

# Non-breeding movements of Black-legged Kittiwakes *Rissa tridactyla* from a North Sea urban colony

Mike Swindells

Email: [mike42trees@gmail.com](mailto:mike42trees@gmail.com) [[orcid.org/0000-0002-0745-9274](https://orcid.org/0000-0002-0745-9274)]  
42 Linden Close, Aldeburgh, Suffolk IP15 5JL, UK.

## Abstract

Early indications of the extensive North Atlantic non-breeding period range of Black-legged Kittiwakes *Rissa tridactyla* (hereafter Kittiwakes) have been reported using ship-based observations, but detailed knowledge of the migration of pelagic birds was difficult to obtain until the development of geolocators gave long-term tracking capabilities. Non-breeding period movements of several oceanic species have now been determined in detail. The current study aimed to establish the wintering tracks of Kittiwakes from Lowestoft, an urban colony in the east of England, and also to determine the similarity of annual tracks in individual birds. Commencing in 2012, geolocators were fitted to adult Kittiwakes breeding on Clarendon Pier, and up to 2018 data from 15 birds were obtained, including up to four years' tracks from individual birds. It was found that Kittiwakes from Lowestoft had highly varied tracks, covering virtually the whole range of wintering areas of birds from other North Atlantic colonies. However, individual birds showed a high degree of track repetition from year to year.

## Introduction

Seabird populations are declining worldwide (Paleczny *et al.* 2015). Various aspects of seabird breeding period behaviour have been studied in a number of species, but this period is often less than half of the year (Cramp *et al.* 1984). Much less is known about the distribution and behaviour of pelagic birds in the non-breeding (winter) period, when birds can face different pressures to those associated with the breeding colony, including pressures from extreme weather, lack of food and developments such as offshore wind farms (Wernham *et al.* 2002). Non-breeding season ringing recoveries are limited, and often from dead birds whose corpses may have travelled for long distances before being found (Coulson 2011). Sightings from ships (Rankin & Duffey 1948; Coulson 2011) are also limited and biased by ocean routes. The advent of geocator tracking devices around the turn of the century has led to a major increase in opportunities for more scientific analysis of seabird distribution and movements outside the breeding season (Harris *et al.* 2009; Coulson 2011; Guilford *et al.* 2012; Fort *et al.* 2012).

Black-legged Kittiwakes *Rissa tridactyla* (hereafter Kittiwakes) are the most numerous gulls in the world and there are many studies on various aspects of their behaviour in the breeding period (Coulson 2011). Outside the breeding period they

are highly pelagic, and during 2008–09 an extensive study of birds from 19 colonies in the North Atlantic was carried out using geolocators (GLS) (Frederiksen *et al.* 2012). The colony locations ranged from Arctic Russia to Wales in the east and from Arctic Canada to Newfoundland in the west. The study gave a large amount of information on movement and distribution, focussing on December, and showed that birds from most colonies covered a large range throughout the area, with a general preference for the northwest Atlantic. However, some birds from Norwegian colonies stayed in the North Sea, and birds from Skomer Island (off the coast of southwest Wales) and Rathlin Island (off the Northern Ireland coast) stayed largely in the Irish Sea and eastern Atlantic around Ireland. Kittiwakes from western Atlantic colonies (Arctic Canada, west Greenland, and Newfoundland) remained almost completely west of longitude 35°W (Frederiksen *et al.* 2012). Further GLS-based studies on wintering Kittiwakes include the effect of breeding success on winter tracks (Bogdanova *et al.* 2011; Ponchon *et al.* 2015; Bogdanova *et al.* 2017), and tracks in the North Pacific (Orben *et al.* 2015).

In many pelagic species individuals tend to return to the same wintering areas each year using similar routes. These include Atlantic Puffin *Fratercula arctica* (Guilford *et al.* 2012; Fayet *et al.* 2016) and Northern Gannet *Morus bassanus* (Kubetzki *et al.* 2009). In contrast, Cory's Shearwaters *Calonectris diomedea* breeding on Selvagem Grande Island (between Madeira and the Canary Islands) have extensive, varied wintering areas, with some individual birds repeating the previous winter track closely, and others not (Dias *et al.* 2010).

Following this information, Kessingland Ringing Group (an informal group formed in 2004 which subsequently became a registered BTO Ringing Group in 2013) decided to investigate whether Kittiwakes from Lowestoft town, adjoining the most easterly point in the UK at 1°46'E 52°29'N, would travel out to the favoured northwest Atlantic area when the apparently suitable North Sea was so close. Lowestoft requires a longer journey to reach the North Atlantic than any of the other southeastern UK colonies, unless an overland route is used. The GLS-based study was intended to be carried out over several years, and so a second investigation concerned the extent to which individual birds would replicate their tracks over a number of years. This characteristic had not been documented in Kittiwakes when the current study started, although it was demonstrated in Puffins from Skomer Island (Guilford *et al.* 2011). Track repetition was subsequently documented for Kittiwakes (*R. tridactyla polycaris* sub-species) from the Bering Sea Pribiloff Islands colonies, which spend the non-breeding period in the Aleutian area of the North Pacific (Orben *et al.* 2015).

## Methods

**Location:** Lowestoft is an urban colony which, in contrast to many UK sea-cliff colonies, is expanding. Nesting takes place in the dock area, the nearby centre of the town, and also the tower of the Roman Catholic Church (Figure 1). The total population is over 400 pairs (A. C. Easton pers. comm.). However, access for catching and retrapping adult birds is limited, and so the study was restricted to





Figure 1. A map of Lowestoft showing the Black-legged Kittiwake *Rissa tridactyla* breeding areas in orange.

birds breeding on Claremont Pier (1°45'E 52°28'N), approximately 1 km south of the town centre (Figure 2). No tracking devices were attached to birds under three years old, as it was considered that younger birds were less likely to be recovered.

**Equipment:** GLS tags were fitted to Kittiwakes starting in 2012, using 10 BioTrack M4083 (BAS type), and then from 2014 using seven Migrate Technology C65, and subsequently 13 C250 and five C330 tags with a longer battery life. Birds were caught using a pole with a noose, and the GLS fitting was carried out under a Special Methods Technical Panel permit (permit numbers 12–32 and 14–89). The devices were attached by cable tie to a colour leg-ring. Each bird was also fitted with a metal BTO ring. The maximum weight of geolocator plus colour ring was 4.0 g (approx. 1.3% of adult body weight), and all fitting was carried out between 17 June and 22 July in each year. Birds were



Figure 2. Claremont Pier Black-legged Kittiwake *Rissa tridactyla* sub-colony, Lowestoft, showing (a) the extent of the sub-colony and (b) typical nest positions. © Andrew Easton

not sexed. On recovery (between 2013 and 2019), light data were downloaded using the manufacturer's interface box and software. Out of the total of 28 birds fitted with GLS from 2012 onwards, 25 were retrapped or sighted a year or more after fitting and three were not recorded again after the year of fitting. K102 (EX56744), one of the original birds fitted with a GLS in 2012, was seen in 2019 with its fourth GLS (as birds were difficult to recover, attempts were always made, even only one year after tagging, and recaptured birds were then fitted with a new GLS). Observers have probably been unable to identify some remaining birds, or they may have moved to other less observed sub-sites in Lowestoft, or elsewhere. In total, 30 useable tracks were obtained from 15 birds. One device failed completely, and one failed after only four months.

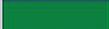
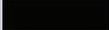
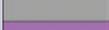
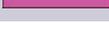
**Data processing:** Processing of light files from both BioTrack and Migrate Technology devices was carried out using IntiProc software (Migrate Technology) to generate dawn and dusk times. Derivation of coordinates was carried out using the 'GeoLight' package (Lisovski & Hahn 2015) in R (R Core Team 2017). The 'GeoLight' package was originally targeted at analysis of stopping areas of predominantly latitudinally migrating birds, and does not have a correction function for longitudinal movement. Kittiwake movement is more longitudinal so movement compensation was implemented. Coordinates were then obtained, after setting parameters (threshold and sun elevation) for the types of GLS used. GLS coordinates have a typical accuracy of c. +/- 180 km (Phillips *et al.* 2004), and so the coordinates were smoothed using the same algorithm as Frederiksen *et al.* (2012). Tracks were then generated, excluding the equinox periods, in which estimates of latitude from GLS data are unreliable. This resulted in using 'valid' dates from 1 August to 7 September, 21 October to 19 February, and 4 April to 30 April, for compatibility with Frederiksen *et al.* (2012). Visual inspection of tracks indicated that these periods did not include any potentially inaccurate coordinates due to autumn or spring equinoxes. Many of the Lowestoft birds returned to the colony before the end of March, making the spring post-equinox period less significant. Individual birds were numbered as K101 to K115, and a capital letter was then appended to denote successive winter tracks from that bird. Details of the birds involved are shown in Table 1.

**Mapping:** Subsequent mapping used equidistant conic projection, with the same parameters as Frederiksen *et al.* (2012). This projection has an origin at 25°W 60°N, approximately the centre of the main wintering areas. Mapping and graphs were produced using R package 'ggplot2' (Wickham 2016).

**Analysis:** For the first objective of comparing Lowestoft colony birds with those from other colonies, only one track from each bird was used to avoid bias. These tracks, denoted as 'primary', were the first track obtained from the bird except where this was incomplete due to GLS battery failure, when the second track (from bird K113) was used (Table 1).

For the second objective of comparing track similarity, mean separation was calculated for every possible pair of tracks by taking the coordinate positions of

**Table 1.** Details of all non-breeding period tracks. Suffix 'A' track is denoted as 'primary' except for K113, which uses 'B' track as primary.

Metal Ring	Code	Map Colour	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19
EX56743	K101		A						
EX56744	K102		A	B	C	D			
EX56745	K103		A	B					
EX56859	K104			A	B	C			
EX56540	K105				A	B			
EX56522	K106				A	B			
ER72491	K107				A				
ER72349	K108					A			
EX56679	K109					A			
EY29676	K110					A	B		
EW72555	K111					A			
EX56565	K112					A	B	C	
ER72486	K113						A	B	
EX56663	K114							A	B
ER72488	K115				A	B	C		

both tracks on each day of the year. The great circle distance between each pair of positions was obtained, using only the first two valid periods, as some GLS did not have data after March, usually due to battery expiry. The distances were then averaged to give a mean separation for the pair. This daily calculation enables some account to be taken of any timing differences between tracks which are spatially very similar. The mean separation for every track pair is shown in Table 2.

The mean separations were then sorted as 'between' bird or 'within' bird. The 'between' pairs of tracks were again sorted as 'primary', where both tracks were 'primary' as defined above, and 'secondary' where one or both tracks were not 'primary'. This eliminated bias towards birds having more than one track. For the 'within' pairs the mean separation of the first two tracks was regarded as 'primary', and pairs which included third or fourth tracks as 'secondary'. This mitigated bias towards birds with more than two tracks.

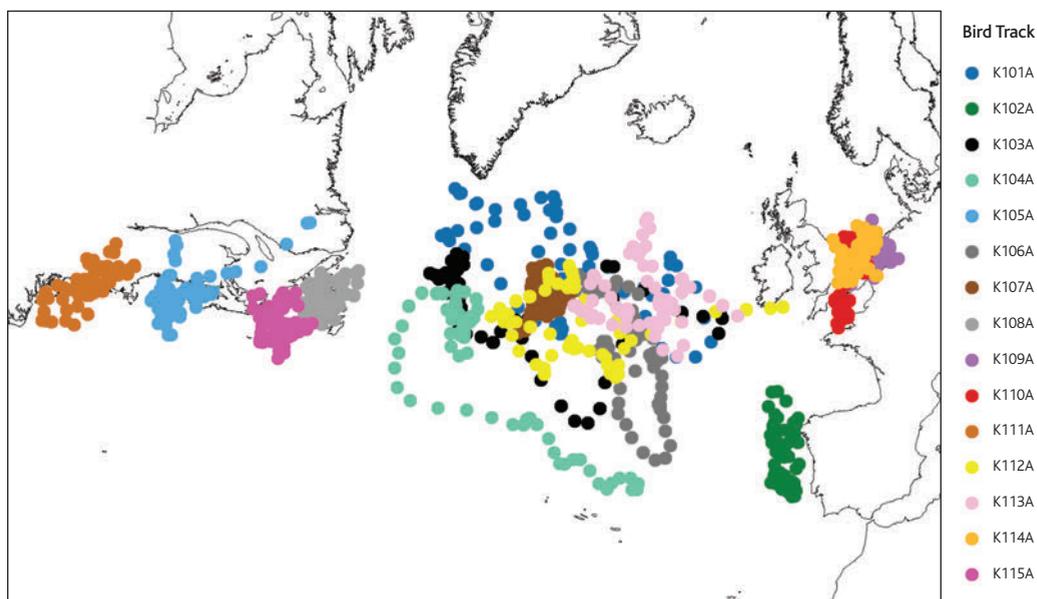
For both between- and within-bird comparisons the remaining track pair mean separations were also grouped and denoted as 'secondary', but not used in the statistical analysis. The mean separation used in all cases actually measures dissimilarity, so that lower values indicate greater similarity.

## Results

The December positions for all primary tracks (Figure 3) show that Lowestoft Kittiwakes dispersed over almost the entire wintering area covered by birds from other colonies studied in Frederiksen *et al.* (2012), omitting only the far northern Norwegian Sea and Arctic Ocean, and the Baffin Bay area west of Greenland. Usage of these areas is generally confined to birds from far northern colonies when moving to the main Atlantic area (Frederiksen *et al.* 2012).

**Table 2.** Mean separation distance (km) for all pairs of tracks from Black-legged Kittiwakes *Rissa tridactyla* tracked from Lowestoft, UK using geolocators.

	<b>102A</b>	<b>102B</b>	<b>102C</b>	<b>102D</b>	<b>103A</b>	<b>103B</b>	<b>104A</b>	<b>104B</b>	<b>104C</b>	<b>105A</b>	<b>105B</b>	<b>106A</b>	<b>106B</b>	<b>107A</b>	<b>108A</b>	<b>109A</b>	<b>110A</b>	<b>110B</b>	<b>111A</b>	<b>112A</b>	<b>112B</b>	<b>113A</b>	<b>113B</b>	<b>114A</b>	
<b>101A</b>	2,139	2,243	1,997	2,542	1,124	1,459	1,220	1,042	1,153	1,618	2,496	1,665	1,809	1,218	1,894	2,219	2,162	2,152	2,627	1,136	1,082	1,017	1,160	1,496	2,087
<b>102A</b>	497	820	695	1,834	1,612	1,529	2,065	1,873	3,043	3,434	1,007	947	1,330	2,543	988	948	830	4,148	1,341	1,912	1,744	1,634	1,102	940	
<b>102B</b>	797	612	1,825	1,601	1,554	2,117	1,962	3,052	3,411	1,185	1,101	1,408	2,508	1,090	1,016	1,005	4,102	1,488	1,983	1,922	1,846	1,296	1,017		
<b>102C</b>	1,074	1,796	1,769	1,820	1,935	1,971	3,070	3,457	833	722	1,170	2,554	601	530	556	4,161	1,318	1,836	1,540	1,568	927	547			
<b>102D</b>	2,219	1,859	1,789	2,501	2,311	3,378	3,764	1,520	1,379	1,801	2,881	1,250	1,232	1,059	4,394	1,807	2,311	2,247	2,160	1,573	1,128				
<b>103A</b>	952	1,078	758	829	1,530	1,840	1,608	1,741	1,031	1,075	2,163	2,109	2,084	2,501	959	676	1,019	1,006	1,442	2,055					
<b>103B</b>	1,059	1,293	1,179	1,797	2,226	1,507	1,644	1,149	1,467	2,159	2,088	2,011	2,691	1,201	1,108	1,543	1,407	1,405	2,028						
<b>104A</b>	1,296	1,042	1,764	2,476	1,586	1,691	1,294	1,778	2,177	2,118	2,016	2,819	1,180	1,106	1,180	1,177	1,404	2,071							
<b>104B</b>	689	1,346	1,730	1,736	1,899	1,055	1,160	2,251	2,205	2,176	2,423	1,123	556	859	871	1,546	2,108								
<b>104C</b>	1,506	1,854	1,665	1,828	1,085	1,185	2,218	2,175	2,146	2,574	1,018	674	906	810	1,468	2,078									
<b>105A</b>	1,035	2,761	2,933	2,105	1,204	3,440	3,354	3,326	1,236	2,083	1,495	1,963	1,891	2,651	3,304										
<b>105B</b>	3,229	3,385	2,552	1,139	3,808	3,776	3,736	846	2,463	1,806	2,341	2,284	3,058	3,694											
<b>106A</b>	485	867	2,315	872	795	905	3,855	983	1,576	1,129	1,097	519	889												
<b>106B</b>	1,067	2,488	664	594	745	4,019	1,063	1,746	1,315	1,298	658	744													
<b>107A</b>	1,644	1,488	1,399	1,443	3,215	721	939	916	743	871	1,362														
<b>108A</b>	2,911	2,861	2,841	1,731	1,569	1,090	1,692	1,448	2,165	2,781															
<b>109A</b>	220	343	4,532	1,478	2,163	1,643	1,697	962	320																
<b>110A</b>	362	4,466	1,429	2,115	1,596	1,646	915	337																	
<b>110B</b>	4,422	1,435	2,053	1,663	1,656	963	379																		
<b>111A</b>	3,150	2,466	3,057	2,988	3,740	4,409																			
<b>112A</b>	1,017	886	763	820	1,393																				
<b>112B</b>	852	683	1,417	2,039																					
<b>112C</b>	603	915	1,532																						
<b>113A</b>	927	1,561																							
<b>113B</b>	930																								



**Figure 3.** All December positions for the primary GLS track from 15 Black-legged Kittiwakes *Rissa tridactyla* tracked from Lowestoft, UK. Compare to Frederiksen *et al.* (2012 Figure 1a). See Table 1 for details of the tracks from each bird.

Figure 4 displays the median monthly positions for all primary tracks, and it is noticeable that in September some birds have already reached the Labrador Sea, while others do not show significant movement from the colony until October.

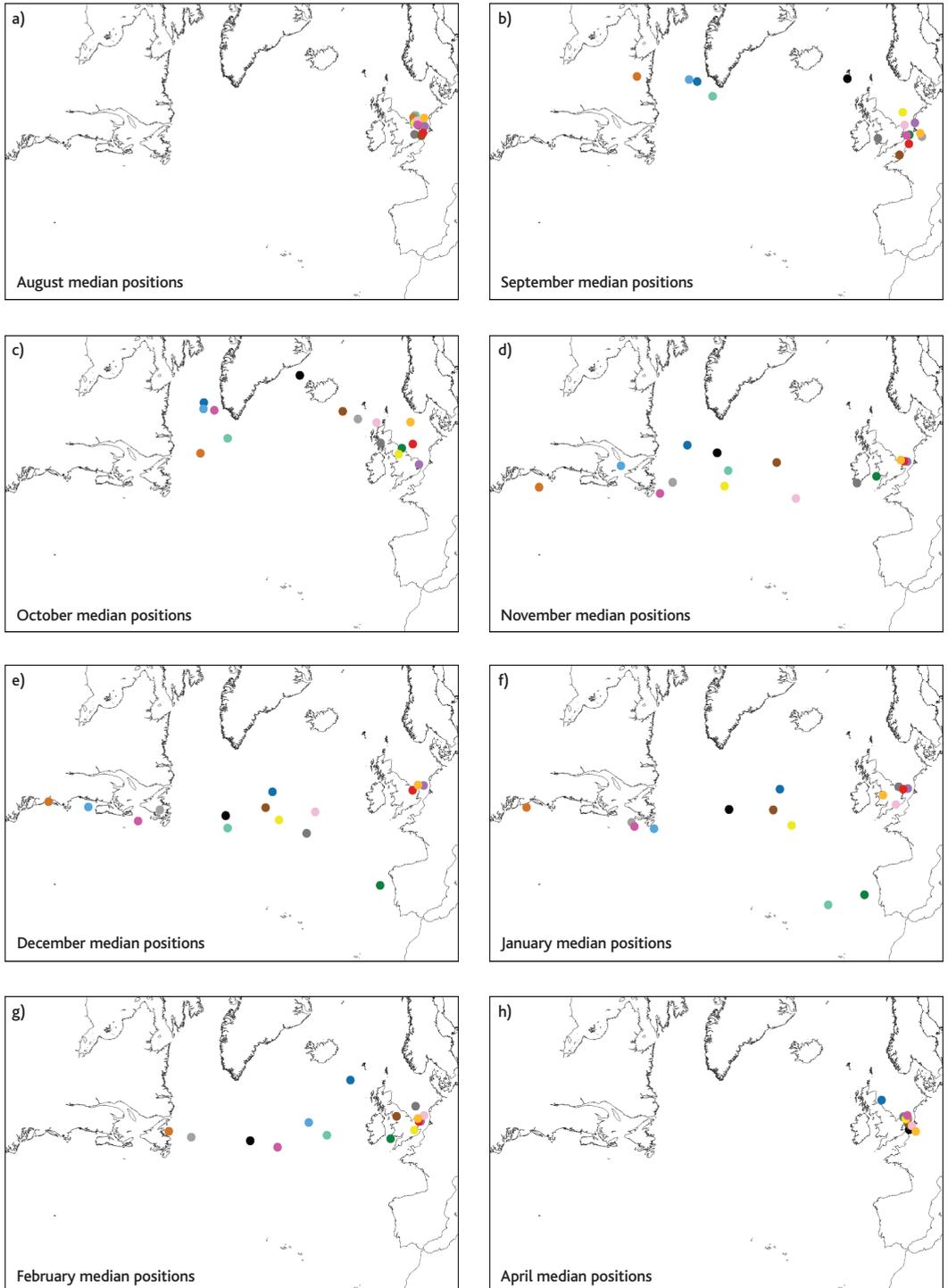
December is the month of maximum distance from the colony for nearly all birds, and in January the drift back towards the colony is noticeable. This continues in February, but there are no valid positional data for March due to the equinox effect. All April medians show that birds were back in the North Sea, with a number actually observed in the colony.

A graph of median distances from the colony, as mapped in Figure 4, is plotted in Figure 5, and the overall median monthly position for all primary track positions is shown by the thick black line which can be compared with data for other colonies in Frederiksen *et al.* (2012, Figure 3).

In summary, Lowestoft colony birds show no marked difference from the other colonies studied in Frederiksen *et al.* (2012), with the main wintering area in the northwest Atlantic. Only two birds remained in the North Sea.

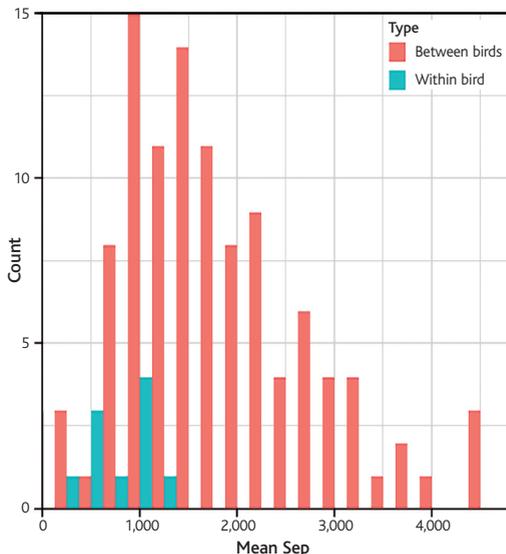
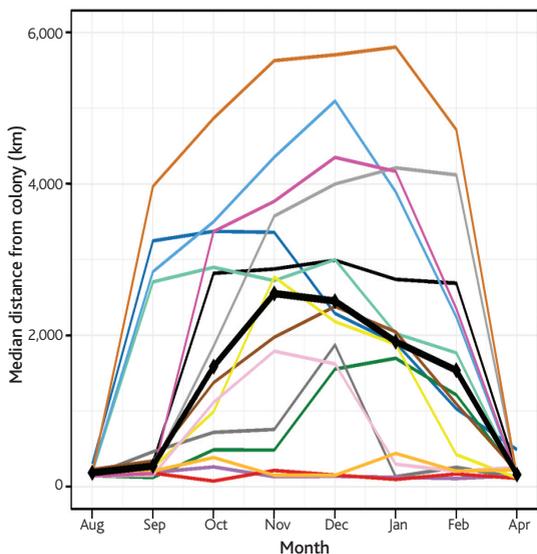
For the second objective of the study the mean separation distributions for primary track pairs are shown as a histogram (Figure 6).

The 'within bird' mean separation distribution had a mean of 771 km (95% CI: 546–996 km) and a maximum of 1,289 km, compared with mean of 1,829 km



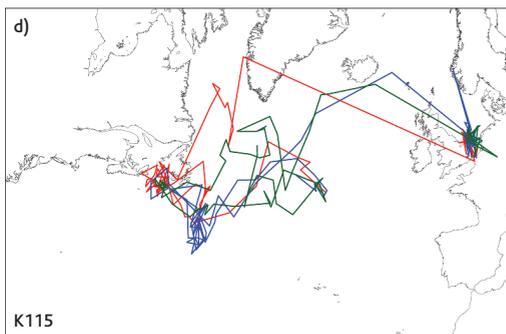
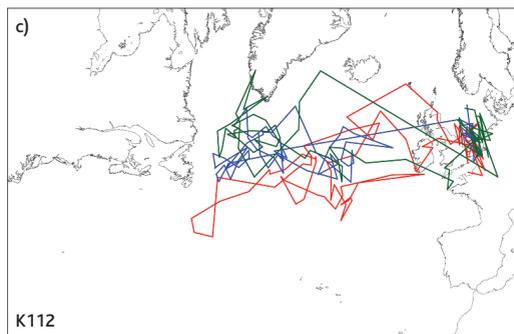
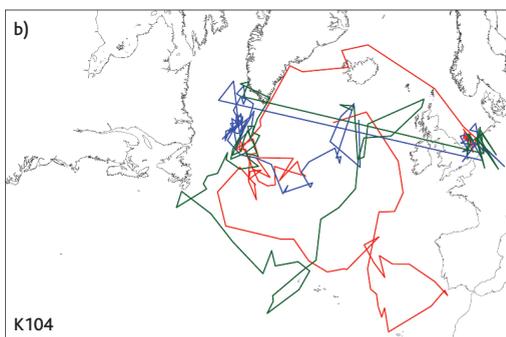
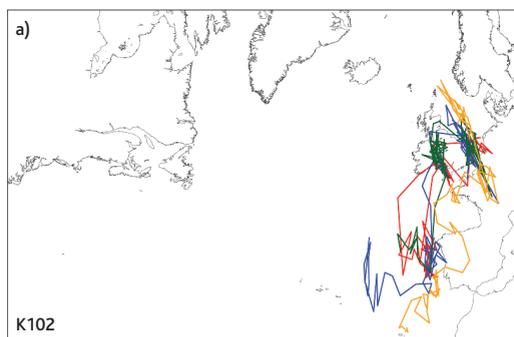
**Figure 4.** Maps showing the median monthly positions of GLS-tracked Black-legged Kittiwakes *Rissa tridactyla* in October to February (a–g) and April (h).

Non-breeding movements of urban Kittiwakes



**Figure 5.** Monthly median great circle distances from the colony (Lowestoft, UK) for the primary GLS track from each of 15 Black-legged Kittiwakes *Rissa tridactyla*. The thick black line shows the overall median monthly distance from the colony for all primary tracks.

**Figure 6.** Histogram of mean separation distance (km) for between-bird and within-bird primary pair distributions of non-breeding Black-legged Kittiwakes *Rissa tridactyla* tracked from Lowestoft, UK.



**Figure 7 (a–d).** GLS tracks for each Black-legged Kittiwake *Rissa tridactyla* where data were available for more than two non-breeding periods. Colour denotes track suffix; red = A, blue = B, green = C, yellow = D (c.f. Table 1).

(95% CI: 1,647–2,011 km) and maximum of 4,505 km for the 'between bird' distribution. Both distributions were tested for normality using the Shapiro-Wilk test. For the 'between' and the 'within' pairs this indicated sufficient divergence from normality for the use of parametric tests to be invalid. This lack of normality led to the use of the non-parametric Mann-Whitney (Wilcoxon) test, which gave  $W = 922$ ,  $P < 0.001$ . The results strongly support that, despite the large variation between birds, individual Kittiwakes do closely repeat their previous years' tracks.

Table 2 gives details of all birds and the tracks obtained from each, and Figure 7 shows track maps for each bird where data is available for more than two non-breeding periods. These tracks have been filtered to show only every fourth position (i.e. every second day), in order to aid visual clarity.

### Discussion

The winter distribution of Lowestoft's breeding Kittiwakes (Figure 3) covered almost the entire area used by birds from 19 other North Atlantic colonies (Frederiksen *et al.* 2012), and this was remarkable considering that the sample involved only 15 birds. The December positions for individual birds ranged from the North Sea (off the coast of East Anglia, UK) to 75°W (off Virginia, USA), just over 6,000 km from the colony. Figure 5 demonstrates that graphs of the monthly mean distances of individual birds from the colony cover a very wide range (compare Frederiksen *et al.* 2012, Figure 3). Visual inspection of tracks showed that birds that travelled further away tended to start their migration earlier and return later, perhaps not a surprising result. However, K102, wintering off the Iberian Peninsula, was very late to go there, spending time in the Irish Sea first. There are four annual tracks for this bird, and in the 2014–15 winter period it did not go to the continental shelf off Portugal until February, starting to return after only eight days. Overall, the distribution of Lowestoft colony birds did not show any major differences from the distributions of birds from other colonies as detailed in Frederiksen *et al.* (2012). The considerable range of wintering areas and the sometimes extensive movement during winter give some protection against adverse weather conditions and changes in the availability of food.

There is some evidence that unsuccessful breeding Kittiwakes winter further from the main colony than successful breeders (Bogdanova *et al.* 2011; 2017). This is based on birds from 10 colonies involved in the Frederiksen *et al.* (2012) study, but the outcome of the Lowestoft birds' breeding season is not known. Catching adult Kittiwakes is not easy, and as our birds were caught at or close to the nest, it is likely that most, if not all, of them were successful breeders, at least in the first year of a GLS fitting and also the year of removal.

Despite the small number of birds in the sample, winter to winter track repetition by individual North Atlantic Kittiwakes is given strong support by this study. Kittiwakes breeding on the Pribiloff Islands in the North Pacific Bering Sea also displayed a wide variety of winter tracks, but with considerable similarity of within-bird tracks relative to between-bird tracks (Orben *et al.* 2015). The Pribiloff

study also showed a core winter range covering approximately 75° longitudinally by 40° latitudinally. The comparative range for Lowestoft birds is 80° by 35°, and there is a general similarity in the variation of tracks between the North Pacific and the North Atlantic birds.

Future study possibilities include obtaining data on breeding success and comparing winter tracks for both successful and unsuccessful breeding years from the same bird, and between different birds, but this would be challenging. Another subject would be use of GLS immersion data to determine dates of leaving and returning to a colony where frequent observation is not feasible, and basic GLS positions are not sufficiently accurate.

### Acknowledgements

The author would like to thank two reviewers for advice which has improved and expanded the paper, Morten Frederiksen and Tom Dickins for advice and encouragement, James Fox (Migrate Technology) for advice on the use of GLS tags, Jez and Laura Blackburn for help at the initial GLS fitting session, Rachel Hallett for advice on the presentation of this paper, and members of Kessingland Ringing Group for their work at sessions to fit and remove GLS tags, particularly Derek Beamish for his catching abilities.

Financial support for the GLS was received from Colin Carter, the Seabird Group, Waveney Bird Club, Lowestoft RSPB Members Group, Lowestoft Lounge Lizards, Mr. John Garbutt, and others.

### Colin Carter (1940–2017)

Colin started ringing as a teenager, and with some breaks due to his career, he remained a dedicated ringer. On retirement he started ringing at Kessingland near Lowestoft in 2004, and was soon joined by the author and progressively more ringers, usually as trainees. In 2012 he initiated the Kittiwake GLS project, and this was continued on the conversion in 2013 to a formal group (Kessingland Ringing Group), with Colin as Group Leader until he died in 2017. He led every ringing session where GLS tags were involved, and without him this project would not have happened.

### References

- Bogdanova, M. I., Daunt, F., Newell, M., Phillips, R. A., Harris, M. P., & Wanless, S. 2011. Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: Links between breeding performance and winter distribution. *Proceedings of the Royal Society B: Biological Sciences* 278: 2412–2418.
- Bogdanova, M. I., Butler, A., Wanless, S., Moe, B., Anker-Nilssen, T., Frederiksen, M., Boulinier, T., Chivers, L. S., Christensen-Dalsgaard, S., Descamps, S., Harris, M. P., Newell, M., Olsen, B., Phillips, R. A., Shaw, D., Steen, H., Strøm, H., Thórarinnsson, T. L. & Daunt, F. 2017. Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series* 578: 167–181.
- Coulson, J. C. 2011. *The Kittiwake*. Poyser, London.

- Cramp, S., Simmons, K. E. L., Brooks, D. J., Collar, N. J., Dunn, E., Gillmor, R., Hollom, P. A. D., Hudson, R., Nicholson, E. M., Ogilvie, M. A., Olney, P. J. S., Roselaar, C. S., Voous, K. H., Wallace, D. I. M., Wattel, J. & Wilson, M. G. 1984. *Handbook of the Birds of Europe, the Middle East and North Africa Volume 3*. Oxford University Press, Oxford.
- Dias, M. P., Granadeiro, J., Phillips, R. A., Alonso, H., Catry, P. 2010. Breaking the routine: Individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society B: Biological Sciences* 278: 1786–1793.
- Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M. & Guilford, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioral Ecology* 27: 1061–1072.
- Fort, J., Beaugrand, C., Grémillet, D. & Phillips, R. A. 2012. Biologging, remotely-sensed oceanography and the continuous plankton recorder reveal the environmental determinants of a seabird wintering hotspot. *PLoS ONE* 7: e41194.
- Frederiksen, M., Moe, B., Daunt, F., Phillips, R. A., Barrett, R. T., Bogdanova, M. I., Boulinier, T., Chardine, J. W., Chastel, O., Chivers, L. S., Christensen-Dalsgaard, S., Clement-Chastel, C., Colhoun, K., Freeman, R., Gaston, A. J., Gonzalez-Solis, J., Goutte, A., Grémillet, D., Guilford, T., Jensen, G. H., Krasnov, Y., Lorentsen, S.-H., Mallory, M. L., Newell, M., Olsen, B., Shaw, D., Steen, H., Strøm, H., Thórarinnson, T. L. & Anker-Nilssen, T. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions* 18: 530–542.
- Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. & Perrins, C. 2011. A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE* 6: e21336.
- Harris, M. P., Daunt, F., Newell, M., Phillips, R. A. & Wanless, S. 2010. Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Marine Biology* 157: 827–836.
- Kubetzki, U., Garthe, S., Fifield, D., Mendel, B. & Furness, R. W. 2009. Individual migratory schedules and wintering areas of northern gannets. *Marine Ecology Progress Series* 391: 257–265.
- Lisovski, S. & Hahn, S. 2013. GeoLight - processing and analysing light-based geolocation in R. *Methods in Ecology and Evolution* 3: 1055–1059.
- Orben, R. A., Paredes, R., Roby, D. D., Irons, D. B. & Shaffer, S. A. 2015. Wintering North Pacific black-legged kittiwakes balance spatial flexibility and consistency. *Movement Ecology* 3: 36.
- Paleczny, M., Hammill, E., Karpouzi, V. & Pauly, D. 2015. Population Trend of the World's Monitored Seabirds, 1950–2010. *PLoS ONE* 10: e0129342.
- Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. & Briggs, D. R. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266: 265–272.
- R Core Team. 2017. R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.
- Rankin, M. N. & Duffey, E. A. 1948. A study of the bird life of the North Atlantic. *British Birds* 41 (Suppl): 1–42.
- Wernham, C., Toms, M., Marchant, J. & Clark, J. 2002. *The Migration Atlas: Movements of the Birds of Britain and Ireland*. Poyser, London.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.