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Source: Ardea, 100(2) : 113-122

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.100.0202

Apparent survival and fecundity of sympatric Lesser Black-backed Gulls and Herring Gulls with contrasting population trends

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Camphuysen C.J. & Gronert A. 2012. Apparent survival and fecundity of sympatric Lesser Black-backed Gulls and Herring Gulls with contrasting population trends. Ardea 100: 113–122.

We investigated apparent survival (i.e. survival confounded by permanent emigration) on the basis of a colour-ring programme in which individual Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus* could be monitored over time. The work was conducted in a large, mixed colony in the western Wadden Sea (Texel), where measures of fecundity were collected simultaneously. In Herring Gulls, we found a mean apparent annual adult survival of 79% in females and 86% in males. Additive year effects rather than sex provided highest model support in Lesser Black-backed Gulls, in which apparent survival for both sexes combined varied between 81% and 100% (mean ≈91%). Breeding success in Lesser Black-backed Gulls was significantly lower than that of Herring Gulls. Lesser Black-backed Gulls experienced four consecutive breeding seasons with very low fledging rates (2006–2009) as a result of cannibalism (60–67% of all hatchlings). Chick predation was generally lower in Herring Gulls. A strong population increase in Lesser Black-backed Gulls coincided with substantial population declines in Herring Gulls in the Wadden Sea in the late 20st and early 21st century. In Lesser Black-backed Gulls, apparent survival declined by about 10% in the last two study years, which could, in combination with the low fecundity, halt the current population increase. We suggest that future work should concentrate on underexplored aspects affecting fecundity and survival such as intermittent breeding and sexual differences in migration, foraging and breeding effort.

Key words: apparent survival, fecundity, *Larus fuscus*, *Larus argentatus*, population trends, sexual segregation, food limitation

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Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus* nest sympatrically in several large colonies throughout the Danish, German and Dutch Wadden Sea (Hagemeijer & Blair 1997). In the late 20st and early 21st century a strong population increase in Lesser Black-backed Gulls coincided with a substantial population decline in Herring Gulls (Spaans 1998a,b, Aarts *et al.* 2008, van Dijk *et al.* 2010). Inspired by these contrasting developments, a comparative study of the feeding ecology, breeding biology and demography of the two species commenced in 2006. Our studies were conducted in one of the largest of these mixed colonies, at Texel (The Netherlands) and involved measurements of phenology (arrivals, laying date), reproductive success (including clutch size, egg volume, egg and chick predation, chick growth and breeding success), plus a colour-ringing programme to assess site-fidelity, recruitment rates and annual survival. Parameters such as fecundity (i.e. fledging rates), population densities, rates of immigration and emigration, recruitment, and survival are particularly relevant for studies of population dynamics (Clobert & Lebreton 1991).

Adult annual survival is a key parameter affecting population trends among long-lived, generally philopatric species (Tinbergen 1953, Harris 1970, Davis

1975, Perrins *et al.* 1991). We investigated apparent survival (i.e. survival confounded by permanent emigration; White & Burnham 1999, Allard *et al.* 2010) on the basis of our colour-ring programme in which individual birds could be monitored over time. We assessed the influence of year, year of capture, sex, and sex-year interactions on apparent survival and resighting probabilities using the program MARK (White & Burnham 1999, 2010), and compared our findings with previously published survival estimates of large gull species with similar or contrasting population trends.

Food supply plays a major role in animal population dynamics and is often an important factor limiting breeding success and survival (Martin 1987, 1995, Pons & Migot 1995). In generalist feeders, such as large gulls (Cramp & Simmons 1983), food supply is notoriously difficult to assess. The observed long-term declines in the Herring Gull population are generally assumed to have been caused by changes in human waste management (covering up landfill areas that provided easy accessible food; Spaans 1998b). The most marked changes therein occurred several decades ago, and the continuing population decline in recent years would suggest that other factors are currently important. The favourable breeding success of Herring Gulls in recent years (Camphuysen & Gronert 2010) was not in accordance with current population trends and the present study was to investigate if levels of annual survival were perhaps reduced. The population increase of Lesser Black-backed Gulls, notorious scavengers at fishing vessels in the breeding season (Camphuysen 1995), mirrored the increase in beam-trawl fleet capacity off the Dutch coast (Spaans 1998a). Breeding success of Lesser Black-backed Gulls was very low in recent years and this study aimed to investigate levels of annual adult mortality. This gull species faces changes in the European Common Fishery Policy that are gradually effectuated (smaller fleets, production of fewer discards; Schou 2011) and high gasoline prices that will all lead to reductions in fishing effort (Rijnsdorp *et al.* 2008). Given these conditions, we expect negative effects on the tendency to breed (birds in poor condition may forego breeding), fecundity and on annual adult survival.

METHODS

Study area and population trends

Ecological data were collected April to August, 2006–2011 in Kelderhuispolder, Texel (53°01'N, 04°43'E), western Wadden Sea, The Netherlands, in a large mixed colony with approximately 11,500 breeding pairs of Lesser Black-backed Gulls and 5000 pairs of Herring Gulls *Larus argentatus*. The colony is situated at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the mainland (Den Helder) and the island. The main food resources are fish (including fisheries discards), benthic fauna, terrestrial infauna, and domestic refuse. The main foraging areas include open sea, intertidal areas (mudflats and coastal breakwaters exposed at low tide), freshwater ponds, tourist resorts (including restaurants) and agricultural land. And at slightly larger distances the gulls frequent sewage plants, rubbish tips and cities. Lesser Black-backed Gulls became established as breeding birds in the early 1970s, at a time when about 1000 pairs of Herring Gulls nested in the area. Herring Gulls increased to just over 10,000 pairs in 1986 and declined since to c. 5500–6000 pairs in 2006 and 2007, when our studies commenced. Since colonisation, Lesser Black-backed Gulls have slowly increased to some 2000 pairs in 1992, but the population exploded to just over 14,000 pairs in 2003–2006 (reconstruction from Staatsbosbeheer (State Forest Management) unpublished annual reports 1967–1990 and SOVON LSB seabird colony database 1991–2007, courtesy Lieuwe Dijksen).

The study area Kelderhuispolder is a valley of 8 ha surrounded by higher dunes (preferred by nesting Herring Gulls) covered with Marram *Ammophila arenaria*, Sea-buckthorn *Hippophae rhamnoides*, and Elder *Sambucus nigra* (Camphuysen & Gronert 2010). The valley itself is mostly covered with grass, including stands with taller Marram, patches with short vegetation, and occasional Elder bushes. Field work commenced early April and lasted until mid August, covering the entire breeding period from prospecting to fledging. Prior to egg-laying (mid-April) the colony was visited with increasing frequency until the first eggs were found along a preset trail leading through each of the study plots into prime Herring Gull and Lesser Black-backed Gull habitats. Nests were marked with a numbered wooden pole and the geographical position (latitude, longitude) of each nest was recorded with a handheld Garmin V GPS.

Ringing and resightings

Breeding gulls were trapped at the nest, roughly halfway through incubation, after we had established that a clutch was completed and fully incubated. Each gull was ringed with a steel band on the right tibia, and on the left tarsus fitted with a 35-mm colour ring of 10 mm diameter made of Polymethyl methacrylate (PMMA; a thermoplastic), engraved with a white inscription of 4 characters (F.xxx for females, M.xxx for males). A total of 180 Lesser Black-backed Gulls and 119 Herring Gulls were ringed between 2006 and 2010, but 26 Lesser Black-backed Gulls fitted with GPS loggers were excluded from the analysis (Table 1). Sex was assessed using head and bill measurements (Coulson *et al.* 1983) and the birds were aged using plumage characteristics (Olsen & Larsson 2003, Svensson & Grant 2009). All birds were weighed to the nearest gram.

Marked gulls were monitored (resighted) using spotting telescopes and binoculars during almost daily visits to the colony between April and August. For analysis, multiple observations of an individual were collapsed to a single 'occasion' per year (Appendix 1), effectively requiring one single sighting to be recorded as 'alive'. Nonetheless, frequent observations were made within the colony to minimise identification error and to reduce the possibility of missing ringed individuals. Sightings were also reported outside the colony, mostly by dedicated birdwatchers, both in The Netherlands and elsewhere in Europe and NW Africa (Camphuysen *et al.* 2011). Only sightings within the colony were used to estimate apparent adult survival, but the other reports were used to check whether particular individuals were still alive even if there were no sightings within the colony (Table 1).

Fecundity

We used fledging rates as measure of fecundity. To assess fledging rates, randomly chosen (groups of) nests in enclosures were monitored. A total of 368 nests were monitored (252 Lesser Black-backed Gulls, 116 Herring Gulls; Table 1). Nests were enclosed during late incubation, by fencing off an area of at least eight square metres using 50 cm high, 2 cm mesh opening chicken wire. Enclosures included vegetation to provide cover for the offspring to hide. Chicks were marked with a numbered aluminium ring on day 1 and subsequently measured and weighed every third day (outside the enclosure) until they were either dead (e.g. predated) or fledged. Chicks of around 30–40 days old, and capable of leaving and entering the enclosures, were colour-ringed on the left tarsus (with similar rings as the adults but with a different code, starting with either P or K) and marked with a steel ring on the right tibia. Chicks of 40 d of age were considered 'fledged', even when they sometimes refused to leave the enclosure at that age. The fate of chicks was assessed, separating birds that died from starvation or disease from those that were killed and predated. The latter category included small chicks (<30 d) that disappeared without a trace from the enclosures, if no evidence for escape could be found. Reproductive success was expressed as the number of fledglings per (monitored) pair (fledglings/pair).

Table 1. Reduced m-array (Burnham *et al.* 1987) summarising capture–mark–resight data from Lesser Black-backed Gulls and Herring Gulls marked as breeding (sub-)adults and monitored at Kelderhuispolder, Texel, from 2006 to 2011. Releases include newly colour-ringed individuals and previously marked birds seen alive within the colony in a particular year. Confirmed survival in 2011 (*n*, %) was based on all sightings recorded (anywhere in Europe), for all birds.

			Encountered for the first time after release						Confirmed	
	Ringed	Released	2007	2008	2009	2010	2011	Total	alive 2011	%
Lesser Black-backed Gull										
2006	23	23	22	1				23	10	43.5
2007	24	46		40	2			42	18	75.0
2008	39	80			66	7		73	22	56.4
2009	53	121				97	1	98	38	71.7
2010	15	119					91	91	14	93.3
Totals	154	389						327	102	66.2
Herring Gull										
2006	7	7	4	2				6	4	57.1
2007	12	15		12	1			13	5	41.7
2008	19	33			23	3		26	11	57.9
2009	37	61				48	3	51	27	73.0
2010	44	95					65	65	34	77.3
Totals	119	211						161	81	68.1

Statistical analysis

Following an assessment of goodness-of-fit (GOF), resighting and apparent survival probabilities were investigated using the capture/mark–resighting data. Single state, open-population, live-encounter, Cormack-Jolly-Seber (CJS) models specified in software program MARK were applied (White & Burnham 2010). Since only six summer seasons (or sampling occasions) were available and because sample sizes were fairly small, violations of the basic assumptions may have been difficult to detect with GOF tests (Choquet *et al.* 2009). Transience is a source of heterogeneity resulting from permanent emigration from the study area or death by some individuals following marking. Trap-dependence can originate from individuals in a population that are relatively easy ('trap-happy') or difficult ('trap-shy') to detect and observe in the field. Transience and trap-dependence were assessed using the GOF tests 3.SR and 2.CT in the U-Care 2.2 program (Choquet *et al.* 2009). The null hypothesis under these tests was that newly released and previously marked animals are subsequently resighted within the colony with the same probability. To test for the effect(s) of grouping data, we conducted GOF tests for pooled data for each species and separately for each sex within species.

The CJS model accounts for differences in survival rates between successive time periods (in our case breeding seasons), cohorts or sexes (Lebreton *et al.* 1992). A 'life history' was compiled for all colour-ringed individuals, including releases (first year sightings) and resightings in subsequent years within the colony. On the basis of individual resighting histories, PROGRAM MARK calculates the likelihood that a living individual is observed within a given period (p) and a survival rate (Φ), which is the likelihood that a given individual has not left the population or is not dead. Different versions of the CJS model were examined, differing in the extent to which survival and resighting rates were held constant (indicated with Φ(.) and p(.), respectively) or whether they were considered year-dependent, sex-dependent or year and sex dependent (indicated with Φ(t) and p(t), respectively). The results were corrected for slight over-dispersion of the data using the value of the goodness of fit parameter $\hat{c}$ (based on 100 bootstraps; see web-based manual to MARK, chapter 5; Anderson *et al.* 1994). Akaike's Information Criterion (AIC; Anderson *et al.* 1998, Anderson & Burnham 1999) was used to determine the version of the CJS model that gave the best fit to the data. In accordance with model weights and evidence ratios presented by Burnham & Anderson (2002), for this assessment only models within 6 AICc units of the top model (ΔAICc = 0) were considered; all others were considered as unsupported by the data. Values reported are means ± SE. For tests of independence, the adjusted *G*-statistic (G_{adj}; Sokal & Rohlf 1981) and χ^2-tests (White & Burnham 2010) were used.

RESULTS

Age and sex of marked birds

Both species of gulls breeding at Texel seem to recruit at a relatively advanced age and incubating birds with immature plumage characteristics are relatively rare. All incubating Lesser Black-backed Gulls that were trapped were in full adult summer plumage. Seven (5%, $n = 145$) trapped and marked Herring Gulls were sub-adults (4th (5×) or 5th calendar year (2×)). One Lesser Black-backed Gulls trapped in 2009 appeared to have been ringed as a chick in 2005, but this bird did not show any plumage features indicating its age (5th calendar year), suggesting that some young breeders (recruits) may have been overlooked. One individual, trapped in 2008, had been ringed as an adult while wintering in Worcestershire (UK) in 1993 and must have been at least 19 years of age when it was colour-ringed at Texel. Another 11 trapped Lesser Black-backed Gulls had been ringed as chicks elsewhere or in earlier years at Texel and these birds averaged 11.8 ± 1.9 years of age (range 9–15 years). Four Herring Gulls were captured that appeared to have been ringed as chicks, respectively 8, 10, 14 and 19 years earlier (average 12.8 ± 4.9 years of age). In total, 85 marked incubating Lesser Black-backed Gulls (55.2%, $n = 154$) and 57 Herring Gulls (47.9%, $n = 119$) were sexed as females. In either case, the sex ratio was not significantly different from even ($G_{adj} = 0.83$ and 0.10 respectively, $df = 1$, n.s.). Two documented cases of colour-ring loss occurred during 2006–2011, both of which were 'solved' by reading the metal tibia ring (one was re-ringed). Three further birds were re-ringed because the colour-ring was either damaged or too badly worn.

Goodness of fit

Heterogeneity (due to, e.g. 'transience' or 'trap-dependence') was negligible in our dataset: 20 releases (11 Lesser Black-backed Gulls, 9 Herring Gulls) eluded detection on the first occasion following release (upper diagonals, Table 1). Otherwise, birds that returned were usually detected in the first season following release (lower diagonals, Table 1). The birds that did not return within two years were never seen again.

Indeed the GOF test results indicated that there was no evidence for transience or trap-dependence in either species, whether tested separately for either sex or for pooled data (Transience test 3.SR: Lesser Black-backed Gull, standardized log odds-ratio $(\text{SLOR})^{\text{females}} = 1.18$, $P = 0.12$, $\text{SLOR}^{\text{males}} = -0.07$, $P = 0.53$, $\text{SLOR}^{\text{pooled}} = 0.57$, $P = 0.28$; Herring Gull, $\text{SLOR}^{\text{females}} = -1.50$, $P = 0.94$, $\text{SLOR}^{\text{males}} = 0.57$, $P = 0.28$, $\text{SLOR}^{\text{pooled}} = 0.13$, $P = 0.4$; Trap-dependence test 2.CT: Lesser Black-backed Gull $\text{SLOR}^{\text{females}} = -0.81$, $P = 0.42$, $\text{SLOR}^{\text{males}}$ = n.d., $\text{SLOR}^{\text{pooled}} = -1.28$, $P = 0.20$; Herring Gull $\text{SLOR}^{\text{females}} = 0.18$, $P = 0.86$, $\text{SLOR}^{\text{males}} = -0.99$, $P = 0.32$, $\text{SLOR}^{\text{pooled}} = -0.68$, $P = 0.50$). We concluded that the CJS model was acceptable.

Factors affecting survival and resighting

Only models fitted to assess structure in the survival process within 6 AICc units of the top model were considered (Table 2). The simplest model (Φ(.) p(.)), yielded slightly but not significantly higher mean apparent survival estimates for Lesser Black-backed Gulls (mean 0.87 ± SE 0.03, CI 0.81–0.91, SE and CI corrected for $\hat{c}$ 1.85) than for Herring Gulls (0.83 ± 0.03, 0.76–0.88, $\hat{c}$ corr. 0.97). Resighting probabilities in Lesser Black-backed Gulls were 0.94 ± 0.02, (CI 0.87–0.97) and 0.87 ± 0.04, (CI 0.75–0.93) in Herring Gulls.

In Lesser Black-backed Gulls, models including additive year effects (models 1 and 2) provided highest model support; the simplest model, or models assessing the effects of sex or year of capture were not supported by the data (ΔAICc >6 units). The top model, fitted to assess annual variation in resighting probability, was not significantly different from the slightly simpler, second best model in which a constant resighting rate was assumed (model 2, Table 2; $\chi^2_1 = 7.32$, $P = 0.06$). We selected Φ(year) p(year) as top model for this species, and estimates of apparent survival and resighting probabilities from 2006 to 2011 are provided in Table 3. The large standard errors for the last survival and resighting probabilities suggest that these parameters were not identifiable (Lebreton *et al.* 1992).

In Herring Gulls, the simplest model provided an adequate description of the data. The model including a sex effect on survival scored second best, and was not significantly different from the simpler top model (Table 2; $\chi^2_1 = 1.76$, $P = 0.185$). This second model deviated only 0.4 ΔAICc units from the first model. Adding the effects of year of capture on survival or a year effect on resighting probability to our models did not lead to further improvements (models 3–5). In particular, those models in which a year effect on survival was assumed were not supported by the data (models 6–7; Table 2). We used the second model for this species (Φ(sex) p(.)), because it was not significantly different from the top model and biologically plausible (see Discussion). Estimates for apparent survival of each sex and pooled resighting probabilities

Table 2. Models and selection criteria used to determine support for competing models and their effects on Lesser Black-backed Gulls (top) and Herring Gulls (bottom). Number of parameters in the models indicated by NP.

	AICc	Δ AICc	AICc weight	Model likelihood	NP	Deviance
Lesser Black-backed Gull models						
(1) Φ(year) p(year)	423.09	0	0.573	1	9	53.156
(2) Φ(year) p(.)	424.06	0.98	0.352	0.614	6	60.388
(3) Φ(.) p(year)	429.44	6.35	0.024	0.042	6	65.762
(4) Φ(year + sex) p(year)	429.68	6.60	0.021	0.037	14	49.105
(5) Φ(.) p(.)	430.11	7.02	0.017	0.030	2	74.624
(6) Φ(sex) p(.)	432.14	9.05	0.006	0.011	3	74.620
(7) Φ(year capture) p()	432.14	9.06	0.006	0.011	3	74.624
Herring Gull models						
(1) Φ(.) p(.)	291.07	0	0.392	1	2	60.143
(2) Φ(sex) p(.)	291.43	0.35	0.329	0.839	3	58.437
(3) Φ(year capture) p()	293.07	1.99	0.145	0.369	3	60.078
(4) Φ(.) p(year)	294.62	3.55	0.067	0.169	6	55.340
(5) Φ(sex) p(year)	295.32	4.25	0.047	0.120	7	53.898
(6) Φ(year) p(.)	297.04	5.96	0.020	0.051	6	57.754
(7) Φ(year + sex) p()	303.59	12.5	0.001	0.002	11	53.387

are provided in Table 3. The reason for our choice is that we wish to explore the causes of an apparently fairly substantial sexual difference in apparent annual survival in our future studies (see Discussion).

Fecundity

The mean breeding success in Lesser Black-backed Gulls (mean ± SD 0.47 ± 0.19 fledglings/pair) was significantly lower than in Herring Gulls (0.86 ± 0.31) at Texel (t_{10} = –2.58, P = 0.027; Table 4). This pattern was consistent, except in 2011 when the breeding success in Herring Gulls was exceptionally low, while Lesser Black-backed Gulls fledged relatively many more chicks in comparison with most other seasons. Lesser Black-backed Gulls experienced four consecutive breeding seasons with very low fledging rates (2006–2009) as a result of high levels of chick predation (cannibalism; 60–67% of all hatchlings). Chick predation was generally lower in Herring Gulls, and the lowest reproductive success was found when levels of chick mortality as a result of starvation and or disease were high (2006, 2011).

DISCUSSION

Overall adult survival in Lesser Black-backed Gulls was higher than in Herring Gulls, but declined in recent years. In Herring Gulls, the annual survival of adults was different between the sexes: notably lower in females. Documented longevity records based on ringing data show that both species are long-lived taxa (Schreiber & Burger 2002) and we had expected similar annual adult survival rates.

Year effects were found to mostly affect survival in Lesser Black-backed Gulls (ranging from 0.81–1.0; model 1). A mean value of 0.91 over this five-year study period agrees nicely with an earlier estimate of 0.91 ± 0.12 for Lesser Black-backed Gulls in the United Kingdom (Wanless *et al.* 1996). Lesser Black-backed Gull fecundity at Texel was inversely related to adult apparent survival (Figure 1). Life history theory predicts that parents should value their own survival over that of their offspring in long-lived species such as seabirds (Erikstad *et al.* 1998, Ghalambor & Martin 2001). Data currently available on fecundity and adult survival in several seabird populations suggest a negative relationship between the two (Weimerskirch 2002). The shape of the relationship is likely convex, similar to the classical figure representing the optimisation of the trade-off between survival and fecundity or

Table 3. Estimates of apparent survival and resighting probabilities from year to year (2006–2011) from models 1 in Table 2 for Lesser Black-backed Gulls, and apparent survival between the sexes and resighting probabilities as a constant from models 2 in Table 2 for Herring Gulls.

Group	Interval/occasion	Estimate	SE	95% CI
Survival probabilities (Φ) **Lesser Black-backed Gull**				
	2006–2007	Fixed = 1.0		
	2007–2008	0.919	0.041	0.795–0.971
	2008–2009	0.932	0.033	0.831–0.975
	2009–2010	0.812	0.036	0.732–0.872
	2010–2011	0.874	197.1	-
Resighting probabilities (p)				
	2006–2007	0.956	0.042	0.750–0.994
	2007–2008	0.949	0.035	0.820–0.987
	2008–2009	0.887	0.040	0.783–0.945
	2009–2010	0.988	0.012	0.918–0.998
	2010–2011	0.874	197.1	-
Survival probabilities (Φ) **Herring Gull**				
	Females	0.787	0.049	0.676–0.868
	Males	0.864	0.038	0.771–0.923
Resighting probabilities (p)		0.871	0.036	0.784–0.927

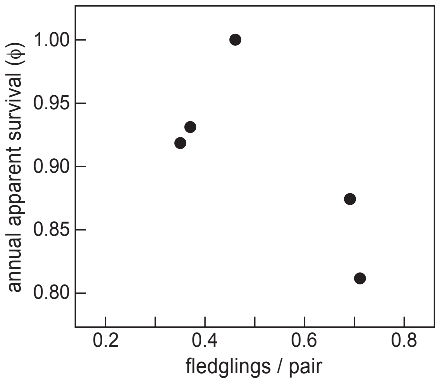

Figure 1. Relationship between fecundity (fledglings/pair) and apparent annual adult survival (ϕ) in Lesser Black-backed Gulls breeding at Texel.

other vital rates (Cody 1966). Cody (1966) proposed a model in which by the "*Principle of Allocation*" maximum contribution to future generations would be achieved by those individuals which utilise, to increase K (carrying capacity), some of the energy conserved by reducing r (the reproductive rate). Hence, if food becomes scarce, adults should reduce their breeding effort rather than jeopardise their residual reproductive value (Drent & Daan 1980, Martin 1995). For Herring Gulls, annual estimates of apparent survival could not be provided based on the current datasets.

We have circumstantial evidence that a substantial number of prospecting Lesser Black-backed Gulls at Texel did forego breeding in some years (no subsequent sightings during the breeding season, numerous empty nests in the colony where eggs were never laid). Our fecundity measure is based on birds that did breed (i.e. laid eggs), while the annual survival is measured over all colour-ringed adults that returned to the colony and were seen; whether they bred or not in later years. Given the observed trends and inverse relationship between fecundity and survival, we feel that more attention must be given to intermittent breeding in these birds (Calladine & Harris 1997, Cam *et al.* 1998). Non-breeding behaviour may constitute an adaptive mechanism which allows maximization of life-time reproductive success in a fluctuating environment (Aebischer & Wanless 1992).

In Herring Gulls, based on the second best model, we found a mean apparent annual adult survival of 0.79 in females and 0.86 in males (model 2). Other studies of the mean adult annual survival using capture–mark–resighting models in Herring Gulls arrived at similar or slightly higher rates as in our males: 0.87 ± 0.03 (Canada; Allard *et al.* 2006), 0.88 ± 0.13 (UK; Wanless *et al.* 1996), 0.88 ± 0.01 (France; Pons & Migot 1995), and 0.91 ± 0.02 (Canada; Breton *et al.* 2008). A sex difference in apparent annual survival in the Herring Gull came as an unexpected result. The studies at Texel, now using advanced GPS loggers, have demonstrated a strong sexual segregation in foraging Lesser Black-backed Gulls in summer (Camphuysen *et al.* MS), a phenomenon that has unfortunately not been investigated for Herring Gulls. A sex difference in resource exploitation in the Herring

Table 4. Fecundity (fledglings/pair) and chick mortality in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, Texel, 2006–2011.

	2006	2007	2008	2009	2010	2011
Lesser Black-backed Gull						
Chick predation, %	60.3	66.7	63.4	62.3	35.4	49.3
Chick mortality, %	25.4	12.3	15.5	17.9	34.8	19.7
Chicks fledged, %	14.3	21.0	16.9	17.0	28.6	31.0
Number of hatchlings	63	81	71	106	161	71
Fledglings per pair	0.26	0.46	0.35	0.37	0.71	0.69
Number of nests	35	37	34	49	65	32
Herring Gull						
Chick predation, %	33.3	39.1	25.0	51.2	20.0	16.7
Chick mortality, %	42.4	8.7	25.0	7.0	21.8	46.7
Chicks fledged, %	24.2	52.2	50.0	39.5	58.2	36.7
Number of hatchlings	33	23	44	43	55	30
Fledglings per pair	0.62	0.80	1.10	0.81	1.33	0.48
Number of nests	13	15	20	21	24	23

Gull breeding at Texel is not unlikely, however. Greig *et al.* 1985 reported different foraging strategies in male and female Herring Gulls breeding in the UK. Bosman *et al.* (2012) examined whether, and to what extent, body size and/or sex-specific differences in competition for resources (e.g. breeding territories or winter food) shaped variation in migration distance and timing of sexually mature males and females of Herring Gulls breeding in Belgium. They found that the larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. Allometry partly explained the sexual segregation in migration behaviour of Herring Gulls and the observed latitudinal segregation between wintering males and females may reflect sex-specific niche specialization, with potential repercussions for annual survival. With our current data, an explanation for the observed differences in survival between the sexes remains speculative. Future work will need to reveal differences in breeding strategies or other traits between male and female Herring Gulls that could help explain the observed sexual differences in annual survival.

The lower survival rates of Herring Gulls compared to Lesser Black-backed Gulls could result from different levels of emigration, the second component next to true survival determining apparent survival. We used only encounters within the colony for this study. There were no confirmed sightings of birds colour-ringed as adults breeding in any other colony (true emigration), but if we were to use *all* sightings, collected anywhere within the flyway of either species, 7% more encounters would have been available (6% more in Lesser Black-backed Gulls, 9% more in Herring Gulls). This difference was not significant ($G_{adj} = 0.13$, $df = 1$, n.s.) and differences in (apparent) emigration rates did not explain the difference between the two species.

Lesser Black-backed Gulls are migratory, wintering generally several thousands of kilometres south of the breeding grounds (in this case mostly at the Iberian Peninsula and in NW Africa; Camphuysen *et al.* 2009, Hallgrimsson *et al.* 2012). Herring Gulls are dispersive or short-range migrants, wintering mostly in The Netherlands, in Belgium or in northern France, and migrating hundreds of kilometres rather than thousands (Camphuysen *et al.* 2011). It is unclear how long distance migration or short-distance dispersal would influence annual adult survival differently. These gulls could potentially forage everywhere along their flyways: there are no crossings of deserts, vast stretches of water, or other inhospitable areas required in either species. The availability of resources in wintering areas or during autumn or spring migration could still be a factor of importance. Alternatively, differences in survival could be related to the food supply and the effort exerted by individual birds during breeding. Several authors concluded that adult mortality in large gulls reaches its maximum at the end of the breeding season (Pons & Migot 1995 and references therein).

Changes in fishing practices are only gradually effectuated, and while Lesser Black-backed Gulls breeding at Texel are currently almost certainly food-stressed (Camphuysen MS), this did not (yet) translate into a reduced annual adult survival. The current reproductive success of both species, on average much higher in Herring Gulls than in Lesser Black-backed Gulls (Table 4), would suggest that the contrasting population trends may soon be reversed. However, the differences in adult survival between the two species are such that this conclusion cannot be drawn. For a breeding population to remain stable, parent birds have to produce enough young that survive to breed themselves, to replace adults that die (Perrins 1991). From the adult annual survival rate, it is possible to deduce the proportion of young that must survive to breed in a stable population (at equilibrium, the number of young surviving per pair to breed must equal twice the annual adult mortality). We will need to continue the concurrent colour-ringing programme of fledglings to be able to assess recruitment rates and age of first breeding, to be able to model current and forecast future population trends.

ACKNOWLEDGEMENTS

We are very grateful to Staatsbosbeheer Texel for permission to work in Kelderhuispolder, a nature reserve closed to the general public. We are particularly thankful to Kees Bruin, Aris Ellen, Marcel Groenendaal, Erik van der Spek en Jan Witte for help and co-operation. A ringing licence was supplied every year by Vogeltrekstation, Heteren. The Royal Netherlands Institute for Sea Research (Royal NIOZ) provided the necessary facilities and finances for these studies and many NIOZ staff have contributed one way or the other. Sharon Boekhout, Cosme Damian Romay, Vicky Hunt, Rim Lucassen, Tim van Nus and Janne Ouwehand, all as students, assisted with field operations in anyone season since 2006. Lieuwe Dijksen (SOVON) provided an update on population censuses of gulls breeding in the area since the 1960s. Risto Juvaste produced the colour-rings. Apart from the authors, Allert Bijleveld, Daniël Camphuijsen, Anja Cervencl, Fred Cottaar, Cosme Damian Romay, Job ten Horn, Roos Kentie, Maarten van Kleinwee, Rim Lucassen, Tim van Nus, Janne Ouwehand, Rebekka Schüller, Mark Tasker, José Verbeek-Cottaar and Jan Zorgdrager, contributed substantially with ring-reading activities in the Kelderhuispolder. Bernard Spaans (NIOZ) kindly introduced the first author into the world of software program MARK and survival analysis.

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SAMENVATTING

Wij onderzochten de schijnbare overleving van voornamelijk volwassen broedvogels op basis van een kleurringprogramma waarbij individuele Kleine Mantelmeeuwen *Larus fuscus* en Zilvermeeuwen *Larus argentatus* van jaar op jaar konden worden gevolgd. De schijnbare overleving is een overlevingsschatting waarbij sterfte en emigratie niet worden onderscheiden. Het onderzoek werd uitgevoerd in een grote, gemengde kolonie van beide soorten op Texel in de westelijke Waddenzee. In deze kolonie werd ook het broedsucces van beide soorten onderzocht. Bij de Zilvermeeuw vonden wij een overleving van 79% bij de vrouwtjes en 86% bij de mannetjes. Bij Kleine Mantelmeeuwen speelde het geslacht geen duidelijke rol, maar hier werden sterke effecten tussen jaren gevonden (overleving variërend van 81–100%, gemiddeld ≈ 91%). Het broedsucces van Kleine Mantelmeeuwen was significant lager dan dat van Zilvermeeuwen in deze kolonie. Dit verschil werd vooral veroorzaakt door vier opeenvolgende jaren (2006–2009) met een zeer laag uitvliegsucces bij de Kleine Mantelmeeuw, vooral als gevolg van wijdverbreid kannibalisme (60–67% van alle kuikens gepredeerd). Kuikenpredatie was aanzienlijk lager bij de Zilvermeeuw. Aan het einde van de twintigste en in het begin van de eenentwintigste eeuw viel een sterke toename van de populatie Kleine Mantelmeeuwen in de Waddenzee samen met een afname bij de Zilvermeeuw. Het sterk verschil in broedsucces tussen beide soorten (waarbij de Zilvermeeuw nu veel beter presteert dan de Kleine Mantelmeeuw) en het minieme verschil in adulte overleving zouden een aanwijzing kunnen zijn dat de beide populaties zich in de toekomst wel eens omgekeerd kunnen ontwikkelen (een toename van Zilvermeeuwen, een afname van Kleine Mantelmeeuwen). Op grond van de hier beschreven resultaten stellen wij voor dat onvoldoende onderzochte aspecten die van invloed zijn op overleving en broedsucces meer aandacht krijgen. Voorbeelden daarvan zijn het overslaan van broedseizoenen door volwassen vogels (keuze voor eigen overleving in plaats van een nieuwe broedpoging) en seksuele verschillen in foerageergedrag en broedzorg.

Corresponding editor: Yvonne I. Verkuil
Received 24 February 2012; accepted 7 August 2012

Appendix 1. Encounter histories of female and male Lesser Black-backed Gulls and Herring Gulls. Capture–mark–resight data for birds marked as breeding (sub-)adults and monitored at Texel, The Netherlands, from 2006–2011.

Lesser Black-backed Gulls	Herring Gulls
000010 1 0;	000010 10 6;
000011 5 9;	000011 12 16;
000100 7 6;	000100 1 3;
000110 5 5;	000101 1 0;
000111 18 12;	000110 6 4;
001000 3 3;	000111 11 11;
001010 1 0;	001000 2 2;
001011 1 1;	001011 2 0;
001100 4 1;	001100 2 1;
001101 1 0;	001110 0 2;
001110 4 3;	001101 1 0;
001111 7 10;	001111 2 5;
010000 1 1;	010000 1 1;
010111 1 0;	010100 1 0;
011011 2 0;	011000 1 1;
011100 1 0;	011100 0 1;
011110 2 1;	011101 0 1;
011111 9 6;	011110 1 0;
101010 1 0;	011111 0 3;
110000 0 2;	100000 1 0;
110111 1 0;	101000 1 0;
111000 0 1;	101111 1 0;
111010 1 0;	111010 0 1;
111100 2 2;	111100 0 1;
111110 3 1;	111111 0 2;
111111 4 5;	