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Short distance migrants travel as far as long distance migrants in lesser black-backed gulls *Larus fuscus*

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Migration strategies differ greatly among and within avian populations. The associated trade-offs and fitness consequences of diverse strategies and how they persist are pertinent questions in migration research. Migration is a costly endeavour, presumably compensated for by better survival conditions in the non-breeding area. One way to assess the cost of alternative strategies is to investigate the investment in movement across the entire annual cycle, an assessment made increasingly feasible with improvements in tracking technology. Our study focuses on lesser black-backed gulls, generalist seabirds that exploit a broad range of resources, exhibit diverse migration strategies and have potentially altered migration strategies in response to human activities and climate change. We used GPS tracking to quantify lesser black-backed gulls' movement throughout their annual cycle and compare trade-offs among four migration strategies. The annual cumulative distance travelled by long distance migrants wintering in west Africa, over 4000 km from their breeding colony, did not differ significantly from individuals of the same breeding colony wintering only a few hundred kilometres away in Great Britain. Short distance migrants returned to the colony first, and long distance migrants returned last. Sex and wing length were not correlated with maximum range, cumulative distance travelled or timing. Individuals spent only a small proportion of their time in flight and spent on average 17% of their time at sea throughout an annual cycle, suggesting a reliance on inland resources for many individuals. Analysing movement throughout the annual cycle can change our perspective and understanding of consequences of different migration strategies. Our study shows that a range of migration strategies coexists and we propose that the long term costs and benefits of these strategies balance out. Diversity in migration strategies may contribute to the resilience of this species in the face of ongoing anthropogenic impact on the environment.

A myriad of migration strategies can coexist within a broad range of species (Lack 1944, Berthold and Querner 1981, Ketterson and Nolan 1982, Lok et al. 2011) and tracking studies are increasingly revealing how diverse strategies can be, even within a single population (Hake et al. 2003, Garthe et al. 2012, Klaassen et al. 2012). These strategies may encompass differences in migration routes, migration distance, timing, stopover behaviour, habitat choice or non-breeding ranges. In some species, these differences may be related to factors such as age (Hake et al. 2003, Jorge et al. 2011, Sergio et al. 2014), sex (Ketterson and Nolan 1983, Kjellén et al. 2001), morphology (Alerstam et al. 2003, Fiedler 2005), social dominance (Ketterson and Nolan 1983, Marra 2000) or individual experience and social learning (Chernetsov et al. 2004, Guilford et al. 2011, Mueller et al. 2013). From an evolutionary perspective, diverse strategies are expected to persist in a population if in the long term, costs and benefits of these strategies balance out (Lack 1968). For example, long distance migrants may incur higher costs than short distance migrants in terms of time and energy during migratory flights, increasing the risk of mortality or delaying arrival in breeding areas. Yet, the

costs of long distance migration may be offset by benefits gained due to better external factors on the non-breeding range, such as reduced competition, predation or pathogens, improved foraging conditions, reduced metabolic costs due to regional climate or reduced winter mortality (Alerstam et al. 2003).

The energetic cost of travel is often considered an important factor shaping migration strategies, but studies have generally focused only on the migratory phase of the annual cycle. Yet, the accompanying period(s) of residency and the associated movements required for self-maintenance during the non-breeding season have their own associated travel costs. An alternative approach to comparing different migration strategies would therefore be to compare the investment in movements throughout the entire annual cycle, incorporating the large scale displacement associated directly with migration and local movements associated with a particular life history strategy and foraging activities. While energetic costs may still be relatively difficult to measure directly, migration distance (the maximum distances between a breeding site and overwintering site) and cumulative distance travelled within an annual cycle are aspects of migration

strategies that we can measure with increasing accuracy due to ongoing developments in tracking technology.

The lesser black-backed gull *Larus fuscus* is an ideal species to examine diversity in migration strategies. Ringing recovery studies have long established that lesser black-backed gulls originating from Great Britain were found in wintering areas along the coast of France, Portugal, Spain, northern Africa and as far south as Senegal (Thomson 1924, Harris 1962); and individual tracking studies have revealed detailed migration routes and timing (Pütz et al. 2008, Klaassen et al. 2012). At the species level, lesser black-backed gulls are omnivorous, while individuals may specialize on different resources (Camphuysen et al. 2015, Tyson et al. 2015). In his seminal book, Alerstam (1990) describes several interconnected aspects of gull ecology and migration, noting that due to their mobile lifestyle and flight efficiency, gulls can roam around in winter more easily than other species, changing their place of residence if environmental conditions deteriorate. He also noted that lesser black-backed gulls breeding along western European coasts and in the North Sea are long distance migrants, but that winter habits were changing, with winter distributions shifting northward (Baker 1980). Alerstam (1990) suggested that the change in migratory habits of the gulls was the result of a large surplus of food available for omnivores in the winter in western Europe and wintering close to the breeding colonies would enable adults to return early to the colony and establish nesting sites. We now have an opportunity to re-examine migratory movements of lesser black-backed gulls first revealed by limited ringing recoveries, and now studied using GPS tracking of individual gulls throughout their annual cycle.

The aim of our study is to determine the extent to which migration strategies differ within a population of lesser black-backed gulls breeding along the North Sea coast. Based on GPS tracking data, we defined four migration strategies according to the geographic region and latitude farthest from the breeding colony where individuals spent the winter. We focused on factors that were relatively easy to measure and compared them across individuals: 1) migration distance (i.e. the maximum distance from the breeding site; Alerstam et al. 2003), 2) annual cumulative distance, 3) timing of departure from the colony in autumn and 4) arrival at the colony in spring. We used annual cumulative distance travelled as a proxy for travel costs associated with a particular migration strategy, which now includes movements during the breeding and non-breeding seasons. Migration distance is often emphasized in migration research; net investment in locomotion (annual cumulative distance) may be expected to be higher for long distance migrants than short distance migrants and timing is likely to differ among migration strategies (McNamara et al. 1998, Kokko 1999, Alerstam et al. 2003). Specifically, we expected that gulls that stayed closer to the colony (short distance migrants) would return earlier. We also tested whether maximum range and annual cumulative distance were related to sex (assuming different strategies between the sexes) or wing length (assuming differences in flight efficiency), although our expectation was that there would be no correlation between these factors (Bosman et al. 2012). To provide additional ecological context when comparing strategies, we estimated both time spent at sea

and time spent in flight throughout the annual cycle for gulls exhibiting different migration strategies. The existence of diverse strategies is especially intriguing in an era of rapid environmental change due to human impact on habitat and climate, and we briefly discuss potential consequences of this diversity in migration strategies.

Methods

Gull tracking

Between 2008 and 2013, 51 adult lesser black-backed gulls were fitted with an 18 g UvA-BiTS GPS tracker (Bouten et al. 2013) using a backpack harness made of a teflon ribbon threaded with a nylon string. Gulls were actively breeding in a mixed-breeding colony of lesser black-backed and herring gulls *Larus argentatus* on the Wadden Sea island of Texel in the Netherlands (53.009°N, 4.717°E). Gulls were captured during incubation using a walk-in trap and were released within 20 min of capture after taking biometric measurements and tagging. In each year, gulls were captured between 20 May and 8 June. For further details about the tagging procedures and the breeding colony see Camphuysen et al. (2015). The GPS trackers are solar-powered with a bi-directional communication system enabling remote download of data and upload of new measurement programs. Although the trackers include a range of sensors, for the current study only data provided by the GPS were used, including: location (mean position error of 30 m for measurement intervals of 600 s), altitude above mean sea level (AMSL) and instantaneous ground speed (m s^{-1}). For further technical details about the tracking system see Bouten et al. (2013). Throughout the year we used different measurement intervals to maximize the number of measurements and minimize data gaps due to low battery power (due to, for example, low solar energy). GPS measurements were generally taken every 5 min during the breeding season and every 20 min during the non-breeding season. Measurements were occasionally taken at higher frequencies, especially during the breeding season.

Data processing

For our analysis we defined each tracking year of a gull from 1 June through 31 May the following year, except where otherwise indicated. We selected 1 June as the start of a gull's year as this generally represented when the tracking of most new-tagged gulls commenced. Tracking data from a total of 51 tagged individuals, ranging from 1 June 2008 to 31 May 2015, were screened and analysed separately per bird and tracking year ('bird-year' from 1 June). We identified days where we had information gaps as any day on which GPS measurements were lacking. As sampling frequency and hence gap days can significantly affect the summary statistics of movement (Ryan et al. 2004, Mills et al. 2006, Shamoun-Baranes et al. 2012b), we only retained those bird-years with a minimum of 75 percent coverage and a sampling rate of 20–30 min in winter. The resulting dataset included 19 individuals and 38 bird-years.

All data were resampled in order to avoid biases in distance estimates due to different sampling rates (Ryan et al. 2004, Mills et al. 2006, Shamoun-Baranes et al. 2012b). After visually exploring measurement intervals from several birds, data were resampled on a 20-min interval. Data were resampled by starting from the first data point and searching for GPS fixes with an interval closest to 20 min and then repeating this process iteratively.

Each bird-year was assigned to one of four migratory strategies: 1) Great Britain (GB), 2) western France (F), 3) Iberian Peninsula (IP) and 4) west Africa (WA) (Fig. 1). These migration strategies were associated with the wintering areas based on an individual's maximum distance from the colony (migration distance), as well as latitude at maximum distance; GB birds were the shortest distance migrants, followed by F, IP and WA respectively.

Summary statistics

We calculated several parameters for each bird-year. Migration distance was calculated as the maximum great circle (orthodromic) distance between the breeding colony and a position in the non-breeding season. Annual cumulative

distance was calculated as the sum of all point-to-point distances in a given bird-year, using the great circle distance between successive points. We corrected the annual cumulative distance for gap days by dividing it by the proportion of coverage. This derived variable, the corrected cumulative distance, was used in subsequent statistical analyses (see 'Comparative analysis of migration strategies'). We calculated the date of departure from the breeding colony in autumn and return to the breeding colony in spring. Breeding colony departure was determined as the first date on which an individual moved away from the breeding colony and did not return to within a 3 km buffer until the following year (Camphuysen et al. 2015). Similarly, arrival date was determined as the first date on which an individual returned to within 3 km of the breeding colony in spring. For the comparative analysis of migration strategies, dates were converted to the number of days since 1 June of the relevant year.

We calculated the time spent in flight based on the instantaneous ground speed measured by the GPS. The frequency histogram of instantaneous ground speed revealed a bimodal distribution with a peaks close to 0 and 30 km h⁻¹. Based on a kernel-density estimate of this histogram, the minimum

Figure 1. Migration routes of lesser black-backed gulls per bird-year and migration strategy (a) Great Britain (GB), (b) western France (F), (c) Iberian Peninsula (IP), (d) west Africa (WA), from 2010 to 2015. Each line represents a bird-year subset.

value between the two peaks (18.6 km h^{-1}) was selected as cut-off value for birds in flight. We then identified flight as all speed values $\geq 18.6 \text{ km h}^{-1}$ and calculated the proportion of measurements in flight per bird-year. Lower speeds will predominantly indicate when birds are stationary, floating or walking (Shamoun-Baranes et al. 2011, 2016a). To calculate time spent at sea we merged the resampled GPS measurements with a 1 km resolution land-sea mask raster (ESRI Ocean Mask World 1 km) using the Overlay-spatial join (Analysis Tools) and Extraction-Extract Values to Points (Spatial Analyst Tools) in ArcGIS 10.1. We then calculated the proportion of measurements over sea per bird-year.

Comparative analysis of migration strategies

The relationships between migration strategy (GB, F, IP, WA), sex and wing length as predictor variables and corrected cumulative distance, departure day and arrival day (as response variables) were investigated with a linear mixed effects model, with individual included as a random effect and each response variable tested separately. After fitting the models and retaining only significant predictor variables, we checked normality, independence, and homoscedasticity of the model residuals visually. All summary statistics and comparative analysis of migration strategies were conducted in R (ver. 3.2.2) (R Core Team), and we used the 'lme4' package to perform linear mixed effects models (Bates et al. 2015). Plots were produced using the package 'ggplot2' (Wickham 2009).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.4271s>> (Shamoun-Baranes et al. 2016b).

Results

Of the 38 bird-years, nine were assigned to Great Britain, eight to western France, 15 to the Iberian Peninsula and six to west Africa (Fig. 1, Table 1, Supplementary material Appendix 1, Table A1). With one exception, lesser black-backed gulls tracked over multiple years used the same migration strategy. Five of the 19 gulls travelled to Great Britain, four to western France, seven to the Iberian Peninsula and four to west Africa (Supplementary material Appendix 1, Table A1). One gull (individual 606) travelled to west Africa in 2013 and to western France in 2014. In 2012, she travelled to western France, however because the number of gap days exceeded our coverage threshold, this bird-year was not included in the analysis. After resampling, the number of GPS fixes retained per bird-year was $21\ 847 \pm 2972$ (Supplementary material

Appendix 1, Table A1). The migration distance (maximum range from the colony) per strategy was $475 \pm 37 \text{ km}$ (mean $\pm$ SD), $815 \pm 121 \text{ km}$, $1894 \pm 135 \text{ km}$ and $4481 \pm 402 \text{ km}$, for GB, F, IP and WA, respectively (Table 1). Among individuals the minimum migration distance was 405 km (GB) and maximum was 4911 km (WA) (Supplementary material Appendix 1, Table A1). The mean corrected annual cumulative distance was longest for GB migrants, and shortest for gulls wintering in France (Table 1), with a minimum of 21 329 km (F) and maximum of 48 211 km (GB) among individuals (Supplementary material Appendix 1, Table A1). On average, birds departed from the breeding colony on $17 \text{ July} \pm 14 \text{ d}$ and returned on $31 \text{ March} \pm 17 \text{ d}$ (Supplementary material Appendix 1, Table A1). The mean duration away from the colony was $256 \pm 23 \text{ d}$ (Supplementary material Appendix 1, Table A1). Exploring the cumulative distance travelled over time revealed similar patterns among individuals within the GB and F strategies, while the temporal patterns appeared more variable within the IP and WA strategies (Fig. 2). The most strikingly different pattern was individual 541 who had the longest maximum range and accumulated distance in a short period of time as it migrated to Africa where it subsequently travelled little on a daily basis (Fig. 2, Supplementary material Appendix 2, kmz file for interactive data exploration in Google Earth).

Among migration strategies (Table 1) and individuals, gulls spent a relatively low proportion of time in flight within an annual cycle (mean $\pm$ SD: 0.12 ± 0.02 , range: 0.08–0.17; Supplementary material Appendix 1, Table A2). The proportion of time gulls spent in flight was significantly and positively correlated with the corrected cumulative distance (marginal $R^2 = 0.55$, conditional $R^2 = 0.71$, $y = 2.7 \times 10^{-6} \times x + 0.033$, with individual as random effect, $n = 38$; Nakagawa and Schielzeth 2013). For this and all other inferential analyses which we report, we did not find any evidence of non-normality, lack of independence or heteroscedasticity in the residuals. Annually, gulls spent $17 \pm 18\%$ (mean $\pm$ SD, range 2–87%) of their time at sea (Supplementary material Appendix 1, Table A2), including time spent in flight as well as other activities (e.g. resting on the sea surface; Shamoun-Baranes et al. 2011). On average WA migrants spent more time at sea than birds using other migration strategies (Table 1). Gulls that migrated to wintering areas in GB and F stayed predominantly inland (Supplementary material Appendix 3, kmz file), while migrants that moved to IP stayed either at the Atlantic coast or inland and the migrants that moved to west Africa spent the winter along the coast (see also Fig. 1, Supplementary material Appendix 2, kmz file). The individual that spent the least amount of time at sea (individual 344 in year 2012, Supplementary material

Table 1. Summary statistics per migration strategy of lesser black-backed gulls from 2010 to 2015. Means $\pm$ SD are presented. Abbreviations in the table header are as follows: n = number of bird-years, Latitude = latitude at maximum distance from the colony, Longitude = longitude at maximum distance from the colony, Migr. dist. = migration distance (km), Cor. cum. dist. = the corrected cumulative distance (km), Prop. flight = proportion of time in flight, Prop. sea = proportion of time at sea.

Destination	n	Latitude	Longitude	Migr. dist.	Cor. cum dist.	Prop. flight	Prop. sea
Great Britain (GB)	9	52.19 ± 0.89	-2.34 ± 0.57	475 ± 37	$40\ 852 \pm 5132$	0.13 ± 0.05	0.13 ± 0.05
Western France (F)	8	46.80 ± 0.15	-1.60 ± 0.29	815 ± 121	$30\ 733 \pm 5900$	0.11 ± 0.02	0.10 ± 0.05
Iberian peninsula (IP)	15	37.94 ± 1.30	-6.86 ± 2.11	1894 ± 135	$34\ 547 \pm 4320$	0.12 ± 0.02	0.11 ± 0.06
West Africa (WA)	6	16.29 ± 3.83	-16.66 ± 0.20	4481 ± 402	$34\ 981 \pm 4660$	0.12 ± 0.02	0.50 ± 0.24

Figure 2. Cumulative distance (km) travelled over time per migration strategy for lesser black-backed gulls from 2010–2015. (a) Great Britain (GB), (b) western France (F), (c) Iberian Peninsula (IP), (d) west Africa (WA), from 2010 to 2015. Each line represents a bird-year subset. Bold lines represent the part of the annual cycle when individuals returned regularly to the colony.

Appendix 1, Table A2) spent the non-breeding season inland in Spain and the individual that spent the most time at sea (individual 541 in year 2011, Supplementary material Appendix 1, Table A2) spent the winter along the coast of west Africa (Fig. 1).

There was a strong and significant relation between migration strategy and each of the response variables that

we considered (corrected cumulative distance, departure day and arrival day; see Table 2 for model parameters and statistics). Individuals migrating to GB remained closest to the breeding colony but the corrected cumulative distance did not differ significantly from IP and WA migrants. In comparison, individuals overwintering in F had a significantly shorter cumulative distance than all other migrants.

Table 2. The effects of migration strategy of lesser black-backed gulls from 2010 to 2015 on different response variables, based on linear mixed-effect models. If an effect was significantly different from the value for Great Britain (GB), it is printed in bold and a p-value is given. For each model $n = 38$ (the number of bird-years) and parameter estimates $\pm$ SE are provided. Departure and arrival day are provided as day of year from 1 January (as used in the model), as well as date format (dd-mm). The marginal and conditional R^2 values (Nakagawa and Schielzeth 2013) are provided for each model, representing the variance explained while ignoring individual information (marginal) or taking the individual information into account (conditional). Migration strategies are assigned as follows: Great Britain (GB), western France (F), Iberian Peninsula (IP) and west Africa (WA). Cor. cum. dist. = the corrected cumulative distance (km).

Response variable	Overwintering area				R^2	
	GB	F	IP	WA	Marginal	Conditional
Cor. cum. dist.	39667 $\pm$ 2167	30 487 $\pm$ 3163 p = 0.010	34624 $\pm$ 2808	34818 $\pm$ 3196	0.27	0.68
Departure day	191 $\pm$ 5.0	194 $\pm$ 7.4	206 $\pm$ 6.5	192 $\pm$ 7.6	0.22	0.47
Date (day-month)	10-07	13-07	25-07 p = 0.036	11-07		
Arrival day	441 $\pm$ 4.5	448 $\pm$ 6.6	457 $\pm$ 5.8	480 $\pm$ 6.8	0.57	0.73
Date (day-month)	11-03	24-03	02-04 p = 0.013	25-04 p < 0.001		

Individuals migrating to IP departed from the breeding colony significantly later (~ 12 d) than all other migrants. Birds migrating to IP and WA arrived back at the breeding colony significantly later in spring than birds migrating to GB and F. Individuals migrating to WA arrived an estimated 39 d after the GB migrants (Fig. 2, Table 2). Sex and wing length did not show a significant relation with any of the response variables (corrected cumulative distance, departure day and arrival day).

Discussion

By comparing migration strategies of lesser black-backed gulls throughout their annual cycle, we have shown that the migration distance from the breeding colony, which is often used to classify migratory strategies (Alerstam et al. 2003), is only a small part of the workload associated with movements throughout a gull's annual cycle. Our findings suggest that the investment in movement across the annual cycle generally balanced out across strategies in the lesser black-backed gull. If we consider the extremes within our study population, the longest distance migrants travelling to west Africa (maximum range 4481 ± 402 km) and the shortest distance migrants travelling to Great Britain (maximum range 475 ± 36 km), they did not differ significantly in the cumulative distance travelled throughout their annual cycles. Yet, western France migrants travelled significantly shorter cumulative distances than migrants using other strategies. Thus, the migrants travelling farthest from the colony were not the ones travelling the longest cumulative distances per year and likely not incurring the highest travel costs.

The proportion of time in flight has been used as a proxy for the cost of locomotion when comparing migration strategies (Garthe et al. 2012). We have shown that corrected cumulative distance travelled and the proportion of time in flight are positively correlated. The energetic cost of flight will depend on numerous intrinsic and external factors. Lesser black-backed gulls are able to use a range of flight modes, from continuous flapping to more energy efficient soaring flight (Tucker 1972, Baudinette and Schmidt-Nielsen 1974, Shamoun-Baranes and van Loon 2006). Flight mode selection is at least partly influenced by atmospheric conditions and the underlying landscape (Woodcock 1975, Shamoun-Baranes et al. 2016a). Similarly, how gulls respond to wind will also have a strong impact on flight costs (Alerstam 1979, McLaren et al. 2016). As the atmospheric conditions experienced during flight and underlying landscape features differ between geographic regions and seasons (Kemp et al. 2010), integrating the impact of atmospheric conditions on flight behaviour is likely to reveal additional differences in the costs and benefits of different migration strategies (Hedenström 1993, Shamoun-Baranes et al. 2010). In some migratory species, flight costs may differ between migratory and local flights, especially in species that go through major physiological changes in preparation for migration (Piersma and Lindström 1997, Sapir et al. 2011). Gulls, in contrast, appear to be highly flexible in their flight behaviour, occasionally making very long foraging trips of several hundred kilometres during the breeding season, or intermittently stopping migratory flights to rest or forage (Camphuysen et al. 2015,

McLaren et al. 2016). The amount of time and energy birds spend on flight throughout their annual cycle is something we still know very little about. While gulls were found to spend relatively little time in flight (~ 12%), we expect this will still contribute significantly to their daily energetic costs. Hedenström and Alerstam (1997), provided a theoretical prediction that the relation between the energetic cost of flight during migration and the energy cost of stopover was 1:2 in passerines and would be even higher for larger birds. If, for the sake of comparison, we follow a similar approach and assume that gulls spend 30% of their flight time soaring and 70% flapping (Shamoun-Baranes et al. 2016a) and that soaring flight costs $2 \times$ BMR while flapping flight costs $7 \times$ BMR (Tucker 1972, Baudinette and Schmidt-Nielsen 1974), and other activities cost $2 \times$ BMR on average, flight would contribute approximately 27% to the daily energy budget despite accounting for only 12% of daily activity. The use of additional bio-logging sensors, such as accelerometers, in combination with GPS tracking throughout the annual cycle to classify behaviour and estimate energy expenditure will likely reduce the uncertainty in estimating the cost of locomotion during different phases of the annual cycle across a range of migratory species (Gleiss et al. 2011, Sapir et al. 2011, Shamoun-Baranes et al. 2012a).

Given its potential consequences for breeding success, timing of arrival to the breeding area in spring may also be an important measure of fitness trade-offs associated with a specific migration strategy (Alerstam 1990, McNamara et al. 1998, Kokko 1999). Early arrival is considered important in areas where competition for breeding sites or partners may be high (Kokko 1999). Alerstam (1990) suggested that wintering closer to the breeding colonies would enable gulls to return earlier. We indeed found that the migrants travelling farthest from the colony (WA migrants) were arriving significantly later than the short distance migrants. Similarly, northern gannets *Morus bassanus* wintering in west Africa arrived later than individuals wintering closer to the colony (Garthe et al. 2012). If late arrival in breeding areas is penalized in some way, these migrants will incur a higher timing-associated costs than shorter distance migrants. These differences in arrival time also raise the possibility of assortative mating within the colony (Bearhop et al. 2005); if short distance migrants generally return earlier to the colony they may be more likely to bond with other short distance migrants than with longer distance migrants, and vice versa. This could be one of several mechanisms maintaining diverse migration strategies within a population. Tracking breeding pairs over multiple years would provide further insight into the process of pair bonding, especially in subsequent breeding season.

Our study confirmed a range of wintering areas similar to those previously reported in ringing recovery studies (Thomson 1924, Harris 1962, Marques et al. 2009, Hallgrimsson et al. 2012) and satellite tracking for other populations (Klaassen et al. 2012) around the North Sea and North Atlantic Ocean. Unlike the previously mentioned ringing studies which provide general spatiotemporal patterns at the population level, our tracking data clearly shows that some individuals do spend the entire non-breeding season in Great Britain. Also, tracking data are crucial for showing intermittent site use (e.g. in Great Britain) by birds

travelling subsequently to western France, the Iberian Peninsula and west Africa, and these patterns may have been underestimated by previous studies. Visual observations and ringing recoveries have previously been used to suggest that gulls were changing their overwintering ecology, possibly in response to the overabundance of human resources, and as a consequence could adjust their migratory behaviour and shorten their migration distance (Lack 1968, Baker 1980, Alerstam 1990). Yet, our present results show that lesser black-backed gulls still employ a broad range of migration strategies, including long distance migrations. While we do not have a baseline to compare with regards to overwintering ecology, as time spent in different environments throughout the annual cycle has never been quantified in gulls, we found that gulls in our study spent little time at sea, suggesting a reliance on inland resources for many individuals. Individuals differ in their foraging strategies in the breeding season (Camphuysen et al. 2015, Tyson et al. 2015); however, individual foraging strategies during the non-breeding season have not yet been explored, and differences in foraging and prospecting behaviour may be crucial in understanding cumulative distances travelled. For example, the long cumulative distances incurred by the GB migrants are likely a combination of their inland movements between nocturnal roosts and terrestrial foraging sites during the non-breeding, but also between different foraging areas throughout the winter (see 'staircase' pattern in Fig. 2a and Supplementary material Appendix 3, kmz file) as well as recurrent trips between Great Britain and the breeding colony during the prospecting phase and breeding season (Supplementary material Appendix 3, kmz file; Camphuysen et al. 2015, McLaren et al. 2016). Information on the cost of locomotion and self-maintenance in variable environments should be integrated with information about foraging strategies throughout the year in order to estimate a net energy budget for each strategy and quantify fitness consequences. Our multiple-year tracking data opens up the possibilities to do so in unprecedented detail.

In summary, our study suggests that costs in terms of time and energy may balance out among the various migration strategies in the lesser black-backed gull, or even lead to counter-intuitive levels of energy expenditure throughout the annual cycle. For example, individuals migrating to Great Britain, only a few hundred kilometres from the breeding colony, were found to travel similar or even longer cumulative distances than long distance migrants. We also expect that the short distance migrants would face relatively high energy expenditure rates by spending the entire annual cycle in the temperate zone, compared to migrants overwintering in coastal west Africa. That said, Great Britain migrants do have a temporal advantage in that they arrive, on average, earlier on the breeding grounds than long distance migrants and are thus potentially more competitive during the prospecting phase prior to breeding. Comparative studies on seabirds have suggested that energetic consequences of different migration strategies balance out (Garthe et al. 2012, Fort et al. 2013), while studies on other species (e.g. waders) revealed contrasting fitness consequences for different strategies (Lok et al. 2011, 2015, Alves et al. 2013). Certain strategies may be more successful in some years than other strategies due to spatiotemporal differences in environmental

conditions and nevertheless result in diverse migration strategies being equally successful in the long term (Lack 1968, Chapman et al. 2011). Alternatively, we may be observing gulls in a state of transition where multiple strategies currently coexist but may eventually disappear if individuals that adapt to exploiting overabundant human resources in western Europe (Alerstam 1990) and migrating only short distances outcompete long distance migrants. How flexible adult gulls are in altering their foraging and migration strategies during their lifetime is unclear. One individual observed in this study showed that at least some individual gulls can have alternative migration strategies within their life span. Previously abundant but already declining anthropogenic resources utilized by gulls, such as human refuse and fishery discards (Camphuysen 1995, Camphuysen et al. 2015, Corman et al. 2016), are likely to decline further due to changes in EU legislation (Bicknell et al. 2013); whether or not individuals can adapt to these changes within their life span will highly depend on their behavioural plasticity and ability to adapt their foraging or migration strategies accordingly. In order to understand the consequences of different migration strategies and changes within the key resources, they should be considered within the context of the annual cycle and life history of an individual (Harrison et al. 2011, Marra et al. 2015). Combining tracking technology, field work and conceptual modelling will be instrumental in addressing this challenge (Bowlin et al. 2010). Understanding the differences among migration strategies can inform us about the potential of a species to keep up with anthropogenic change. We believe that the diverse migration strategies exhibited by these gulls and other species (Gilroy et al. 2016) will contribute to their resilience and enable them to persist in a system continuously being changed by humans.

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Supplementary material (Appendix JAV-01229 at <www.avianbiology.org/appendix/jav-01229-0>). Appendix 1–3.