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The annual cycle, breeding biology and feeding ecology of the Lesser Black-backed Gull *Larus fuscus*

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The population increase of Lesser Black-backed Gulls in The Netherlands triggered investigations into life-history, migratory movements and foraging ecology during 16 years of nest-monitoring, colour-ringing and GPS-tracking on the island of Texel (Wadden Sea). The main objective was to obtain comprehensive ecological data on breeding performance within the context of the annual cycle, shifts in resources, prey types and habitat use. Migration strategies ranged from short- (France, England), medium- (Portugal, Spain) to long-distance (NW Africa), utilising marine, coastal or terrestrial, region-specific resources. Young birds travelled on average further than older individuals. Strong within-colony philopatry was found, this was strongest in males. Assessments of mate-fidelity indicated serial, social monogamy. Unexpectedly, given increasing population trends when the study commenced, fledging rates were low and declining egg volumes, smaller hatchlings, declining mass at fledging and high levels of cannibalism indicated structural food stress. Fledgling mass was well below that of chicks in historical studies, suggesting insufficient provisioning. Breeding was highly synchronised and early nesters fledged more young than late pairs. The onset of breeding was significantly delayed over the years, chick depredation rates declined, overall breeding success became more variable. Marine, urban and rural habitats, mostly within 80 km from the colony were used for foraging. Marine prey, mostly fisheries discards, formed the principal prey for most birds, supplemented with food found in agricultural areas. Human waste was found in only 7% of prey samples. A consistent decline of marine prey (in line with developing restrictions in fisheries), combined with signals pointing at food stress, suggests that the population is unable to boost reproductive success with currently existing foraging opportunities.

Key words: reproductive success, migratory movements, foraging ecology, chick growth, cannibalism, timing, site-fidelity

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The Lesser Black-backed Gull *Larus fuscus* is a coastal breeding, sexually dimorphic seabird, that has shown a population increase and range expansion in northwestern Europe since the mid-1900s, most notably since the 1960s (Cramp & Simmons 1983, Camphuysen 2013). The first breeding pairs in The Netherlands and in Germany were recorded in 1926 and 1927 (Brouwer 1927, Goethe 1957), but numbers remained low for decades. In the early 1970s, however, c. 40 years after initial colonisation, there was an exponential increase in breeding numbers (Spaans 1998ab). Belgium was colonised as recently as 1985 (Seys *et al.* 1998).

The observed range expansion, at a time when the closely related and sympatric European Herring Gull *Larus argentatus* showed poor reproductive success and declined following a threefold population increase (Spaans 1987), puzzled scientists for years. Interspecific competition was investigated as a possible explanation of the contrasting trends (Noordhuis & Spaans 1992, Camphuysen 1995), but consensus was reached with the suggestion that the newcomer, a more genuine seabird, had filled an empty niche rather than that it had outcompeted the coastal orientated Herring Gull (Garthe *et al.* 1999a, Camphuysen 2013). The puzzle continued, because the foraging behaviour and the resource base of Lesser Black-backed Gulls were by no means consistent, neither between breeding sites (spatial variation; Corman *et al.* 2016, Enners *et al.* 2018), nor between years within colonies (temporal variation; Noordhuis 1987, Kubetzki & Garthe 2003, Kim & Monaghan 2006, Coulson & Coulson 2008). The Dutch breeding population peaked at c. 100,000 pairs around 2013–2015, when stabilisation in numbers occurred, while ten years earlier the first declines were reported from the Wadden Sea islands (Koffijberg *et al.* 2021). Therefore, the original scope of our research, to examine the expansion of lesser black-backed gulls alongside the decline of an established species, subsequently altered to examining more recent population dynamics. To enhance our understanding, we put the current reproductive performance of Lesser Black-backed Gulls, now no longer in a phase of colonisation and range expansion, in context with novel information on seasonality and timing, migratory movements, habitat choice, and foraging ecology, throughout the annual cycle.

Ring recoveries have shown that Lesser Black-backed Gulls are long-distance migrants, wintering up to c. 5000 km southwest of the breeding grounds (Landsborough Thomson 1924, Wernham *et al.* 2002, Hallgrimsson *et al.* 2012). Modern satellite and GPS tracking studies conducted in Germany (Corman *et al.* 2016, Garthe *et al.* 2016, Sommerfield *et al.* 2016), The Netherlands (Camphuysen *et al.* 2012, 2015, Tyson *et al.* 2014, Brown *et al.* 2021) and in Belgium (Baert *et al.* 2018, Sotillo *et al.* 2019ab) confirmed this flyway and revealed their terrestrial and marine foraging and staging areas in unprecedented detail. Although gull populations have been much researched in recent decades, few comprehensive and integrative studies on the breeding biology and foraging ecology of Lesser Black-backed Gulls have been published. For The Netherlands, some short-term studies were reported in the 1980s and 1990s, hinting at the (combined) effects of increased population size and interspecific competition on food-supply, parental effort and chick survival of the established species (Herring Gull) and the newcomer (Lesser Black-backed Gull; Spaans & de Wit 1986, Spaans *et al.* 1987, Noordhuis & Spaans 1992, Spaans *et al.* 1994, Bukacinski *et al.* 1998). In Germany and Belgium, there have been only a few comprehensive studies of their breeding biology. These studies were again often short-term (Garthe *et al.* 1999b, Dierschke & Hüppop 2003, Kubetzki & Garthe 2003, Dierschke 2005, Bosman *et al.* 2013, Kavelaars *et al.* 2018, Salasa *et al.* 2020). The most frequently cited work is decades old, when environmental conditions were entirely different (Lockley 1932, Darling 1938, Paludan 1951, Goethe 1957, Harris 1964, Brown 1967b, Davis & Dunn 1976). As a result, knowledge of breeding biology is outdated, ageing, incomplete or simply lacking.

The main objective of this study, therefore, was to obtain recent, comprehensive ecological data of the breeding of the Lesser Black-backed Gull, shifts in resources, prey types, and habitat use. Studies were conducted at the Wadden Sea island Texel, a colony with few mammalian predators, no risk of flooding, no public disturbance and no health issues known to have ever affected the nesting birds on a detectable scale. The Lesser Black-backed Gull is a strictly protected species within this National Park and the colony was therefore an excellent place to investigate why this species performed so well in comparison with the sympatric Herring Gulls at the start of our studies. Population trends were in line with neighbouring colonies on other Wadden Sea islands (Koffijberg *et al.* 2021) and were therefore considered to be representative of a larger area. We studied the entire annual cycle to put the breeding biology and foraging ecology in a wider context. The studies on Texel reported here are unique for several reasons. While most historical gull studies in Europe have spanned only a few years, we (1) monitored gull breeding for 16 consecutive seasons (2006–2021), (2) collected information on diet and resources simultaneously, (3) colour-ringed adults and nestlings to monitor site fidelity, return rates, habitat use, dispersal and migration throughout the annual cycle and (4) deployed GPS tracking devices to study foraging behaviour and foraging grounds during breeding, as well as to outline migratory pathways and wintering grounds without 'human intervention', i.e. no observers on the ground required, even though ground truthing is always necessary.

METHODS

Study colony

The main study was conducted in one of the largest breeding colonies on the island Texel (Kelderhuispolder, Geulduinen; 53°00.5'N, 04°43.1'E), The Netherlands, at the crossroads of the western Wadden Sea and the southern North Sea (Camphuysen & Gronert 2010, Camphuysen 2013). The Lesser Black-backed Gull colonised this area in 1970 (Dijksen & Dijksen 1977, Dijksen 1996) and the colony has not been studied before. The study colony is part of a much larger colony, on the south tip of the island where, around 2006, when the study started, over 11,000 pairs of Lesser Black-backed Gulls bred in a mixed colony together with c. 4000 pairs of Herring Gulls. It is within Natura 2000 area NL2003060 ('Duinen en Lage land Texel') and the Lesser Black-backed Gull is listed by conservationists with the specific objective to maintain a breeding population of c. 14,000 pairs (Aarts *et al.* 2008). The study colony is an undisturbed and ungrazed nature reserve, inaccessible to public in summer. There are few mammalian predators: Feral Cats *Felis catus*, Stoats *Mustela erminea*, European Hedgehogs *Erinaceus europaeus* and Brown Rats *Rattus norvegicus*. Colony data were collected from April to August, 2006–2021. Two prime study plots for Lesser Black-backed Gulls were chosen initially, but in later years, following gradual changes in the distribution of nests in the core colonies (areas gradually being abandoned and new sites colonised), four further study plots were selected to ensure a sufficiently large sample of nests available for research.

Annual cycle and non-breeding distribution: colour-ringing and GPS tracking

The annual cycle was reconstructed using field observations in and around the colony, plus re-sightings of colour-ringed individuals (adults and juveniles), captured as breeding birds or fledglings, throughout their (annual) range. The colour-ring data will be instrumental to assess apparent annual mortality in a follow-up study, and have provided information on changes with increasing age in timing, range, and the use of stop-over or wintering sites age during annual migrations for this study. Breeding birds were captured at Texel while incubating and marked with a permanent stainless-steel ring on one leg and a four-letter coded, green PMMA colour ring on the other, to allow for individual recognition (first letter F for females, M for males). Walk-in traps were deployed over well-incubated clutches (eggs c. 10–22 d old). During ringing,

standard biometrics were taken always by the same observer. Head length (head+bill) was used as a non-invasive method to indicate the sex of adults or sub-adults (males are on average larger than females, cut-off point 113 mm, accuracy 95.0 ± 2.0%, ±SD), following Coulson *et al.* (1983). Over the first years it appeared that some of the smaller males had been wrongly sexed, indicating that Dutch birds were on average larger than birds from the United Kingdom. After sexing birds with molecular techniques (blood samples) and during necropsies (gonadal inspection), a new cut-off point between the sexes of 116 mm was chosen, which fitted the bi-modal pattern in head length well (Camphuysen 2013). Breeding gulls were aged using plumage characteristics (Adriaens *et al.* 2021). Age was expressed in (annual) cycles, i.e. from the start of one primary moult to the next (1st–4th cycle, versus adults; following Adriaens *et al.* 2021).

Chicks were colour-ringed just before fledging, using the same rings as for adults but with different codes (first letter K or P), when the tarsus had reached a length of c. 60 mm, or when the intertarsal joint was thin enough (young chicks have a thick intertarsal joint, but when around 30–35 d of age, the leg becomes much thinner, just as in later life). To enlarge numbers of colour-ringed fledglings in anyone season, to allow the study of apparent survival and return rates with meaningful samples, an additional 40–80 free-running near-fledglings were captured annually in July. To boost the total number of Lesser Black-backed Gulls colour-ringed in the same general breeding area even further, c. 30 adults and c. 40 near-fledglings were captured annually in a large neighbouring colony at IJmuiden (52°27.5'N, 04°34.3'E; using the Y as first engraved character). Total numbers colour-ringed arrived at 428 adults and 757 fledglings on Texel (2006–2021) and 394 breeding adults plus 551 fledglings at IJmuiden (2008–2021). The result was a population of 'known' individuals, used to assess return rates, site- and mate-fidelity in either colony, but also to track foraging trips and to reveal timing and migratory pathways across ages throughout the annual cycle.

Colour-ring reading was conducted within and outside the colony during the entire prospecting phase (with increasing frequency, Jan–Apr), and during all field work associated with nest marking and nest controls (May–August, with declining frequency in Sep–Oct), to assess individual colony returns, pair bonds, (potential) recruits, prospectors and (known) nest owners (32,658 sightings in all; 2006–2021: 1226 colony visits, 4561 field hours of observation). Within and around the colony at IJmuiden, 31,932 sightings

were obtained from prospecting through breeding (courtesy Fred Cottaar and co-workers; no field time recorded; 2008–2021: 716 field days with over 25 sightings), while another 4344 sightings were obtained from elsewhere along the flyway. In addition, a 'world-wide' network of colour-ring readers provided re-sightings of colour-ringed individuals all over the known flyway of this species. The 2130 ringed individuals yielded 73,700 re-sightings in 17 European and NW African countries. To track movements from colour-ring re-sightings for all age categories (1st–4th cycle and adults) as discrete groups, for each individual, each month (each year) the mean latitude and longitude positions were calculated and plotted against time throughout the annual cycle (Figure 1, Table S1).

A GPS tracking system was used since 2008, to study foraging whereabouts and flyways continuously and over the entire annual cycle. The system was developed at the University of Amsterdam and consists of c. 17-g solar-powered GPS tags, with a wireless ZigBee transceiver that communicates with a base station in the centre of the breeding colony (Bouten *et al.* 2013). The GPS tags were attached to the back of adult breeding birds using a Teflon three-strap permanent backpack harness configuration with one strap fitting across each wing and one strap below the crop. Birds were immediately released following standard biometric measurements, ringing, and secure placement of the tags. Data logged on the tags were downloaded to a base station and new tag settings could be uploaded to the instruments if needed. Speed, direction and time duration were calculated between consecutive GPS fixes. The GPS data were collected for a whole range of detailed studies, including flight energetics (e.g. McLaren *et al.* 2016, Shamoun-Baranes *et al.* 2016). Tracking individuals by using colour rings or by using GPS tags has its own specific pros and cons and depending on the research question the suitability of the techniques may differ (see e.g. Thorup *et al.* 2014 for a more detailed review). Here specifically, we used the GPS data to complement the migration data collected with colour rings (in which all age categories could be followed simultaneously, while GPS trackers were deployed on breeding adults only), as well as the use of foraging habitats, especially those away from land (no observers) or in areas where colour-ringed birds cannot be detected easily.

Time intervals between fixes longer than 60 minutes indicated data gaps, generally due to low battery power, and were excluded from analysis. The time interval between consecutive GPS positions was attributed to the first of two consecutive locations. This interval and the first GPS position was then used to calculate the presence of birds (hours) in 2'N × 3'E rectangles within 150 km around the colony. For this paper, we summarised seven years' worth of data (51 adult Lesser Black-backed Gulls, 24 males and 27 females), trapped and fitted with GPS tags between 2008 and 2014 on Texel. Individual differences in foraging whereabouts, just exemplifying individual site fidelity, were mapped for ten adult nesting birds, tagged at Texel in 2020 and 2021, now using plots of all fixes, but only for the first 30 d worth of data after tag deployment (i.e. late egg phase, well into chick phase).

Timing of egg-laying, monitoring incubation (egg phase)

From late April to early June, nest searches were conducted along a pre-set trail through fixed study plots, to mark 80–100 nests covering the main laying period. Exceptionally late nests (outside the normal distribution; mean ± 2 SD and beyond) were ignored in our studies (maximally 1–2 nests within the study area per annum). Nests containing at least a single egg were marked (unique numbers), photographed, described and a GPS position was recorded (latitude, longitude). Nest descriptions involved position in a dune landscape (at the top, along a slope (steep or gradual) of a dune, or in flat valley areas) and the amount of vegetation covering the nest bowl, assessed using an 8-point scale, with categories ranging from open ground nest (just a scrape in the soil) via more or less half-covered (25–75% cover) to completely covered in tall grass or bushes (invisible from above). For the analysis, nest cover categories were grouped as 'open' (<10% nest cover: category 1–2), 'half covered' (10–75% hidden in vegetation: cat. 3–5) or largely 'hidden from view' (>75% concealed by vegetation: cat. 6–8).

Over the years, 1356 nests were monitored until hatching (84.8 ± 12.5 nests/yr; ±SD), in these nests 3658 eggs were laid (228.6 ± 33.8 eggs/yr). During each nest visit, the presence and incubation stage of the eggs were checked and recorded into a logbook. For each egg, a prediction was made of the expected day of hatching (assuming an incubation time of 27 d), but the exact duration of incubation (d) was assessed and used for analysis if laying and hatching dates were both exactly known. Marked nests were visited every third day until all eggs had hatched, were lost, or were abandoned.

During incubation, laying date, clutch size (*n*/nest), laying sequence (A, B, or C-eggs), egg size (max. length [L], max. width [B], mm) to calculate egg volume (ml),

egg depredation, egg mortality and hatching success were assessed. Egg measurements were all taken by the same observer or after calibration by a frequent co-worker. Egg volume was calculated from linear egg dimensions, using Volume = kLB^2, where k is a constant (Barth 1968, Hoyt 1979). The constant (k) used was derived from Spaans & Spaans (1975), to allow for direct comparisons with earlier Dutch data: k = 0.5035. Differences in egg shape were ignored, even though some eggs were considerably rounder or more pear-shaped than others (Barth 1968, Makatsch 1974). Truly unusual eggs, such as dwarf eggs or bright blue eggs were recorded and described. The timing of egg laying was based on all eggs laid in marked nests within a season (expressed as mean or median laying date), whereas in some earlier studies the onset of laying (first eggs) for each nest has been used. If mean or median dates of clutch initiation would be preferred, the difference with data presented in this paper would mean a 1.5 ± 0.7d shift forward (1314 nests).

Trends in most vital rates over time were tested using linear least squares regression. Nesting attempts were grouped as 'early', 'peak' and 'late' relative to median egg laying for each year. The interquartile range (IQR) is presented as the laying peak (d), used to illustrate the level of synchronisation in a given season, where 'early' nesting attempts occurred prior to the 1st quartile, 'late' nests after the 3rd quartile, and 'peak laying' in between. Vital statistics over early, peak or late breeding attempts (timing relative to annual colony laying median) were compared by means of one-way ANOVA. To test whether hatching success (number of eggs/nest) was related to relative laying date (nest versus annual colony mean), a generalized linear mixed effect model with a Poisson distribution was used (R-package 'lme4'). Model fit, and whether such a relationship was linear or quadratic, was compared with a log-likelihood test. To account for annual variation, year was included as a random effect.

From hatching to fledging (chick phase)

The colony is situated in a well-vegetated area and hatchlings quickly disappear in the vegetation if not somehow contained. To be able to study the development of chicks, a randomly selected subset of marked nests was fenced in with 50 cm high chicken wire to form an enclosure (minimum size for isolated nests: $2 \times 2 = 4$ m^2, ensuring inclusion of the chick provi-

Lesser Black-backed Gull chicks, Kelderhuispolder, Texel, The Netherlands (photo CJC, 27 June 2011).

sioning patch near each nest and sufficient vegetation for chick cover), where chicks could be retrieved during colony visits every third day until fledging or death. The use of enclosures was a choice, even though unwanted side-effects may occur (Griffiths 1992, Gyimesi *et al.* 2016), because it would provide detailed data on growth, causes of mortality and fledging rates. Because it was our aim to obtain productivity data representative for the colony at large, enclosed plots should not be more nor less susceptible to (chick) depredation than unenclosed sections of the colony. Fortunately, the study colony was not (or known to be; pers. obs.) under particular stress from rats or other mammalian predators, in which case enclosure data might have resulted in biased data. Of the 1356 nests that were initially marked during laying, 37% were randomly selected to be enclosed (497 nests, or 31.1 ± 8.0 nests/yr, ±SD). In these enclosures, 989 hatchlings were monitored (61.8 ± 23.7 chicks/yr), of which 251 (25.6%) individuals fledged (15.7 ± 8.9 fledglings/yr).

Levels of chick survival, depredation, or mortality were based on regular enclosure controls: every third day until fledging. Hatchlings were allocated to the appropriate egg number when possible and marked with numbered aluminium tarsus rings, so that they could be recognised during handling. Aluminium rings were replaced by stainless steel and PMMA colour-rings (see above) later in life. Data gathered from chicks in enclosures to assess growth included structural size measurements (see below; mm/d), mass increments (g/d) and primary moult scores. Measurements included total head+bill length (mm), bill length (exposed culmen, 0.1 mm), wing (flattened, mm), tarsus (diagonal, mm, not in 2006; methods following Balwin *et al.* 1931) and body mass (g), all taken by the same observer or after thorough calibration by a frequent co-worker. The primary moult score was a description of the stages of flight feather growth using a 5-point scale, from 0 (down), 1 (feather shafts emerging), 2 (feather shafts opening), 3 (feathers between 1/3 and 2/3 final length), 4 (>2/3, not fully grown) to 5 (fully grown), following Camphuysen *et al.* (2009). With few exceptions (some specific projects), chicks were not sexed. Chicks were recorded as 'predated' when they had entirely vanished from the (intact) enclosure while very young (<10 days of age, incapable of escaping), or when partly scavenged remains were found at later age in or outside the enclosure on the first nest visited after an earlier control. Chicks were recorded as 'died' when intact remains were found on such a subsequent control (even if scavenged later).

Chicks were recorded as 'fledged' when they reached 40 d of age; any individuals that died within the colony when older were logged under 'first year mortality'.

Reproductive output (fledglings/nest) was calculated over all randomly selected, enclosed nests combined, separately for each year of study or for any other grouping with biological relevance, such as for nests with different clutch size or laying date (timing). The World Seabird Union and the Circumpolar Seabird Group prefer fledglings per nest over mean clutch size (F/CS×100) as productivity indices (PI) to facilitate comparisons between colonies and seabird species over larger geographical scales (CSG 2010). From that perspective, good productivity for 'seabirds' is ≥50%, poor productivity ≤ 10% and moderate productivity between >10% to <50% of eggs producing fledglings. As in the egg phase, trends over the years were tested using linear least squares regression. Mean values over (grouped) early, peak or late breeding attempts are presented and compared by means of one-way ANOVA. To test whether fledging rate (chicks/nest) was related to relative laying date (nest versus annual colony mean), a generalized linear mixed effect model with a Poisson distribution was used (R-package 'lme4'). Model fit, and whether such a relationship was linear or quadratic, was compared with a log-likelihood test. To account for annual variation, year was included as a random effect.

Censuses of the colony, breeding densities and non-breeders

Colony counts were conducted late May (incubation) in 2009, 2010, 2011, 2015 and 2016, in one day, timed such that both sympatric breeding species had completed clutches and could be included. Active territories with at least one well-constructed nest (so-called 'play nests' were excluded using expert judgement) were counted within a 10 m wide strip-transect, walking band-transects through the colonies, using three observers tied together along an 8 m long rope, preceded by a navigator/recorder to lead the way. Nesting species were identified on the basis of observations ahead (birds flushed while approaching), but especially based on prey remains found on the territories (prey remains dominated by crab or shellfish in Herring Gulls, clean sites with fish remains or grass pellets characterizing Lesser Black-backed Gulls). During nest marking, the same method was used to identify the nesting species, but with the possibility of checking results during later nest controls. This showed that an error occurred of around 1.3% misidentified Lesser Black-backed Gull nests ($n = 1316$). During the

colony census, clutch size or occasional brood size (hatchlings) were recorded. Densities were expressed as number of nests per unit area (per m^2 or ha) for c. 25–35-m long stretches of transect. Extrapolations for non-surveyed parts of the colony (between transects) were used to assess relative abundance and breeding numbers within study plots and within the study colony as a whole. The transect sampling technique provided insight in spatial patterns in species composition and breeding densities throughout the study area.

Recruitment, age at first breeding, colony exchanges

Prior to egg laying and throughout the breeding period, the colony was rigorously checked for colour-ringed individuals. Indications of immigration were based on 'foreign' rings observed (prospecting, likely breeding or definitely breeding) and similar scans in other colonies were used to obtain evidence for breeding dispersal. Age at first breeding was based on birds trapped on nests to be ringed, with age being based on plumage characteristics.

Resource base (foraging habitat and diet)

Diets were studied from spontaneously regurgitated matter (pellets, large chunks of regurgitated matter, partly eaten food remains, food boluses produced during handling of adults and chicks) and from chick-feed sub-sampled within the territories, each considered as individual samples. During colony visits, marked territories were always inspected for the presence of discarded prey items, and these were bagged, thereby keeping individual pellets and boluses apart as discrete samples, numbered, and kept frozen for later analysis. Additional prey samples (pellets mostly) were collected from study plots, to enhance the overall sample in each of the phases of breeding. With pellets, boluses and regurgitated matter, some easily and fully digested prey are overlooked, but the microscopical inspection of prey samples ensured that even very small remains (such as earthworm setae and minute otoliths) were detected. This paper is not intended as a diet paper, and therefore the results were simply summarised and expressed as 'frequency of occurrence' (FO, %, see Barrett *et al.* 2007) for individual prey types over all analysed prey samples, per phase in the breeding cycle.

In the following results section, we present our findings based on the above methods. To provide a comprehensive overview, wherever necessary, we also provide findings already published elsewhere.

RESULTS

Annual cycle and non-breeding distribution

Colour-ring data showed that most adults left the breeding grounds after late August (Jul–Oct), and that successful breeding birds were preceded by failed breeders and prospecting immature (sub-adult) non-breeders (Figure 1, Table S1). Winter (Dec–Jan) sightings of colour-ringed adult birds (580 individuals) were recorded in Spain (49.8% of the individuals), France (21.7%), Morocco (10.9%), Portugal (10.2%) and the UK (5.3%), with far fewer birds in Nigeria, Gambia, Senegal, Mauritania, Algeria, Tunisia, Italy or Belgium. The GPS tracking data largely confirmed these results, but indicated that the UK is of greater significance than colour-ring data had suggested (a likely effect of differences in ring-reading observation effort). Virtually all birds migrated in a south-westerly direction (c. 200°) and all age groups reached their southernmost destinations around January. Colour-ringed juveniles abandoned the breeding grounds late (Sep–Nov) and travelled on average 37% in kms further away than adults (Figure S1, Table S1). Later in life, as immatures (2nd–4th cycle), they still tended to travel further to the south than adults (up to 10–25% in kms). Many birds used stop-over sites in northern France (Aug–Nov), roosting mostly in industrial areas, for up to a few months before travelling towards their southernmost winter destinations. Immatures leaving the breeding grounds used these same stopovers earlier on (Jun–Sep), juveniles later than adults (Oct–Nov). Adults showed strong winter site fidelity, over a smaller wintering range than most immature birds: almost a quarter of individual adult re-sightings were reported in at least three years (up to 13 consecutive non-breeding seasons) in the same country, usually at the exact same location. Strong site-fidelity throughout the annual cycle (nests, stop-overs and winter destinations) was confirmed with GPS tracking data (Brown *et al.* 2021).

Most adults returned in March and April (range: Jan–May), followed by older immatures (3rd and 4th cycle, mostly April–May), that were more likely to travel towards their breeding grounds in summer than younger birds (1st and 2nd cycle; Figure S1). Prospecting immatures arrived later than most adults in the breeding colonies, but returned earlier every season when growing older. Juveniles that survived their first winter sometimes travelled to the northeast in May and June of their second year, but normally without reaching their natal breeding grounds (mean latitude ± SD: 48.8 ± 4.9°N; Table S3). Adults that returned early (Feb–Mar) on the breeding grounds assembled for

weeks on roosts on nearby beaches, before the colony itself was visited (field observations and GPS tracking results). Adults that spent the winter in Africa arrived last (later than birds wintering within the temperate zone), sometimes not before May, to join colony life (Shamoun-Baranes *et al.* 2016, Kentie *et al.* 2023). Pair bonds were seen to be established or renewed, at least partially, in assemblies or roosts on beaches around the colony, often well before territories within the colony were re-occupied. The longest-distance migrants largely missed these earliest periods of pair-bond (re-) establishments. Overnight stays, territorial defence and nest-building within the colony area itself were observed no earlier than mid-April (GPS data and visual observations during regular colony visits), three weeks to a month before the first eggs were laid. The

breeding grounds were in use from February (early arrivals) to October (late departures), but colonies were only occupied in April–August (earliest prospectors in March; Figure 1).

Nesting habitat, pair-bond renewals, site and mate fidelity (pre-laying phase)

Lesser Black-backed Gulls established breeding territories mainly on grassy, flat surface areas (44.8%) or on gradual hill slopes (52.3%), largely avoiding steep slopes (0.7%) and dune tops (1.3%; 1356 nests), thereby differing from the sympatric Herring Gull that had a larger preference for steep slopes and dune tops. In all, rather few (11.1%) of the 1356 marked nests were open (poorly covered), another small fraction (8.9%) were largely or completely hidden from view.
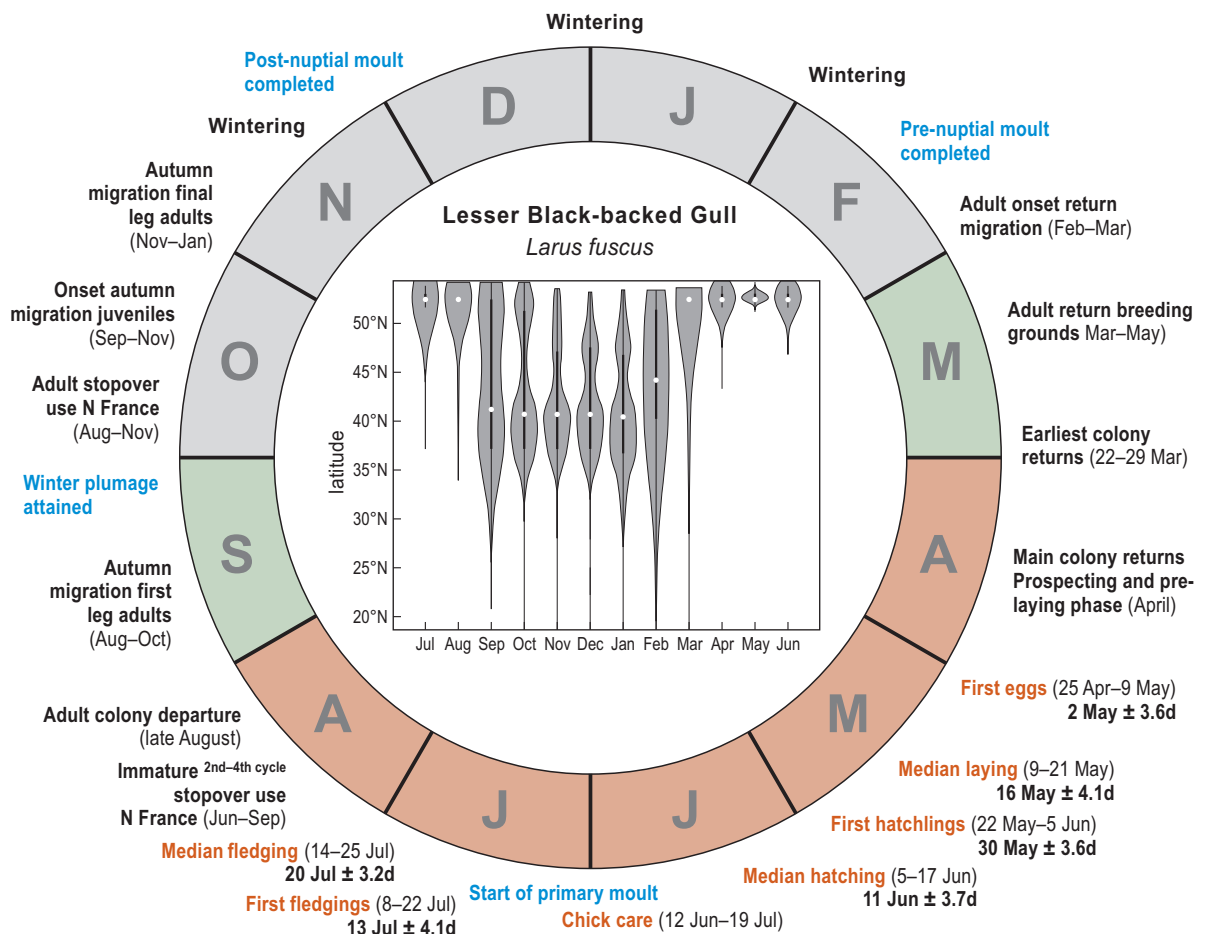
Figure 1. Schematic representation of the annual cycle of Lesser Black-backed Gulls *Larus fuscus* based on systematic colony observations at Texel (2006–2021) and on migratory movements of adult birds that were colour-ringed at Texel or in IJmuiden (Netherlands). For details on mean values (bold, ± SD) and range (in parentheses) of timings and annual fluctuations therein, see Results. Inset: violin-plot of average latitudinal distribution of sightings of colour-ringed adult birds ringed at Texel and IJmuiden, throughout Europe and NW Africa. Median values are indicated with a dot. Main colony attendance: April–August, main wintering: period September–February.

Of 42 males with known pair-bonds lasting more than one season (range spanning 2–14 years per individual), 29 birds (69%) were with the same female partner in subsequent seasons (range: 2–6 years), 13 changed a partner once (2–8 years) and two birds had three partners (5–14 breeding years). Nine partner changes were the result of a divorce (47.4%), ten followed the death of the initial partner (52.6%). Similar statistics were found for 42 females with known pair-bonds lasting more than one season (range: 2–10 years): 27 (62.3%) with the same (male) partner (2–5 years), 13 with one partner change (31.0%, 2–10 years), one with three partners (over 6 years) and one with four partners (6 years): 12 changes (66.7%) occurred following a divorce, six (33.3%) because the earlier partner died. These results suggest that the likelihood of encountering the same pair was 87% from one year to the next and 79% over a three-year period, eventually declining to 45% over five years, and to below 20% over longer time intervals.

Lesser Black-backed Gulls displayed a high degree of nest site-fidelity, generally choosing breeding sites but also club sites within or very near the study plot where they were found as breeding birds when they were ringed. Based on colour-ring data, only five re-nesting males (8%) abandoned their original study plot, and these were always small displacements (20–40 m) in immediately adjacent nesting areas. Area displacements between nesting attempts were commoner in females (8 cases, 16%), but again, most changes were minor and towards neighbouring study plots. With 30 study plots used for ring-reading in the main study colony and with 1223 individuals ringed, re-sightings were typically within the same or perhaps in one other, neighbouring plot. Only 159 (13%) were seen in three or more study plots and only 52 (4%) in four or more sites. Multi-year GPS tracking data confirmed that re-nesting attempts by adult breeders far away from initial (ringing) sites in later seasons were rare. Of 110 subsequent breeding attempts or confirmed territoriality (one year to the next), 90% re-nested within only 20 m of the original nest site, 96% within 40 m (median distance between subsequent nests: 3 m, IQR: 1.4–8.6 m). Longer distances between two subsequent nesting attempts of GPS carrying individuals were rare but included 87 and 118 m in females and 154, 194, and 210 m in males. One exceptional bird, a female, GPS-tagged in 2012 and re-nesting on the exact same location in 2013 and 2014, was rediscovered in 2017 as a breeding bird in Havergate NNR, Orfordness, Suffolk (UK), 238 km to the WSW of Texel, and returned there annually until at least 2022.

Laying date, clutch size, egg volumes, incubation and hatching success (egg phase)

Laying was highly synchronised (peak duration: 8.7 ± 2.0 d, ±SD), but the median laying date, initially around 12 May became progressively later after 2008 and stabilised on c. 20 May since 2013, widening the gap in laying with the consistently earlier nesting Herring Gulls from 2.9 ± 0.8 d (2.3–3.8 d) in 2006–2008 to 9.2 ± 3.2 d in 2010–2021 (7.3–12.7, but 4.3 d in 2019 as a result of a particularly 'late' season in Herring Gulls). The delay in egg-laying was highly significant, and while the duration of the (short) laying peak was variable, there was also a significant tendency for the peak to become wider over the years (Table 1, annual details in Table S2).

Clutches contained on average 2.7 ± 0.1 eggs (excluding disturbed nests followed by relaying: 7.4% single egg clutch (C/1), 18.9% C/2, 73.7% C/3, 1324 nests). Clutches with four or even five eggs were only encountered during the colony census (0.2% of nests checked, see below). Clutch size varied slightly, with no consistent change over the years (Table 1).

The difference in volume between A-eggs (first egg in a clutch; 74.3 ± 6.2 ml, $n = 878$) and B-eggs (76.8 ± 6.5 ml; $n = 617$) was small and not significant, whereas C-eggs (third egg in a clutch; 70.2 ± 6.4 ml, $n = 707$) were significantly smaller ($t_{1322} = 10.4$, $P < 0.001$). Dwarf eggs (<50 ml) were rare (<0.1%, $n = 3979$), bright blue eggs occurred 20 times (0.5%), of which 12 eggs (four clutches) were produced by the same female. By volume, A-eggs in two-egg (1.0%) and three-egg (4.3%) clutches were larger than in single egg clutches and this difference was considerably larger in late-laying pairs (5.6 and 10.5% larger, respectively; Table S5). Highly consistent was a long-term, significant decline in mean total volume of three-egg clutches from 225 ml to 215 ml (–4.4%) between 2006 and 2021 (Table 1).

Incubation typically commenced when at least two eggs were laid (egg temperature when touched, logbook notes). GPS tracking data had revealed that males remained longer at the nest than females during incubation bouts in the egg phase, thereby taking a greater share in the incubation process (7.3 ± 6.2 h versus 5.4 ± 4.7 h per bout in males ($n = 387$) and females ($n = 514$ bouts), respectively; Camphuysen *et al.* 2015). Eggs hatched on average after 26.2 ± 0.4 days of incubation, with the first hatchlings being found 30 May ± 3.6 d, median hatching around 11 June ± 3.7 d. Hatching success was fairly stable throughout the study period (71.0 ± 8.4% of eggs laid). There were no apparent trends in either of these

Table 1. Statistics describing the egg laying and incubation phase based on all marked nests in Lesser Black-backed Gulls breeding in the Kelderhuispolder, Texel, 2006–2021.

Egg laying and incubation	Mean	± SD	min	max	Trend	R^2	P	signf
First eggs	2-May	± 3.6	25-Apr	9-May	±	0.00	0.330	n.s.
Duration of peak-laying (d)	8.7	± 2.0	5	11	+	0.31	0.015	*
Median egg-laying	16-May	± 4.1	9-May	21-May	++	0.62	<0.001	***
Mean egg-laying	17-May	± 3.7	10-May	21-May	++	0.62	<0.001	***
eggs (n)	3622							
Clutch size (n)	2.67	± 0.1	2.40	2.83	±	0.02	0.280	n.s.
nests (n)	1323							
3-egg clutch volume (cc)	219.7	± 4.3	213.4	226.0	––	0.60	<0.001	***
nests (n)	998							
Incubation (d)	26.2	± 0.4	25.7	27.4	–	–0.01	0.370	n.s.
First hatchlings	30-May	± 3.6	22-May	5-Jun	+	0.18	0.150	n.s.
Duration peak-hatching (d)	7.8	± 1.7	5	11	+	0.03	0.250	n.s.
Median hatching	11-Jun	± 3.7	5-Jun	17-Jun	++	0.46	<0.005	**
Egg depredation (%)[1]	21.1	± 8.1	9.5	40.3	±	–0.07	0.970	n.s.
Egg mortality (%)[2]	7.8	± 1.8	5.6	11.0	±	–0.06	0.740	n.s.
Hatching eggs (%)	70.7	± 8.5	50.2	82.9	±	–0.07	0.970	n.s.
eggs (n)	3658							
Failed clutches (% of all nests)	19.0	± 8.4	9.1	36.3	±	–0.04	0.510	n.s.
Relaying attempts (% of failed nests)	14.8	± 13.7	0	46.2	–	0.14	0.090	n.s.
All marked nests (n)	1356							

[1] 18.7 ± 8.2% when correcting for eggs that were predated after the expected date of hatching; >26 days after being laid (see text).
[2] 10.3 ± 2.3% when correcting for eggs that were predated after the expected date of hatching (see text).

Table 2. Statistics describing chick development in the chick care phase including fledging rates (n/pair) in Lesser Black-backed Gulls breeding in the Kelderhuispolder based on randomly selected nests in enclosures, Texel, 2006–2021.

Egg laying and incubation	Mean	± SD	min	max	Trend	R^2	P	signf
Hatchling mass, <3 d (g)	56.2	± 1.9	51.4	59.1	––	0.24	0.03	*
Chick depredation (%)	52.4	± 13.3	26.9	78.4	––	0.30	0.02	*
Chicks that died (%)	22.1	± 9.8	12.3	42.3	+	0.17	0.06	n.s.
Chicks fledged (%)	25.0	± 10.6	4.8	43.9	+	0.03	0.26	n.s.
hatchlings (n)	989							
Mass increments, 10–20 d (g/d)*	23.9	± 3.9	13.6	33.7	–	0.14	0.09	n.s.
First fledglings, 40 d of age (date)	13-Jul	± 4.1	8-Jul	22-Jul	+	0.04	0.22	n.s.
Head length fledglings**	102.7	± 3.2	95.7	106.6	–	χ^2_1 2.70	0.10	n.s.
Wing length fledglings**	292.8	± 17.6	248.5	315.1	–	χ^2_1 2.23	0.13	n.s.
Body mass fledglings**	656.4	± 64.9	493.3	738.3	–	χ^2_1 3.67	0.05	*
Fledglings/pair	0.49	± 0.2	0.09	0.94	±	0.01	0.35	n.s.
Productivity index (%)	18.4	± 8.8	3	35	+	0.01	0.29	n.s.
All enclosed nests (n)	497							

*Only chicks that reached 40d of age and were considered as fledglings, **no data for 2013.
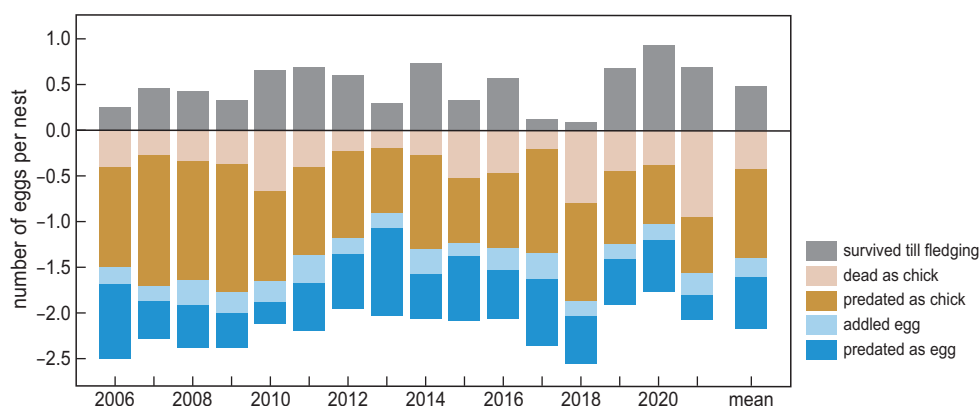
Figure 2. Reproductive success (chicks fledged/nest, grey bars) and factors reducing the output, portraying losses from the initial clutch size (i.e. entire bar length) as negative values.

egg parameters over the years of study (Table 1). Hatching success was similar for all eggs in which the sequence of laying could be established without doubt (A: 69.1%, B: 75.0%, C: 72.5%). Relaying frequencies varied (14.8 ± 13.7% of predated nests, range: 0–46.2%), but the likelihood more than halved when the laying window of the colony as a whole became substantially delayed (2006–2013: 20.3 ± 17.0% failed pairs relayed, 2014–2021: 9.3 ± 7.5% relaying).

Egg predation amounted to 21.0 ± 8.1% per annum (Table 1), varied between 15 and 30% in most years, and one third of the eggs that were predated disappeared within five days after being laid. As expected, nest cover reduced the risk of egg predation (27.4% of the eggs in open nests, 21.0% in half covered nests, versus 11.7% in clutches that were almost completely hidden from view; G_{adj} = 12.6, df = 2, P < 0.01, 3642 eggs). There was some anecdotal evidence for egg depredation by Carrion Crows *Corvus corone* roaming the colonies, but by far the most eggs were taken by conspecifics or Herring Gulls (pers. obs.). A-eggs (30.7%) suffered higher losses from predation than B (20.3%) or C-eggs (16.9%), and late clutches (33.8%) suffered more than eggs laid early (20.3%) or in the peak period (21.7%; all Table S5). Predation levels per egg were much higher in single-egg clutches (78.8% of all eggs laid, n = 99) than in two-egg clutches (33.8%, n = 494) and three-egg clutches (15.9%, n = 2927). The relatively high hatching success in C-eggs is the result of the overall much higher success rates of three-egg clutches (76.7% of all eggs hatched) over two- (67.1% hatched) and one-egg clutches (23.1% hatched).

Less than a tenth of all eggs produced were addled or died during incubation and did not hatch (7.9

± 1.9%). However, of all eggs recorded as 'predated' of which the laying date is precisely known, 12.1% were taken after the expected date of hatching (>27 days after being laid; n = 711). Adding these eggs to the category that died, would lower the fraction that was predated to 18.7 ± 8.2% and increase the proportion of eggs that failed to hatch to 10.3 ± 2.3%. After correction for addled eggs predated after 27 days (see above), 53% of the eggs were predated within the first 9 d after nest initiation, 24% during the next and 23% during the nine final days prior to hatching. Egg predation was particularly high in 2013: 41.4% (n = 215, or 37.7% after correction for eggs taken >27 d after being laid), which led to an all-time low in hatching success of 51.6%.

Overall, 1.92 ± 0.29 eggs/pair hatched to produce chicks of the original clutch of on average 2.70 ± 0.14 eggs (interannual variability in Figure 2).

Hatchling mass, chick growth, chick mortality, fledging success and productivity index (chick phase)

Overall, 0.49 ± 0.23 eggs/pair fledged chicks of the original clutch of the on average 1.92 ± 0.29 eggs/pair that had hatched (c. 25% of all hatchlings; interannual variability in Figure 2). The productivity index (PI), using fledglings over clutch size (CSG 2010), showed that reproductive success was moderate to poor in all years (16.3 ± 8.2, range: 3–40%), even in the 'best' season (2020). Single egg clutches fledged not a single chick, two-egg clutches fledged 0.25 chicks/nest, whereas three-egg clutches were the most productive (0.6 chicks/nest; Table S5).

Hatchlings weighed 56.2 ± 1.9 g, but their body mass declined significantly over the years (Table 2,

annual details in Table S4), likely as a result of the progressively smaller eggs that were produced (see above). Duties were shared between nest partners and GPS tracking data revealed that males spent only marginally longer at territories than females in the chick phase (3.8 ± 3.4 h versus 3.0 ± 2.8 h per nest bout in males ($n = 698$) and females ($n = 1008$ bouts), respectively; Camphuysen *et al.* 2015). While hatching success was similar for all properly sequenced eggs (A, B, C), rather fewer hatchlings fledged from C-eggs (22.7%, $n = 172$) than from either A- (31.6%, $n = 190$) or B-eggs (32.0% $n = 153$), but the difference was not significant ($G_{adj} = 4.65$, $df = 2$, $P > 0.05$;

Table S5). Two thirds of the breeding pairs lost all chicks or even failed to hatch any eggs (Table 3). The body mass of chicks at around 40 d of age (while fledging) was highly similar, between pairs fledging one, two or the maximum of three chicks (Table 3).

About one fifth of the chicks died from starvation, disease or for other (unknown) reasons (21.7 ± 9.2%). Chick body mass gain was least variable, and usually uninterrupted during the first 20 d of life (Figure 3). Logistic growth models, based on chicks that fledged successfully, typically showed a point of inflection at c. 15 d of age (period of linear growth: c. 10–20 d of age). Between day 10 and day 20 (linear phase of growth)

Table 3. Brood size fledged in Lesser Black-backed Gulls, Texel, 2006–2021 based on randomly selected nests in enclosures, and the mean mass (± SD and range) of fledglings against brood size.

Fledglings (n)	Nests (n)	%	Fledgling mass (37–43 d)			
			Mean	SD	Min	Max
0	331	66.6				
1	92	18.5	648.9	± 163.7	325	957
2	63	12.7	645.9	± 122.3	300	913
3	11	2.3	665.1	± 120.2	396	876
	497					

Table 4. Chick size with age (left) and growth increments to reach that size (right) in 5-day intervals for Lesser Black-backed Gull chicks raised and successfully fledged in the Kelderhuispolder, Texel, 2006–2021 based on randomly selected nests in enclosures. Growth increments are based on individual assessments every third day from first handling (usually 0–3 d of age) until fledging (40 d). In the second half of the table, biometrics of adult breeding individuals are provided, to be compared with the size of various body components (mm) and the body mass (g) of (unsexed) fledglings around 40 days of age.

|	Mean size (mm) or mass (g)							Growth increments (mm or g/day)					
Age	Head	Bill	Wing	Tarsus	Mass	Moult	Sample	Age	Head	Bill	Wing	Tarsus	Mass
Hatchlings	47	17.8	25	26	57	0	103						
4–6 d	56	20.7	31	32	104	0	264	1–5d	2.2	0.8	1.6	1.4	12.3
9–11 d	67	25.5	51	41	211	0–1	268	6–10d	2.3	1.0	3.2	1.8	19.9
14–16 d	76	29.6	87	49	332	1	270	11–15d	1.9	0.9	6.9	1.8	24.2
19–21 d	84	33.4	134	56	454	2	262	16–20d	1.6	0.8	8.9	1.4	24.1
24–26 d	91	36.7	182	60	550	2–3	269	21–25d	1.4	0.7	9.5	0.9	18.9
29–31 d	96	39.4	227	62	613	3	261	26–30d	1.2	0.6	9.3	0.5	15.4
34–36 d	101	41.8	265	63	653	3–4	231	31–35d	0.9	0.5	8.1	0.2	9.8
39–41 d	104	43.3	297	63	659	4	80	36–40d	0.7	0.4	6.8	0.1	3.7
Adult Female	111.1	51.0	415.7	61.6	737.8	5	283						
± SD	2.4	1.9	8.7	2.2	51.9								
Adult Male	122.3	56.7	438.9	66.8	911.1	5	299						
± SD	2.9	2.2	10.7	2.5	65.3								
Sex ignored	116.9	53.9	427.6	64.3	826.9		582						
Fledglings	89	80	70	98	80	%	80	Fledgling size (%), compared with (unsexed) adults					
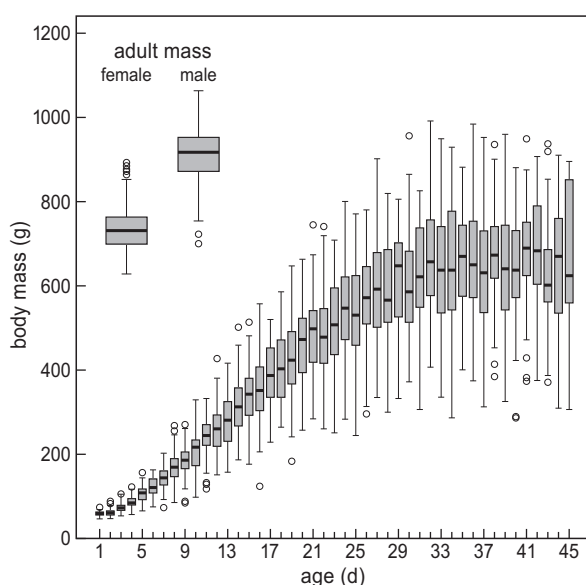
Figure 3. Box plot of body mass increments with age of chicks that fledged successfully (*n* = 296), compared with median body mass of (sexed) breeding adults (*n* = 538) ringed at Texel, 2006–2021 (inset). The body mass of 234 fledglings weighed between 36 and 45 days of age averaged 658.7 ± 132.4, range: 300–971 g. The body mass of unsexed adult breeding birds averaged 826.5 ± 105.1, range: 630–1065 g.

body mass increased by on average 24 g/d (Table 4). Of 3686 measurements over the years of young chicks (<21 d of age), only 5.5% demonstrated mass loss between subsequent assessments. In later stages of chick care, mass losses between subsequent checks became increasingly more common: age 20–25 d: 20.3% (*n* = 644), 26–30 d 24.7% (*n* = 543), 31–35 d 27.6% (*n* = 431), 36–40 d 43.2% (*n* = 315) of the measurements indicating mass loss. Raising a full brood (three chicks) from hatching to fledging was rare: 2.3% of all cases (*n* = 497 nests).

With 2.70 ± 0.14 eggs as mean clutch size over all seasons, 37.1 ± 9.1% of all losses between laying and fledging could be attributed to chick depredation, making this the prime factor influencing fledging rates. Chick predation, largely by conspecifics and by Herring Gulls, but occasionally by raptors such as Marsh Harriers *Circus aeruginosus*, Goshawks *Accipiter gentilis* and perhaps crows (Corvidae), varied around 52.8 ± 13.2% over all hatchlings, with a significantly declining trend over the years. Chick depredation could reach very high levels such as 67% (2007, 2009) or even 78% (2017) of all hatchlings in some seasons. In such years, chick depredation occurred mostly in sudden, particularly violent, often initially localised but

gradually spreading cannibalistic events during which, when observed, numerous agitated, fighting adults were involved, pecking at and eventually killing free roaming chicks. During such outbreaks, chicks were attacked and killed or torn apart by adult gulls rather than eaten, although carcasses were later scavenged (gulls typically aim at the intestines and fleshy thighs). Major outbreaks tended to spread like oil-slicks, with some parts of the colony severely impacted, and other sectors relatively spared. The advantage of nest cover was absent during chick care. More or less open ground nests did not suffer from higher chick predation rates (57.0% of the chicks) than the half-covered nests or nests that were largely hidden from view (51.9 and 53.5%, respectively; G_{adj} = 0.22, *df* = 2, *P* > 0.05, 1019 chicks). Overall, 49.3% of all 515 chicks with known hatching dates were predated before they had reached an age of only 10 d, a further 29% were taken before 20 d of age, another 18% before 30 d and only 4% during the last 10 days prior to fledging. The median age of chicks when depredated was relatively high (16–18 d) in 2006, 2008 and 2021, very low (3–4 d) in 2019 and 2020, and varied between 6–13 d in the other years.

At c. 40 d of age, most chicks were capable of flight and could leave the enclosures at will. Around that age, while flying around, the offspring were still considerably smaller than the adults. Head and bill were around 80–90% of adult size, the wings were c. 70% and the body mass was c. 80% of an adult bird. Only the feet (tarsus) were fully developed (98%; Table 4). While head length in adults differed between males and females such that a barely overlapping bimodal frequency distribution occurred (see Coulson 1983), the size-distribution in free running near-fledglings (exact age unknown), captured for colour-ringing, was normally distributed with a considerable spread: mean: 105.8 ± 5.8 mm, range: 88–121 (*n* = 954). The same was true for properly aged chicks in enclosures at c. 40 d of age (mean: 103.5 ± 5.9 mm, range: 88–120, *n* = 179). Structural size (head, wing) and mass around fledging declined over the years, but this decline was only significant when considering chick body mass (Table 2). A similar (non-significant) decline was found when a body mass index was calculated (body mass corrected for size, i.e. using head length as proxy; ANOVA χ^2_1 = 3.53, *P* = 0.06).

Breeding densities

Breeding numbers of Lesser Black-backed Gulls within the two adjacent valleys of the Kelderhuispolder colony (15 ha), ranged from 2336–4817 (mean: 3640 ± 1025) 'active' territories in each of the colony censuses

(2009–2016). Breeding densities in 2015 and 2016 (hence, breeding numbers), were distinctly lower than in the earlier counts (2009, 2010 and 2011): 0.015 and 0.019 nests/m^2 (156–193 nests/ha) in 2015–2016 versus 0.025–0.032 nests/m^2 (250–320 nests/ha) in 2009–2011. Of 2810 inspected nests during area censuses, 5.7% were single egg clutches, 14.7% 2-eggs, 54.2% 3-eggs, 0.2% 4–5-egg clutches and 23.5% were territories with empty nests. Empty nests were more frequent in 2011 (33.1%, $n = 483$) and 2016 (32.8%, $n = 808$) than in 2010 (18.6%, $n = 802$) and 2015 (11.9%, $n = 707$), so non-breeding varied irrespective of fluctuations in breeding densities. Peak densities of up to 0.14 nests/m occurred in sections of counting strips averaging 298 ± 131 m^2 in surface area, and such high densities occurred only in the flat ground valley areas, or on the lower gradual dune slopes.

Consequences of nesting late
Nest cover (ranked along an 8-point scale) was similar, irrespective of laying date, but clutches produced in late nests were significantly smaller than in earlier breeding attempts (Table 5). Egg size, expressed as three-egg clutch volumes, did not differ between early, late or peak-produced clutches. Both the number of hatchlings and the number of fledglings were significantly reduced in late nests. but the penalty for being late was most obvious in the chick phase. Early nests had the lowest incidence of failed broods (54.2%), while 87% of the late nests did not fledge a single chick (Table S7). From these late nests, just under 10% of the hatchlings fledged, 21% died and nearly 70% was predated. Of the early nesting birds, over all seasons, 7% fledged full broods (three chicks), against 2% of nests from the peak laying period and none of the late-nesting birds. Hatching and fledging rates and egg volumes for properly sequenced A-, B-, and C-eggs for gull pairs incubating 1-, 2- or 3-egg clutches, all relative to (grouped) laying date, are tabulated in Table S5.

The number of eggs hatched per nest had a significant, linear, negative relationship with laying date ($\chi^2_1 = 16.63$, $P < 0.001$; Figure 4A, Table S4). The number of chicks produced per nest, showed a significant quadratic relationship with median laying date ($\chi^2_1 = 12.98$, $P < 0.001$; Figure 4B, Table S4). The earliest nests produced slightly fewer chicks per nest than those that were initiated later, but still before the median laying date. Note that the confidence intervals for early nests are wide, indicating variation in fledging success for early nests. Nests that were initiated after the median laying date hardly produced any chicks, with low confidence intervals around the prediction.

Recruitment, age at first breeding, colony exchanges
Of the breeding birds trapped for colour-ringing (with a breeding history otherwise unknown), 0.4% were in late 3rd cycle, 1.0% in 4th cycle and 98.6% were in adult plumage when captured ($n = 507$). Immatures were even uncommon as prospecting 'visitors'. During ring-reading, 78 colour-ringed immature individuals were seen, including seven for the first time as 2nd cycle (9.0%), 38 as 3rd cycle (48.7%) and 33 as 4th cycle birds (42.3%; all true age from rings). One of these was ringed as chick in Zeebrugge (Belgium; 1.4%), one at

Table 5. Vital statistics describing nest cover, egg production, hatching and fledging rates, failures and brood size (fledglings) relative to the timing of nesting attempts in Lesser Black-backed Gulls, Texel, 2006–2021.

| Timing	Early	Peak-laying	Late	One-way ANOVA		
				F	P	Signf
Nest cover (1–8)	4.13 ± 1.3	4.05 ± 1.2	4.07 ± 1.3	0.365	0.694	n.s.
Clutch size	2.67 ± 0.64	2.70 ± 0.59	2.55 ± 0.63	6.068	0.002	**
3-egg clutch volume	218.7 ± 15.7	220.7 ± 16.1	219.7 ± 17.0	1.149	0.318	n.s.
Hatchlings per nest	2.09 ± 1.1	2.00 ± 1.1	1.63 ± 1.1	13.78	<0.001	***
Fledglings per nest	0.73 ± 0.9	0.61 ± 0.8	0.16 ± 0.46	16.87	<0.001	***
Chick predation	38.4%	50.8%	69.6%			
Failed broods	54.2%	60.2%	87.3%			
1-chick fledged	25.3%	21.1%	9.3%			
2-chicks fledged	13.3%	16.9%	3.4%			
3-chicks fledged	7.2%	1.8%	0.0%			
All nests (n)	269	766	268			
Enclosed nests (n)	81	280	116			
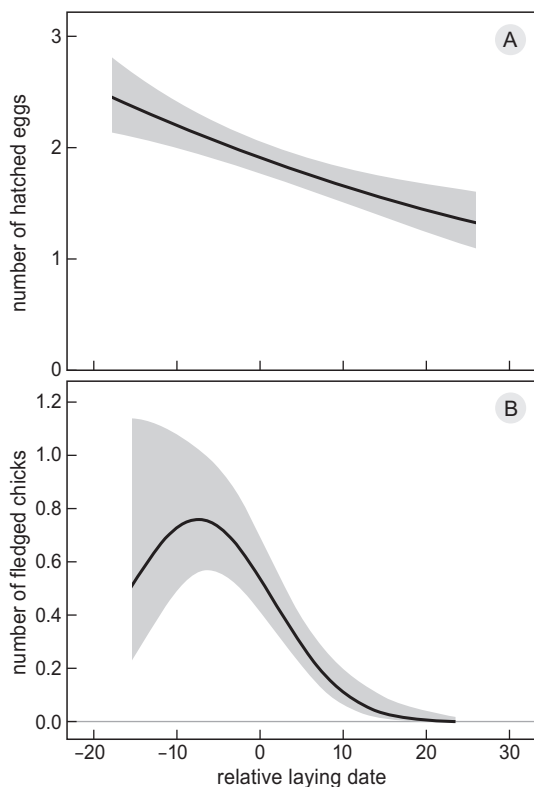
Figure 4. (A) Number of hatched eggs and (B) fledged chicks in relation to relative laying date (annual colony median laying date). The light grey area represents the confidence interval. Early nests, compared to the median laying date, hatched significantly more eggs than late nests, while nests produced just after the first nests, but before the laying peak, fledged most chicks.

Helgoland-Düne, Schleswig-Holstein (Germany; 1.4%), two in IJmuiden (2.9%) and the rest originated from the study colony itself (94.3%). At the nearby colony of IJmuiden, where breeding success is not measured, but where visual observations of assemblies of fledglings in August 2008–2021 indicated that the reproductive success is much higher than on Texel (Fred Cottaar pers. comm.), a higher proportion of breeding subadults was found during ringing: 1.4% in 3rd cycle, 5.6% in 4th cycle and 93.0% in adult plumage (484 incubating individuals). Subsequent ring-reading activities in the colony IJmuiden yielded nearly 1634 sightings of immature prospecting birds, representing 162 individuals: two (1.2%) for the first time during their first cycle, 59 (36.4%) as 2nd cycle, 83 (51.2%) as 3rd cycle and 18 (11.1%) as 4th cycle individuals.

Of fledglings ringed on Texel prior to 2018, only 91 individuals were confirmed to have returned as a prospector or to breed (9.2%, $n = 994$). For 17 chicks raised at Texel (1.7%), breeding evidence was obtained

from other colonies: two on Helgoland (FRG, 247 km distance), four in IJmuiden (61 km), five individuals elsewhere in the Dutch Wadden Sea (4–129 km), and six in urban and industrial areas, deeper inland in The Netherlands (66–147 km). Three birds ringed as breeding adults were found breeding in later years in the UK (238 km), in IJmuiden (61 km) and near Petten in Noord-Holland (30 km). Confirmed breeding at Texel of birds fledged in other colonies included 11 individuals that had fledged in industrial areas at Europoort/Maasvlakte and Moerdijk (125 km distance), one from Zeebrugge harbour (Belgium, 212 km), one from Helgoland (FRG, 247 km) and one from Havergate in the UK (238 km). Seven other ringed individuals from other colonies were seen as prospectors on Texel and four juveniles fledged from Texel were seen prospecting other breeding sites.

Resource base (foraging habitat and diet)

Using 13,624 hours of GPS tracking data of 51 adult Lesser Black-backed Gulls (24 males, 27 females) within 150 km from the colony (Apr–Jul, 2008–2014), it appeared that 50% of the time spent away from the colony was recorded within a radius of action of 28 km (85% <41 km, 95% <72 km). Most foraging activities, sexes alike, were within a crescent shaped area to the west, southwest and south of the colony (Figure 5). As a result, the overlap in feeding whereabouts with Lesser Black-backed Gulls breeding at Vlieland and Terschelling (53°14'N, 04°55'E and 53°25'N, 5°27'E) or IJmuiden was minimal (Sage 2022). The foraging habitat of birds breeding in Texel ranged from pelagic to inshore, coastal and almost entirely terrestrial. 'Time spent' includes commuting (flight) and roosting. Terrestrial foraging activities focussed on 'old' polders on the mainland (often circumnavigating 'modern' polders with larger farms and monocultures that were constructed over the past 100 years), and waste or wastewater processing plants.

GPS tracking data also revealed considerable individual variation in foraging locations. Strong site-fidelity plus a tendency to behave similarly across years occurred primarily in individuals foraging in terrestrial habitats, where foraging flights were usually highly directed flights to and from frequently visited foraging opportunities (Figure 6). Amsterdam was used as a distant urban foraging area by some specialised individuals, or opportunistically by other birds. Individual foraging site-fidelity in urban areas was often quite extreme, visiting the same bridge, square, building or street over and over. In more recent years (2017–2021), much longer inland foraging trips were recorded, that

often went beyond the Amsterdam region and well into Friesland (especially in 2019), than in the earlier years of GPS tracking (2008–2016). This material still awaits further analysis. The North Sea was used for 'wide-range searching' (pelagic or free-swimming surface prey) and trawler visits (discards), while the Wadden Sea was almost exclusively used to forage behind shrimpers (discards). Intertidal mudflats, important foraging grounds for numerous other waterbird species in the Wadden Sea, were utilised only by one specialist.

Prey items collected around nests confirmed the use of habitats as indicated by the tracking data (Table 6). The dietary spectrum was enormous (307 prey species or types) and varied in response to availability (seasonal, diurnal, tidal, lunar cycles, otherwise), but probably also by (individual) preference. Of all prey samples collected (8203 samples), at least 82.2% (FO) contained marine prey, 31.0% contained terrestrial prey. The third most important category was waste material with an anthropogenic origin (FO: 7.3%). Prey
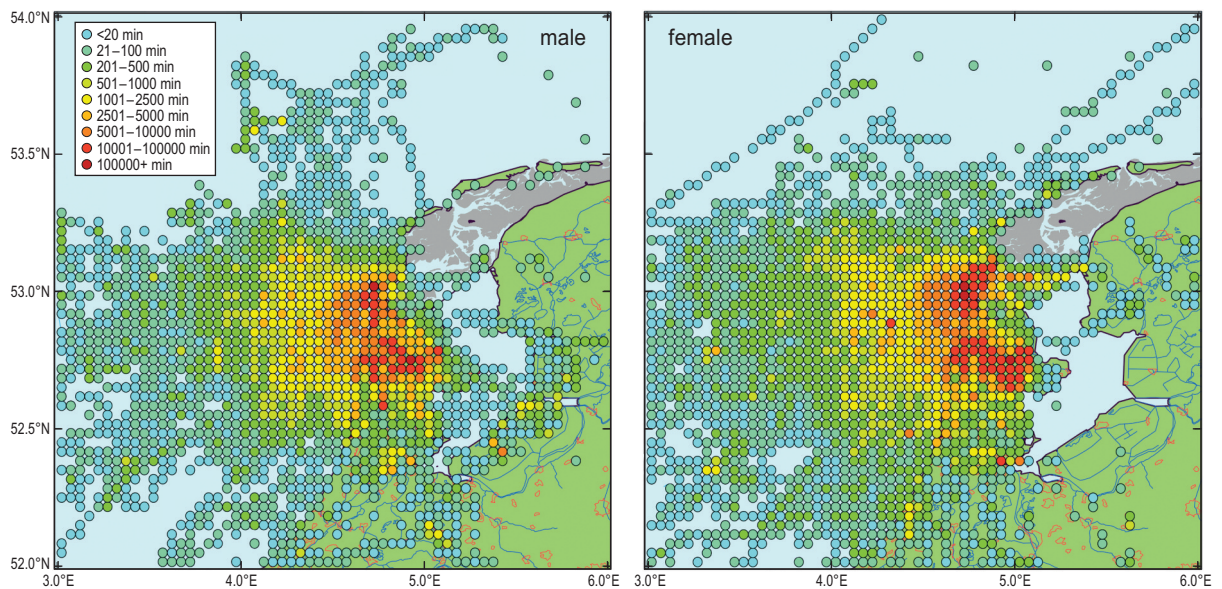
Figure 5. Prime foraging distribution based on GPS tracking data (time spent (min) per 2 × 3' rectangle) for adult male (24 individuals, 29,106 h) and female (27 individuals, 46,503 h of tracking) Lesser Black-backed Gulls breeding at Texel (Kelderhuispolder), 2008–2014, Apr–Jul data combined.
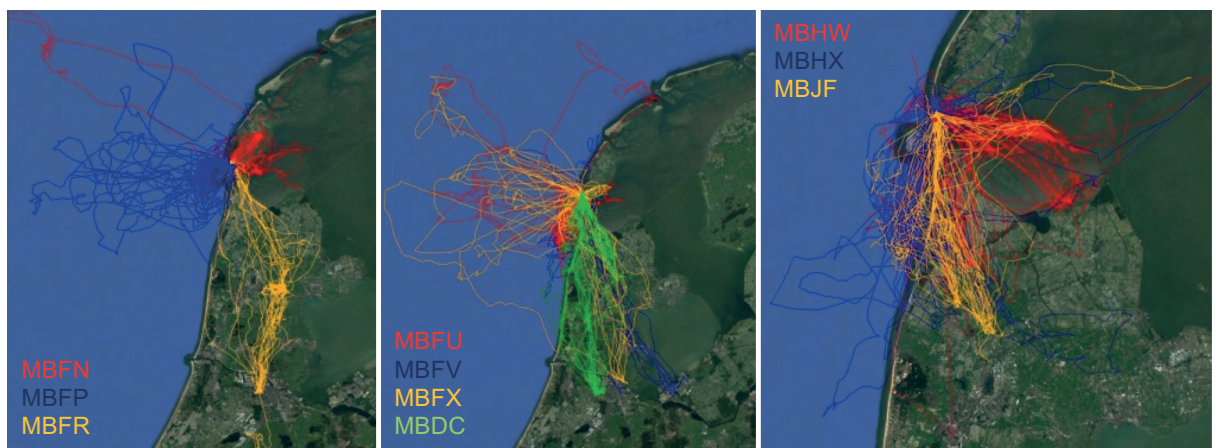
Figure 6. Examples of individual foraging trips using GPS tracking data of 10 individuals during the first month after capture (late egg phase and half-way into chick care phase). Four-letter codes represent colour-ring codes and colours match the colours used on the maps. Left two maps: 3 June – 3 July 2020, right map 5 June – 5 July 2021.

types normally found along the tideline or on the intertidal zone were very scarce (FO: 3.0%, while abundantly represented around nests of the sympatric Herring Gulls). Another rare category was freshwater prey (FO: 1.4%), in which 75% of remains found around marked nests (105 samples) originated from one specialised individual bird or pair in two seasons.

The most frequently encountered marine prey were roundfish (FO: O 67.7%, *n* = 6739) and flatfish (FO: 52.5%), which were mostly Whiting *Merlangius merlangus*, Horse Mackerel *Trachurus trachurus*, Grey Gurnard *Eutrigla gurnardus*, Plaice *Pleuronectes platessa*, Dab Limanda limanda and Dover Sole *Solea solea*, most of which are demersal fish species, only available as discards from large beam trawlers. Marine crustaceans were represented in 27.2% of all prey samples holding marine prey, and these were typically swimming crabs (primarily Swimming Crab *Liocarcinus holsatus*), while marine polychaetes (FO: 14.7%) formed a final important group, mostly represented by *Eunereis longissimi*.

From pre-laying through the egg phase and into the chick phase, the frequency of occurrence of particularly lean (Gadidae, Syngnathidae, Trachinidae), difficult to handle (Belonidae, Bothidae, Pleuronectidae) or bony fish (Callionymidae, Cottidae, Triglidae) species declined, whereas fatty, small pelagics (Ammodytidae, Clupeidae, Osmeridae, Scombridae) doubled during the chick phase (Table 6). Swimming crabs and marine polychaetes typically occurred in pulses, pointing at shifts in availability for foraging gulls at sea.

Table 6. The origin and frequency of occurrence (FO, %) of remains of principal prey of Lesser Black-backed Gulls breeding in the Kelderhuispolder, sorted by relative abundance per breeding phase, Apr–Aug 2006–2021.

Origin	Pre-laying	Egg-phase	Chick-phase	Overall	Totals (*n*)
Sample (*n*)	1329	3403	3471		8203
Marine	86.3	78.8	83.8	82.2	6739
Terrestrial	22.8	38.0	27.2	31.0	2541
Anthropogenic	7.4	7.4	7.1	7.3	597
Intertidal	7.4	2.3	2.1	3.0	250
Freshwater	2.6	1.4	0.9	1.4	113
Undetermined	1.0	1.0	1.4	1.2	97
Sample pollution[1]	6.3	6.7	3.1	5.1	421

Origin	Taxonomic group	Pre-laying	Egg-phase	Chick-phase	Overall	Totals (*n*)
Freshwater	Freshwater fish	91.2	100	93.3	95.6	113
	Other prey	8.8	0	2.7	2.0	
Intertidal	Bivalves	37.8	48.1	35.6	40.4	250
	Crustaceans	9.2	31.6	56.2	30.0	
	Polychaetes	54.1	19.0	6.8	29.2	
	Other prey	2.0	1.3	4.1	2.4	
Marine	Roundfish	62.9	70.7	66.7	67.7	6739
	- Fatty small pelagics	*10.3*	*12.5*	*22.2*	*16.3*	
	Flatfish	67.0	54.9	44.5	52.5	
	Crustaceans	27.2	20.5	33.5	27.2	
	Polychaetes	24.4	18.4	7.4	14.7	
	Gastropods	3.1	2.2	0.6	1.6	
	Other prey	0.0	0.3	0.2	0.2	
Terrestrial	Insects & spiders	51.2	55.5	41.3	49.7	2541
	Plants	30.4	16.8	28.6	22.8	
	Oligochaetes	13.9	28.9	14.1	21.6	
	Non-passerine birds	4.0	9.4	26.9	15.3	
	Mammals	9.9	11.4	6.1	9.2	
	Other prey	7.9	4.2	3.4	4.3	
	Passerine birds	2.6	0.8	1.3	1.2	

[1]Pollution indicates food sample contents that were probably not intentionally taken by the birds, or had otherwise been added to the sample during collection (e.g. tiny plant seeds of locally abundant vegetation).

Species or types of most frequently recorded terrestrial prey were various insects and spiders (49.7%, $n = 2541$), plant materials (mostly livestock food from farms, seasonally also *Empetrum nigrum* berries), Oligochaetes (mostly earthworms *Lumbricus terrestris*, 21.6%), plus non-passerine birds (mostly gull eggs) among some 95 other, less commonly encountered terrestrial prey types. A remarkable peak in small rodents (mostly Common Vole *Microtus arvalis*) was recorded in 2019 (12× usual levels given long-term results, FO in 2019: 14.3%, versus 1.9 ± 1.8% over all other years).

Among the anthropogenic waste materials (597 samples) were mostly plastic fragments, bread seeds, plastic line, thread, plastic packaging, bread, chicken, plastic pellets and paper, plus 75 other, less frequent types, which points at a mixture of items from a marine origin (free floating plastics), rubbish bin contents (most likely from urban environments) and human interventions (e.g. feeding birds bread). The likely origin of food identified as garbage were cities and pickings from holiday resorts and one waste processing plant on the mainland (Opperdoes, 36 km to the SE). Open landfills do not exist within the foraging range around Texel.

The frequency of occurrence of terrestrial prey in analysed samples (not considering species composition) was similar throughout the study, with no apparent trend ($r^2 = –0.067$, $P = 0.68$, $P > 0.05$.). The occurrence of marine prey, however, declined substantially and significantly, from a representation between 80 and 95% in all food samples in earlier years to around two-thirds or sometimes even less in recent years ($r^2 = 0.399$, $P = 0.009$). Prey items with an anthropogenic origin, even though consistently at low levels, increased in frequency ($r^2 = 0.269$, $P = 0.033$).

DISCUSSION

The Lesser Black-backed Gull is one of several Northern Hemisphere gull species, in which numbers, that were low initially (often because of intensive human exploitation), suddenly increased exponentially, reached some maximum and then declined (Morais *et al.* 1998, Spaans 1998ab, Skórka *et al.* 2005, Camphuysen 2013, Anderson *et al.* 2016, Giroux *et al.* 2016, Chytil *et al.* 2021, Litwiniak *et al.* 2021). The ability of large gulls to adapt to human-related environments and food is the usual explanation, and this includes foraging and feeding on landfills, in urban or rural environments, or behind fishing vessels, but also a fairly recently devel-

oped readiness to nest on roofs of buildings in cities and industrial areas (Blokpoel & Scharf 1991, Belant 1997, Duhem *et al.* 2003, Rock 2005, Spelt *et al.* 2020). Being "opportunistic" or even "catholic in feeding habits" are characterisations that have been used to explain their success (Cramp & Simmons 1983, Burger *et al.* 2020, Moore 2020), but while both aspects might contribute to a population increase and range expansion, they do not help us understand a population decline. That the Lesser Black-backed Gull, as an explanation for the rapid range expansion and population increase, had filled an empty niche (mainly fishery discards at newly developed large offshore beam trawlers) rather than outcompeted other coastal large gull species (Garthe *et al.* 1999a, Camphuysen 2013) would thus be an example of successful adaptation to human-related environments. Our studies coincided with a change of fortune, considering the poor breeding success within the study colony, and a stabilisation or decline in breeding numbers in the whole country (Boele *et al.* 2021).

Annual cycle

Lesser Black-backed Gulls are long-distance migrants that leave their breeding grounds in early autumn and return in spring. Colour-ring data and GPS tracking results revealed a south-westerly flyway of this subspecies up to NW Africa (Morocco to Gambia and Senegal), but with the majority of the birds wintering in Europe (mainly Portugal and Spain; Brown *et al.* 2021). This is in accordance with even the earliest published work (Landsborough Thomson 1924, Barnes 1953, Harris 1962). Shifts in wintering areas have been reported some decades ago, with an increasing proportion remaining in the UK or in northern France in winter (Lack 1986, Alerstam 1990). That perceived shift northwards, estimated at 1.6 latitudinal degrees or 150–200 km per year between 1965 and 1975, has not continued (as predicted in Alerstam 1990, p. 213). In fact, the entire original flyway still exists (Brown 2022), with more northerly breeding birds leapfrogging populations breeding in The Netherlands and in the UK (Hallgrimsson *et al.* 2021). Only birds wintering in NW Africa are almost entirely marine in their orientation (coastal fish factories, fisheries and offshore resources; own unpublished GPS tracking data). Birds wintering on the Iberian Peninsula have a large variety of foraging areas including open sea and the seashore (Oro & Ruiz 1997), but including numerous terrestrial options such as large, open landfill areas, rice fields, and olive plantations (Martin-Velez *et al.* 2020, Martin-Velez 2021). Birds wintering in France and in the UK

are largely terrestrial in winter, where they mostly feed on landfills, pig farms, and agricultural fields (Lack 1986, Shamoun-Baranes *et al.* 2016, Baert *et al.* 2018).

The gradual, stepwise change in wintering destinations, range, and timing for birds with increasing age (1st–4th cycle versus adults), now only available from colour-ring re-sightings, supports the exploratory migration model (Baker 1978, 1980), in which, by a process of area exploration, young birds become familiar with a larger area than that they will eventually use as adults (Figure S1, Table S1). Juvenile birds had a different timetable and alternative routes compared to adults (see Kilpi & Saurola 1984, Helberg *et al.* 2009, Marques *et al.* 2009). Colour-ring data have provided evidence for strong site-fidelity as adults, with regard to stopover use and wintering destinations (as in Helberg *et al.* 2009), which would mean that individuals develop intimate knowledge of foraging opportunities at only a few preferred locations. GPS tracking data have confirmed that strong site-fidelity in stopover sites and wintering quarters in adults, with considerable individual variation in timing (Shamoun-Baranes *et al.* 2016, Brown 2022). Only a handful of tracked individuals changed their winter destinations completely from one year to the next, thereby suggesting that gulls can be flexible if needed (Brown *et al.* 2021). Unexpectedly, the annual cumulative distance travelled by long distance migrants did not differ significantly from individuals wintering further to the north (Shamoun-Baranes *et al.* 2016), indicating that the travel required to feed particularly in wintering areas was negatively correlated with distance travelled along the entire flyway.

Adults that returned in late winter and early spring assembled at nearby beaches weeks before they visited the colony itself, and initially only briefly on days with calm weather and overnight stays within the colony occurred no earlier than mid-April. As a result, the breeding grounds on Texel are in use from February (early arrivals) to October (late departures), but residency at the colony effectively spans only April–August. As long-distance migrants returned so much later than most birds that spent their winter within the temperate zone (Shamoun-Baranes *et al.* 2016, Kentie *et al.* 2023), this meant that the available time to (re-)establish pair bonds, to (re-)occupy and successfully defend territories, or to boost energy reserves required to produce eggs, were all compromised for the birds wintering furthest away.

The absence of gulls in the colony from September to March will discourage potential predators from staying in the area between seasons. Frequent rains in winter will likely wash away rotting prey remains that have accumulated around nests and on roosts and leftovers of dead chicks from the previous breeding season (in part, a hygienic reset). The complete absence of birds within the colony during the non-breeding season is typical for this site, but perhaps not a general rule for all colonies (see however Paludan 1951).

Breeding strategy

Historical published work on the breeding biology of the Lesser Black-backed Gull was conducted during that expanding phase of Lesser Black-backed Gull with colonisations around Europe (Lockley 1932, Darling 1938, Paludan 1951, Goethe 1957, Harris 1964, Brown 1967b, Hausmann 1969, Davis & Dunn 1976). Clutch size (c. 2.7), hatching success (c. 79%) and fledging rates (c. 1.2–1.8 fledglings/nest; Darling 1938, Davis & Dunn 1976, Wanders 1980) were revealed and assuming an adult annual survival of 85 to 90% (i.e. typical for long-lived large gulls; Schreiber & Burger 2002, Ross Smith *et al.* 2013, Dierschke *et al.* 2021), such life history parameters would certainly stimulate population growth. More recent studies were often short term (student) projects (de Wijs 1982, 1984, Bekhuis 1994, Calladine 1997), conducted as a sideline of experimental work such as food supplementation (Spaans *et al.* 1994, Bukacinski *et al.* 1998), crossfostering (Harris 1970), courtship behaviour (Brown 1967a), GPS tracking and diet studies (Garthe *et al.* 1999b, Gyimesi *et al.* 2016) or colonies suffering from culling (Duncan 1981, Wanless *et al.* 1996), floodings (Davis *et al.* 2018), botulism (Kim & Monaghan 2006), fox depredation (Wanders 1985, Davis *et al.* 2018) or other additional mortality factors enhancing variability in the measured reproductive success. Annual variations in reproductive output are difficult to appreciate from such short-term studies.

At the onset of the studies at Texel (2006–2010), while still investigating factors underlying the apparently ongoing increase of the Lesser Black-backed Gull against consistent declines of the sympatric Herring Gull, good reproductive output was expected, but the opposite was found (Camphuysen & Gronert 2010). Reproductive success at Texel remained low, certainly in comparison with historical work (cited above), in virtually all seasons that followed. At the time at Texel (2006–2011), with additive year effects rather than sex providing highest model support, apparent annual survival for both sexes combined averaged 91% (range: 81–100%; Camphuysen & Gronert 2012). Low reproductive success in combination with a 'high' (or normal) apparent annual survival of the adults

breeding on Texel would lead to an 'ageing' population, but it remains to be seen how survival probabilities have changed in recent years.

PRE-LAYING PHASE

Large gulls, as many other colonial species, exhibit a high degree of nest site-fidelity or within-colony 'micro-philopatry', choosing sections, clubs and territories in sectors of the colony from which they originated, year after year (Goethe 1937, Paludan 1951, Tinbergen 1953, Chabryzk & Coulson 1976, Klomp & Furness 1992, Spaans & de Wit 1986, Ross-Smith 2013). This was confirmed in our studies, with territorial shifts that were typically over short distances only (90% <20m). Yet, field observations suggested that some popular sectors within the colony were gradually abandoned over the years, while others were colonised, leading to gradual shifts in distribution patterns and breeding densities over the area at large (see Methods on study plots). Some of these collective displacements may have been the result of disturbances inflicted by the research itself, but the gradual changes occurred also outside the study plots and new colonisations were recorded also in frequently 'visited' (studied) parts of the terrain. Long-distance territorial displacements (>200 m) within the colony were not recorded. The impact of site-fidelity on mate-fidelity was difficult to assess, but long-lasting pair-bonds were the exception rather than the rule (<20% over five years or more), nearly 60% as a result of divorces, the rest because one of the partners died. It is interesting to note that new partners were typically recruited from the same general area within the colony (Brown 1967a), suggesting that new partners were probably not 'randomly' picked overflying birds that were lured in by displaying territorial males (contra Tinbergen & Falkus 1970).

EGG PHASE

Most parameters characterizing the egg-phase (clutch, predation pressure and hatching success) were in line with earlier studies of Lesser Black-backed Gulls, Herring Gulls or closely related species (Drent 1967, Paludan 1951, Harris 1964, Ross-Smith 2013). Egg predation was slightly more frequent at Texel (c. 21%) than in earlier published work, but the difference was small. Drent (1967) found a preponderance of egg predation in the laying and early incubation periods, thereby explaining these early losses by the initially low parental attentiveness to the clutch, which increased and became more aggressive later in the incubation period. At Texel, egg predation occurred throughout the incubation period and c. 25% of the eggs were lost during the last week of incubation. Ross-Smith *et al.* (2016) found that hatching success was significantly positively associated with egg volume and clutch size (based on 1600 eggs in 2007 and 2008 at Flat Holm, Wales), with eggs in clutches of two and three eggs significantly more likely to hatch than those in clutches of one. Trends found on Texel are in full agreement with these findings (Table S5-S7) and the reason might be that experienced, higher quality females are more likely to lay early in the season and produce 'complete' clutches with relatively large eggs.

The various parameters characterising the egg phase varied between seasons, without a clear trend, with two clear exceptions: (1) laying was substantially delayed, from the first to the second half of May during the 16 years of study, and (2) and a highly significant decline in 3-egg clutch volumes occurred over the years (both Table 1). Between 2007 and 2013, Lesser Black-backed Gulls at Texel commenced laying progressively later (median egg laying: 9, 10, 12, 14, 15, 19, 21 May, respectively) and it stabilised around 17–21 May between 2014 and 2021, about 10 days later than before. With adults returning to the breeding grounds as before, the pre-laying phase became substantially extended, with pairs occupying territories for almost a month, but still refrained from laying (field observations of colour-ringed birds and unpublished GPS tracking data). Also, the laying peak widened (Table 1), suggesting that laying synchronisation somewhat declined in recent years. As stressed before, few earlier studies were longer-term investigations, such that while differences in for example clutch volume could be assessed, time-trends from other sites are not available. The only comparable (unpublished) datasets that could be explored were collected at the neighbouring colony in IJmuiden (Fred Cottaar unpubl. data), where Lesser Black-backed gulls produced eggs on average 1–2 weeks earlier than at Texel, but where egg laying was not studied with a similar precision to assess more subtle changes in laying dates. At IJmuiden, however, using annual measurements collected 2008–2022, three-egg clutch volumes decline at a similar rate as at Texel.

In gulls, reproductive success usually declines in the course of a breeding season (Davis & Dunn 1976, Spaans *et al.* 1987, Brouwer *et al.* 1995). The onset of laying in gulls is probably an individually based compromise, between an expected seasonal peak of food abundance for the offspring and energetic requirements for the females when forming the eggs (Perrins 1970, Drent 2006), with nest initiation being subject to local environmental conditions. The seasonal pattern in

breeding output may thus either be a consequence of timing per se, affecting all individuals in the same way (the date hypothesis), or reflect quality differences between individual breeders, irrespective of timing (the quality hypothesis), with 'quality' referring to the phenotypic quality or condition of the breeding individuals (Verhulst & Nilsson 2008). Experienced adults are expected to lay well before inexperienced individuals and recruits (Davis 1975, Bosman *et al.* 2013). In accordance with earlier work, within seasons, late-nesting Lesser Black-backed Gulls on Texel fledged very few young compared to early- or peak-nesting birds (Figure 4). The better breeding results obtained by 'timely' or even earlier laying birds could confirm that more experienced, (potentially high quality) birds take initiative each season, while less experienced birds and first-timers follow.

Egg size can decline under conditions of low food availability prior to egg-laying (Pons 1992, Bolton *et al.* 1992). Between seasons, there was a highly significant negative correlation between median laying dates and 3-egg clutch volumes (Table S4, $r^2 = 0.65$, $df = 14$, $P < 0.001$), and there was an overall decline in egg volume over the years (Table 1). Did a generally late start to egg-laying have negative consequences for egg volumes in the colony as a whole, or was the population structurally (perhaps even increasingly) unable to store sufficient resources to produce larger eggs, or to advance laying?

Migratory birds may accumulate stores at the breeding grounds and females then react to the rate of change of in body condition to commence breeding ('income breeders'; Drent & Daan 1980). Alternatively, as Perrins (1970) pointed out, long-distant migrants may circumvent problems by bringing nutrients with them in the form of body stores ('capital breeders'). In Lesser Black-backed Gulls breeding on Texel, the high synchronisation of laying (50% of all eggs produced in 8.7 ± 2.0 days, range: 5–11 days; Table 1) suggests that most breeding pairs are affected by social stimulation or respond to environmental conditions in the same way. Tracking data have shown thatbirds travelling all the way to NW Africa in winter arrive rather late, while still breeding within the synchronised laying peak (Kentie *et al.* 2023). Such birds are more likely to have to rely on body stores to commence nesting, but for in fact most other birds, with a pre-laying phase spanning up to four months, accumulated stores in the breeding grounds themselves will be most relevant. If nest initiation is indeed subject to local environmental conditions, and all these birds cannot keep up with an earlier laying date, or with clutch volumes as in earlier

years, the resources on which the population is currently depending must be a limiting factor.

A flaw in the setup of our studies was that non-breeding (territorial adults that did not produce any eggs) was not systematically recorded. Camphuysen (2013, p. 326), from colour-ring re-sightings, estimated that individual Lesser Black-backed Gulls bred on average only once every 2.1 years (in the apparently more productive control colony at IJmuiden once every 1.8 years). Migot (1992) found that a large proportion of potentially mature birds did not breed in a study of demographic changes in French Herring Gulls and annual nest counts of Lesser Black-backed Gulls at the Tarnbrook Fell gullery (Lancashire, UK) between 1981 and the mid-1990s showed that around half the constructed nests did not receive eggs (O'Connell *et al.* 1997). Calladine & Harris (1997) found that 30–40% of adult Lesser Black-backed Gulls, all with previous breeding experience, skipped seasons and observed that smaller individuals, birds with low survival probabilities and comparatively unsuccessful breeders were common amongst intermittent breeders. We have no evidence to confirm that suggestion, but the fact that numerous territorial pairs forego egg-laying in some years is apparently far from unique.

CHICK PHASE

Problems in the Texel population were particularly evident during the chick phase: chick depredation rates (largely by conspecifics or Herring Gulls) were spectacularly high in some seasons and contributed to poor or at best moderate breeding results in nearly all years (Figure 2, Table 2). Fledging rates such as in historical studies (1.2–1.8 fledglings/nest; Darling 1938, Davis & Dunn 1976, Wanders 1985) were never even approached on Texel in recent years. When breeding became delayed in the most recent seasons, distinctly lower levels of chick depredation were found. However, whatever the patterns of causation, the delay in nest initiations brought greater variability in reproductive output between seasons: two of the worst years on record (2017–2018), but also four of the best seasons in terms of fledging rates (2014, 2019–2021). The significant decline in egg volume led to smaller hatchlings (Table 1) and both the structural size and body mass of chicks around fledging declined significantly from 2006–2021 (Table 2). These trends resulted in smaller, lower quality offspring.

The depredation of chicks by conspecifics, or by closely related gull species in mixed colonies, is often referred to as 'cannibalism' (Tinbergen 1959, Brown 1967b, Gillett *et al.* 1975, Burger & Gochfeld 1981,

Hario 1990, Nurhan & Henson 2021). Such cannibalism (or infanticide) is a behavioural trait found in a wide variety of animals (Fox 1975), but it is a clear disadvantage of coloniality that is particularly obvious in large gulls (Paynter 1949, Emlen 1956, Parsons 1971, Hunt & Hunt 1975, Davis & Dunn 1976, Montevecchi 1977). Cannibalism is believed to be an adaptive behaviour that might enable a population to survive periods of scarcity, a mechanism known as the 'lifeboat strategy' (van den Bosch *et al.* 1988). Hide observations by David & Dunn (1976) revealed that the bulk of egg losses, and to a lesser extent chick loss, in a colony of Lesser Black-backed Gulls arose through predation not just by conspecifics, but usually by nearest neighbours. Often, the protagonists had lost their own clutch shortly before turning predator. A chain reaction could lead to a steady build-up of aggressive failed breeders and so account for further losses. During the most violent outbreaks of cannibalism at Texel, the spreading of this phenomenon as an oil-slick pattern was striking: large areas of the colony could suffer near-complete losses of offspring, whereas neighbouring, similar areas remained, at least initially, unaffected. Hunt & Hunt (1976), in a study of colonial Glaucous-winged Gulls *Larus glaucescens*, observed that pecking of trespassing chicks by neighbouring adults was the major cause of chick mortality. Chicks that grew slowly were more likely to be killed by neighbours than fast-growing chicks, and among slow-growing chicks, those hatched early in the season on large territories had better survival rates than late hatching chicks on small territories. At Texel, chicks entering neighbouring territories were usually received with hostility by the defending adults (field observations). That slow-growing chicks had a greater tendency to wander around (as in Hunt & Hunt 1976) has not been demonstrated on Texel but could be expected if starving chicks try to find food in times of poor provisioning. Examination of corpses of chicks during cannibalistic outbreaks at Texel showed that the birds were not just killed but must have been pecked at many of times before they died. Numerous bald-headed or bleeding young wandering around in the colony during years with high chick depredation rates were testimonies of these confrontations.

During mass cannibalistic outbreaks, chicks were initially just killed (and often torn apart by multiple adults together), but not eaten, with their remains being scavenged by adult and juvenile gulls on later days (typically aiming at intestines and flesh of the legs). Such outbreaks had nothing to do with the few specialised cannibalistic birds that took eggs or chicks of conspecifics as part of their diet or to feed their chicks ('professional cannibals'; Camphuysen 2011). That free-roaming (hungry) chicks entering neighbouring territories were more likely to be killed could mean that enclosures potentially formed safe havens, thereby affecting the results of our studies. Camera traps revealed that adults readily attacked chicks hidden within enclosures, and if a study plot fell within a sudden cannibalistic outbreak, adult gulls would attack any chick they could see, thereby sometimes even flying straight into the fence by which targeted chicks were enclosed. That the use of enclosures led to slightly better breeding results cannot completely be excluded.

Overall, the body mass of fledglings (around 40 d of age) arrived on average at 650 g, or nearly 80% of adult body mass (Figure 3, Table 4). There is, unfortunately, little published material to compare such values with. Studies on Lesser Black-backed Gulls in Vlissingen (NL) and Zeebrugge (B) in 2016 showed that male fledglings were heavier (asymptotic body mass: 778.4 ± 20.3 g) and larger (tarsus length: 64.7 ± 0.5 mm) than female chicks (mass: 660.3 ± 17.7 g; tarsus length: 59.6 ± 0.6 mm; Kavelaars *et al.* 2018), which would be c. 10% heavier than the (unsexed) chicks fledging at Texel. The fledgling mass of Lesser Black-backed Gull chicks on Texel was on average far below that of chicks of similar age at Terschelling in the early 1990s. Spaans *et al.* (1994) compared the mass of chicks with a wing length > 260 mm (i.e. probably ≥ 35 d; Table 4) for eight colonies in 1992–1993 and found values of 780–800 g for IJmuiden, Texel, Vlieland and Terschelling in 1992, or 20–23% more than at Texel in recent years and 800–950 g for Terschelling in 1993, which is 23–45% more than in the present study). A decline in chick growth (slower growth, lower mass at fledging) of Herring Gulls at Terschelling in the early 1980s compared with that in the late 1960s, was reported as a density-dependent response of a population that had tripled in size (Spaans *et al.* 1987). In Lesser Black-backed Gulls at Terschelling in 1992, food-supplemented chicks experienced more rapid growth and achieved a higher body mass around fledging than controls (Spaans *et al.* 1994, Bukacinski *et al.* 1998). Fledging success (in controls) was reduced as a result of high levels of chick starvation and depredation. In 1993, however, resources were apparently so plentiful, that experimental food did not make a difference: controls grew faster and to a higher mass around fledging than in 1992 (Bekhuis 1994, Spaans *et al.* 1994). The low and declining fledgling mass of Lesser Black-backed Gulls on Texel must be seen as another indication of low provisioning rates during chick care.

Fledging a full brood of three chicks was rare on Texel, even though the body mass of chicks at c. 40 d of age was similar between pairs fledging one, two or three chicks (Table 3). Similar growth rates and mass of fledglings in broods of various sizes were surprising, given the fact that siblings compete actively for food, while single chicks have no competitors. Similar growth rates of chicks in broods of two and three chicks was also found by Vermeer (1963) for Glaucous-winged Gulls, where even manipulated 'supernormal' broods (adding one, two or three eggs to clutches of three) were highly successful and experimental pairs taking care of three, four, five or six hatchlings fledged 2.1, 2.9, 3.4 and 4.8 chicks/nest, respectively.

Wilkens & Exo (1998) estimated that 0.6 chicks/ pair should fledge to maintain a stable population size for Herring Gulls. Obviously, not just breeding success, but also levels of annual mortality, immigration and emigration should be known, including their relative importance regarding the functioning of the population (Migot 1992). However, all signals from the chick phase of Lesser Black-backed Gulls breeding at Texel point at poor results as a result of insufficient provisioning by most parents in virtually all years of study. A mean reproductive output of only 0.49 ± 0.2 (0.09– 0.94) chicks/pair on average over a 16-year period such as at Texel between 2006 and 2021 would be consistent for a breeding population in decline. The logical next step would be a comprehensive analysis of life history parameters such as age of first breeding, occurrence of non-breeding seasons, age dependent survival, and levels of recruitment; which can now be based on a long-term dataset of colour-ringed individuals, from which to calculate lifetime reproductive success and to understand current, as well as near-future (likely) population trends.

CONSEQUENCES OF NESTING LATE

Within seasons, breeding success in Herring Gulls studied on Terschelling was highest for early breeders, decreasing to almost zero for late breeders (Spaans *et al.* 1987). In an experimental study in the same colony, years later, Brouwer *et al.* (1995) found that the optimal hatching date, leading to the highest fledging rates, coincided with the colony mean hatching date (synchronization advantage) when resources were plentiful. When food was less abundant, early breeders were more successful. A consistently higher reproductive success of 'early' versus 'late' laying birds (Figure 4B), would point at food stress following the model of Brouwer *et al.* (1994). The success of early breeders did not lead to advances in colony breeding in later years

as suggested by Spaans *et al.* (1987). In fact, the onset shifted 10 days towards the second half of May, while the differences between early, peak and late nesting individuals within seasons was generally maintained, but with two notable exceptions: 'early' nesters in 2017 and 2018 did not fledge a single young, when the entire (poor) reproduction in these years relied on birds that started during the peak of laying.

Breeding densities and population trends

For colonial seabirds, one of the often-highlighted advantages of nesting synchronised and in high densities is: safety in numbers (collectively defending eggs and chicks when disturbed by predators; Danchin & Wagner 1997). In large gulls, however, most eggs and chicks are taken by conspecifics, so next-door neighbours may suddenly change from co-defenders to predators. Wilkens & Exo (1998) compared the reproductive success for Herring Gulls at two plots with different population densities at the island Mellum (German Wadden Sea island). With similar clutch sizes, the lower density area produced more offspring than the high-density area, largely as a result of higher (conspecific) chick depredation rates in the more densely populated parts. A three-fold increase in nesting density coincided with a significant reduction of reproductive success in Herring Gulls breeding on Terschelling (Dutch Wadden Sea), again, largely as a result of strongly increased levels of chick depredation by conspecifics (Spaans *et al.* 1987). The breeding density of the two (sympatric) species at Texel (2009–2016) was at least two times higher than that in the mixed colony at Terschelling at the time, but the reproductive output at Texel was even marginally higher than that measured at Terschelling (Spaans *et al.* 1987). There is no evidence for a shortage of nesting space or suitable habitat at the Wadden Sea islands in most of the larger colonies studied in dune areas along the North Sea in recent decades. Breeding density itself is probably not the issue. That populations in which the nesting density has increased suffer more from cannibalism than before, has probably more to do with increased levels of intra-specific competition for food: with a resource base now shared with more competitors.

Resource base and foraging opportunities

Central place foragers often segregate in space, even without signs of direct agonistic interactions: a common avoidance strategy among and within species from neighbouring breeding colonies (Wakefield *et al.* 2013, Sage 2022). Individual-level memory of resource availability can be sufficient to cause spatial segregation in

the foraging range of neighbouring colonial animals (Aarts *et al.* 2021), but that seabirds from neighbouring colonies forage in largely mutually exclusive areas is often assumed to result from density-dependent competition (Wakefield *et al.* 2013). Lesser Black-backed Gulls equipped with GPS data loggers from six study colonies along the German North Sea coast did indeed forage in barely overlapping home ranges, and that range increased with increasing colony size (Corman *et al.* 2016). Colony-specific foraging patterns, habitats, and resources could reduce intra-specific competition. Similarly, with most foraging activities of Lesser Black-backed Gulls breeding on Texel directed to the west, southwest and south of the colony (Figure 5), an overlap in feeding whereabouts with large neighbouring colonies at Vlieland, Terschelling and IJmuiden was indeed almost non-existent (Ens *et al.* 2009, Sage 2022). As a result of the spatial segregation with birds breeding on Vlieland and Terschelling, the Frisian Front area (c. 53°45'N, 04°30'E), an important feeding ground for Lesser Black-backed Gulls (Camphuysen 1995, Baptist *et al.* 2019), was for Texel birds within range (c. 52 km to the NNW), but effectively 'out of reach', and thus rarely visited (Figure 5).

Individual foraging site fidelity, another widespread phenomenon in nature (Bormann *et al.* 2019), probably benefits individuals through higher foraging efficiency. It may arise as a consequence of dietary specialisation, and the resulting resource partitioning might guarantee semi-exclusive foraging opportunities for individual birds (Ceia & Ramos 2015). From the diet studies at Texel, it appeared that only few birds specialised on mammals (mostly rodents) or freshwater fish. Birds that otherwise shared a common resource with many others, often specialised on specific locations. So, while numerous birds foraged on farmland on Texel, or in old polders on the mainland, GPS tracking data typically showed that individuals used only two or three different 'preferred' feeding areas out of multiple options (given the population at large) for most of their time during breeding (Figure 5). Flexibility was demonstrated when several GPS tracked individuals suddenly ventured into Friesland grasslands in 2019, while the frequency of occurrence of common voles in prey samples throughout the colony peaked at 12× long-term average levels, during a major outbreak of common voles in agriculture grasslands (Wymenga *et al.* 2021). Flexibility was also shown in short-lived, but distinct peaks in the frequency of occurrence of prey types such as swimming crabs, marine polychaetes (only available during spawning bouts), ripening berries or insects.

Marine prey (primarily obtained in the North Sea and in deeper parts of the Wadden Sea) supplemented by food found in agricultural areas (Texel and mainland) and small amounts of junk food (garbage from urban areas mostly) currently forms the basis for Lesser Black-backed Gulls breeding at Texel (Table 6). In an earlier analysis of tracking data, it appeared that males travelled on average further from the colony than females, and spent more foraging time at sea, offshore (Camphuysen *et al.* 2015). Males fed mostly on fisheries discards at offshore trawlers while females foraged predominantly on land or near-shore and in the Wadden Sea around shrimpers (Tyson *et al.* 2014). Discards from large offshore beam trawlers (to a lesser extent nearshore shrimpers), formed the most important resource base, given prey remains found in c. 8200 food samples. For Lesser Black-backed Gulls at Terschelling in the 1990s, the presence or absence of small pelagics (clupeids) was at the time seen to influence chick growth and reproductive success most (Spaans *et al.* 1994), but even though small pelagics were frequent prey for birds breeding on Texel, they were too uncommon (in mass) to likely 'drive' success or failure for the breeding population as a whole. Beam trawlers typically return to the harbours for the weekend (Rijnsdorp *et al.* 2011) and discard-scavenging specialists, tracked with GPS, responded by switching to foraging on terrestrial habitats (Tyson *et al.* 2014).

The demonstrated dependence on discards, of this colony, but in fact of most colonies in this part of the North Sea (Flore 1999, Schwemmer & Garthe 2005, Sotillo *et al.* 2014), has shed a different light on the rather sudden increase in breeding numbers that occurred in the 1970s and 1980s. This increase followed the modernisation of the Dutch fishing fleet: from otter trawl to beam trawl that commenced in the 1960s (Rijnsdorp *et al.* 2008). Beam trawling is a discards-intense form of fishing (Van Beek 1998), that seemingly formed a sound foundation, at the time, for the colonising species all over the Southern and German Bights (see also Camphuysen 1995). A successful utilisation of discards from large (offshore) beam trawlers can explain the timing and the scale of the population increase throughout the 1970s–1990s. So, rather than outcompeting other gulls for existing foraging opportunities (Noordhuis 1987, Noordhuis & Spaans 1992), the increase was more likely driven by the successful exploitation of an emerging (marine) resource, associated with offshore beam trawlers (Camphuysen 1995, Garthe *et al.* 1999a). The decline in fishing effort, especially a shrinking beam trawl fleet, and the EU discards ban (Bicknell *et al.* 2013, Borges

2013, Anon. 2014, Kuhlman & Van Oostenbrugge 2014) is an ongoing and gradual process that commenced earlier this century, and that will reduce this anthropogenic resource base more and more. A consistent decline of prey samples containing marine prey over the study period, in line with various other signals in the breeding colony pointing at food stress, are clear indications that the birds breeding on Texel find it difficult to adapt within the constraints of their colony-specific foraging home range. An increasing tendency to utilise inland rather than marine foraging opportunities in Lesser Black-backed Gulls was reported from many areas in Europe, even though factual evidence was sometimes sparse, but indeed, some recently established colonies are even almost entirely terrestrial, and often with great success (Gyimesi *et al.* 2016, Sotillo *et al.* 2019ab). The birds breeding at Texel, despite their longer inland foraging trips in recent years, are seemingly unable to boost their current reproductive success with existing (gradually changing) foraging opportunities, as if still 'hopeful' for returning fishing fleets offshore.

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SAMENVATTING

Kleine Mantelmeeuwen *Larus fuscus* hebben zich in 1926 als broedvogel in Nederland gevestigd. Tot aan de jaren zestig van de vorige eeuw bleven de aantallen broedvogels tamelijk klein, maar daarna ontwikkelde de populatie zich snel. In 2006 werd op Texel (Nederlandse Waddenzee) begonnen met een langjarig onderzoek naar de broedbiologie, trekbewegingen en foerageerecologie door middel van nestmonitoring, het (kleur-)ringen van vogels, voedselonderzoek en het volgen van individuen met geavanceerde gps-loggers. Het hoofddoel was het verkrijgen van uitgebreide ecologische gegevens over de broedprestaties, de jaarlijkse cyclus (van broedkolonie tot overwinteringsgebieden), kenmerkende prooisoorten, verschuivingen in de voornaamste voedselbronnen en habitatgebruik. Trekstrategieën varieerden van korte (Frankrijk, Engeland), via middellange (Portugal, Spanje) tot lange afstanden (NW-Afrika). Jonge vogels trokken gemiddeld wat verder weg dan oudere exemplaren en er ontwikkelde zich een opmerkelijke individuele plaatstrouw bij het gebruik van nestplaats binnen de kolonie, op stop-overs tijdens de najaarstrek en in de winter. Broedvogels keerden jaarlijks terug naar vrijwel hetzelfde territorium, en die plaatstrouw was het sterkst bij de mannelijke dieren. Seriële, sociale monogamie kon worden aangetoond, waarbij zowel scheidingen als sterfte van een van beide partners tot nieuwe paarbanden konden leiden. Onverwacht, gezien de in het begin van het onderzoek nog groeiende aantallen broedvogels, waren de van jaar op jaar significant afnemende eivolumes, kleinere jongen, het geleidelijk afnemende gewicht van uitvliegende kuikens, enorm hoge niveaus van kannibalisme (kuikenpredatie door soortgenoten of Zilvermeeuwen *Larus argentatus*) en lage uitvliegpercentages, zo te zien allemaal het gevolg van structureel voedselgebrek. De gemeten uitvlieggewichten waren laag, in vergelijking met historisch onderzoek, wat duidt op onvoldoende voedselaanvoer voor de jongen. Het broedseizoen was in hoge mate gesynchroniseerd en vroeg leggende vogels produceerden aanzienlijk meer nakomelingen dan 'late' paren. Toch verschoof de piek van de eileg in de loop van de jaren van begin mei naar de tweede helft van mei en daarbij liep het percentage gepredeerde kuikens gemiddeld weliswaar wat terug, maar het algehele broedsucces werd meer variabel. Mariene, stedelijke en terrestrische habitats, meestal binnen 80 km van de kolonie, werden gebruikt om in te foerageren. Mariene prooien, meestal teruggegooide bijvangst uit de boomkorvisserij, vormden het hoofdbestanddeel van het menu, vooral aangevuld met voedsel wat in landbouwgebieden werd gevonden. Menselijk afval werd aangetroffen in slechts 7% van de voedselmonsters. Een consistente daling van het aandeel mariene prooien (in overeenstemming met zich ontwikkelende beperkingen in de visserij en een krimpende vloot), gecombineerd met signalen die wezen op chronische voedseltekorten, laat zien dat de populatie op Texel niet in staat is om voldoende jongen te produceren binnen de huidige foerageermogelijkheden.

SUPPLEMENTARY MATERIAL 1
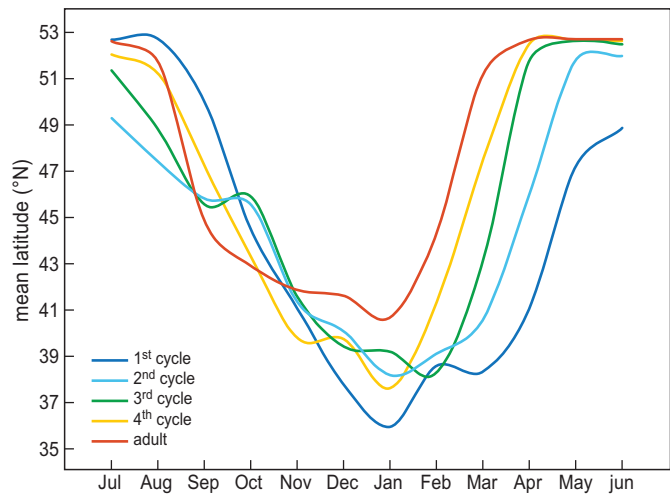
Figure S1. Based on sightings of colour-ringed Lesser Black-backed Gulls marked as adults or fledglings at Texel (2006–2021) and IJmuiden (2008–2021), the mean latitude (°N) for birds during their first, second, third, fourth and subsequent cycles was calculated, using a mean Latitude for each individual for each month in a given year (Table S1). Monthly mean values and standard deviations are provided in Table S3. It shows that juveniles (post-fledging, first cycle, dark blue) leave their breeding grounds on average relatively late and travel on average further to the SW (c. 200°) than later in life (c. 37% further away than adults). All immatures (2nd–4th cycle) utilise a larger area than adults (10–25% further away on average than adults), and most leave the breeding grounds before the adults. Older immatures (3rd and 4th cycle) are more likely to travel towards their breeding grounds in summer and arrive earlier with progressing age. The results support the exploratory migration model (Baker 1978, 1980), in which by a process of area exploration, young birds build up a familiar area, larger than that they will later use as adults. Assessment of the relative suitability of different habitats encountered during explorations early in life, and the subsequent restriction of movements to suitable habitats, results in an adult home range of familiarity (see Baker 1980), but with a considerable level of individual specialization and wintering site-fidelity in place.

Table S1. Breeding grounds (Texel and IJmuiden combined): c. 52.78°N, 4.66°E, mean and max distance away from breeding grounds, and the overriding (mean) direction, α (°) in January for each age group.

Age group	Mean distance	Max distance	α (°)	Sample
Adults	1516 km	4870 km	205°	456
4th cycle	1893 km	2780 km	205°	29
3rd cycle	1689 km	4871 km	205°	40
2nd cycle	1802 km	2780 km	204°	44
1st cycle	2064 km	4578 km	203°	69

Supplementary Material is available online
www.ardeajournal.nl/supplement/s111-###-###.zip

SUPPLEMENTARY MATERIAL 2

Table S2. Model estimates from the best supported generalized linear mixed effect model of number of eggs hatched and number of chicks fledged, relative to colony median laying date. Note that the model is run on log scale due to the Poisson distribution of the data.

|	Estimate	SE	z	P
Nr hatched eggs (log scale)				
Intercept	0.645	0.037	17.533	< 0.0001
Relative laying date	–0.014	0.003	–4.057	< 0.0001
Random effect (Year)				
Variance	0.015			
SD	0.123			
n	1323			
Nr fledged chicks (log scale)				
Intercept	–0.653	0.137	–4.774	< 0.0001
Relative laying date	–0.096	0.015	–6.452	< 0.0001
Relative laying date^2	–0.006	0.002	–3.318	< 0.0001
Random effect (Year)				
Variance	0.181			
SD	0.426			
n	478			

Table S3. Based on sightings of colour-ringed Lesser Black-backed Gulls marked at Texel (2006–2021) and IJmuiden (2008–2021), the monthly mean latitude (°N)/longitude (°W/E) for individuals during their first, second, third, fourth and subsequent cycles was calculated (sample size n, monthly mean values and standard deviations).

	Mean latitude	SD	Mean longitude	SD	n
First cycle, post-fledging					
Aug	52.68	0.9	4.52	1.0	1027
Sep	49.91	4.4	1.48	4.7	233
Oct	44.43	6.2	–3.18	5.3	124
Nov	41.05	6.2	–4.99	4.8	99
Dec	37.78	5.1	–5.24	3.9	65
Jan	35.96	5.0	–5.58	4.0	69
Feb	38.56	5.7	–4.55	4.1	48
Mar	38.33	3.1	–4.23	2.4	43
Apr	41.01	6.1	–4.16	4.5	36
May	47.17	5.6	–1.40	4.3	39
Jun	48.82	4.9	0.37	4.2	48

Table S3. Continued

	Mean latitude	SD	Mean longitude	SD	n
Second cycle					
Jul	49.23	4.9	1.41	4.7	51
Aug	47.37	5.8	–0.11	5.5	58
Sep	45.78	6.8	–1.29	5.6	55
Oct	45.51	6.1	–1.63	5.2	61
Nov	41.31	4.1	–4.11	4.4	55
Dec	40.06	3.9	–3.90	2.9	51
Jan	38.16	3.9	–4.56	2.8	44
Feb	39.10	4.6	–4.58	3.0	38
Mar	40.56	4.8	–3.51	3.1	33
Apr	45.94	7.4	–0.22	5.6	21
May	51.76	2.5	3.53	3.1	79
Jun	51.95	1.5	4.00	1.8	86
Third cycle					
Jul	51.29	2.7	2.63	3.3	89
Aug	48.74	5.2	0.62	4.7	59
Sep	45.52	7.5	–1.44	5.7	47
Oct	45.85	6.2	–1.71	5.1	54
Nov	41.54	5.6	–4.19	3.3	46
Dec	39.41	4.9	–4.46	3.4	39
Jan	39.19	6.2	–4.37	4.0	40
Feb	38.29	4.8	–4.97	3.4	35
Mar	43.05	5.9	–2.16	4.2	25
Apr	51.72	2.8	3.86	2.5	84
May	52.62	0.6	4.60	1.0	164
Jun	52.46	0.4	4.53	0.5	127
Fourth cycle					
Jul	52.0	2.1	3.97	2.3	117
Aug	51.2	3.4	2.84	3.5	76
Sep	47.1	6.9	–0.02	5.4	53
Oct	43.3	6.3	–3.18	4.9	37
Nov	39.8	5.4	–5.33	3.2	42
Dec	39.7	4.2	–4.87	2.9	35
Jan	37.6	4.0	–5.58	2.6	29
Feb	41.3	4.4	–3.51	3.1	31
Mar	47.4	6.2	0.82	4.3	45
Apr	52.5	1.5	4.49	1.4	128
May	52.6	0.3	4.66	0.3	129
Jun	52.6	0.4	4.68	0.4	120
Adults					
Jul	52.58	0.66	4.57	0.73	2284
Aug	51.66	3.08	3.67	2.76	1484
Sep	44.76	6.92	–1.60	5.23	583
Oct	42.90	6.28	–2.77	4.40	348
Nov	41.87	5.55	–3.66	3.67	469
Dec	41.61	5.75	–3.50	3.35	475
Jan	40.68	5.76	–3.81	3.22	456
Feb	44.32	6.74	–1.47	4.44	522
Mar	51.16	4.13	3.57	2.98	1229
Apr	52.65	0.42	4.60	0.45	3121
May	52.68	0.30	4.64	0.16	3834
Jun	52.68	0.35	4.64	0.28	2775

Table S4. Vital rates for Lesser Black-backed Gulls breeding at Texel, 2006–2021.

Breeding season	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
First eggs	03-May	25-Apr	01-May	30-Apr	04-May	01-May	04-May	09-May	03-May	08-May	06-May	06-May	05-May	29-Apr	29-Apr	04-May
Peak egg-laying	10-15/5	6-15/5	7-12/5	9-17/5	11-17/5	10-18/5	16-23/5	20-24/5	14-20/5	17-27/5	15-24/5	15-24/5	17-25/5	13-23/5	14-23/5	17-27/5
Duration of peak-laying	6	10	6	9	7	9	8	5	7	11	10	10	9	11	10	11
Median egg-laying	13-May	09-May	12-May	12-May	14-May	15-May	19-May	21-May	17-May	21-May	20-May	20-May	20-May	17-May	19-May	21-May
Mean egg-laying	14-May	11-May	10-May	13-May	14-May	13-May	19-May	21-May	17-May	21-May	20-May	19-May	21-May	18-May	19-May	21-May
± SD	8.8	7.6	4.1	6.0	5.4	5.3	5.6	4.4	5.0	6.3	5.9	6.7	6.7	7.6	8.0	6.6
(n) eggs	164	224	255	304	210	243	238	213	258	232	219	223	202	230	226	181
Clutch size	2.75	2.73	2.83	2.79	2.76	2.82	2.52	2.40	2.81	2.44	2.62	2.49	2.66	2.61	2.68	2.77
± SD	0.5	0.5	0.5	0.5	0.5	0.5	0.7	0.7	0.5	0.7	0.6	0.8	0.6	0.6	0.6	0.6
(n) nests (excl relays)	57	79	92	108	74	87	90	84	88	93	84	90	62	88	82	65
3-egg clutch volume	226.0	225.3	223.1	222.1	225.6	224.5	217.4	215.7	221.9	214.1	216.5	216.5	217.5	213.4	216.8	218.8
± SD	17.2	15.1	14.6	15.5	15.1	19.2	14.7	14.4	14.4	15.9	15.8	20.4	17.4	18.4	13.2	14.7
(n) nests (3 eggs only)	47	59	81	87	61	75	54	44	75	53	66	60	48	57	56	75
Incubation (d)	26.4	26.6	25.9	27.4	26.0	26.1	26.2	26.5	26.0	25.9	26.1	25.7	25.9	26.1	26.0	26.9
Breeding period	14/5-7/6	10/5-5/6	11/5-4/6	13/5-7/6	15/5-9/6	16/5-8/6	20/5-14/6	22/5-16/6	18/5-11/6	22/5-11/6	21/5-13/6	21/5-11/6	21/5-14/6	19/5-11/6	20/5-11/6	22/5-15/6
First hatchlings	01-Jun	22-May	29-May	28-May	30-May	27-May	1-Jun	5-Jun	1-Jun	5-Jun	3-Jun	2-Jun	1-Jun	27-May	31-May	1-Jun
Peak hatching	6-11/6	1-11/6	3-8/6	6-13/6	7-14/6	6-12/6	12-17/6	15-19/6	10-15/6	12-19/6	11-19/6	8-17/6	11-17/6	8-16/6	9-16/6	13-22/6
Duration of peak-hatching	6	11	6	8	8	7	6	5	6	8	9	10	7	9	8	10
Median hatching	08-Jun	06-Jun	05-Jun	08-Jun	10-Jun	09-Jun	15-Jun	17-Jun	12-Jun	16-Jun	14-Jun	12-Jun	15-Jun	12-Jun	12-Jun	16-Jun
Egg predation (%)	29.5	15.0	16.5	13.9	9.5	18.9	24.1	40.3	18.2	29.5	20.6	29.8	20.1	19.7	21.1	9.8
Egg mortality (%)	7.1	5.6	9.6	8.4	7.6	10.8	6.2	6.8	8.9	5.7	9.0	11.0	5.9	6.4	6.6	8.7
Hatching eggs (%)	60.7	78.1	73.1	77.7	82.9	70.3	69.7	50.2	72.9	64.8	70.4	59.2	74.0	73.9	72.4	81.5
(n) eggs	183	233	260	310	210	249	241	221	258	227	223	228	169	234	228	184
Failed clutches (%)	20.6	10.8	15.2	9.1	9.2	18.2	20.4	36.0	14.3	26.9	20.0	36.3	19.0	16.9	21.4	9.1
Failed clutches (n)	13	9	14	10	7	16	19	32	13	25	17	33	12	15	18	6
Relaying attempts (n)	6	4	0	2	1	1	3	5	3	0	1	1	1	1	2	1
Relaying failures (%)	46.2	44.4	0.0	20.0	14.3	6.3	15.8	15.6	23.1	0.0	5.5	3.0	8.4	6.7	11.2	16.7
Relaying overall (%)	9.5	4.8	0.0	1.8	1.3	1.1	3.2	5.6	3.3	0.0	1.1	1.1	1.6	1.1	2.4	1.5
(n) marked nests	63	83	92	110	76	88	93	89	91	93	85	91	63	89	84	66
Nests within enclosures	(random selection)		2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
(n) hatchlings	62	81	57	94	121	71	58	32	65	27	71	37	42	53	66	52
Hatchling mass <3d	57.2	58.8	59.1	56.8	57.4	55.2	55.8	57.4	56.7	54.7	51.4	56.4	57.7	53.9	55.3	55.7
Chick care (40d)	09/6-19/7	07/6-17/7	06/6-16/7	9/6-19/7	11/6-21/7	10/6-20/7	16/6-26/7	18/6-28/7	13/6-23/7	17/6-27/7	15/6-25/7	13/6-23/7	16/6-26/7	13/6-23/7	13/6-23/7	16/6-26/7
Chick predation %	62.9	66.7	63.2	64.9	43.3	49.3	55.4	57.1	51.6	44.4	44.3	78.4	54.8	41.5	33.3	26.9
Chick mortality %	22.6	12.3	15.8	17.0	29.2	19.7	12.5	14.3	12.5	33.3	25.7	13.5	40.5	22.6	19.7	42.3
Chicks fledged %	14.5	21.0	21.1	14.9	27.5	31.0	30.4	28.6	35.9	22.2	30.0	8.1	4.8	35.8	43.9	30.8
First fledglings	13-Jul	14-Jul	11-Jul	08-Jul	11-Jul	09-Jul	11-Jul	20-Jul	16-Jul	17-Jul	14-Jul	17-Jul	21-Jul	11-Jul	9-Jul	13-Jul
Median fledging	18-Jul	14-Jul	14-Jul	17-Jul	18-Jul	19-Jul	23-Jul	25-Jul	21-Jul	23-Jul	21-Jul	21-Jul	22-Jul	23-Jul	19-Jul	22-Jul
No. fledglings	9	17	12	14	33	22	17	8	23	6	21	3	2	19	29	16
Fledgling mass 36-44d	706.0	665.2	684.2	657.8	692.2	613.4	622.2	n.d.	639.4	628.9	662.0	466.1	435.8	611.0	622.4	699.0
Fledglings pair-1	0.26	0.46	0.43	0.33	0.66	0.69	0.61	0.30	0.74	0.33	0.57	0.12	0.09	0.68	0.94	0.70
(n) nests	35	37	28	43	50	32	28	27	31	18	37	26	23	28	31	23
First year survival %	33.3	47.4	36.1	37.5	34.5	45.6	39.7	46.2	30.9	30.1	39.1	40.0	5.7	6.3	2.2	
(n)	69	116	83	96	110	114	68	39	110	73	87	10	35	95	139	45

Provisional fledgling survival based on unmodelled re-sightings anywhere within range

Incubation duration based on [hatching date - exp laying date] of properly sequenced 1, 2, and 3 eggs only

Productivity index	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Clutch size (CS)	2.75	2.73	2.83	2.79	2.76	2.82	2.52	2.40	2.81	2.44	2.62	2.49	2.66	2.61	2.68	2.77
Fledglings (F)	0.26	0.46	0.43	0.33	0.66	0.69	0.61	0.30	0.74	0.33	0.57	0.12	0.09	0.68	0.94	0.70
PI (%)	9	17	15	12	24	24	24	12	26	14	22	5	3	26	35	25
Qualification	poor	moderate	moderate	moderate	moderate	moderate	moderate	moderate	moderate	moderate	moderate	poor	poor	moderate	moderate	moderate

Poor ≤ 10%, Moderate 10-50%, Good ≥50%   Worst   Best

Main contributors to breeding failures

Breeding season	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Initial clutch (n, all)	2.75	2.73	2.83	2.79	2.76	2.82	2.52	2.40	2.81	2.44	2.62	2.49	2.66	2.61	2.68	2.77
Predated as egg (n)	0.81	0.41	0.47	0.39	0.26	0.53	0.61	0.97	0.51	0.72	0.54	0.74	0.54	0.51	0.56	0.27
Addled egg (n)	0.20	0.15	0.27	0.23	0.21	0.31	0.16	0.16	0.25	0.14	0.23	0.27	0.16	0.17	0.18	0.24
Remaining hatchlings (n)	1.75	2.17	2.09	2.17	2.29	1.98	1.76	1.27	2.05	1.58	1.84	1.47	1.97	1.93	1.94	2.26
Predated as chick (n)	1.10	1.45	1.32	1.41	0.99	0.98	0.97	0.73	1.05	0.70	0.82	1.16	1.08	0.80	0.65	0.61
Died as chick (n)	0.39	0.27	0.33	0.37	0.67	0.39	0.22	0.18	0.26	0.53	0.47	0.20	0.80	0.44	0.38	0.96
Fledglings per nest (n)	0.25	0.46	0.44	0.39	0.63	0.61	0.57	0.36	0.74	0.35	0.55	0.12	0.09	0.69	0.91	0.69
Losses proportional (%)	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**
Predated as egg	29.5	15.0	16.5	13.9	9.5	18.9	24.1	40.3	18.2	29.5	20.6	29.8	20.1	19.7	21.1	9.8
Addled egg	7.1	5.6	9.6	8.4	7.6	10.8	6.2	6.8	8.9	5.7	9.0	11.0	5.9	6.4	6.6	8.7
Predated as chick	39.9	52.9	46.6	50.4	35.9	34.6	38.6	30.3	37.6	28.8	31.2	46.4	40.5	30.7	24.1	21.9
Died as chick	14.3	9.8	11.7	13.2	24.2	13.9	8.7	7.6	9.1	21.6	18.1	8.0	29.9	16.7	14.3	34.5
Survived till fledging	9.2	16.7	15.5	14.1	22.8	21.8	22.4	15.1	26.2	14.4	21.1	4.8	3.5	26.5	34.0	25.1

The difference in reproductive success (fledglings nest-1) in the above table and in this one is the result of deploying chick mortality data (from enclosed nests) over egg losses using all clutches marked initially

Egg laying period	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Median egg-laying	13-May	09-May	10-May	12-May	14-May	15-May	19-May	21-May	17-May	21-May	20-May	20-May	20-May	17-May	19-May	21-May
Peak starts	10-May	06-May	07-May	09-May	11-May	10-May	16-May	20-May	14-May	17-May	15-May	15-May	17-May	13-May	14-May	17-May
Peak ends	15-May	15-May	12-May	17-May	17-May	18-May	23-May	24-May	20-May	27-May	24-May	24-May	25-May	23-May	23-May	27-May
First eggs	03-May	25-Apr	01-May	30-Apr	04-May	01-May	04-May	09-May	03-May	08-May	06-May	06-May	05-May	29-Apr	29-Apr	04-May
Peak duration	6	10	6	9	7	9	8	5	7	11	10	10	9	11	10	11

Table S5. Hatching and fledging success (%) for properly sequenced A, B, and C-eggs of Lesser Black-backed Gulls relative to laying date, but irrespective of clutch size, Kelderhuispolder 2006–2021.

Egg[*]	Egg fate	Early	%	Peak	%	Late	%	Totals	%
					Timing of laying				
A	Dead	9	5.1	25	5.0	14	9.8	48	5.9
	Predated	53	30.3	143	28.6	55	38.5	251	30.7
	Hatched	113	64.6	332	66.4	74	51.7	519	63.4
B	Dead	7	6.0	22	6.1	8	8.1	37	6.4
	Predated	17	14.7	69	19.1	31	31.3	117	20.3
	Hatched	92	79.3	270	74.8	60	60.6	422	73.3
C	Dead	13	9.8	41	9.8	16	17.4	70	10.9
	Predated	16	12.0	66	15.7	27	29.3	109	16.9
	Hatched	104	78.2	313	74.5	49	53.3	466	72.2
A–C	% Hatched	(424)	72.9	(1281)	71.4	(334)	54.8	(2039)	69.0

Egg	Chick fate	Early	%	Peak	%	Late	%	Totals	%
A	Dead	15	42.9	23	18.3	4	13.8	42	22.1
	Predated	11	31.4	59	46.8	18	62.1	88	46.3
	Fledged	9	25.7	44	34.9	7	24.1	60	31.6
B	Dead	8	25.8	16	16.0	4	18.2	28	18.3
	Predated	12	38.7	49	49.0	15	68.2	76	49.7
	Fledged	11	35.5	35	35.0	3	13.6	49	32.0
C	Dead	11	31.4	32	27.1	5	26.3	48	27.9
	Predated	14	40.0	60	50.8	11	57.9	85	49.4
	Fledged	10	28.6	26	22.0	3	15.8	39	22.7
A–C	% Fledged	(101)	29.7	(344)	30.5	(70)	18.6	(515)	28.7

[*]Only properly sequenced eggs in breeding attempts of which the laying dates were exactly known; egg phase based on all nests, fledging based on enclosed nests.

Table S6. Egg volumes (ml) and egg predation rates (%) for Lesser Black-backed Gulls incubating 1-, 2- or 3-egg clutches relative to laying date, Kelderhuispolder 2006–2021.

	Nests	Clutch	Volume			% Predated		
			A	B	C	A	B	C
Early nests	25	1	73.9			84.0		
	39	2	72.1	69.7		40.7	32.0	
	205	3	74.2	74.0	69.9	12.1	8.2	11.6
Peak nests	52	1	72.6			86.3		
	123	2	73.3	70.5		26.8	32.9	
	591	3	75.3	75.5	70.0	17.6	14.4	16.1
Late nests	20	1	67.9			60.0		
	79	2	71.8	69.2		36.6	36.6	
	169	3	75.0	74.7	70.2	28.0	22.2	29.5
All nests	98	1	71.9			80.2		
	250	2	72.7	70.0		32.0	33.8	
	977	3	75.0	75.1	70.0	17.9	14.1	17.1

Table S7. Fledging rates (chicks/nest) for Lesser Black-backed Gulls incubating 1-, 2- or 3-egg clutches relative to laying date (based on randomly selected nests in enclosures), Kelderhuispolder 2006–2021. Note that single egg clutches did thus far not fledge a single chick, essentially because relatively few of these eggs hatched. Early large ('complete') clutches were most productive overall (PI 30%, moderate).

Nests[*]	Clutch	Timing	Eggs	Eggs hatched	Hatchlings fledged	%Hatched	%Fledged	Fledging rates Chicks/nest	PI
6	1	Early	6	1	0	16.7	0	0	0 %
9	1	Peak	9	1	0	11.1	0	0	0 %
11	1	Late	11	4	0	36.4	0	0	0 %
Σ 26			26	6	0	23.1	0	0	0 %
10	2	Early	20	17	3	85.0	17.6	0.3	15 %
40	2	Peak	81	50	15	61.7	30.0	0.4	20 %
30	2	Late	60	41	2	68.3	4.9	0.1	5 %
Σ 80			161	108	20	67.1	18.5	0.25	13 %
65	3	Early	195	162	56	83.1	34.6	0.9	30 %
231	3	Peak	693	542	156	78.2	28.8	0.7	23 %
75	3	Late	224	149	17	66.5	11.4	0.2	7 %
Σ 371			1112	853	229	76.7	26.8	0.6	20 %

[*]Only breeding attempts of which the laying dates were exactly known; relaying pairs were excluded.