged at fish docks and at refuse tips. We discuss the extent to which changes in environmental circumstances in breeding and wintering areas may be responsible for the strikingly different population trends of the two species.

Methods

Ratio of birds going to different feeding sites

Several discernible flight lines of gulls from Walney lead to feeding sites used by the breeding birds (Brown, 1967; Verbeek, 1977). To compare the current situation with that in the 1970s, we used methods similar to those of Verbeek (1977). We counted the relative proportions of the two species in these flight lines to examine whether the ratio was constant across the different foraging locations. The flight lines were clearly directed to the Irish Sea (marine area with fishing vessels), Barrow (urban area with refuse tips), Fleetwood (fish dock and urban area) and Morecambe Bay (tidal area with mussel and starfish beds) as shown in Fig. 1. The data were collected in April 2002 before egg laying in either species, because different timings of breeding between herring and lesser black-backed gulls (laying dates in 2003 expressed as number of days from 1 April = 1, herring gull: means $\pm$ SE, 39.41 ± 0.32; median, 39, $n = 256$; lesser black-backed gull: means $\pm$ SE, 46.49 ± 0.59; median, 47, $n = 111$; Mann–Whitney test: $U = 5611.50$, $P < 0.001$) could influence the results if the foraging behaviour of the majority of pairs of one species was restricted by incubation regimes, whereas that of the other was not (see also Verbeek, 1977). Counting was conducted from two hides and two points on the shore, where each flight line was observed easily using 8×20 binoculars. The data were collected during 20–60 min of observation five and eight times at each site, and the overall ratios of the two species for each flight line were used for analysis. Because we were interested in the relative proportions of the two species using the differing foraging opportunities when they are available, we timed observations to coincide with the availability of the feeding areas as in the other studies (Verbeek, 1977; Sibly & McCleery, 1983). Particularly, the flight line to Morecambe Bay was observed during the low tide when gulls are able to feed on intertidal molluscs. Verbeek's counting included one more feeding site than ours, the Walney refuse tip, located very close to the colony and where herring gulls predominated in 1973–1974. However, this closed in 2001.

Gull diets

Data on the diet composition of adult herring and lesser black-backed gulls were obtained from analysis of their regurgitated pellets. Although this method under-represents

soft-bodied prey, it is useful for assessing differences between species or changes in diet composition (Spaans, 1971; González-Solís *et al*., 1997*b*; Votier *et al*., 2001). Pellets from adult birds were collected from mid-April to May 2002 and 2003 during egg laying and incubation, because the pellets of adults and chicks are indistinguishable. The study areas were surveyed once daily and fresh pellets were identified and recorded. To facilitate comparisons with the earlier data, we categorized the food types as fish, marine mollusc, crab, grain/grass and refuse. As the boundary of each gull territory is often indistinguishable, it was not possible to identify precisely the individual that regurgitated each pellet. However, the species involved was readily identified because the nesting habitats of the two species are relatively segregated throughout the colony. Lesser black-backed gulls prefer topologically low areas whereas herring gulls most frequently nest in sand dunes (Kim & Monaghan, 2005). The analysed pellets were destroyed or retained to avoid replications in sampling. Pellets containing more than one item, although unusual, were categorized according to the main item in the pellet. These data were compared with those collected by Shaffer (1971) using similar methods.

Breeding performance

The data on breeding parameters of herring and lesser black-backed gulls were collected in 2003. The study areas were surveyed once daily during egg laying. All new nests containing an egg were recorded and marked with numbered bamboo sticks. Laying dates and clutch size were recorded for 256 herring and 111 lesser black-backed gull pairs. We visited each study nest until clutch completion. A total of 67 herring and 88 lesser black-backed gull nests with a complete three egg clutch (the modal clutch size in both species) were then randomly selected from the recorded nests to investigate reproductive performance. Eggs were individually marked on the day of laying. The expected hatching date was estimated by adding 30 days to the first egg-laying date and we checked each nest once daily beginning 2 days before the estimated hatching date until all the chicks were hatched. All chicks were marked with coloured leg flags on the day of hatching (day 0) for identification within each brood. Each nest was visited every 4 days until day 23 to check survival of chicks. Because chicks become more mobile and move further from their nest sites as they grow, it was not possible to track them after day 23 without causing undue disturbance. The breeding parameters, clutch size, hatching success and chick survival rate were compared between the two species using generalized linear models taking the egg-laying date into account. Models initially included all explanatory variables and two-way interactions. Final models were selected by sequentially dropping non-significant interactions and then non-significant main effects (Crawley, 2003). Because the timing of breeding differed slightly between the two species, lesser black-backed gulls laying slightly later than herring gulls, the proportional rank of laying date by species was used as a factor in all the models.

Investigation of disease incidence

The numbers of adult birds and chicks found dead at the nest site showing symptoms characteristic of botulism were also counted among the study nests for comparison between the two species. Botulism is a form of poisoning caused by ingestion of toxins produced by the anaerobic bacterium *Clostridium botulinum*. Birds with botulism were recognized by the typical symptoms of flaccid paralysis of the limbs and neck, ocular disturbances and respiratory distress (Smith, 1976). Birds that had died of botulism symptoms were recognizable as they kept the paralysed postures.

Results

Relative use of feeding sites

The observed numbers of the two species going to each feeding site were compared with the expected ratio based on the breeding populations at the South Walney colony in 2002. Birds going to the Irish Sea were significantly biased towards lesser black-backed gulls whereas those going to Barrow were in a ratio similar to that in which the two species were present in the breeding colony; Fleetwood and Morecambe Bay were herring gull biased (Table 1). This pattern was broadly similar to that recorded by Verbeek (1977) in 1973–1974.

Adult diet

The composition of regurgitated pellets of adult herring and lesser black-backed gulls during egg laying and incubation in 1970–1971 (reanalysis of Shaffer, 1971) and 2002–2003 is shown in Table 2. The proportion of pellets containing different prey types differed significantly between the two species in all the years when data were collected (Table 2; 1970: $\chi^2_4 = 36.68$, $P<0.001$; 1971: $\chi^2_4 = 47.19$, $P<0.001$; 2002: $\chi^2_4 = 18.06$, $P = 0.001$; 2003: $\chi^2_4 = 41.10$, $P<0.001$). Lesser black-backed gulls fed on fish more frequently than herring gulls in 3 out of 4 years, whereas herring gulls fed on marine molluscs more frequently. In 1970–1971, lesser black-backed gulls fed on crab more frequently, but there was no difference between the two species in 2002–2003. In most years, the two species fed on grain/grass and refuse with equal frequencies. Overall, in both time periods, the herring gull appeared to make more use of the intertidal areas with marine molluscs than did the lesser black-backed gull.

Interspecific comparison of breeding performance

Clutch size did not differ between herring and lesser black-backed gulls, with around 80% of birds producing three eggs (Table 3; generalized linear model with a Poisson error distribution and a log link: deviance $=-0.26$, d.f. $= 1$, $P = 0.607$), and egg-laying date did not influence clutch size in the study birds (deviance $=-0.57$, d.f. $= 1$, $P = 0.452$). Hatching success (proportion of eggs hatched) and chick survival rate to day 23 (proportion of chicks survived) were

Table 1 Percentage of herring *Larus argentatus* (HG) and lesser black-backed gulls *Larus fuscus* (LBG) in flight lines leading to different feeding sites

Feeding area	Duration of counting period (min)	HG (%)	LBG (%)	Total number	Interspecific comparison	
					χ^2_1	*P*
(a) *2002 (April)*						
Irish Sea	150	2.2	97.8	138	24.51	<0.001
Barrow	235	18.5	81.5	1317	0.33	0.57
Fleetwood	235	21.1	78.9	2369	5.03	<0.05
Morecambe Bay	225	32.1	67.9	1342	133.60	<0.001
Population (breeding pairs)		19.1	80.9	23000		
(b) *1973, 1974 (March–April)*[a]						
Irish Sea	361	4.3	95.7	1021	832.95	<0.001
Barrow	460	49.6	50.4	639	0.02	0.88
Fleetwood	488	63.3	36.7	3042	202.09	<0.001
Morecambe Bay	440	60.5	39.5	835	35.62	<0.001
Walney Dump	255	76.5	23.5	2092	563.09	<0.001
Population (breeding pairs)		50.0	50.0	47000		

The *P*-values are based on χ^2 tests comparing the numbers of the two species going to each feeding site, with expected values based on the population ratio at the Walney colony at the time.
[a]Verbeek (1977).

Table 2 Food composition (percentage of pellets of each type) of adult herring *Larus argentatus* (HG) and lesser black-backed gulls *Larus fuscus* (LBG) during egg laying and incubation phases

Food type	HG (%)	LBG (%)	Interspecific comparison		HG (%)	LBG (%)	Interspecific comparison	
			χ^2_1	*P*			χ^2_1	*P*
	(a) *1970 (19 April–18 June)*[a]				(b) *1971 (24 April–8 June)*[a]			
Fish	8.6	11.1	1.66	0.20	8.5	15.5	14.18	<0.001
Marine mollusc	30.9	14.2	35.49	<0.001	43.1	26.1	31.72	<0.001
Crab	17.5	22.5	4.10	<0.05	14.6	23.4	14.75	<0.001
Grain/grass	6.8	7.7	0.18	0.67	3.5	2.4	0.63	0.43
Refuse	36.2	44.4	7.23	<0.01	30.3	32.5	0.54	0.46
Total no. of pellets	1300	324			1493	329		
	(c) *2002 (5 April–31 May)*				(d) *2003 (12 April–5 May)*			
Fish	13.5	28.4	8.16	<0.01	9.2	29.5	19.46	<0.001
Marine mollusc	16.5	9.9	2.07	0.15	52.3	18.9	28.82	<0.001
Crab	8.3	10.6	0.21	0.64	7.3	5.3	0.18	0.67
Grain/grass	30.8	14.9	9.04	<0.01	7.8	15.8	3.77	0.05
Refuse	30.8	36.2	0.65	0.42	23.4	30.5	1.41	0.23
Total no. of pellets	133	141			218	95		

[a]Shaffer (1971).

examined in the nests with the modal three egg clutches in order to see if either of the two species appeared to be experiencing difficulties in finding food. The proportion of eggs hatched differed little between the two species (Table 3; generalized linear model with a binomial error distribution and a logit link: $F = 0.74$, d.f. = 1, $P = 0.390$) when relative egg-laying date was taken into account ($F = 3.91$, d.f. = 1, $P = 0.048$). Overall, 62.8% of herring gull chicks and 56.04% of lesser black-backed gull chicks survived to day 23. When the effect of egg-laying date was taken into account ($F = 6.74$, d.f. = 1, $P = 0.009$), the proportion of chicks surviving to day 23 in each brood did not differ between the species (Table 3; $F = 1.90$, d.f. = 1, $P = 0.168$).

Interspecific comparison of disease incidence

The ratio of herring gulls to lesser black-backed gulls among birds that died of apparent botulism in the study nest sites did not differ from that expected from the total numbers of the two species in both adults and chicks during the 2003 breeding season (Table 4).

Discussion

A number of factors are likely to be involved in the population changes of herring and lesser black-backed gulls at Walney, but the different pattern in the two species since

Table 3 Breeding parameters of herring *Larus argentatus* (HG) and lesser black-backed gulls *Larus fuscus* (LBG) at the Walney colony in 2003

	Number of eggs or chicks at the nes†					Total number
	0 (%)	1 (%)	2 (%)	3 (%)	4 (%)	of nests
(a) *Clutch size*						
HG		6.3	15.2	78.5		256
LBG		2.7	15.3	79.3	2.7	111
(b) *Number of eggs hatched from three egg clutches*						
HG	4.5	7.5	26.9	61.2		67
LBG	9.1	4.5	28.4	58.0		88
(c) *Number of chicks surviving until day 23 from three egg clutches*						
HG	18.8	21.9	39.1	20.3		64
LBG	33.8	12.5	28.8	25.0		80

Table 4 Numbers of adult birds and chicks dying of botulism in herring *Larus argentatus* (HG) and lesser black-backed gulls *Larus fuscus* (LBG)

	HG		LBG		Interspecific comparison	
	Total	Botulism	Total	Botulism	χ^2_1	*P*
Adult	134	5	176	7	0.03	0.85
Chick	164	9	206	7	0.52	0.47

The χ^2 test are based on comparisons of the numbers of the two species to expected values based on the ratio in the study birds.

the 1980s is particularly interesting and potentially illuminating. Since 1975, many gulls at the Walney colony have apparently died of botulism (Smith, 1982; Ortiz & Smith, 1994). The number of gulls dying of this cause is increasing every year (T. Chadwick, pers. obs.), but there is scant information on its effect on breeding numbers of the two species. Our data on this are limited to one breeding season and involve relatively small numbers of birds. Nonetheless, if there was a major difference in susceptibility of the two species, as would be required for this to explain the striking difference in population trends, this should have been evident from our sample. In fact, the relative mortality at the colony attributable to botulism (or whatever disease shows similar symptoms) during the breeding season did not differ between the two species in either adults or chicks during 2003. This suggests that the herring gull is not more susceptible than the lesser black-backed gull. Thus, differences in adult mortality at the colony from this cause during the breeding season do not appear to explain the different population dynamics of the two species. However, more detailed studies are needed of the potential role of disease in the population dynamics of the two species.

There is a possibility that culling of gulls may have influenced the population trends. The large gull species were culled at many colonies throughout the UK (Coulson, Duncan & Thomas, 1982), but no significant culling has taken place at the Walney colony itself. Since 1978, large-scale culls have been carried out at the Abbeystead gull colony close to Walney, which could influence recruitment into the Walney colony. However, this does not explain the herring gull-biased population decline at Walney, because the Abbeystead colony is mainly lesser black-backed gulls, and consequently many more lesser black-backed gulls have been culled there than herring gulls (Duncan, 1981; Wanless & Langslow, 1983).

Many studies have reported interspecific competition for food between herring and lesser black-backed gulls (Den Boer, 1986; Furness, Ensor & Hudson, 1992; Noordhuis & Spaans, 1992). However, they do show some differences in feeding preferences, with the lesser black-backed gull generally being considered more marine (Cramp, Bourne & Saunders, 1974). Our data are based on the relative proportions of the two species in flight lines, and the diet as indicated by pellets. Both have their limitations in that the proportional use of food sources by the two species when they are available does not tell us about the overall use of that feeding area, and the pellets do not provide information on food without hard parts, for example fish offal and earthworms. Together though, the two methods provide information on any major differences between the two species. Overall, our results on percentage of herring and lesser black-backed gulls in flight lines leading to different feeding sites before egg laying supported this. Although we made our observations over shorter time periods than did Verbeek (1977), our result effectively confirms the general behaviour pattern typical of this species. Birds going to the Irish Sea were biased towards lesser black-backed gulls. It is known that lesser black-backed gulls are more successful than herring gulls in feeding on fishery wastes from fishing boats at sea (Furness *et al*., 1992; Noordhuis & Spaans, 1992). The ratio of birds flying to the Morecambe Bay area was herring gull biased, reflecting their more intertidal foraging, as also shown in other studies (Garthe *et al*., 1999; Kubetzki & Garthe, 2003) and supported by the pellet data in this study. The ratio of the two species flying to urban areas did not differ from that at the colony, suggesting that this source was equally used by the two gulls. Barrow town, where there are several refuse tips, has long been one of the main food resources for the Walney gulls. The refuse tip at Walney Island was in the past more frequently used by herring gulls than lesser black-backed gulls, probably because the herring gull is more competitive at such feeding sites, particularly when the sites are close to the breeding colony (Mudge & Ferns, 1982; Sibly & McCleery, 1983). However, the closure of this tip (in 2001) occurred well after the herring gull had started to decline. Fleetwood has been a major fishing port for the last 90 years and it has facilities for fish handling and a fish hall with a daily auction. Even though a number of lesser black-backed gulls also flew towards Fleetwood, Verbeek (1977) found that most of the gulls feeding on fish scraps around the fish hall were herring gulls (99.4%).

Over the past 10 years or so, there has been an influx of itinerant mussel fishermen all around the Morecambe Bay area, and recently cockling has also taken place in this area (Andrews, 2003). Wildfowl species feeding in the intertidal

area have been hit badly by commercial shellfishing, although some species show a reduction in the rate of decline in recent years (Makin, 1998). Such a change in shellfish availability may have negatively influenced food availability for the more intertidal herring gull during both breeding and wintering periods.

The importance of fishery wastes as a food resource for *Larus* species has been reported in many studies (Furness & Monaghan, 1987; Furness *et al*., 1992; Oro, 1996; Oro *et al*., 1997; Arcos & Oro, 2002). The fishery management report of ICES shows that the catch of fish in the Irish Sea has declined dramatically since the mid-1980s. However, whiting discard data, the most important index of food availability for gulls that forage in the Irish Sea, have not shown declines of the same magnitude (Fig. 3a). The majority of vessels in the Irish Sea target *Nephrops* with either single or twin-rig otter trawls. These vessels have bycatches of whiting (most of which are discarded), haddock, cod and plaice (ICES, 2003). Although discarding whiting is considered a major problem for the *Nephrops* fishery in a fish conservation context, the discards can provide high-quality diet to the gulls that forage round the fishing vessels in the Irish Sea, particularly lesser black-backed gulls. The amount of fish landings in the Fleetwood fish dock has decreased sharply (Fig. 3b), probably suggesting that food became less available for the scavengers that forage around the dock and fish hall, particularly herring gulls. In contrast, refuse tips seem a relatively stable and predictable food resource for the gulls all year around. In North West England, between 1996 and 2002, the amount of municipal waste taken to refuse tips increased by around 10% from 3 278 000 to 3 612 000 tonnes in total, and currently there are 18 refuse tips in Cumbria (DEFRA, 2003). Refuse tips have contributed to the growth of some gull populations by providing a local and abundant food resource (Pons, 1992; Sol, Arcos & Senar, 1995).

How might such changes in food supply result in different population fluctuations in herring and lesser black-backed gulls? It would appear that changes in food availability in the intertidal area and at the fish dock have occurred, and this would be expected to influence particularly the herring gull. Fishery discards at sea on the other hand, favoured by the lesser black-backed gull, do not seem to have changed to much extent. Many studies have shown the importance of food availability for breeding success in seabird species (Monaghan *et al*., 1989; Danchin, 1992; Monaghan, Uttley & Burns, 1992; Uttley *et al*., 1994; Oro, Bosch & Ruiz, 1995). Even though diet composition during the breeding season differed between herring and lesser black-backed gulls, our results from 2003 showed that breeding success did not differ between the two species and is relatively good. It is possible that post fledging survival is poorer in herring than in lesser black-backs. Furthermore, because the distribution of the two species differs depending on the time of year, one has to consider the effects of food supply separately on their breeding success and winter survival.

Lesser black-backed gulls typically migrate to the coast of the Mediterranean and North Africa. Although the winter-

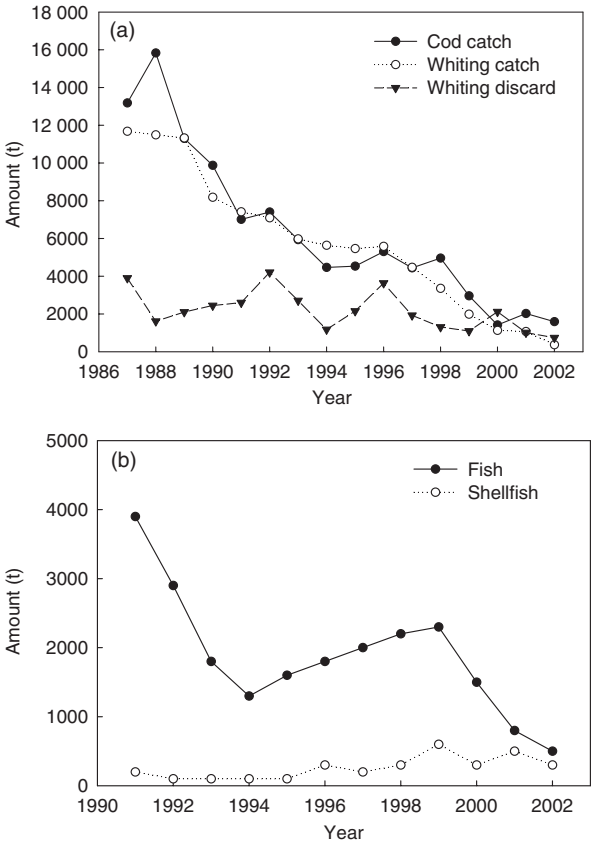

Figure 3 Changes in food availability around the Walney colony: (a) amount of fish catch and discards in the Irish Sea; (b) amount of fish and shellfish landings at Fleetwood fish dock (ICES, 2003).

ing pattern of the lesser black-backed gull is changing, relatively few winter in northern England or the Solway Firth area (Burton *et al*., 2003). Herring gulls generally undergo some southerly movements, but are broadly resident within the UK (Snow & Perrins, 1998; Malling-Olsen & Larsson, 2003). Because of their different winter distribution and difference in wintering environments, the two species may show different winter survival rates. It is therefore possible that changes in winter food supply in the intertidal zone have altered herring gull mortality. Such changes may have also altered the wintering behaviour of immature birds and reduced recruitment to the Walney colony, because the locations to which young birds disperse in winter play a part in their subsequent recruitment to breeding colonies (Duncan & Monaghan, 1977). It is clear from the recent Seabird 2000 census (Mitchell *et al*., 2004) that the distribution of the lesser black-backed gull in the UK is becoming more southerly. Although the species has continued to increase overall in the UK and Ireland, colonies in north-east Scotland have shown substantial declines. Despite their being relatively common birds, we do in fact know relatively little about regional variation in the diet of the two species or of the wintering ecology of the lesser black-backed gull in particular. Interestingly, numbers have generally increased in urban

areas for both species, although urban nesting still involves a relatively small percentage of the breeding birds (Mitchell *et al*., 2004). More extensive studies on breeding and wintering ecology of the two species are needed in populations showing different population trends.

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References

Andrews, J. (2003). Sands of change portrait of the cockle fishery in Morecambe Bay: November 2002–October 2003. *CEFAS: Shellfish News* **16**, 21–24.

Arcos, J.M. & Oro, D. (2002). Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). *Mar. Biol.* **141**, 277–286.

Brown, R.G.B. (1967). Species isolation between the herring gull *Larus argentatus* and lesser black-backed gull *L. fuscus*. *Ibis* **109**, 310–317.

Bukacińska, M., Bukaciński, D. & Spaans, A.L. (1996). Attendance and diet in relation to breeding success in herring gulls (*Larus argentatus*). *Auk* **113**, 300–309.

Burton, N.H.K., Musgraove, A.J., Rehfish, M., Sutcliffe, A. & Waters, R. (2003). Numbers of wintering gulls in the United Kingdom, Channel Islands and Isle of Man: a review of the 1993 and previous winter gull roost surveys. *Br. Birds* **96**, 376–401.

Calladine, J. (2004). Lesser black-backed gull *Larus fuscus*. In *Seabird population of Britain and Ireland*: 242–261. Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T.E. (Eds). London: T & AD Poyser.

Chudzik, J.M., Graham, K.D. & Morris, R.D. (1994). Comparative breeding success and diet of ring-billed and herring gulls on South Limestone Island, Georgian Bay. *Colon. Waterbird* **17**, 18–27.

Coulson, J.C., Duncan, N. & Thomas, C. (1982). Changes in the breeding biology of the herring gull (*Larus argentatus*) induced by reduction in the size and density of the colony. *J. Anim. Ecol.* **51**, 739–756.

Cramp, S., Bourne, W.R.P. & Saunders, D. (1974). *The seabirds of Britain and Ireland*. London: Collins.

Crawley, M.J. (2003). *Statistical computing: an introduction to data analysis using S-Plus*. Chichester: John Wiley & Sons.

Danchin, É. (1992). Food shortage as a factor in the 1988 kittiwake *Rissa tridactyla* breeding failure in Shetland. *Ardea* **80**, 93–98.

Dean, T. (1991). *Walney Island*. London: Hodder & Stoughton.

DEFRA (2003). *E-digest of environmental statistics*. At http://www.defra.gov.uk/environment/statistics/index.htm

Den Boer, P.J. (1986). The present status of the competitive exclusion principle. *Trends Ecol. Evol.* **1**, 25–28.

Duncan, N. (1981). The Abbeystead and Mallowdale gull colony before colony. *Bird Study* **28**, 133–138.

Duncan, N. & Monaghan, P. (1977). Infidelity to the natal colony by breeding herring gulls. *Ring. Migr.* **1**, 166–172.

Furness, R.W., Ensor, K. & Hudson, A.V. (1992). The use of fishery waste by gull populations around the British Isles. *Ardea* **80**, 105–113.

Furness, R.W. & Monaghan, P. (1987). *Seabird ecology*. Glasgow: Blackie.

Garthe, S., Freyer, T., Hüppop, O. & Wölke, D. (1999). Breeding lesser black-backed gulls *Larus graellsii* and herring gulls *Larus argentatus*: coexistence or competition? *Ardea* **87**, 227–236.

González-Solís, J., Oro, D., Jover, L., Ruiz, X. & Pedrocchi, V. (1997*a*). Trophic niche width and overlap of two sympatric gulls in the south western Mediterranean. *Oecologia* **112**, 75–80.

González-Solís, J., Oro, D., Pedrocchi, V., Jover, L. & Ruiz, X. (1997*b*). Bias associated with diet samples in Audouin's gulls. *Condor* **99**, 773–779.

ICES (2003). *Report of the Advisory Committee on Fishery Management, 2003*. ICES Cooperative Research Report No. 261, Copenhagen.

Kim, S.-Y. & Monaghan, P. (2005). Interacting effects of nest shelter and breeder quality on behaviour and breeding performance of herring gulls. *Anim. Behav.* **69**, 301–306.

Kubetzki, U. & Garthe, S. (2003). Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. *Mar. Biol.* **143**, 199–207.

MacRoberts, B.R. & MacRoberts, M.H. (1972). Social stimulation of reproduction in herring and lesser black-backed gulls. *Ibis* **114**, 495–506.

Madden, B. & Newton, S.F. (2004). Herring gull *Larus argentatus*. In *Seabird population of Britain and Ireland*: 242–261. Mitchell, P.I., Newton, S.F., Ratcliffe, N. & Dunn, T.E. (Eds). London: T & AD Poyser.

Makin, B. (1998). South Walney – past, present and future. *Cumbria Wildl.* **51**, 9–13.

Malling-Olsen, K. & Larsson, H. (2003). *Gulls of Europe, Asia and North America*. London: Christopher Helm.

Mitchell, I.P., Newton, S.F., Ratcliffe, N. & Dunn, T.E. (2004). *Seabird populations of Britain and Ireland*. London: T & AD Poyser.

Monaghan, P., Uttley, J.D. & Burns, M.D. (1992). Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea*. *Ardea* **80**, 71–81.

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C. & Blackwood, J. (1989). The relationship between food supply, reproductive effort and breeding success in Arctic terns *Sterna paradisaea*. *J. Anim. Ecol.* **58**, 261–274.

Mudge, G.P. & Ferns, P.N. (1982). The feeding ecology of five species of gulls (Aves: Larini) in the inner Bristol Channel. *J. Zool. (Lond.)* **197**, 497–510.

Noordhuis, R. & Spaans, A.L. (1992). Interspecific competition for food between herring *Larus argentatus* and lesser black-backed gulls *L. fuscus* in the Dutch Wadden Sea area. *Ardea* **80**, 115–132.

Oro, D. (1996). Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. *Mar. Ecol. Prog. Ser.* **132**, 43–46.

Oro, D., Bosch, M. & Ruiz, X. (1995). Effects of a trawling moratorium on the breeding success of the yellow-legged gull *Larus cachinnans*. *Ibis* **137**, 547–549.

Oro, D., Ruiz, X., Jover, L., Pedrocchi, V. & González-Solís, J. (1997). Diet and adult time budgets of Audouin's gull *Larus audouinii* in response to changes in commercial fisheries. *Ibis* **139**, 631–637.

Ortiz, N.E. & Smith, G.R. (1994). Landfill sites, botulism and gulls. *Epidemiol. Infect.* **112**, 385–391.

Pierotti, R. & Annett, C.A. (1991). Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. *Ecology* **72**, 319–328.

Pons, J.-M. (1992). Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. *Ardea* **80**, 143–150.

Shaffer, L.C. (1971). *Specialisations in the feeding behaviour of gulls and other birds*. PhD thesis, University of Oxford.

Sibly, R.M. & McCleery, R.H. (1983). The distribution between feeding sites of herring gulls breeding at Walney Island, U.K. *J. Anim. Ecol.* **52**, 51–68.

Smith, G.R. (1976). Botulism in waterfowl. *Wildfowl* **27**, 129–138.

Smith, G.R. (1982). Botulism in waterfowl. *Symp. Zool. Soc. Lond.* **50**, 97–119.

Snow, D. & Perrins, C.M. (1998). *The birds of the western Palearctic*. Oxford: Oxford University Press.

Sol, D., Arcos, J.M. & Senar, J.C. (1995). The influence of refuse tips on the winter distribution of yellow-legged gulls *Larus cachinnans*. *Bird Study* **42**, 216–221.

Spaans, A.L. (1971). On the feeding ecology of the herring gull *Larus argentatus* Pont. in the northern part of the Netherlands. *Ardea* **59**, 73–188.

Uttley, J.D., Walton, P., Monaghan, P. & Austin, G. (1994). The effects of food abundance on breeding performance and adult time budgets of guillemots *Uria aalge*. *Ibis* **136**, 205–213.

Verbeek, N.A.M. (1977). Comparative feeding ecology of herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus*. *Ardea* **65**, 25–42.

Votier, S.C., Bearhop, S., Ratcliffe, N. & Furness, R.W. (2001). Pellets as indicators of diet in great skuas *Catharacta skua*. *Bird Study* **48**, 373–376.

Wanless, S. & Langslow, D.R. (1983). The effects of culling on the Abbeystead and Mallowdale gullery. *Bird Study* **30**, 17–23.

Witt, H.-H., Crespo, J., De Juana, E. & Varela, J. (1981). Comparative feeding ecology of Audouin's gull *Larus audouinii* and the herring gull *L. argentatus* in the Mediterranean. *Ibis* **123**, 519–526.