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ORIGINAL ARTICLE

Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands

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Abstract The Herring Gull population in The Netherlands went through phases of exploitation, protection, persecution and again (partial) protection during the nineteenth and twentieth centuries. The numbers of breeding pairs peaked in the 1980s at approximately 90,000 pairs, at which point a colour-ringing campaign was organised to evaluate dispersal and distribution patterns. Herring Gulls were ringed as chicks, predominately near-fledglings, in 12 colonies in 1986 (1,247 individuals), 13 colonies in 1987 (1,354 individuals) and 14 colonies in 1988 (1,396 individuals). Between 1986 and 2009, of the 3,997 Herring Gull chicks colour-ringed, 3,124 individuals (78.2%) were seen and reported at least once, while 453 (11.3%) were recovered dead. In total, 86,247 ring-readings of living gulls were received and processed, originating from 1,358 locations by 868 observers. One-fifth (20.5%) of all sightings originated from the home-ranges (areas within a radius of 5 km around the ringing place). Only 691 sightings (0.8%) were reported at over 300 km from the natal colony (10.7% at 6–10 km, 8.9% at 11–25 km, 17.7% at 26–50 km, 22.9% at 51–100 km, 14.4% at 101–200 km and 4.1% at 201–300 km). Colony-specific differences in travelling distance, dispersal rate and direction of movements suggest a grouping of colonies in three areas: (1) eastern Wadden Sea islands (Rottumeroog–Vlieland), with significantly higher dispersal rates and movements mostly towards the south-west to south-east; (2) Texel and the four colonies along the mainland coast (Callantsoog–Wassenaar), with shorter mean range and movements mostly to the south; (3) colonies in the Delta area (Europoort–Saeftinghe), with rather short range movements and dispersal in many directions. The maximum distance travelled did not vary much between adults, immatures and juveniles, but the timing of outward and return movements was different for each of these age categories. Adult birds reached their greatest mean distances on average 1 month earlier than immatures, which in turn arrived at this point 1 month earlier than juveniles. These age-specific differences were enhanced in the spring, when birds were moving towards the (natal) colonies, but when adults moved on average closer and 2 months ahead of immatures, which in turn moved earlier and closer to the natal home-range than juveniles. With reference to findings from other studies in other European countries, Herring Gulls breeding in The Netherlands occupies a mid-position between dispersive and sedentary tendencies.

Keywords *Larus argentatus* · Colour-ringing · Dispersal · Timing · Distribution · Long-term trends

Zusammenfassung Die niederländische Population der Silbermöwe durchlief während des 19ten und 20ten Jahrhunderts Phasen der Ausbeutung, des Schutzes, starker Verfolgung und wieder (teilweisen) Schutzes. Die Anzahl brütender Silbermöwen erreichten in den 1980er Jahren ihren Höchststand bei ca. 90 000 Brutpaaren. In dieser Zeit

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wurde ein Farbringprogramm initiiert um Dispersions- und Verbreitungsmuster zu untersuchen. Silbermöwen wurden als Küken, möglichst kurz vor dem Flüggewerden beringt, jeweils in 12 Kolonien 1986 (1 247 Ind.), 13 Kolonien 1987 (1 354 Ind.) und 14 Kolonien 1988 (1 396 Ind.). Zwischen 1986 und 2009 wurden von insgesamt 3997 als juvenil beringten Silbermöwen 3124 Individuen (78,2%) mindestens einmal lebend zurückgemeldet, wohingegen 453 (11,3%) als Totfunde gemeldet wurden. Insgesamt wurden 86 247 Ablesungen lebender Silbermöwen erziehlt und bearbeitet, welche von 1358 verschiedenen Orten und 868 Beobachtern stammen. Ein Fünftel (20,5%) aller Sichtungen beruhen auf Meldungen aus dem Home-Range (Gebiete innerhalb eines Radius von 5 km um den Beringungsort). Nur 691 Sichtungen (0,8%) wurden aus über 300 km Entfernung vom Geburtsort gemeldet (10,7% aus 6–10 km, 8,9% aus 11–25 km, 17,7% aus 26–50 km, 22,9% aus 51–100 km, 14,4% aus 101–200 km und 4,1% aus 201–300 km). Koloniespezifische Unterschiede in Zugdistanzen, Dispersionsrate und Zugrichtung lassen eine Einteilung in drei Gruppen zu: (1) Östliche niederländische Wattenmeerinseln (Rottumeroog–Vlieland), mit signifikant höheren Dispersionsraten und Bewegungen meist in Richtung südwest bis südost, (2) Texel und die vier Kolonien entlang der Festlandsküste (Callantsoog—Wassenaar), mit kürzeren mittleren Entfernungen und Bewegungen, meist nach Süden und (3) Kolonien im Deltaareal (Europoort–Saeftinghe) mit eher geringen Entfernungen und Dispersion in viele Richtungen. Die maximal zurückgelegten Distanzen zeigen keine starke Variation zwischen adulten, immaturen und juvenielen Tieren, jedoch zeigten sich unterschiedliche Zeitmuster für Wegzug und Rückkehrbewegungen für jede Altersklasse. Adulte Vögel erreichten die größte mittlere Distanz im Schnitt einen Monat früher als die Immaturen, welche dieses Stadium wiederum einen Monat vor den Juvenilen erreichten. Diese altersspezifischen Unterschiede wurden im Frühjahr noch vergrößert, wenn die Vögel sich in Richtung ihrer Geburtsorte bzw. Kolonien bewegten, wobei sich Adulte im Schnitt näher und zwei Monate vor den Immaturen in Richtung der Kolonie begaben, während die Immaturen sich wiederum früher und näher in Richtung ihrer Geburtsorte begaben, als die Juvenilen. Unter Berücksichtigung anderer europäischer Studien, zeigen niederländische Silbermöwen eine Zwischenstellung zwischen dispersieven und ortsgebundenen Bewegungsmustern.

Introduction

Palaearctic Herring Gulls *Larus argentatus*, with the exception of more migratory populations breeding in northern Scandinavia and Russia, are known as either resident or dispersive to a varying degree (Glutz von Blotzheim and Bauer 1982; Cramp and Simmons 1983). Seasonal dispersal patterns have been shown to vary with age as well as with breeding area (Landsborough Thomson 1924; Eaton 1933; Schüz 1933; Coulson and Butterfield 1985; Calladine 2002). In The Netherlands, where the species is generally regarded as a common resident or at best a short-distance migrant [Commissie Nederlandse Avifauna (CNA) 1970; Bijlsma et al. 2001], a review of migratory movements and dispersal patterns of Herring Gulls has thus far only been undertaken on the basis of metal ring recoveries (Spaans 1971). Tinbergen (1952) reported an apparent discrepancy between the results of an early analysis of ringing results (Drost and Schilling 1940), in which Herring Gulls were described as residents with some dispersal in all directions after the breeding season, and observations of endless streams of southbound Herring Gulls along the coast, which led him to call for more data. Spaans (1971) also concluded that during the 1950s and 1960s, after the breeding season, Herring Gulls dispersed in all directions, "more or less random around the ringing localities", and that only birds from Texel in their first year moved predominantly to the south.

The Herring Gull population in The Netherlands went through phases of exploitation, protection, persecution and again (partial) protection in the late nineteenth and throughout the twentieth centuries (Spaans 2007). In the early twentieth century, the breeding population was small (approx. 2,500 pairs), and colonies were frequently raided by humans in search of eggs (food) and feathers (fashion). This changed around 1912, when protective measures were implemented to safeguard colonies from egging and other forms of disturbance and the demand for seabird feathers had come to a halt. The population increased from the mid-1910s to approximately 15,000 pairs in the late 1930s (12.2% increase per annum; Spaans 1998). By that time, however, even conservationists became concerned about the impact of what was called an "overpopulation" of Herring Gulls. Measures to restrict the number of nesting Herring Gulls were taken and, in the absence of immediate success, this developed into a systematic campaign of destruction. From 1947 to 1966, some 90,000 adults were either shot or poisoned, and some 500,000 eggs were destroyed (Spaans 2007). In the mid-1960s, this type of destruction came to an end, partially because the effect of culling was "disappointing", but also because of an alarming decline in the breeding success of a number of seabirds and marine mammals in the Wadden Sea area due to intoxication following continuous leakages of pesticides (e.g. dieldrin, aldrin) by Shell Chemie in Botlek near the mouth of the Rhine River (Koeman et al. 1969). The Herring Gull population, which had peaked at 24,000 pairs in 1954 when the persecution was intensified, had dropped to some 16,000 pairs in the mid-1960s.

Following the relaxation of persecution in the late 1960s, the population rapidly increased, to reach an all-time high of nearly 90,000 pairs in 1984 and 1985 (11.5% increase per annum; Spaans 1998). Now that the Herring Gull population was so large, investigations into the whereabouts of gulls from each of the major colonies were instigated. A large-scale colour-ringing programme (plastic colour-rings with inscriptions that could be read from a distance; a rather novel tool at the time for gull studies) seemed to be the most appropriate approach to achieve that goal (Spaans and De Wit 1985; Noordhuis 1989). The colour-ringing campaign, in which approximately 100 large chicks were marked annually in each of 12–14 participating colonies, lasted from 1986 through 1988. The colonies have undergone rather different fates since this project started: some are still intact, with roughly the same number of breeding pairs, others were abandoned within a few years after the ringing campaign, others increased markedly and others declined once again (Spaans 1998). The wealth of information that has accumulated over the years following this colour-ringing campaign is now fit for analysis, and the first results are evaluated in this paper.

The sightings of colour-ringed individuals observed between 1986 and 2009 were analysed in search of patterns of dispersal and seasonal movements, and for associated differences between colonies, cohorts and age categories. The specific questions addressed were: (1) Is there evidence for migration (i.e. regular seasonal journeys) in Herring Gulls that fledged from colonies in The Netherlands, or are movements usually irregular and mostly in response to, for example, weather or prey resources? (2) Do these Herring Gulls move in all possible directions away from the natal colonies, or is there a tendency to travel in a set direction? (3) What is the difference between annual and seasonal movements of juvenile, immature and adult Herring Gulls? (4) Is there a difference between colonies or regions with respect to the distance and direction of (annual or seasonal) movements (see Coulson and Butterfield 1985)? Finally, (5) do Herring Gulls in winter completely mix, or is there a difference in wintering areas for birds originating from different breeding colonies or breeding regions?

Material and methods

Herring Gulls were ringed as chicks, mainly near-fledglings, in 12 colonies in 1986 (1,247 individuals), 13 colonies in 1987 (1,354 individuals), and 14 colonies in 1988 (1,396 individuals). The 14 colonies (Fig. 1), the number of chicks ringed in each colony and the years during which colour-ringing took place in of each of the sites are listed in Table 1.

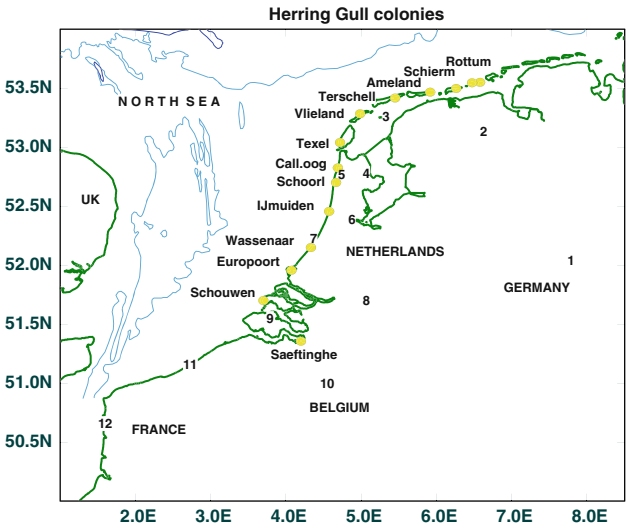

Fig. 1 Colonies (Rottum through Saeftinghe) of Herring Gull (*Larus argentatus*) where chicks were colour-ringed during 1986–1988 (see also Table 1). *Rottum* refers to two colonies next to each other: Rottumerplaat in the west, Rottumeroog in the east. *Numbers* refer to clusters of particularly productive sighting areas ("mega-sites"), including German refuse tips and sewage works (*1*), refuse tips Groningen and Drenthe (Usquert, Veendam, Wijster) (*2*), central Wadden Sea, also including refuse tip at Terschelling, Harlingen harbour, and Griend (*3*), refuse tip in Wieringermeer (*4*), northern Noord-Holland (Julianadorp-Camperduin, coastal sites) (*5*), Amsterdam (*6*), mainland coast south of and including IJmuiden (IJmuiden-Hoek van Holland, coastal sites) (*7*), inland areas southern Netherlands (refuse tips Breda, Geldermalsen, Tilburg, Waalwijk) (*8*), Zeeland (refuse tips and coastal sites) (*9*), inland refuse tips in Belgium (Antwerpen, Helchteren, Mont-Saint-Guibert, Vlierzele) (*10*), Belgian coast (coastal sites) (*11*), and French coast (coastal sites) (*12*)

Colonies were categorised as having *collapsed* (†) if they ceased to exist within 15 years after ringing (Wassenaar and Schoorl), as *declining* (—) when 50% or less of the population remained in the early twenty-first century when compared to the late 1980s and early 1990s (Rottumeroog, Rottumerplaat, Terschelling, Vlieland, Callantsoog, and Schouwen), *stable* (±) if the population remained within ±50% of the number of breeding pairs during ringing (Schiermonnikoog, Texel, Saeftinghe) and as *increasing* (+) if the number of breeding pairs had more than doubled in recent years in comparison with the situation during the ringing campaign (Ameland, IJmuiden, Europoort; Table 1).

Colour-rings

The rings used, one on each tarsus, were large and conspicuous; the colours deployed included blue, red, green, orange, white, yellow and black (Camphuysen 2008). Inscriptions were a single letter (A, B, D, G, H, J, L, N, P, S, T, X, Y and Z), a number (1, 2, 4, 7, 9) or one to three

Table 1 Numbers of Herring Gull (*Larus argentatus*) chicks colour-ringed during 1986–1988 and estimated breeding populations between 1985 and 2005

Colony	Numbers ringed				Number of breeding pairs					
	1986	1987	1988	Total	1985	1990	1995	2000	2005	Trend[a]
Rottumeroog	103	103	105	311	5,600	3,500	3,200	2,400	2,800	–
Rottumerplaat	105	105	100	310	2,800	6,200	2,100	1,700	1,300	——
Schiermonnikoog	105	105	105	315	5,000	5,200	4,800	7,200	3,100	±
Ameland	102	105	104	311	2,000	3,000	2,500	3,600	4,900	++
Terschelling	103	105	105	313	16,900	16,000	11,700	5,000	3,200	——
Vlieland	105	105	106	316	12,500	10,000	8,000	3,100	4,700	——
Texel	103	104	105	312	8,800	9,500	7,600	6,500	6,100	±
Callantsoog	105	104	104	313	1,500	730	1,400	510	350	——
Schoorl	102	99	103	304	3,200	1,200	25	0	0	†
IJmuiden			105	105	300	1,400	1,100	1,400	1,500	++
Wassenaar	105	104	40	249	5,100	200	0	0	0	†
Europoort	104	105	105	314	1,300	5,000	7,800	7,000	5,000	++
Schouwen	105	105	104	314	7,250[c]	7,400	4,000	3,000	2,300	——
Saeftinghe		105	105	210	6,100	7,000	8,500	8,000	8,000	±
Total[b]	1,247	1,354	1,396	3,997	88,850	77,150	70,000	62,800	53,000	–

Estimates have been rounded-off and provided by SOVON (SOVON Dutch Centre for Field Ornithology) and Waterdienst (National service of the Directorate General of Public Works and Water Management)

[a] Trends in breeding numbers of colonies since colour-ringing took place are indicated as well, and qualified as either increasing (+), stable (±), declining (—), or having collapsed (†). Strong trends are indicated by double symbols

[b] The bottom line refers to the total number of chicks colour-ringed (left) and the total Dutch breeding population estimates (pairs), including other colonies as well (right)

[c] A 1987 count was preferred over an apparently unreliable estimate of 13,000 pairs in 1985 (see Vercruijsse 1999 for further details)

parallel bars (-, =, Ξ). The inscription was repeated three times so that a ring could be read from all angles of observation; the bars ran around the ring (horizontally). For notation, the protocol suggested mentioning the left ring first, followed by the right ring, and to use B for blue and Z for black. It was also suggested to write "—" for a single bar, F for a double bar and 3 for triple bar inscriptions. No metal ring was added. The position of the rings (left or right tarsus), the colour and the inscriptions formed unique code combinations (further referred to as "ring-codes").

The plastic rings were prone to wear, and many rings were eventually lost. Incomplete codes were omitted from the analysis (1,706 sightings of 170 incomplete ring-codes), except in rare cases in which local knowledge allowed the correct original code for sightings of well-known individuals that had lost one of their rings to be entered into the dataset. Fading colours formed a second problem. Ring loss became a frequent issue after 10 calendar years, and ring fading occurred in some colours after 6 years. Colours of rings were not randomly distributed over the various colonies/ringing years. However, differences in sighting probability were site specific rather than colour specific, and sightings rates were rather similar for colours with different "hardiness" (dark rings being apparently slightly stronger than light-coloured rings) within subregions, while they were rather different between areas with similar "hardiness" of the rings.

Sightings of colour-rings were all entered into the database by a central database manager upon receipt, while each entry was immediately examined in the context of previous sightings. Because the movements of many individual birds were characteristic, ''unusual'' records (outliers in time or space) were double-checked, and observers were consulted, where needed, to confirm sightings. During this procedure, numerous misreportings were found where colour-fading had been an issue. Where uncertainties remained, records were omitted. It was soon found that individuals were so site-faithful throughout their annual cycle (both in winter and in summer) that outliers were easy to spot. In later years, therefore, with more prolonged individual dispersal patterns at hand, further checks for consistency were performed during which at least several hundreds of records (probably <0.5% of all reported sightings) were either corrected or deleted. All these thorough checks have resulted in the database now being, despite its large size and numerous contributors, relatively "free" of errors.

Age and plumage

Herring Gulls were labelled as juveniles during the entire first year following ringing (July of first calendar year until June of second calendar year) and as immatures in the second (July–December), third (January–December) and fourth (January–December) calendar year following ringing. Older birds were referred to as adults. For the summer analyses (April–August or April–September), however, all second calendar year individuals (at least 10 months old in that season) were included with the immatures.

Analysis

With all gulls ringed as chicks, the exact age was known for all birds for which a complete ring code could be read during later encounters. For each sighting, date, observer and location were logged, while distance (km) and angle (°) from the natal colony were calculated for each locality and used for further analysis. Angles were subsequently grouped into octants (N, NE, E, SE, S, SW, W and NW), while distances were either used as they were measured (km) or grouped into categories. Data were analysed on the basis of spatial or temporal patterns in sightings. Reported sightings were either plotted exactly (latitude–longitude co-ordinates; 1′ resolution) or grouped (within certain popular ring-reading locations, or particular distance zones) for analysis. All sightings within 5 km from the ringing location were labelled as "home-range" records. For each of the sightings, distance to the nearest North Sea coast was calculated (km) in order to facilitate the analysis of inland movements. Distances were grouped into categories for analysis. Sightings within 5 km from the North Sea coast were taken as "coastal reports".

In order to analyse the dispersal rate (r) from the natal colonies, sightings within the home-range were omitted. The rate of dispersal was calculated using the method described by Coulson and Brazendale (1968) for the Cormorant *Phalacrocorax carbo*. The sightings were grouped into equal-distance zones from the natal area (50-km intervals). To avoid pseudo-replication and to have individual birds as units rather than individual sightings, the representation of birds, as a proportion (%) of all sightings of that individual, within each of the distance bins was assessed, and the average representation for all individuals within each of the distance bins was subsequently determined. The percentage of birds recorded within each zone as well as those recorded at greater distances from the natal colonies were determined, and the logarithm of these numbers were plotted against distance. A linear relationship would imply that a constant proportion of the birds which enter a zone remain in it, irrespective of the distance to the colony. This constant (r), or the rate of dispersal, may vary between different age categories of gulls or between gulls from different colonies or areas, and it can be calculated (± standard error) in the same manner as the average annual survival rate in birds (Lack 1943; Parsons and Duncan 1978). The dispersal rate r is provided to illustrate and quantify whether the dispersal of a particular category of birds was greater or smaller than another.

Some sites were particularly productive in terms of sightings ("mega-sites"). For example, a frequently explored site such as the Tilburg refuse tip alone yielded 8,606 observations of 795 ring-codes. Another site, IJmuiden harbour, yielded 4,529 sightings of 557 individual birds over the years. In a further attempt to discover colony-specific dispersal and movements, 12 clusters of such "mega-sites" (i.e. groups of particularly productive sites within the same general area; Fig. 1, Table 2) were analysed to investigate the representation of individual colonies in each of them. Some of these clusters produced sightings over a distinctly shorter period of years than the others (Wieringermeer 1987–1995, inland areas southern Netherlands 1988–1996, Belgian refuse tips 1986–1995; Table 2). Because fewer chicks were ringed in some colonies than in others, correction factors were needed to avoid underrepresentation of certain ringing sites in the analysis: Rottumeroog (×0.92), Rottumerplaat (×0.92), Schiermonnikoog (×0.91), Ameland (×0.92), Terschelling (×0.91), Vlieland (×0.90), Texel (×0.92), Callantsoog (×0.91), Schoorl (×0.94), IJmuiden (×2.72), Wassenaar (×1.15), Europoort (×0.91), Schouwen (×0.91) and Saeftinghe (×1.36; see Table 1).

Results

Sightings and recoveries

A total of 3,997 Herring Gull chicks were colour-ringed between the summers of 1986 and 2009 (23 years); of these, 3,124 individuals (78.2%) were read and reported at least once, while 453 (11.3%) were eventually recovered dead. In total, 86,247 ring-readings of living gulls were received and processed, originating from 1,358 locations and by 868 observers. In all, 72.4% were reported at least once as juveniles (range 39.8–95.2%), 49.6% as immatures (30.5–74.3%) and 33.9% as adults (17.7–61.0%; Table 3). There were relatively few ring-readings in all age categories at Rottumerplaat (colony declined), Ameland (increased) and, in particular, Wassenaar (collapsed) (Table 3). Most reported sightings came from coastal areas (in particular the mainland provinces of Noord-Holland and Zuid-Holland) and from refuse tips in the north-eastern part of the country and in the province of Noord-Brabant. An overwhelming majority (93.6%) of all sightings came

Table 2 Clusters of "mega-sites" (sites from where at least 100 sightings of colour-ringed Herring Gulls were reported[a], with the number of sightings and ring-codes during winter and summer for each cluster and in total

Number of site	Description of mega-site clusters	Period	Winter (October–March)		Summer (April–September)		Total
			Sightings	Ring-codes	Sightings	Ring-codes	Ring-codes
1	Germany, refuse tips and sewage works	1987–2003	168	85	2	2	86
2	Groningen and Drenthe, refuse tips	1986–2009	3,462	599	1,354	468	744
3	Central Wadden Sea and refuse tip Terschelling	1986–2003	179	58	2,184	341	360
4	Wieringermeer, refuse tip	1987–1995	1,444	296	1,413	259	396
5	Coast northern Noord-Holland	1986–2009	4,341	476	9,471	786	901
6	Amsterdam	1986–2003	217	59	72	36	79
7	Mainland coast from IJmuiden to the south	1986–2006	9,425	1,020	10,154	903	1,301
8	Inland areas southern Netherlands, refuse tips	1986–1996	7,863	739	3,092	516	883
9	Zeeland, refuse tips and coastal sites	1986–2008	2,745	474	3,466	465	621
10	Inland refuse tips Belgium	1986–1995	666	318	163	105	348
11	Belgian coast (coastal sites)	1986–2009	555	134	748	170	225
12	French coast (coastal sites)	1988–2008	919	189	240	95	205

[a] See Fig. 1

Table 3 Sightings according to age of Herring Gull chicks colour-ringed in The Netherlands between 1986 and 1988

Colony	Juvenile	Immature	Adult	Number of birds colour-ringed
Rottumeroog	231 (74.3)	138 (44.4)	79 (25.4)	311
Rottumerplaat	171 (55.2)	115 (37.1)	62 (20.0)	310
Schiermonnikoog	195 (61.9)	126 (40.0)	72 (22.9)	315
Ameland	162 (52.1)	96 (30.9)	55 (17.7)	311
Terschelling	259 (82.7)	120 (38.3)	87 (27.8)	313
Vlieland	264 (83.5)	129 (40.8)	74 (23.4)	316
Texel	262 (84.0)	164 (52.6)	119 (38.1)	312
Callantsoog	244 (78.0)	197 (62.9)	137 (43.8)	313
Schoorl	243 (79.9)	213 (70.1)	183 (60.2)	304
IJmuiden	100 (95.2)	78 (74.3)	64 (61.0)	105
Wassenaar	99 (39.8)	76 (30.5)	58 (23.3)	249
Europoort	238 (75.8)	208 (66.2)	142 (45.2)	314
Schouwen	268 (85.4)	202 (64.3)	153 (48.7)	314
Saeftinghe	157 (74.8)	120 (57.1)	70 (33.3)	210
Total	2,893 (72.4)	1,982 (49.6)	1,355 (33.9)	3,997

Data are given as the number (*n*) of sightings, with the proportion (%) of ring-codes given in parenthesis

from The Netherlands ($n = 86{,}247$; 3,073 ring-codes), 3.5% from Belgium (614 ring-codes), 2.1% from France (292 ring-codes) and 0.7% from Germany (214 ring-codes). Only five sightings were reported from Denmark (3 birds), one sighting from Poland (1 bird) and three sightings from the UK (3 birds).

Distances

One-fifth (20.5%) of all reported sightings ($n = 86{,}247$) originated from the home-range areas. Only 691 sightings (0.8%), including 144 birds (3.6%), were reported at distances of >300 km from the natal colony (10.7% 6–10 km, 8.9% 11–25 km, 17.7% 26–50 km, 22.9% 51–100 km, 14.4% 101–200 km, 4.1% 201–300 km). Wintering birds were reported on average at approximately 80–95 km from the natal colonies, with a tendency for birds from the Wadden Sea area to travel further away (Table 4). Adults in summer were normally seen within 20–40 km of their natal colonies, but long-distances (200–500 km) were still frequently reported during the breeding season for all colonies (Table 5).

Exceptional distances (>500 km) were covered by three individuals. O2WJ (ringed at Rottummeroog) was seen in

Table 4 Mean and maximum distances from the natal colony in the winter (October–March) according to age of Herring Gulls ringed as a chick in The Netherlands between 1986 and 1988

Colony	Juvenile		Immature		Adult	
	Mean distance (km)	Maximum distance (km)	Mean distance (km)	Maximum distance (km)	Mean distance (km)	Maximum distance (km)
Rottumeroog	98	506	69	478	107	504
Rottumerplaat	97	370	95	484	128	300
Schiermonnikoog	101	451	103	485	152	442
Ameland	137	426	159	461	156	432
Terschelling	119	406	133	412	167	412
Vlieland	101	417	143	404	151	414
Texel	99	388	105	388	95	357
Callantsoog	69	327	77	736	56	333
Schoorl	68	350	78	339	54	349
IJmuiden	53	292	52	326	24	327
Wassenaar	27	172	52	289	66	287
Europoort	54	431	60	262	64	264
Schouwen	80	366	90	262	63	354
Saeftinghe	57	221	52	264	44	199
Overall	83	506	91	736	95	504

Table 5 Mean and maximum distances from the natal colony in the summer (April–September) according to age of Herring Gulls ringed as a chick in The Netherlands between 1986 and 1988

Colony	Second calendar year		Third calendar year		Fourth calendar year		Adult	
	Mean distance (km)	Maximum distance (km)	Mean distance (km)	Maximum distance (km)	Mean distance (km)	Maximum distance (km)	Mean distance (km)	Maximum distance (km)
Rottumeroog	105	473	72	349	44	274	20	504
Rottumerplaat	101	376	72	373	61	237	61	237
Schiermonnikoog	132	338	81	354	86	399	57	338
Ameland	142	426	57	330	79	265	74	264
Terschelling	79	406	72	397	59	226	53	203
Vlieland	63	380	63	292	52	222	59	419
Texel	74	351	64	376	65	344	49	376
Callantsoog	37	327	39	327	39	327	28	350
Schoorl	43	308	43	315	45	313	28	347
IJmuiden	46	292	53	327	17	282	5	327
Wassenaar	40	182	69	167	45	187	50	287
Europoort	60	429	59	231	50	231	45	264
Schouwen	78	223	72	227	51	213	18	227
Saeftinghe	49	224	52	225	49	177	40	198
Overall	75	473	62	397	53	399	42	504

France as a juvenile at the refuse tip of Boismont, Somme (506 km from natal colony) and as an adult on the mudflats near Le Crotoy, Somme (504 km). WLZA (Callantsoog) was found dead in France in its third calendar year at Courseulles-sur-Mer, Calvados (529 km). WTZB (Callantsoog) was sighted in its fourth calendar year in Poland, at Kolobrzeg on the Baltic coast (736 km). The two birds seen alive were re-sighted later, much nearer to the natal colony: O2WJ until 2008 (20 years), WTZB until 1995 (7 years).

The mean distance from the natal colony throughout the year fluctuated most strongly in Herring Gulls from the eastern Wadden Sea islands (Rottumeroog–Vlieland), with a mean range of 160 km away from the natal colonies in winter, but gradually approaching closer to the home-range areas in the summer with increasing age (Fig. 2a). Herring Gulls from Texel and the four colonies along the mainland coast (Callantsoog–Wassenaar) were seen at a mean distance of 80–100 km from the natal colonies in winter and at considerable shorter distances from the natal colonies in immature stages during the summer than seen for immatures in the Rottumeroog–Vlieland group (Fig. 2b). In the Delta area (Europoort–Saeftinghe), rather smaller differences in mean range between summer and winter were found, particularly in younger birds (within 50–70 km from the natal colonies), but a more distinct seasonal pattern in distances was found in adults (Fig. 2c). Long-distance movements (>200 km from the natal colony) were more common in the first group of colonies (12.9% of all sightings, 20.6% of all ring-codes) than in colonies situated along the mainland coast (2.6 and 16.5%, respectively) and in the Delta area (1.4 and 11.7%, respectively).

Dispersal rates (r) in winter (October–March) and summer (April–September) according to age for each of the 14 colonies are shown in Table 6. Winter dispersal rates were remarkably similar for each of the three age categories (adults vs. immatures $t_{26} = 0.1$, nonsignificant; immatures vs. juveniles $t_{26} = 1.13$, nonsignificant), but in summer, immatures dispersed further than adults ($t_{26} = 1.84$, $P < 0.05$). In all age categories and seasons, dispersal rates of Herring Gulls from Rottumeroog–Vlieland significantly exceeded those of the other colonies (Texel–Saeftinghe; Table 6).

The mean distance of winter movements away from the natal colony did not change with age [0–23 years, log-transformed mean distances in winter, excluding home-range sightings (y) against true age in years (x); $y = 0.52x + 74.273$, $r^2_{23} = 0.03$], but the maximum reported distances declined gradually, suggesting a progressively smaller winter range with increasing age ($y = -14.627x + 555.09$, $r^2_{23} = 0.49$). The difference in dispersal range between colonies in the north-east and those in the rest of The Netherlands (north-west and south-west; see Fig. 2) and the annual cycle of departure and return towards the home-range remained intact during at least the first 10 years of life, after which a seriously reduced sample size (a combination of ring loss and mortality) led to a more confusing picture (Fig. 3). The difference in dispersal distance between colonies in the north-western region (Fig. 2b) and those in the south-west (Fig. 2c) disappeared when the birds matured, leading to a highly similar seasonal pattern in range of adult birds in either region.

Direction of movements

The analysis of flight directions away from the natal colonies revealed that most colonies, with the exception of those situated in the Delta area (Europoort–Saeftinghe), have a distinct southerly or south-westerly component (occasionally south-easterly) in their movements and that this component applies to both the winter (Table 7) and summer reports (Table 8). Most (78%) of the sightings during the winter were from locations south of the natal colonies, with the highest proportion for the ten northern colonies. With longitudes ranging from 6°35′E (Rottumeroog) to 4°42′E (Callantsoog), the data suggest some degree of spatial segregation in wintering areas between colonies. There was, however, a split in the main direction between colonies, with birds from Rottumeroog–Schiermonnikoog mainly moving to the south and south-east, and those from Ameland–Vlieland mainly moving to the south and south-west (Fig. 4). Vlieland could also be included in another cluster of colonies (with Texel, Callantsoog and Schoorl), in which 70–80% of all winter sightings were directly south of the breeding colonies. The flight directions of gulls that had fledged in the five southern colonies (IJmuiden–Saeftinghe) were more to north and north-east than those of gulls had fledged in the other colonies. In fact, in all but one colony (the exception being IJmuiden), few birds moved straight to the south (Table 7; Fig. 4).

These patterns were more or less retained in the summer (Table 8), when sightings from Herring Gulls originating from the easternmost three Wadden Sea islands were mostly to the south and south-east, from those originating from Ameland and Terschelling mostly to the south-west, from those originating from Vlieland, Texel, Callantsoog and Schoorl mostly to the south (but note 39% of the Vlieland birds to the east of the natal colony, and rather frequent sightings north of the natal colony of birds originating from Schoorl). Most sightings of birds from the Delta area were to the east and north-east. Summer sightings from birds originating from the (collapsed) Wassenaar colony were most diverse, with 44% to the north and north-east, and 42% to the south-west of the natal colony.

The results of travelling distances (Fig. 2), dispersal rates (Table 6) and directions of movements (Tables 7, 8) suggest that each colony can be placed into one of three groups. The first group is formed by the eastern Wadden Sea islands (Rottumeroog–Vlieland), with the longest seasonal movements away from the natal colonies in winter and a gradual approach closer to the natal colonies in the summer with increasing age, significantly higher dispersal rates (Table 6) and movements mostly in directions varying from south-west to south-east. A second group of colonies comprises Texel and the four colonies along the

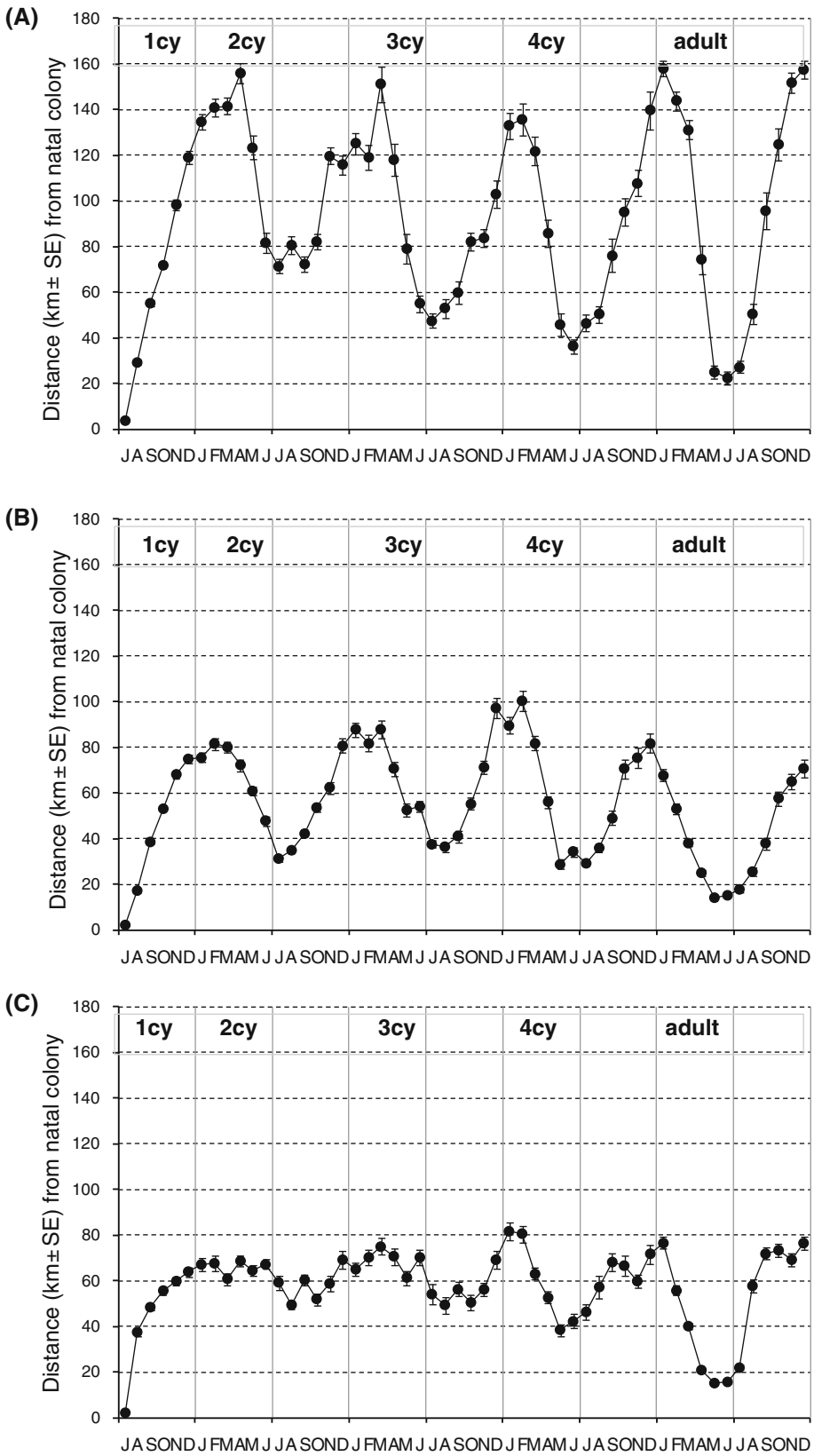

Fig. 2 Mean distance [km; ± standard error (*SE*)] from natal colony of fledgings up to and including adults for Herring Gulls colour-ringed as chick at: **a** the eastern Wadden Sea islands (Rottumeroog–Vlieland; $n = 18{,}902$ sightings), **b** Texel and in the mainland coast colonies (Callantsoog–Wassenaar; $n = 45{,}467$ sightings), **c** in the Delta area colonies Europoort–Saeftinghe ($n = 21{,}869$ sightings) between 1986 and 1988. *X-axis gridlines* indicate 9 half-yearly periods [beginning with July (*J*) of the year of ringing]. *cy* Calendar year

Table 6 Dispersal rates[a] for various categories of Herring Gulls colour-ringed as chick in The Netherlands between 1986 and 1988, based on 50-km distance bins for distances up to 250 km from the natal colonies

Number of colony	Colony	Winter dispersal rates (Oct–Mar)						Summer dispersal (Apr–Sep)			
		Adult		Immature		Juvenile		Adult		Immature	
		r	SE	*r*	SE	*r*	SE	*r*	SE	*r*	SE
1	Rottumeroog	0.65	±0.13	0.60	±0.12	0.63	±0.12	0.35	±0.07	0.58	±0.13
2	Rottumerplaat	0.61	±0.12	0.62	±0.03	0.60	±0.07	0.48	±0.10	0.50	±0.07
3	Schiermonnikoog	0.64	±0.08	0.61	±0.07	0.64	±0.11	0.41	±0.07	0.57	±0.08
4	Ameland	0.74	±0.08	0.71	±0.10	0.60	±0.09	0.52	±0.09	0.62	±0.02
5	Terschelling	0.73	±0.06	0.67	±0.10	0.60	±0.09	0.47	±0.05	0.59	±0.07
6	Vlieland	0.66	±0.10	0.58	±0.12	0.44	±0.14	0.55	±0.10	0.47	±0.04
7	Texel	0.47	±0.12	0.52	±0.11	0.48	±0.14	0.38	±0.08	0.42	±0.09
8	Callantsoog	0.47	±0.12	0.51	±0.09	0.52	±0.15	0.25	±0.09	0.48	±0.09
9	Schoorl	0.41	±0.05	0.49	±0.08	0.52	±0.09	0.35	±0.05	0.46	±0.07
10	IJmuiden	0.50	±0.10	0.44	±0.12	0.42	±0.06	0.48	±0.07	0.39	±0.10
11	Wassenaar	0.42	±0.14	0.35	±0.11	0.24	±0.11	0.41	±0.09	0.24	±0.12
12	Europoort	0.53	±0.08	0.58	±0.09	0.48	±0.07	0.40	±0.12	0.46	±0.05
13	Schouwen	0.43	±0.14	0.50	±0.14	0.44	±0.10	0.32	±0.09	0.45	±0.10
14	Saeftinghe	0.29	±0.13	0.43	±0.08	0.36	±0.11	0.23	±0.11	0.34	±0.06
Colonies 1–6[b]		0.67	±0.04	0.63	±0.04	0.58	±0.04	0.46	±0.03	0.56	±0.03
Colonies 7–14[b]		0.44	±0.11	0.48	±0.10	0.43	±0.10	0.35	±0.09	0.40	±0.08
t_{12} 1–6 versus 7–14[b]		6.59	***	4.62	***	3.28	**	2.58	*	3.86	*

SE Standard error

[a] See "Material and Methods"

[b] Groupings of colonies with highly similar values and *t* test results (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

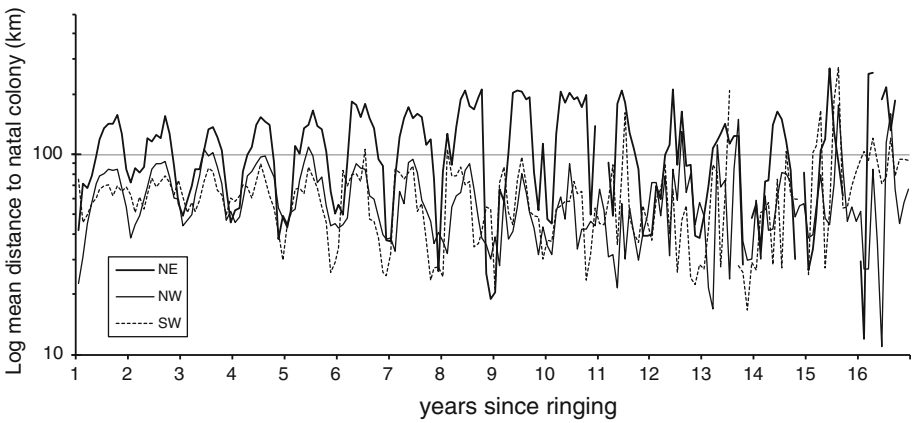

Fig. 3 Mean distance (km, $\log^{10}$ transformed) from the natal colony with increasing age for Herring Gulls colour-ringed as chick on the eastern Wadden Sea islands Rottumeroog–Vlieland (*NE*), at Texel and in the mainland colonies Callantsoog–Wassenaar (*NW*), and in the Delta colonies Europoort–Saeftinghe (*SW*). Mean distances were calculated for each month over a period of 16 years

mainland coast (Callantsoog–Wassenaar), with a mean range of 80–100 km in winter, considerably shorter distances to the natal colonies in immatures in the summer than in immatures from the Wadden Sea islands group and mostly moving strictly to the south. Finally, colonies in the Delta area (Europoort–Saeftinghe) show rather smaller differences in mean range between summer and winter in younger birds, a distinct seasonal pattern in adults, short range movements and a dispersal in many directions.

Dispersal from the perspective of the main wintering areas

From the perspective of sites at which particularly large numbers of sightings were reported (clusters of "mega-sites"; Fig. 1, Table 2), it is clear that most were visited during the winter by birds from all 14 breeding colonies. All clusters of "mega-sites", however, were particularly important for certain (groups of) colonies (Table 9).

Table 7 Direction of sightings (1986–2009) at distances of greater than 5 km from natal colonies during the winter period (October–March) of Herring Gulls (all age classes combined) ringed as a chick in The Netherlands between 1986 and 1988

Colony	N	NW	W	SW	S	SE	E	NE	Sightings
Rottumeroog	0		1	20	**76**	2	0	1	1,662
Rottumerplaat			1	**29**	**40**	20	9	0	1,480
Schiermonnikoog			2	21	**35**	**41**	1	1	1,825
Ameland			3	**44**	**26**	22	4	0	1,370
Terschelling	0		4	**23**	**39**	17	17	1	1,678
Vlieland				7	**79**	7	4	2	2,163
Texel				4	**79**	15	1	1	3,267
Callantsoog	1			13	**79**	0	5	1	5,694
Schoorl	9			11	**73**	2	5	0	5,359
IJmuiden	11			**56**	**29**	1	1	2	1,105
Wassenaar	11			**33**	4	18	1	**33**	1,828
Europoort	2	0	1	15	9	**28**	3	**41**	3,253
Schouwen			0	**32**	14	15	**28**	11	3,037
Saeftinghe	11	2	8	3	1	8	1	**64**	2,318
Total	3	0	1	18	**48**	12	6	11	36,039

Data for each colony are given as a percentage of the number of sightings for that colony

Predominant directions (>25%) are given in bold

Table 8 Direction of sightings (1986–2009) at distances greater than 5 km from natal colonies during the summer period (April–September) of Herring Gulls (all age classes combined) ringed as a chick in The Netherlands between 1986 and1988

	N	NW	W	SW	S	SE	E	NE	Sightings
Rottumeroog	0		10	23	**57**	8	0	1	866
Rottumerplaat			5	**36**	**41**	9	8	0	773
Schiermonnikoog			10	21	24	**32**	8	4	873
Ameland			8	**64**	11	8	9		839
Terschelling	0		7	**40**	**29**	11	13	1	1,085
Vlieland				14	**43**	1	**39**	3	1,571
Texel				3	**69**	19	6	4	3,584
Callantsoog	6			17	**67**	0	4	6	5,826
Schoorl	**29**			11	**50**	1	5	4	4,856
IJmuiden	21			**55**	14	1	1	9	930
Wassenaar	18			**42**	2	11	2	**26**	2,056
Europoort	6	0	1	15	6	21	1	**51**	3,554
Schouwen				**26**	21	7	**34**	12	3,827
Saeftinghe	21	6	13	1	0	6	1	**52**	1,848
Total	9	0	2	20	**37**	8	9	14	32,488

Data for each colony are given as a percentage of the number of sightings for that colony

Predominant directions (>25%) are given in bold

Sightings of Dutch Herring Gulls at German refuse tips and sewage works (FRG, cluster 1) were dominated by birds originating from the Wadden Sea islands (Texel excluded; 91% of all reported rings). Only a handful of birds originated from colonies in the west. Refuse tips in Groningen and Drenthe (Gr, cluster 2) were dominated by Herring Gulls from Rottumeroog–Terschelling (89%), with only rare reports of birds from IJmuiden–Saeftinghe. Local birds were most frequently represented in the central Wadden Sea (WdC, cluster 3), with most Herring Gulls originating from Ameland, Terschelling, Vlieland, and, slightly odd, Callantsoog (73%). At the Wieringermeer refuse tip (Wr, 4), wintering Herring Gulls were dominated by birds ringed on Vlieland and Texel and in Callantsoog and Schoorl (60% of all birds seen). The mainland coast between Julianadorp and Camperduin (NH, cluster 5) received mainly Herring Gulls from Texel, Callantsoog and Schoorl (64%). In Amsterdam (Ams, cluster 6), sightings were dominated by birds from Texel, Callantsoog and Schoorl (64%). The absence of birds from nearby IJmuiden is striking. The mainland coast between IJmuiden–Hoek van Holland (ZH, cluster 7) had sightings being clearly dominated by Herring Gulls originating from Texel, Callantsoog, Schoorl, IJmuiden and Europoort (69%). Inland refuse tips at Breda, Geldermalsen, Tilburg, Waalwijk (Brab, cluster 8) were attended by a rather wide variety of birds (minimum colony representation 3%, maximum 14%), with 55% from colonies in the west, but also from colonies as wide apart as Texel, Callantsoog, Schoorl, Europoort and Saeftinghe. In clusters 9–12, Herring Gulls originating from southern colonies (Schoorl–Saeftinghe) dominated: 82% in Zeeland (refuse tips and coastal sites; Zeel, cluster 9), 74% at Belgian refuse tips (Binll, cluster 10), 78% along the Belgian coast (Bcst, cluster 11) and 77% along the French coast (F, cluster 12).

Birds from Wassenaar, even after correction for ringing effort, were not commonly represented in any of these 12 areas. Relatively high numbers were seen at some inland refuse tips (cluster 8, 6%), along the coast of Zuid-Holland (i.e. immediate surroundings of the home-range, cluster 7, 7%) and in Amsterdam (cluster 6, 8%; Table 9).

Using a similar approach, but with all sightings (including sightings outside the clusters of "mega-sites" as well) within Germany (214 ring-codes reported), Belgium (614 codes) and France (292 codes), a clear split in regions was found. In Germany, 74% of all reported ring-codes originated from the easternmost five Wadden Sea Islands (85% from all Wadden Sea islands combined). In Belgium and France, the representation of Dutch colonies was rather similar, with 61% from the southernmost five colonies (IJmuiden–Saeftinghe) in Belgium and 64% in France (79 and 82%, respectively, when birds from the two next colonies in line (Schoorl and Callantsoog) are also included.

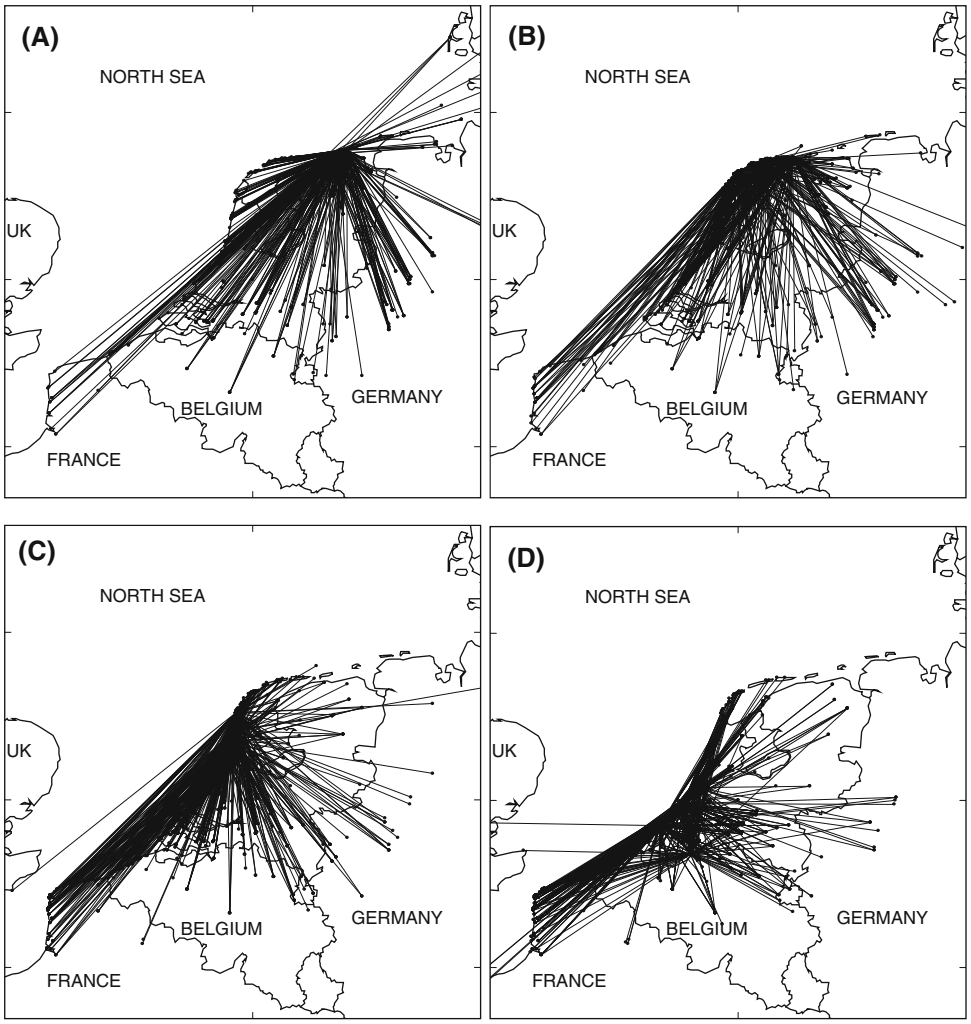

Fig. 4 Direction of sightings (1986–2009) at distances greater than 5 km from natal colonies during the winter period (October–March; $n = 36{,}039$ sightings) of Herring Gulls (all age classes combined) colour-ringed as a chick on Rottumeroog–Schiermonnikoog (**a**), on Ameland–Vlieland (**b**) on Texel and in Callantsoog–IJmuiden (**c**), in Wassenaar–Saeftinghe (**d**)

Seasonality and age

The maximum distance travelled away from the natal colony did not vary much between adults, immatures and juveniles, but the timing of the outward and return movements was different for each of the age categories (Fig. 2). Adult birds returned towards the colonies from December and January onwards, with a relatively fast return in March and April, whereas young immatures did not even show a tendency to travel towards the natal colony region until very late in the spring or early summer. Adult birds reached their greatest mean distances, on average, 1 month earlier than immatures, which in turn arrived 1 month earlier than juveniles (Fig. 5). These age-specific differences are enlarged in spring, when mean distances were progressively closer to the natal colony, but in which adults moved on average closer towards the home-range and 2 months ahead of immatures, which in turn were earlier and closer to the home-range than juveniles (Fig. 5).

Home-range sightings of adult Herring Gulls peaked in May (nearly 60%) and were lowest in November–December (9%; Fig. 6a). Some 40% of all sightings of adult birds in winter were at distances of greater than 100 km from the natal colony. In immatures, considerably lower proportions of home-range sightings were found in all months, but the fraction seen within 100 km from the natal colony was quite similar to that in adults (Fig. 6b). Juveniles abandoned the home-range later than the other age groups, and less than 10% of the sightings of juveniles originated from within the home-range in any month after August of the first calendar year (Fig. 6c). The period in which 35–40% or more of the sightings came from distances of over 100 km from the natal colony lasted from December to January in adults, from January to February in immatures, but from January to April in juveniles.

Table 9 Proportion (%) of colour-ringed Herring Gulls from 14 Dutch colonies within 12 clusters of "mega-sites" (see Fig. 1, Table 2) in winter (October–March)

Colony	1 FRG	2 Gr	3 WdC	4 Wr	5 NH	6 Ams	7 ZH	8 Brab	9 Zeel	10 Binll	11 Bcst	12 F
Rottumeroog	**12**	**25**	3	3			1	3	1	3		1
Rottumerplaat	**30**	**20**	5	5	1	3	2	3	1	2	2	
Schiermonnikoog	**19**	**20**	2	4	2	2	2	4	2	3	3	2
Ameland	9	**11**	**17**	5	2	5	3	4	3	3	1	3
Terschelling	**12**	**13**	**20**	8	2		4	5	1	2		2
Vlieland	**10**	4	**26**	**9**	9	7	7	5	3	4	5	2
Texel	2	1	3	**17**	**13**	**22**	**10**	**8**	3	3	3	6
Callantsoog	1	1	**10**	**18**	**26**	**25**	**14**	**9**	4	6	9	6
Schoorl	2	2	5	**16**	**25**	**17**	**15**	**10**	6	8	**11**	7
IJmuiden			5	7	9		**20**	7	**13**	**10**	**15**	**14**
Wassenaar		1		2	4	8	7	6	4	3	3	3
Europoort	1	1	2	3	5	8	**10**	**13**	**10**	8	**11**	**14**
Schouwen	1		2	1	1		4	8	**23**	**12**	**27**	**29**
Saeftinghe							1	**14**	**27**	**33**	**10**	**11**
n	78	551	55	286	469	55	1100	756	529	355	143	199
Area in bold (Σ)	82	89	73	60	64	64	69	55	72	55	75	68

Representation was based on the number of ring-codes, corrected for differences in ringing effort between colonies of origin

Colonies indicated in bold were particularly well represented (≥10%). For header abbreviations. see text in Sect. "Dispersal from the perspective of the main wintering areas"

Inland movements

Adults and immatures, all colonies combined, showed a bi-modal pattern in sightings with respect to the distance to the nearest North Sea coast (Fig. 7). The peak at sites within 5 km from the North Sea coastline in May can best be explained by home-range returns (all natal colonies being coastal), but a distinct second peak occurred in August-September, during wing moult, after the breeding season. The percentage of coastal sightings of juveniles declined gradually during the first autumn, and some return towards the coast was witnessed in April and May, as in immatures and adults, but with fewer sightings near the natal home-range areas (Fig. 7).

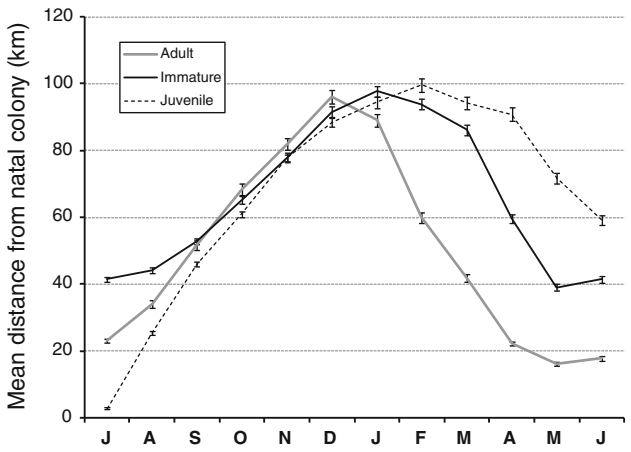

Fig. 5 Seasonality in mean distance (km ± SE) from natal colony (n = 86,247 sightings) for adult, immature and juvenile Herring Gulls (all colonies combined) colour-ringed as a chick in The Netherlands between 1986 and 1988. *X-axis* Months of the year beginning with July (*J*)

When seasonality is compared in terms of distance to the North Sea shoreline for adult Herring Gulls originating from each of the three main breeding regions (Fig. 8), it is clear that only mainland and Delta gulls (Texel–Saeftinghe) show the bi-modal seasonality, with the strongest tendency to stay in coastal habitats for birds originating from Texel–Wassenaar (Fig. 8). A very high proportion of Herring Gulls from Rottumerplaat–Vlieland was observed at greater distances from the North Sea coast, in particular in winter, followed by a return in April through June. The post-breeding peak in coastal habitats was less obvious, although a marked decline in sightings in these areas was found only after September.

Discussion

Studies of the migratory movements of Herring Gulls in Europe have been based on field observations (Sluiters 1939; Tinbergen 1952; Meltofte and Faldborg 1987),

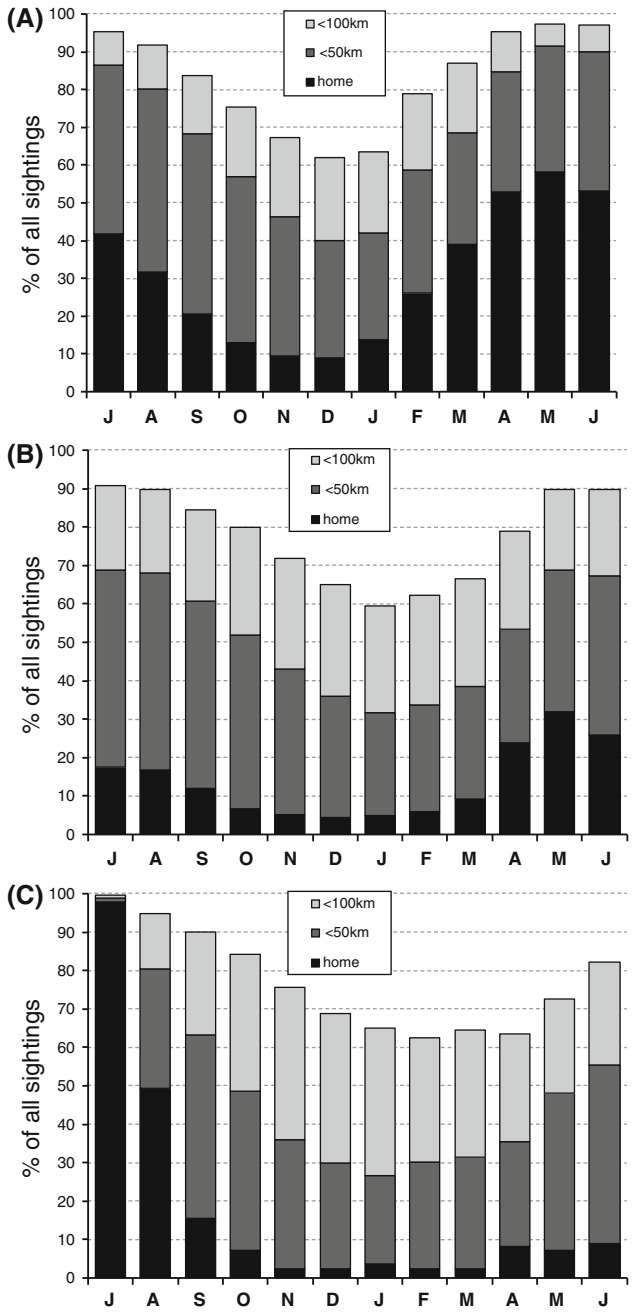

Fig. 6 Seasonality in dispersal for adult (**a**), immature (**b**), juvenile (**c**) Herring Gulls (all colonies combined) colour-ringed as a chick in The Netherlands between 1986 and 1988. Shown are the proportions of sightings within the home-range and within 50 and 100 km from the natal colony ($n =$ **a** 26,158 sightings of adults, **b** 33,518 immatures, **c** 26,258 juveniles). *X-axis* Months of the year beginning with July (*J*)

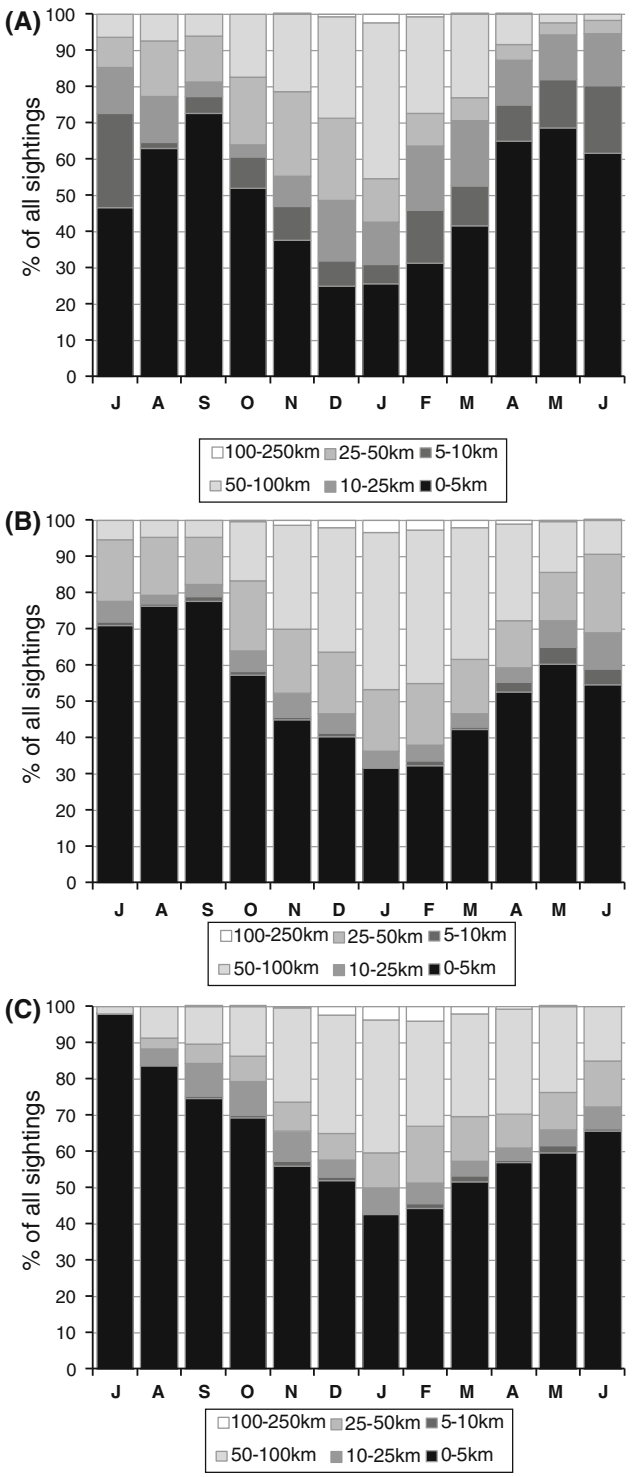

Fig. 7 Seasonality in inland dispersal for adult (**a**), immature (**b**), and juvenile (**c**) Herring Gulls (all colonies combined) colour-ringed as a chick in The Netherlands between 1986 and 1988. Shown are the proportions of sightings within distance bands measured from the North Sea shoreline ($n =$ **a** 26,212 sightings of adults, **b** 32,456 of immatures, **c** 30,268 of juveniles). *X-axis* Months of the year beginning with July (*J*)

ringing recoveries (Landsborough Thomson 1924; Spaans 1971; Jörgensen 1973; Prüter 1984; Calladine 2002), occasionally on reported sightings of colour-rings (Rock 1999; Klein 2001; Markones and Guse 2007) and, more

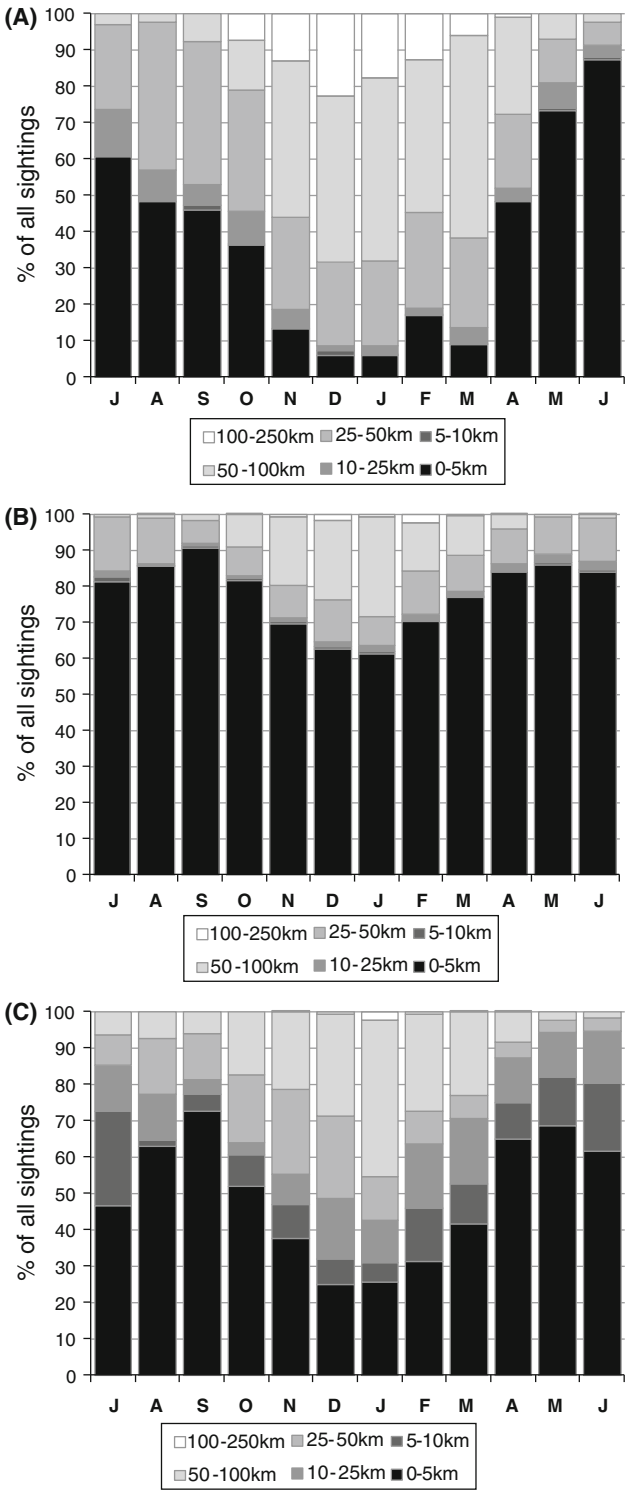

Fig. 8 Seasonality in inland dispersal for adult Herring Gulls from: **a** eastern Wadden Sea colonies (Rottumerplaat–Vlieland; $n = 2{,}814$ sightings), **b** Texel and the mainland coast (Callantsoog–Wassenaar; $n = 16{,}653$ sightings), **c** the Delta area colonies (Europoort–Saeftinghe, $n = 7{,}745$ sightings), colour-ringed as a chick between 1986 and 1988. Shown are the proportions of sightings within distance bands measured from the North Sea shoreline. *X-axis* Months of the year beginning with July (*J*)

recently, on data downloads of electronic devices, such as satellite and radio transmitters, attached to free-flying gulls (Ens et al. 2009). Each method has advantages as well as disadvantages, and the results are complementary rather than stand-alone descriptions of migratory pathways and dispersal patterns. Colour-ringing programmes have a clear advantage over traditional ringing recoveries given the multiple sightings of individual birds (without the need to retrap) over a large number of years and generally provide a much larger sample size (number of individual birds monitored) than high-tech methods currently used to track individual birds (Ens et al. 2009). A clear disadvantage is caused by the fact that the colour-ringing data are influenced by spatial and temporal patterns in observer effort. That complication is true for metal ringing data as well. As a result, colour-rings of Herring Gulls are seldom read at sea (birds usually in flight or swimming) or in other important foraging areas, such as on mudflats in the Wadden Sea area, where birds occur in relatively low densities and where ring-reading is not very profitable from the point of view of observer effort.

Bias resulting from ring-reading effort

Enthusiast ring-readers (volunteers, amateur bird-watchers mostly) tend to collect data in areas where the reward (i.e. the frequency of colour-ring sightings) is considerable. Consequently, they strongly prefer refuse tips, harbours, breakwaters, beaches and other areas where gulls occur in groups and can be read rather easily. The top-10 ring-readers of the Herring Gull programme described in this paper together have reported 54,269 sightings (62.9% of all 86,247 reports). They found nearly 50% of all ring codes ever deployed, while visiting "only" 36.9% of all 1,358 sites from which colour-ringed Herring Gulls have ever been reported alive (Table 10). The top-10 ring-reading sites, where 33,114 sightings originated from (38.4% of all reported sightings), produced 1,828 ring codes (45.7% of all ring codes deployed). These locations included two harbours (IJmuiden and Scheveningen), three refuse tips (Tilburg, Wieringermeer, Breda), three beach locations (Camperduin, IJmuiden, Katwijk aan Zee) and two particularly well-studied colonies (Schouwen and IJmuiden; Table 11).

Because there are regional differences in the likelihood that colour-rings would be found and reported, we have analysed the data not only from the perspective of the natal colonies ("where did they go"), but also from the perspective of the sighting areas from where many rings were reported ("from where did they come" and "how are different breeding areas represented within a sample of sightings somewhere"). After reviewing the data from these two angles, we feel confident that questions such as

Table 10 Top-10 ring-readers (A–J) and individual number of ring codes observed, percentage of all ring-reports, number of individual ring codes found, percentage of all codes available, number of visited locations and percentage of all ring-report locations

Observer	Rings read	% Rings read	Codes	% Codes	Locations	% Locations
A	16,842	19.5	1,338	33.5	222	16.3
B	6,076	7.0	634	15.9	57	4.2
C	5,813	6.7	742	18.6	55	4.1
D	4,481	5.2	507	12.7	37	2.7
E	4,226	4.9	436	10.9	51	3.8
F	3,745	4.3	489	12.2	39	2.9
G	3,733	4.3	642	16.1	47	3.5
H	3,482	4.0	662	16.6	28	2.1
I	3,001	3.5	639	16.0	105	7.7
J	2,870	3.3	681	17.0	87	6.4
Total	54,269	62.9	1,975	49.4	501	36.9

Table 11 Top-10 ring reading sites and individual number of ring codes reported, percentage of all ring-reports, number of individual ring codes found and percentage of all codes available

Location	Type	Rings read	% Rings read	Codes	% Codes
Tilburg, refuse tip	Dump	8,606	10.0	795	19.9
IJmuiden, harbour	Harbour	4,529	5.3	557	13.9
IJmuiden, IJbunker colony	Colony	3,838	4.5	124	3.1
Wieringermeer, refuse tip	Dump	2,857	3.3	396	9.9
Camperduin, beach site	Beach	2,848	3.3	561	14.0
Schouwen, breeding colony	Colony	2,477	2.9	218	5.5
Scheveningen, harbour	Harbour	2,055	2.4	438	11.0
IJmuiden, beach site	Beach	2,021	2.3	502	12.6
Breda, refuse tip	Dump	1,959	2.3	444	11.1
Katwijk aan Zee, river mouth	Beach	1,924	2.2	477	11.9
Total		33,114	38.4	1,828	45.7

"is there evidence for migration in Herring Gulls breeding in The Netherlands" and "do Herring Gulls move in random directions away from their breeding grounds?" can be addressed.

Migration versus dispersal

Bird migration, as regular seasonal journeys undertaken by birds, is marked by its annual seasonality (Berthold 2001). Migrants tend to breed in area A and perform a seasonal migration to overwinter in area B. The seasonality of movements according to the colour-ring sightings was strong, as a characteristic of true bird migration, but the home-range and immediate surroundings of natal colonies were never completely abandoned outside the breeding period. Dispersal refers to movements away from an existing population through simply moving from one habitat patch into the next. If it is accepted that dispersal is a random movement with respect to distance, the distribution can be represented by a mathematical relationship which describes the smaller numbers of sightings at progressively greater distances from the natal colony. Coulson and Brazendale (1968) expressed this relationship as $p_j = r^j$, where j is the number of distance zones from the colony, p_j is the proportion of birds moving beyond the outer limit of zone j and r is a constant for each colony, being the proportion entering each zone and moving beyond (Table 6). A linear relationship between the percentage of birds recorded within each distance zone, plus those recorded at greater distances from the natal colonies (the logarithm of these numbers plotted against distance), would imply that a constant proportion of the birds which enter a zone remain in it, irrespective of the distance to the colony. In the case of a true migration, it would be impossible to predict the extent and position of the wintering area from the more local sightings. The sighting data of our colour-ringed Herring Gulls have thus provided more evidence for colony- or area-specific dispersal than for true seasonal migration.

Distance and direction of movements

Dutch colour-ringed Herring Gulls predominately moved in a southerly direction away from their natal colonies and were rarely observed at distances greater than 300 km from the natal colony. Note, however, that dispersal in northerly or north-westerly directions away from most colonies could not be recorded due to an absence of observation possibilities on the North Sea. A lack of observers also makes sightings within the Wadden Sea area itself a rather rare event (Ens et al. 2009). Hence, while there is a strong seasonality in the whereabouts of Herring Gulls relative to the natal colonies, the observed patterns have been influenced by the (abundant or persistent) presence, scarcity or even complete absence of observers, depending on the location, which is a problem that plagues every ringing scheme. Our data suggest that there are distinct differences in wintering areas between birds originating from the north-east (longer range, predominantly south-west, south and south-east), the north-west (intermediate range, predominantly to the south) and the south-west (shortest range, frequent movements in most directions; Fig. 2, Table 7). The overwhelming majority of winter sightings

of the ten northernmost colonies (Rottumeroog–IJmuiden) occurred south (south-west through south-east) of the natal colony, despite there being suitable habitats to the east and north-east. With the same predominant direction of dispersal of Herring Gulls from different colonies, spatial segregation of main wintering grounds is inevitable and was indeed found. While the likelihood of sighting an eastern bird was probably relatively higher in the central west of the country, as a result of differences in observer effort, we still find consistent patterns in dispersal between colonies (Table 9).

The fact that dispersal rates were higher in the more northerly colonies than in the southern subset also has a certain amount of geographical context. Birds from colonies on Wadden Sea islands often roost on the mainland to the south of the colony, but these birds have to cover a greater distance in comparison with mainland birds because of the mere presence of the Wadden Sea basin where they cannot roost. Suggested groupings based on range, dispersal rate and directions of movements would include six colonies in the north-east (Rottumeroog–Vlieland), five colonies in the West and north-west (Texel–Wassenaar) and three colonies in the South-west (Europoort–Saeftinghe). The step between the first group of colonies and the second is larger than the step between the second group and the third. A geographical explanation for this difference could be the existence of the Wadden Sea. Ring-reading activity is low within that basin so that the mean distance travelled calculated for birds from the Wadden Sea islands may be biased (exaggerated) as a result of a spatial gap in observer effort. However, the much greater tendency to abandon home-range areas by gulls from the Wadden Sea area could be an argument to label these birds as short-distance migrants rather than as dispersive.

Dispersal and age

With increasing age, Herring Gulls arrive earlier within the home-range each spring until a regular pattern of approach (February–April), shortest range (May–July), departure (August–October) and longest range (November–January) relative to the natal colonies is achieved. Age-specific differences in mean travelling distance, however, were relatively small (Fig. 2), and winter dispersal rates were similar for all age groups.

Adults and immatures showed a bi-modal pattern in sightings with respect to the distance to the nearest North Sea coast (Fig. 7). Post-breeding peak numbers within 5 km of the North Sea coast were found in August–September, just after the breeding season, when adults are engaged in post-nuptial (complete) moult. It is interesting to note that at-sea sightings of Herring Gulls throughout the North Sea are at their lowest during this period (Camphuysen and Leopold 1994; Stone et al. 1995). Lensink (2002) reports a coastal "summer migration" from June through to early August and explains these movements as "birds abandoning colonies". According to this author, autumn movements do not start before October, with a peak in early December, and inland movements in autumn have a median value of 1 week later than coastal displacements. All this would fit the picture emerging from our colour-ring sightings (Fig. 7): Herring Gulls finalise their wing moult (which has commenced during breeding) at coastal sites and disperse to some extent—and later in the autumn and winter—into inland habitats (colour-ring sightings) and to the open sea (as suggested from ship-based surveys; Camphuysen and Leopold 1994), returning to the coast (and colonies) in the spring.

There have been 6 years since 1990 during which sightings from inland sites located 50–100 km from the coast were frequently reported. Most sightings were from refuse tips, which became unavailable for gulls one after the other through changes in waste management (open refuse tips were closed or covered up, gulls were actively scared away with the help of falconers and organic waste materials were increasingly separated from other waste products and processed elsewhere). In the next period (1997–2003), with many more deep inland sightings, mostly at German refuse tips, the peak may have been an observer effect (most sightings are from only few dedicated, but apparently temporarily active observers).

The exceptional season, 1995–1996, with a very high proportion of winter sightings of adult Herring gulls at coastal locations, was the coldest winter in the entire series (IJnsen Index De Kooy, data KNMI, De Bilt). For a second group of seasons with high proportions in coastal areas (2001–2002 through 2003–2004), however, winter conditions were mild, as in most of the other years. The colour-ring sightings cannot therefore support the suggestion that Herring Gulls have a stronger tendency to disperse inland in mild seasons (SOVON 1987). After 2003, winter sightings of colour-ringed adult birds were typically within a narrow band of 25 km from the North Sea coast.

Spaans (1971) highlighted the attraction of inland refuse tips as "relatively recent food sources". Many of these sites are now defunct and therefore unattractive to Herring Gulls; their numbers have subsequently declined at these locations, and the birds must have redistributed themselves during the winter since the 1980s and 1990s. If the observer bias cannot be held responsible for the decline in sightings at inland localities since the winter of 2001–2002, the stronger tendency to overwinter in coastal areas may have been the result of this change in waste management within the country. Between 1986 and 2001, the proportion of winter sightings from refuse tips fluctuated between 25 and

63% (mean ± SD 39.8 ± 15.4%, $n = 36{,}179$ sightings; 1996 with only 5.1% excluded), but this fell to less than 1% in nearly all years thereafter (9.3 ± 8.1%, $n = 316$ sightings). van Waeyenberge et al. (2002) reported that Belgian Herring Gulls tended to visit rubbish dumps less frequently in the course of their lifetime, suggesting a change in food choice with age, rather than a change in food availability. A similar tendency was reported by Vercruijsse (1999), suggesting that adult Herring Gulls prefer a more natural habitat and natural (i.e. mostly intertidal) prey.

Herring Gulls breeding in The Netherlands seem to occupy a mid-position between being dispersive and sedentary; they certainly are not clearly migratory. Of all sightings, 99% were reported at distances of less than 300 km from the natal colony. Yet, even within a small country as The Netherlands, there is evidence that birds originating from the more northerly colonies have a stronger tendency than those from colonies further to the south to cover some distance in the winter. The conclusions drawn by Spaans (1971) that the gulls disperse in all directions and that the distribution of the autumn and winter recoveries is more or less random around the ringing localities are not supported by our study. We found colony-specific and age-specific patterns in dispersal and timing, as well as predominantly southward dispersal for most colonies after breeding. Belgian Herring Gulls also dispersed mostly in a southerly direction and generally covered only small distances (van Waeyenberge et al. 2002). However, the Dutch Delta area was one of the main wintering areas, indicating northward and north-eastward dispersal similar to the birds nesting in Saeftinghe. Furthermore, the coastline of northern France and the Belgian coast itself were the most important areas. As in The Netherlands, immature birds returned later to the breeding grounds in spring than adults.

Landsborough Thomson (1924) described the movements of Herring Gulls in the UK as dispersal, with every gradation of distance but mostly within the limits of the British Isles. He reported the greatest distance travelled to be approximately 960 km. He failed to find regularity in movements with regard to timing or direction. Parsons and Duncan (1978), however, found that dispersal was predominantly in a southerly direction. There was no difference between the proportion of young and adult birds recovered inland, nor in range, except in the summer when adults had returned to their coastal home grounds. The seasonality and range found by Parsons and Duncan (1978) for juvenile, immature and adult Herring Gulls ringed on the Isle of May were remarkably similar to those in The Netherlands. The former also explained the movements in terms of directional dispersal, rather than as a migration from the natal colony. Calladine (2002) confirmed that Herring Gull dispersal had a marked tendency for southward autumn movements. He also found slight regional variations in the distances moved between breeding and wintering areas, with birds from Ireland being more sedentary than birds from northern and south-west UK. In an earlier analysis, Drost and Schilling (1940) concluded that German Herring Gulls did not migrate, but dispersed irregularly, with a maximum distance of 550 km from the natal colony. They also failed to find a structural difference in dispersal range for juvenile, immature and adult gulls. Gabrey (1996), on the contrary, recorded a monthly mean distance of approximately 1,600 km in winter for juvenile Herring Gulls ringed in breeding colonies in the Great Lakes (USA), but distinctly shorter mean distances in immature (700 km) and adult (500–800 km) birds. We failed to find a difference between age groups in terms of travelling distance for Herring Gulls colour-ringed within The Netherlands. Finnish Herring Gulls were found to migrate (abandoning breeding grounds), with a mean winter distance of winter recoveries of 737 km in adult birds (range 24–1,336 km) and 634 km in juveniles (range 19–1,019 km; Kilpi and Saurola 1984). As in the Dutch data, juveniles were found to perform a return migration in spring, but 2–3 months later than adults. Juveniles tended to stay far south of the natal area in their first summer (Kilpi and Saurola 1983a). So, again, no difference in range between adults and juveniles, but a difference in timing and in tendencies to return to home grounds in the first years after fledging.

Only three sightings from the British Isles were received of birds (three) colour-ringed between 1986 and 1988, suggesting that the southern North Sea acts as an effective barrier for Dutch Herring Gulls. Speek and Speek (1984) listed quite a number of recoveries in the UK of Herring Gulls ringed within The Netherlands, but their analysis was seemingly "polluted" by misidentified chicks (actually Lesser Black-backed Gulls; see also Spaans 1971). Stanley et al. (1981) listed 28 recoveries, mainly in south-eastern counties of England. Calladine (2002) showed that many Herring Gulls originating from north-east Scotland and east England were recovered in The Netherlands and gave further indications for North Sea crossings by Herring Gulls from Scandinavia, The Netherlands and Belgium. While it is probable that birds from Dutch colonies occur regularly along the south and east coasts of England (Stanley et al. 1981; Calladine 2002), we can only conclude that on the basis of our colour-ring sightings, the British Isles are normally off-range for Dutch Herring Gulls.

Klein (2001) reported on 14,500 sightings from Herring Gulls colour-ringed as chicks in Mecklenburg–Vorpommern (western Baltic, Germany) between 1991 and 1999. Winter sightings confirmed that approximately 75% of the gulls remained within the western Baltic area, that 20% moved inland and that 5% travelled towards the North Sea

coast and down to Pas-de-Calais in France. With a distinctly larger range (e.g. mean distances in winter 300–400 km from the natal area in immature birds), similar aspects of timing were found, with juveniles departing later from the breeding grounds than older birds and having a less pronounced tendency than the older birds (later and fairly distant to the home grounds) to return the next spring. He also found that gulls originating from the Rostock area did not disperse as widely as birds from other colonies and explained this fact by more readily accessible, year-round food sources. He finally concluded that female Herring Gulls had a greater "mobility" than males, which also returned earlier in the home-ground regions. Most of these aspects (with the exception of a sexual difference in dispersal strategy) were corroborated by our work in The Netherlands, albeit at slightly different scales and with slightly different patterns due to local conditions.

Kilpi and Saurola (1983b) examined pre-migration movements of coastal Finnish Herring Gulls after the breeding season and found that adults primarily exploited the nearest possible feeding sites upon leaving the colonies. This finding resembles the peak in occurrence of adult birds in coastal sites (as profitable feeding areas close to the breeding colonies) in The Netherlands in early autumn, prior to the dispersal to winter grounds. It is likely that such areas provide easy meals for birds actively engaged in post-nuptial (complete) moult, minimising the needs for energetically expensive foraging flights.

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References

Berthold P (2001) Bird migration: a general survey. Oxford ornithology series. Oxford University Press, Oxford

Bijlsma RG, Hustings F, Camphuysen CJ (2001) Schaarse en algemene vogels van Nederland. Avifauna van Nederland, vol 2. KNNV/GMB, Utrecht/Haarlem

Calladine J (2002) Herring Gull *Larus argentatus*. In: Wernham C, Toms MP, Marchant JH et al (eds) The migration atlas: movements of the birds of Britain and Ireland. T&AD Poyser, London, pp 369–372

Camphuysen CJ (2008) Aflezingen van gekleurringde Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *Larus fuscus* in Nederland. Sula 21:3–32

Camphuysen CJ, Leopold MF (1994) Atlas of seabirds in the southern North Sea. IBN Research report 94/6, Institute for Forestry and Nature Research, Texel/NIOZ-Report 1994-8, Institute for Sea Research and Dutch Seabird Group, Texel

Commissie Nederlandse Avifauna (CNA) (1970) Avifauna van Nederland. Brill, Leiden

Coulson JC, Brazendale MG (1968) Movements of Cormorants ringed in the British Isles and evidence of colony-specific dispersal. Brit Birds 61:1–21

Coulson JC, Butterfield J (1985) Movements of British Herring Gulls. Bird Study 32:91–103

Cramp S, Simmons KEL (eds) (1983) The birds of the Western Palearctic, vol 3. Oxford University Press, Oxford

Drost R, Schilling L (1940) Über den Lebensraum deutscher Silbermöwen, *Larus a. argentatus* Pontopp., auf Grund von Beringungsergebnisse. Vogelzug 11:1–22

Eaton RJ (1933) The migratory movements of certain colonies of Herring Gulls (*Larus argentatus smithsonianus* Coues) in eastern North America. J Field Ornithol 4:165–176

Ens BJ, Bairlein F, Camphuysen CJ, de Boer P, Exo K-M, Gallego N, Klaassen R, Oosterbeek K, Shamoun-Baranes J (2009) Onderzoek aan meeuwen met satellietzenders. Limosa 82:33–42

Gabrey SW (1996) Migration and dispersal in Great Lakes Ring-billed and Herring Gulls. J Field Ornithol 67:327–339

Glutz von Blotzheim UN, Bauer KM (1982) Handbuch der Vögel Mitteleuropas, 8/I. Akademischer Verlag, Wiesbaden

Jörgensen OM (1973) Some results of Herring Gull ringing in Denmark, 1958–1969. Dansk Orn Foren Tidsskr 67:53–63

Kilpi M, Saurola P (1983a) Geographic distribution of breeding season recoveries of adult and immature *Larus marinus*, *L. argentatus* and *L. fuscus* ringed in Finland. Ornis Fenn 60:117–125

Kilpi M, Saurola P (1983b) Pre-migration movements of coastal Finnish Herring Gulls (*Larus argentatus*) in autumn. Ann Zool Fenn 20:245–254

Kilpi M, Saurola P (1984) Migration and wintering strategies of juvenile and adult *Larus marinus*, *L. argentatus* and *L. fuscus* ringed from Finland. Ornis Fenn 61:1–8

Klein R (2001) Raum-Zeit-Strategien der Silbermöwe *Larus argentatus* und verwandter Taxa im westlichen Ostseeraum. PhD thesis. Universität Rostock, Rostock. Available at: http://www.greengull.de/img/dissertation_rklein.pdf. Accessed 27 Aug 2009

Koeman JH, de Brauw MC, de Vos RH (1969) Chlorinated biphenyls in fish, mussels and birds from the River Rhine and the Netherlands coastal area. Nature 221(5186):1126–1128

Lack D (1943) The age of the Blackbird. Brit Birds 36:166–175

Landsborough Thomson A (1924) The migrations of the Herring Gull and Lesser Black-backed Gull: results of the marking method. Brit Birds 18:34–44

Lensink R (2002) Zilvermeeuw (*Larus argentatus*). In: Lensink R, van Gasteren H, Hustings F, Buurma L, van Duin G, Linnartz L, Vogelzang F, Witkamp C (eds) Vogeltrek over Nederland, 1976–1993. Schuyt & Co, Haarlem, pp 154–155

Markones N, Guse N (2007) Räumlich-zeitliche Verteilung und Nahrungserwerbsstrategien von Silbermöwen *Larus argentatus* der westlichen Ostsee:Erkenntnisse einer Ringfundanalyse. Vogelwarte 45:1–13

Meltofte H, Faldborg J (1987) Forekomsten af måger og terner på Blåvandshuk 1963–1977. Dansk Orn Foren Tidsskr 81:137–166

Noordhuis R (1989) De relatie tussen zilvermeeuwen op vuilstortplaatsen en de schade op mosselpercelen en in weidevogelgebieden in Zuidwest-Nederland. RIN-rapport 89/4. Rijksinstituut voor Natuurbeheer, Arnhem

Parsons J, Duncan N (1978) Recoveries and dispersal of Herring Gulls from the Isle of May. J Anim Ecol 47:993–1005

Prüter J (1984) Methoden und vorläufige Ergebnisse der Großmöwenberingung auf Helgoland. Seevögel 5 (Sonderband):61–65

Rock P (1999) The efficacy of the colour-ringing system used for Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*Larus fuscus*). Ringing Migration 19:306–310

Schüz E (1933) Von den Wanderungen der Eismeer- und Ostsee-Silbermöwen (*Larus a. argentatus*). Orn Fenn 10:17–19

Sluiters JE (1939) Van slapen en slaapvlucht bij verschillende vogelsoorten, II. Levende Nat 44:112–117

SOVON (1987) Atlas van de Nederlandse vogels. SOVON, Arnhem

Spaans AL (1971) On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of The Netherlands. Ardea 59:73–188

Spaans AL (1998) The Herring Gull *Larus argentatus* as a breeding bird in The Netherlands during the 20th century. Sula 12:183–196

Spaans AL (2007) Meeuwenbestrijding in historisch perspectief. In: Saris F (ed) Een eeuw vogels beschermen. KNNV Uitgeverij, Zeist, pp 154–163

Spaans AL, de Wit AAN (1985) Verspreiding van Zilvermeeuwen:vogels op de voet gevolgd. Vogeljaar 33:200–207

Speek BJ, Speek G (1984) Thieme's vogeltrekatlas. Thieme, Zutphen

Stanley PI, Brough T, Fletcher MR, Horton N, Rochard JBA (1981) The origins of Herring Gulls wintering in south-east England. Bird Study 28:123–132

Stone CJ, Webb A, Barton C, Ratcliffe N, Reed TC, Tasker ML, Camphuysen CJ, Pienkowski MW (1995) An atlas of seabird distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough

Tinbergen N (1952) De trek van Zilvermeeuwen langs de Nederlandse kust. Ardea 40:77–80

van Waeyenberge J, Stienen EWM, Vercruijsse HJP (2002) Kleurringproject van Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* aan de Belgische kust:overzicht van algemene resultaten. Natuur oriolus 68:146–156

Vercruijsse HJP (1999) Zilvermeeuwen uit de duinen van Schouwen:verspreiding, sterfte en broedbiologie. Private publication. HJP Vercruijsse, Tilburg