

# Post-fledging migration and wintering strategies of individual juvenile Lesser Black-backed Gulls (*Larus fuscus*)

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Research into the patterns and drivers of juvenile migration is important for understanding the development of individual migration strategies. Although several recent studies have tracked adult large gulls throughout the annual cycle, the movements of juveniles remain poorly understood. We fitted Global Positioning System (GPS) devices that transmit locations through the Global System for Mobile Communications (GSM) to ten juvenile Lesser Black-backed Gulls *Larus fuscus* prior to fledging on the island of Spiekeroog, Germany, to study their first autumn migration and wintering behaviour. The tracked birds initially departed on similar compass bearings south to south-west, after which migration routes diverged. Individuals took 38–107 days to reach their wintering sites in Algeria, Morocco or Spain. Birds visited  $6.7 \pm 3.7$  (mean  $\pm$  sd) stopover sites *en route* and spent substantial time in northern Europe, with some individuals converging at the same sites over small spatial scales (<1 km), but not over the same time periods. Birds increased travel speeds in the second half of their migration. They showed relatively high site-fidelity after arrival at wintering sites, and there was no evidence that the size of foraging areas increased over time, suggesting limited exploratory behaviour. Individuals used the same predominant habitats – cropland, open water and built-up areas – to varying degrees, but showed limited variation in habitat use over time. Overall, the migration routes and timings of juveniles broadly resembled those of previously tracked adults. Given their similar initial bearings and abundance of large gulls on the flyway, we suggest that social learning is likely to be an important process shaping the individual migration and wintering strategies of juvenile gulls.

**Keywords:** Bhattacharyya's affinity index, navigation, ontogeny of behaviour, orientation, tracking.

The dispersive movements of juveniles during the first months post-fledging have important implications for the fate of individuals (Dingle & Drake 2007, Vardanis *et al.* 2011). Individual movements probably reflect a variety of intrinsic and extrinsic drivers (Newton 2011, 2012); indeed, migration strategies of birds appear to be influenced by innate and learned behaviour (Berthold & Helbig 1992, Mueller *et al.* 2013, Riotte-Lambert & Weimerskirch 2013). Juveniles probably have

reduced navigation capabilities compared with adults (Guilford *et al.* 2011) and potentially face challenges in every new environment (stopover or wintering site) that they visit (Newton 2006). As such, individuals need to acquire information about their environments, while improving their foraging proficiency (de Grissac *et al.* 2017, Mendez *et al.* 2017). A greater foraging efficiency or better body condition should increase competitiveness, and consequently limit the extent of energetically costly movements between sites during the post-fledging winter. Ultimately, the responses of individuals to conditions encountered during their

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initial post-fledging migration have a major influence on survival and recruitment, and gene flow (Berthold & Helbig 1992, Newton 2006, Weimerskirch *et al.* 2015).

Tracking technology has provided new insights into individual movements of juvenile birds, and has shown, for example, that they may acquire similar flight capabilities to adults in the first months post-fledging (e.g. Wandering Albatrosses *Diomedea exulans*; de Grissac *et al.* 2017). Juveniles may learn behaviour from more experienced individuals (Alerstam *et al.* 2003, Mueller *et al.* 2013). For example, in White Storks *Ciconia ciconia*, juveniles adopt adult migration strategies by travelling in mixed-aged groups, despite their lower flight capabilities (Rotics *et al.* 2016). In contrast, for several seabird and raptor species which do not appear to migrate with kin (e.g. Scopoli's Shearwaters *Calonectris diomedea*, Black-footed Albatrosses *Phoebastria nigripes*, Egyptian Vultures *Neophron percnopterus*, Cory's Shearwaters *Calonectris borealis*) juveniles may learn independently (Perón & Grémillet 2013, Gutowsky *et al.* 2014, Phipps *et al.* 2019, Ramos *et al.* 2019) and consequently may have different migration strategies or spatial distributions to adults. As juvenile space use can differ remarkably between species and populations (Flack *et al.* 2016), further studies are needed to better understand variation in movement patterns and the main drivers.

With the development of smaller and lighter tracking devices, studies on large gulls have focused in recent years on understanding how movement strategies relate to population trends, and, for some species, to range expansions associated with changes in land use or increased availability of discards from fisheries (Tyson *et al.* 2015, van Toor *et al.* 2017, O'Hanlon & Nager 2018). The Lesser Black-backed Gull *Larus fuscus* is probably the most intensively studied large gull, but there are few reported impacts of long-term attachment of devices to adults on development of their chicks (Kavelaars *et al.* 2018), migration patterns (Pütz *et al.* 2007) or survival (Thaxter *et al.* 2014, Wikelski *et al.* 2015). Prior to the advent of biologging, the migration strategies of Lesser Black-backed Gulls of different age-classes were determined from ring recoveries and resightings (e.g. Helberg *et al.* 2009, Bairlein *et al.* 2014). More detailed information has since been obtained by deployment of satellite-transmitters (platform terminal transmitters (PTTs)) on juveniles and

adults (Pütz *et al.* 2007, Wikelski *et al.* 2015) and by GPS tracking of adults (Klaassen *et al.* 2012, Shamoun-Baranes *et al.* 2017). Birds from the German, Dutch and Belgian coast of the North Sea generally migrate on a south-westerly route to the Iberian Peninsula and North Africa, making intensive use of stopover sites in the Netherlands, Belgium and northern France (Klaassen *et al.* 2012, Bairlein *et al.* 2014, Baert *et al.* 2018). Some adults may also winter in these areas as well as in the UK (Bairlein *et al.* 2014, Shamoun-Baranes *et al.* 2017). There can also be substantial variation within populations; for example, individuals from Texel (The Netherlands) adopted strategies ranging from short- (c. 500 km) to long-distance migration (c. 5000 km) (Shamoun-Baranes *et al.* 2017).

As with the great majority of other seabird species (Phillips *et al.* 2017), migration strategies of adult gulls appear to remain stable across several years (Shamoun-Baranes *et al.* 2017). During their long-distance migrations, adult Lesser Black-backed Gulls do not take the shortest possible route, preferring to travel along coastal areas probably due to higher food predictability, and to use favourable wind conditions that reduce energetic costs of flight (Klaassen *et al.* 2012, Bustnes *et al.* 2013). As adult Lesser Black-backed Gulls leave the breeding colony earlier than juveniles, families presumably do not routinely travel together (Camphuysen 2013), although this has been observed on occasion (Holley 1986). It is suggested that Lesser Black-backed Gulls migrate solitarily (Wikelski *et al.* 2015). During the non-breeding period, however, they are gregarious and form flocks when feeding or roosting (Martín-Vélez *et al.* 2020). Little is known about the post-fledging migrations of juveniles, but long-term satellite-tracking data from one individual gull from Denmark indicated high fidelity to migration routes and wintering sites (Pütz *et al.* 2008). Differences in ranging behaviour of different age classes at wintering sites have been reported for other species of large gulls: juvenile Yellow-legged Gulls *Larus michahellis* are more widely dispersed around roosts and juvenile Herring Gulls *Larus argentatus* around feeding sites during the non-breeding period than adults, most probably due to their lower competitiveness (Monaghan 1980, Sol *et al.* 1995).

The aim of this study was to track the post-fledging migration of juvenile Lesser Black-backed Gulls and provide new insights into initial

movement patterns and the development of navigation, migration and wintering strategies. Specifically, we document the timing of migration, routes taken, use of stopover and wintering sites, and habitat use. We also tested how migration speed is adjusted *en route* and investigated the extent to which juveniles switch foraging sites after arrival in wintering areas. We predicted that as a result of their explorative behaviour and their reduced experience and competitiveness, individuals would exhibit large variation in migration strategies and would switch foraging sites and habitats frequently after arrival at their wintering site.

## METHODS

### Fieldwork

We fitted Global Positioning System (GPS) devices (OT15-2G; Ornitela, Lithuania) that transmit locations through the Global System for Mobile Communications (GSM) to 10 Lesser Black-backed Gull chicks (two females and eight males, based on molecular sexing using body feathers) prior to fledging on the island of Spiekeroog, Germany (53°33'N, 7°38'E) on 13 and 14 July 2017. Devices were attached using a harness made of Teflon, heat shrink and thread (Mettler, No. 36; Amann Handel, Boennigheim, Germany), secured with aluminium crimps and glue (Loctite 406; Henkel, Duesseldorf, Germany). Birds weighed 800–933 g. Devices and harnesses weighed 19.5–20.2 g, representing 2.1–2.4% of body mass. The devices were programmed to take positions every 10 min, 1 h or 24 h according to battery status (setting changed when the battery charge dropped below 50%, or 25% of total capacity, respectively) once the birds started flying. Battery recharge was through a solar panel, and GPS data were transmitted via the GSM network. All tracked individuals fledged successfully, and nine birds left the wider area (100 km) of the colony 28–72 days thereafter. The study period was defined as from 20 July 2017 (i.e. fledging, based on approximate age at logger deployment) until 12 December 2017–28 January 2018, covering autumn migration and the first 2 months at the wintering site. Eight individuals were tracked for the entire study period considered here. One individual was presumed to have died or lost the device (based on accelerometer data indicating an unusual, i.e. upside-down, orientation of the

device) before leaving the breeding area, 61 days after deployment, and the GPS device of another bird stopped recording because of mortality, device loss or failure, 143 days post-deployment. The post-fledging survival rate during the first 7 months was high (80%), substantially greater than the first-year survival rate (mean  $\pm$  sd,  $30.6 \pm 7.5\%$ ) estimated for a large sample size of colour-banded birds from colonies in the Netherlands by Camphuysen (2013). We hypothesized that high survival rates were due to the availability during the deployment period of chicks in good body condition from single-chick broods, probably raised by high-quality parents in a year with overall low breeding success.

### Spatial analysis

All analyses were carried out in R v. 3.6.1 (R Core Team 2019) unless indicated otherwise. Prior to analyses, a speed filter of 70 km/h (Klaassen *et al.* 2012) between consecutive locations was applied using the *adehabitatLT* package (Calenge 2006) to remove locations associated with unrealistic flight speeds. This resulted in the removal of 20 data points. Duplicated time stamps were also removed.

We defined autumn migration as the period from departure beyond a 100-km radius of the breeding colony, to arrival at the wintering site. Visual inspection of initial movements confirmed that 100 km was an appropriate cut-off, and that arrival at wintering sites was indicated by a transition from directed, long-distance flight to small-scale stationary movements, usually at the maximum or southernmost distance from the natal colony (see Figure S1). Raw GPS fixes during autumn migration were linearly interpolated at a daily interval using the function *approx* within the *stats* package, thereby generating new positions. The interpolation was used to account for differences in the GPS interval among individuals. Stop-over sites were defined as at least two consecutive daily GPS fixes of the same individual within a radius of 25 km (following Klaassen *et al.* 2012) to allow comparison with other studies. Cumulative distance travelled during autumn migration was calculated from consecutive daily GPS fixes, and migratory range was the distance between the first and the last GPS fix during autumn migration. Values were great circle distances calculated using the *distVincentyEllipsoid* function in the *geosphere* package (Hijmans 2019). Travel days were defined

as those with a daily travel distance of at least 25 km following Klaassen *et al.* (2012). We calculated both the travel speed considering all locations (migration speed) and those associated with travel days (hereafter travel speed). Migration duration was calculated as the time (number of days) between departure from the wider surroundings of the colony until arrival at the wintering site. Bearing was calculated between the first position during autumn migration and the following 10 positions, using the *circular* package (Agostinelli & Lund 2017). We excluded two individuals from migration analyses as they were missing positions for 7 and 39 days, respectively, during autumn migration; tracking data of the remaining individuals did not have missing days.

Spatial behaviour at wintering sites was analysed for 2 months from the day of arrival and included all activities such as roosting and foraging. To map habitat use at wintering sites, we identified positions during daytime using the *sunclac* package (Thieurmél & Elmarhraoui 2019), selected at least five consecutive GPS fixes at an interval of < 70 min within the day, and interpolated the raw GPS fixes at an hourly interval, as detailed above. We used an hourly interval, as we were interested in detecting changes over shorter time spans and could rely on greater temporal resolution of GPS fixes due to better solar recharge at the wintering sites. We estimated 50% utilization distributions (UDs) representing core areas, using the *adehabitatHR* package (Calenge 2006), selecting a cell size of 0.5 km and smoothing factor ( $h$ ) of 1.5 km. We determined the  $h$  value based on visual inspection of three realistic  $h$  values derived from the href method (4.5, 3 and 1.5 km), and selected 1.5 km as it appeared the most appropriate to characterize gull core ranges. We then tested for wintering-site fidelity over two temporal scales: short-term (daily for the 14 days post-arrival) and long-term (weekly for the 8 weeks post-arrival). By considering two time periods, we aimed to investigate whether birds initially moved between multiple foraging areas characteristic of explorative behaviour, before specializing on a particular area or resource. For both analyses, we calculated the spatial overlap of consecutive UD for each individual using Bhattacharyya's affinity index (BA; Fieberg & Kochanny 2005), and also compared the size of the core areas.

To quantify habitats visited, we overlaid all daily GPS fixes onto freely available raster maps of

land use. Data in Europe and Africa were available at the scale of 100 and 20 m, respectively (ESA Climate Change Initiative 2017, Copernicus Land Monitoring Service CLC 2018). We matched the 27 habitat categories from the European dataset to the nine categories from the African dataset to compare birds wintering in Europe or Africa (see Table S1): (1) woodland, (2) shrubland, (3) grassland, (4) sparse vegetation, (5) bare areas, (6) cropland, (7) built-up areas, (8) open water and (9) (semi-) aquatic vegetation. Information on habitat type was cross-checked and further resolved with satellite imagery in Google Earth v. 7.3.2.5776 (Google LLC 2019).

### Statistical analysis

To test whether all tracked juveniles changed speed similarly during autumn migration, we split tracks into locations before or after the half-way point, based on the straight-line distance between the first and the last GPS fixes during migration. We used paired *t*-tests to compare the total number of days taken and the number of travel days (i.e. total days minus stopover days) in each half of the route. Additionally, Spearman rank correlations were used to compare migration duration with both the distance of the wintering site (migratory range) from natal colony and cumulative distance travelled using the *stats* package.

To explore individual wintering-site fidelity over time, we ran generalized linear mixed-effects models (GLMMs) using the *lme4* package (Bates *et al.* 2015), with BA overlap between consecutive core areas as the response variable, time as a fixed effect (14 days and 8 weeks, respectively) and individual ID as a random effect to account for multiple values per individual. The response variable followed a binomial distribution with a logit link function. To determine whether juveniles reduce the size of foraging areas over time, indicative of a refinement of foraging sites, we ran linear mixed-effect models with size of core areas as the response variable, time as a fixed effect (14 days and 8 weeks, respectively) and individual ID as a random effect to account for multiple values per individual. The response variable was log-transformed to follow a normal distribution. In each case, we compared the full model with one where the covariate (time) had been removed, using likelihood ratio tests.

To characterize habitat use at wintering sites over time, we identified the number of GPS fixes

assigned to habitat classes. The most common habitat types were open water, built-up areas and cropland, which accounted for an average of 89% of time spent during the first 14 days (range 42–100%) and 87.9% during the first 2 months (range 62–100%). Therefore, we focused on these habitats. We ran GLMMs separately for each habitat and time period, with the proportion of time spent in the habitat as the response variable, time as a fixed effect (14 days and 8 weeks, respectively) and individual ID as a random effect to account for multiple values per individual. The response variable followed a binomial distribution. In each case, we compared the full model with one where the covariate (time) had been removed, using likelihood ratio tests.

## RESULTS

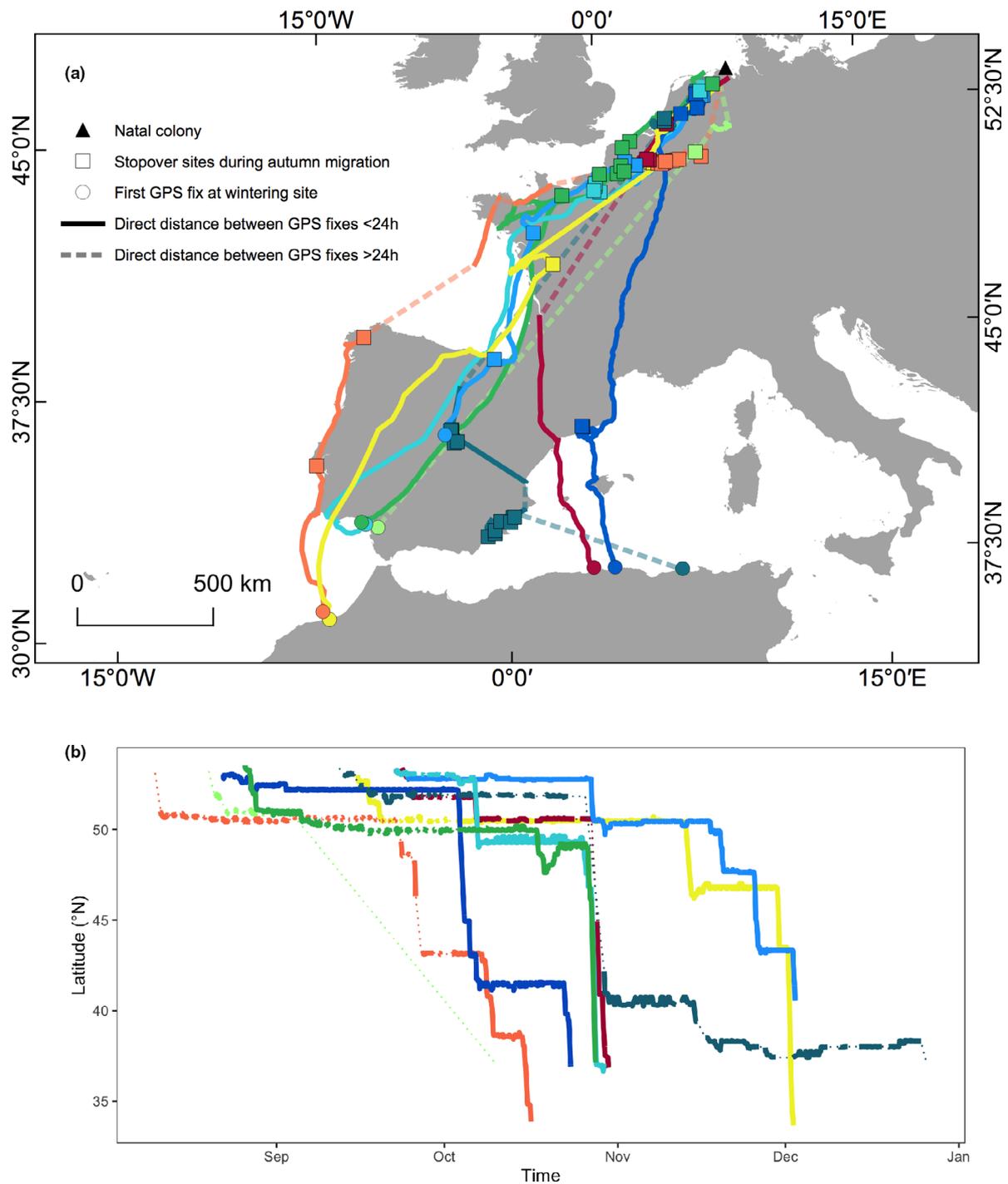
In total, 117 734 GPS fixes were collected from the tracked juvenile Lesser Black-backed Gulls between 20 July 2017 and 28 February 2018, of which 26 332 GPS fixes from nine individuals were classified as autumn migration and 52 086 GPS fixes from seven individuals as overwintering. GPS-GSM devices differed in battery recharge performance but provided  $48.1 \pm 40.2$  fixes per day ( $n = 9$ ) during migration, and  $65.2 \pm 23$  fixes per day or  $2.7 \pm 1$  fixes per hour ( $n = 7$ ) during the wintering period.

### Migratory routes

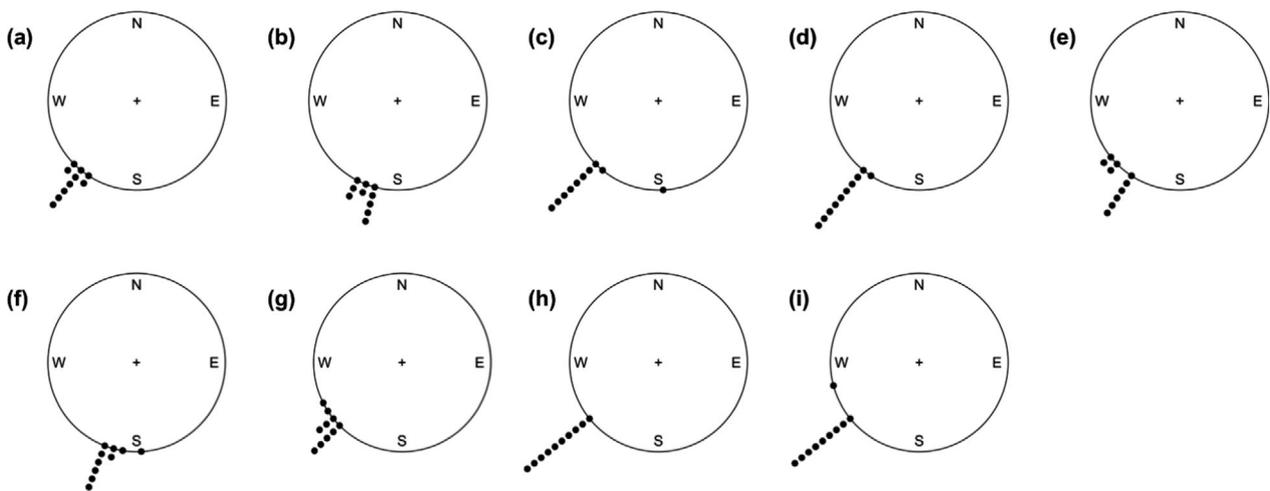
Juveniles left the wider surroundings (within 100 km) of the natal colony on a southerly or south-westerly bearing (mean  $218.1 \pm 0.6^\circ$ ),  $47.7 \pm 17.1$  days after fledging between 10 August and 24 September 2017 ( $n = 9$ ; Figures 1 and 2). Individuals used 3–10 stopover sites in Germany, the Netherlands, Belgium, northern France and on the Iberian Peninsula ( $6.7 \pm 3.7$ ,  $n = 9$ ), reaching their wintering sites in Algeria, Morocco, and south and central Spain after a further  $64 \pm 21$  days ( $n = 9$ ). During migration, they covered a minimum total travel distance (based on a single daily GPS fix) of  $2869 \pm 684$  km (range 2032–4041 km), resulting in an average daily distance travelled of  $47 \pm 13$  km ( $n = 9$ ). Only  $27.1 \pm 4.4\%$  of daily distances travelled exceeded 25 km ( $n = 7$ ), corresponding to a mean of  $16.6 \pm 5.4$  travel days per individual and an

average travel speed of  $165 \pm 55$  km/day. There was no correlation between migratory range and duration ( $S = 42.88$ ,  $\rho = 0.23$ ,  $P = 0.613$ ,  $n = 7$ ) or cumulative distance travelled and duration ( $S = 33.8$ ,  $\rho = 0.4$ ,  $P = 0.379$ ,  $n = 7$ ).

There was considerable individual variation in movement patterns during migration in terms of the overall timing and route (Figure 1b). Nevertheless, the seven individuals for which daily fixes were available appeared to have more directed movements after leaving stopover sites in northern France, Belgium and the Netherlands compared with the movements from the breeding colony to these stopover sites. During the second half of migration, there was an increased migration speed (i.e. shorter duration) ( $t_6 = 6.06$ ,  $P < 0.001$ ,  $n = 7$ ). Indeed,  $86.2 \pm 12\%$  of daily positions were reached over the first half of the route, with daily travel distances of  $28 \pm 73$  km and a maximum range of 169–709 km. After leaving northern Europe, individuals covered daily travel distances of  $158 \pm 261$  km, with a maximum range of 353–1168 km. However, although travel speeds increased, the number of travel days did not differ between the first ( $11.4 \pm 5.9$  days) and second half of migration ( $5.1 \pm 3.9$  days,  $t_6 = 2$ ,  $P = 0.094$ ,  $n = 7$ ), indicating that throughout the journey, birds mixed travel days with days spent at stopover sites. All nine individuals showed convergent movements both at stopover and at wintering sites, i.e. multiple individuals used the same sites over small spatial scales (i.e.  $< 1$  km; Figures 1 and 3), although separated in time. Four birds migrated along the French coast and then across Spain. One bird probably crossed the Bay of Biscay (missing GPS data on exact route across the open sea) and then travelled south along the Portuguese coast. This individual and one other flew *c.* 370 km over open water in the Atlantic to reach their wintering sites in Morocco. Two birds migrated from southern Spain across the Strait of Gibraltar. After leaving a stopover site in central Spain, one bird switched from its previous predominantly south-westerly bearing to an easterly bearing, reaching the Spanish coast and crossing the Mediterranean Sea to winter in Algeria (using more stopover sites and taking longer than the other tracked individuals). Two birds migrated to the Catalan coast, then travelled *c.* 500 km across the Mediterranean Sea, in one case following the coast of Mallorca, to winter on the Algerian coast.



**Figure 1.** (a) Migratory movements of nine juvenile Lesser Black-backed Gulls *Larus fuscus* tracked using GPS-GSM devices after leaving the wider surroundings (100 km) of the natal colony on the island of Spiekeroog, Germany, in 2017. Different colours represent different individuals. Colony position is marked with a black triangle. GPS tracking intervals varied between 10 min and 24 h, and dotted lines indicate a time difference greater than 24 h between consecutive GPS fixes. At least one GPS fix was available per day for all but two individuals. Stopover sites are centroids, i.e. the mean longitude and latitude of consecutive GPS fixes within 25-km distance (maps produced with QGIS 3.4.9-Madeira software, <https://qgis.org>, using Natural Earth free vector map data, <https://www.naturalearthdata.com>). (b) Variation in timing of autumn migration in nine juvenile Lesser Black-backed Gulls tracked with GPS-GSM devices in July 2017.



**Figure 2.** (a–i) Bearings during days 2–11 of autumn migration relative to the first migratory position for nine juvenile Lesser Black-backed Gulls *Larus fuscus* from Spiekeroog, Germany, tracked using GPS-GSM devices in 2017.

### Space use at wintering sites

The date of arrival at wintering sites varied between individuals, from 10 October to 26 December 2017 (median 29 October 2017). Movements at wintering sites were over much smaller spatial scales than during migration, and the spatial scale did not exceed 300 km (Figure 4, Figure S1). The size of core areas ranged from 127 to 330 km<sup>2</sup> (mean of 190 ± 65 km<sup>2</sup>).

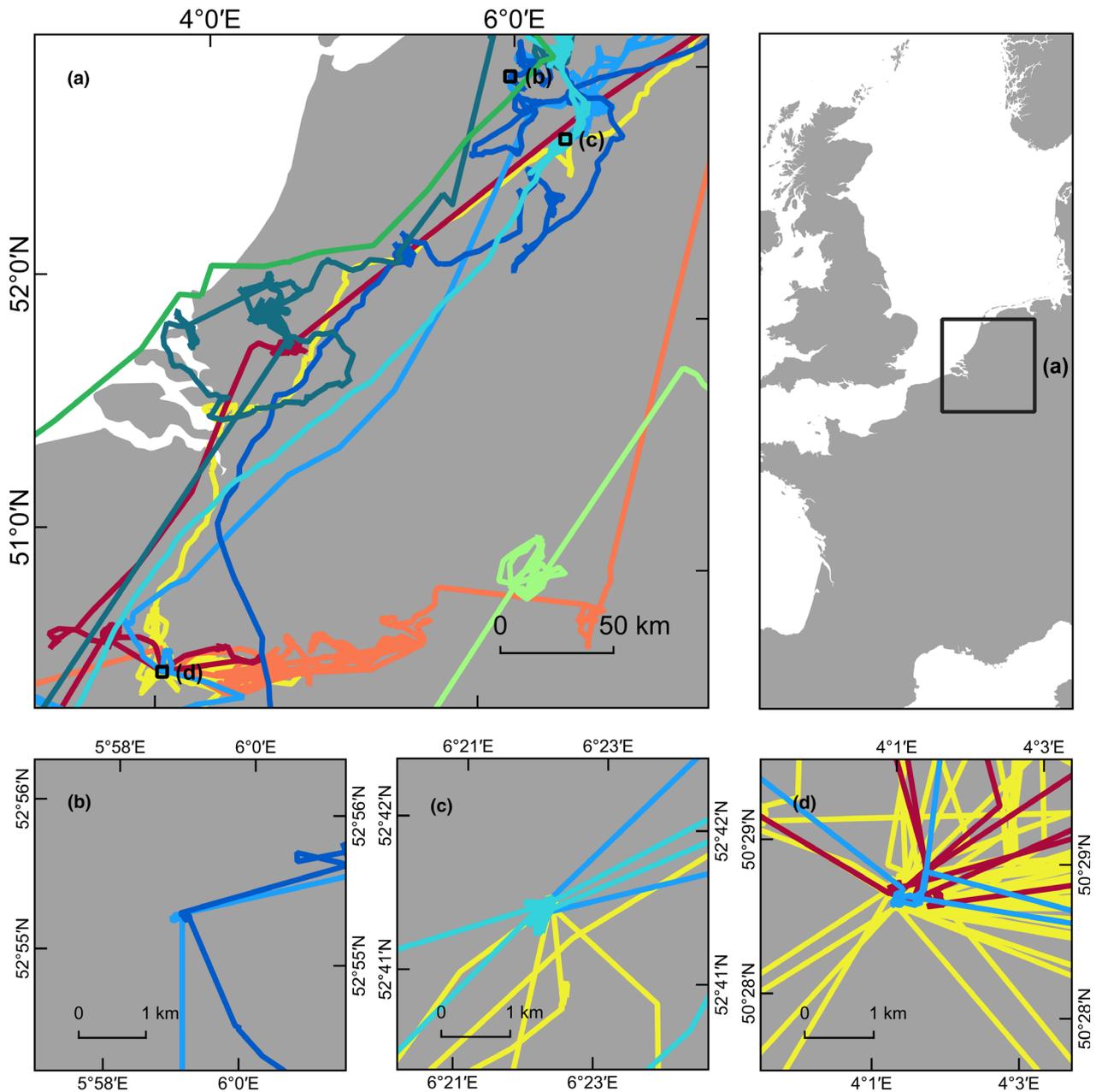
BA values varied between individuals over both the short and the long term (Figure S2a). There was no evidence of a change in individual site fidelity over the short term (i.e. at the daily level over the first 2 weeks;  $\chi^2_1 = 0.45$ ,  $P = 0.501$ ) or the long term (i.e. weekly level over the first 2 months;  $\chi^2_1 = 1.8$ ,  $P = 0.180$ ). Equally, the size of core areas appeared to vary between individuals over both the short and the long term (Figure S2b), yet there was no evidence of a change over time (short term:  $\chi^2_1 = 0.53$ ,  $P = 0.465$ ; long term:  $\chi^2_1 = 1.15$ ,  $P = 0.283$ ). These results suggest birds exhibit idiosyncratic foraging behaviour that appears to vary little after arrival at wintering sites, with little evidence of a wider exploration of the surrounding area (Figure 4).

### Habitat use at wintering sites

Habitat use appeared to differ substantially between individuals and also appeared to be linked to wintering site (Figure 5, Figure S3). Except for

one individual overwintering in central Spain (ind. 17980), which spent extensive time in freshwater habitats, at open landfills and in urban areas, all other juveniles explored a variety of habitats in coastal areas (based on visual inspection in Google Earth). Important areas were located inshore in estuaries, on small islets off the coast, at ports and on piers, in urban and industrial areas, at open landfills, on agricultural land and at freshwater sites. Although a similar range of habitat types were exploited by the juveniles wintering in various locations, use of specific site characteristics was apparent, e.g. irrigated agricultural fields in southern Spain (Figure 5; ind. 17985 and 17986). Similar habitat use was also observed at the remaining two wintering sites, each shared by two individuals (ind. 17977 and 17978 in Morocco, and ind. 17979 and 17981 in Algeria). One individual showed a switch in habitat use over the long-term (ind. 17985, Figure 5b).

Over the short term (i.e. the first 14 days), individuals increasingly used terrestrial habitats, as demonstrated by a decrease in use of open water habitat ( $\chi^2_1 = 4.0$ ,  $P = 0.047$ ). However, there was no change in use of the two major terrestrial habitat types (cropland:  $\chi^2_1 = 0.81$ ,  $P = 0.369$ ; built-up areas:  $\chi^2_1 = 1.62$ ,  $P = 0.204$ ; Figure S3a), nor was there evidence of a change in use of any of the three habitat types over the long term (i.e. the first 8 weeks; cropland:  $\chi^2_1 = 2.62$ ,  $P = 0.105$ ; built-up areas:  $\chi^2_1 = 0.62$ ,  $P = 0.432$ ; open water:  $\chi^2_1 = 0.31$ ,  $P = 0.581$ ; Figure S3b).



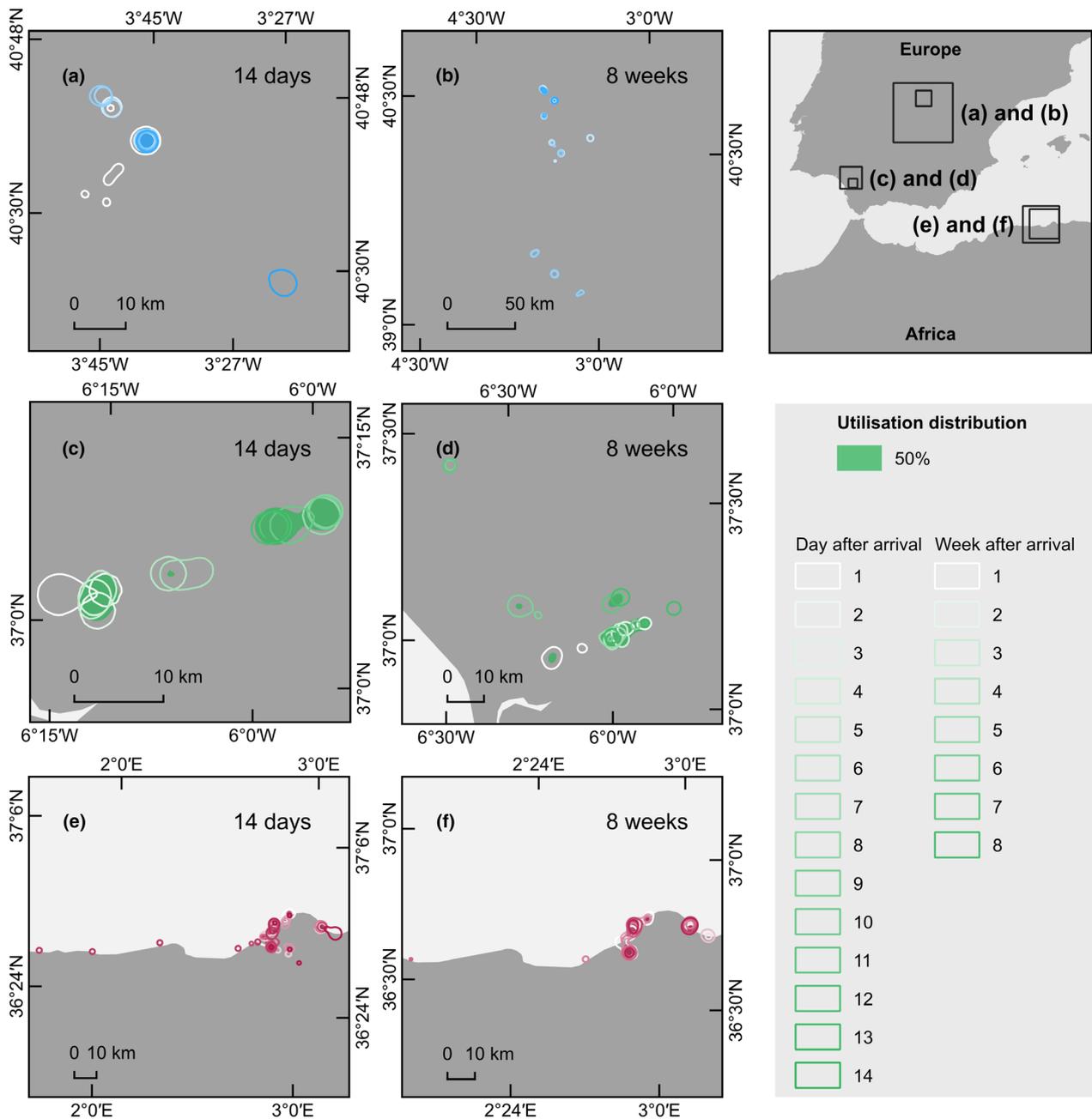
**Figure 3.** (a) Early migratory movements of nine juvenile Lesser Black-backed Gulls *Larus fuscus* across north-western Europe, tracked with GPS-GSM devices from Spiekeroog, Germany, in 2017. Different colours represent different individuals. (b–d) Stopover sites visited by several juveniles during migration, demonstrating convergent movements in space (but not time) (maps produced with QGIS 3.4.9-Madeira software, <https://qgis.org>, using Natural Earth free vector map data, <https://www.naturalearthdata.com>).

## DISCUSSION

### Juvenile migration strategies

Whereas adult Lesser Black-backed Gulls from northern Europe perform a range of migration

strategies, from short (500 km) to long distance (5000 km) (Shamoun-Baranes *et al.* 2017), all juveniles in this study migrated several thousand kilometres to winter in southwest Europe or North Africa. Juveniles left the vicinity of the breeding colony over a period of 1.5 months and mixed

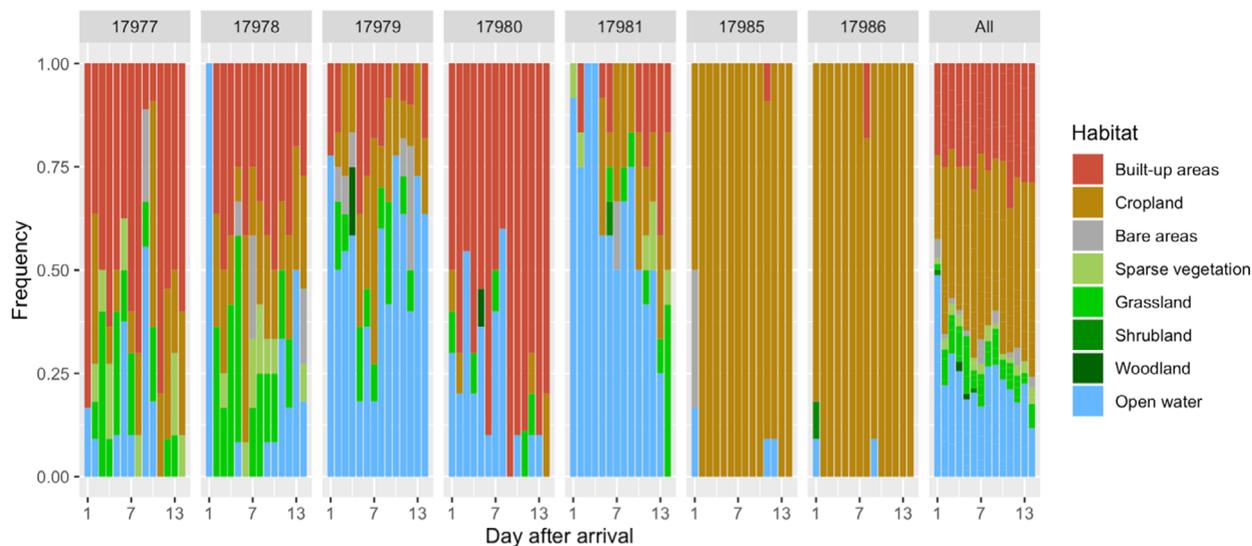


**Figure 4.** (a–f) 50% utilization distributions (UDs) of three juvenile Lesser Black-backed Gulls *Larus fuscus* at their wintering sites in central and southwest Spain, and Algeria, tracked with GPS-GSM devices from Spiekerroog, Germany, in 2017/2018. Each row represents a different individual, and UD for each individual and day (a,c,e) or week (b,d,f) after arrival are shown in colours alongside 50% UD for the entire time period (maps produced with QGIS 3.4.9-Madeira software, <https://qgis.org>, using Natural Earth free vector map data, <https://www.naturalearthdata.com>).

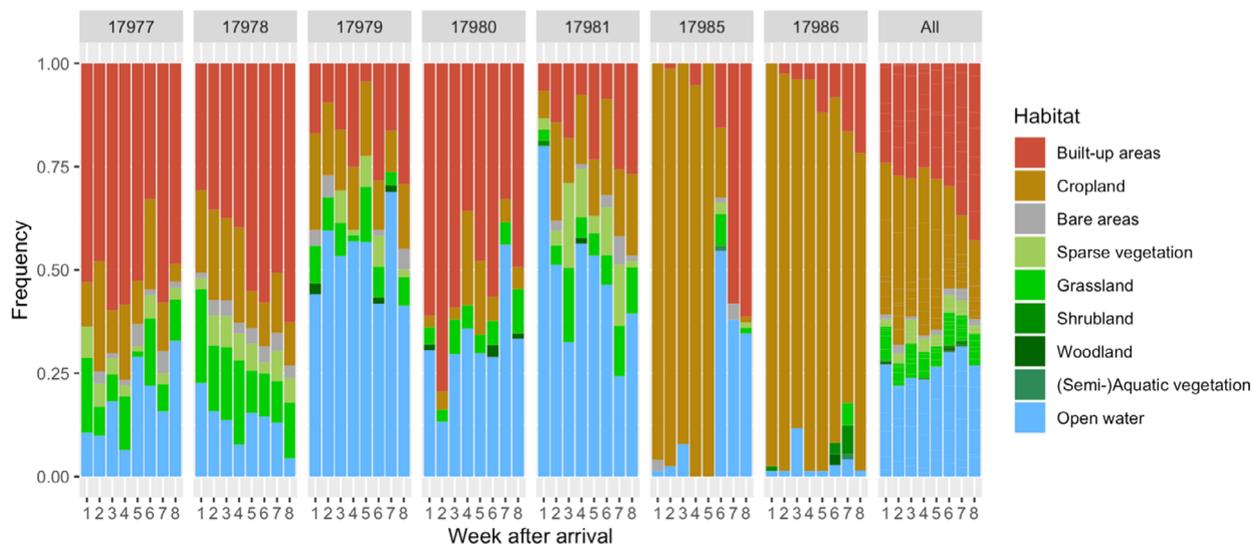
travel days with multiple days at stopover sites. This resulted in a slow migration strategy (47 km/day), similar to adult Lesser Black-backed Gulls in autumn (44 km/day; Klaassen *et al.* 2012). However, there was extensive variation in

the choice of route in the tracked juveniles, particularly south of 40°N, and in wintering destinations, which ranged from 7°W in Morocco to 8°E in Algeria. The sexes might differ in habitat use during autumn migration, and adult females have

(a)



(b)



**Figure 5.** Winter habitat use by seven individual Lesser Black-backed Gulls *Larus fuscus* tracked with GPS-GSM devices from Spiekeroog, Germany, over (a) 14 days and (b) 8 weeks after arrival at their wintering sites.

been found to arrive 2 weeks later than males at wintering sites (Baert *et al.* 2018). However, given the low sample size and the bias towards males in this study, we could not test for similar effects.

All tracked juveniles departed the breeding area in a south-westerly direction, which suggests that the initial bearing of migration might be genetically determined, but may also be influenced by

environmental conditions *en route* (Vardanis *et al.* 2011, Vansteelant *et al.* 2017). Alternatively, social learning could shape the initial migration routes of gulls, as suggested by Baker (1980) and Pütz *et al.* (2007) and reported for White Storks (Rotics *et al.* 2016) and Whooping Cranes *Grus americana* (Mueller *et al.* 2013). Large gulls are gregarious during the non-breeding period (Sol

*et al.* 1995, Martín-Vélez *et al.* 2020) and could orientate themselves according to the flight direction of other individuals when searching for suitable foraging habitats, particularly if following other birds from the same night roosts. Directed large-scale and convergent movements during migration could be a hint that juveniles follow more experienced conspecifics. In this study, all tracked individuals migrated separately, although they sometimes visited the same locations on different days. Individuals from different populations presumably mix at stopover sites along their migratory route (Dingle & Drake 2007), and hence information about alternative migratory routes, foraging and wintering sites could be transferred between age-classes and among populations.

According to analyses of ring recoveries, Lesser Black-backed Gulls ringed in Germany rarely overwinter on Mediterranean coasts, and even fewer individuals have been recorded at the Algerian coast (Bairlein *et al.* 2014). While a lower rate of recovery could reflect reduced observer effort in the region, GPS tracking of migrants indicates that those areas are not used by many adult Lesser Black-backed Gulls from breeding colonies in the Netherlands and Belgium (Klaassen *et al.* 2012, Shamoun-Baranes *et al.* 2017, Baert *et al.* 2018). In contrast to these studies, we found a third of the tracked juveniles overwintered on the coast of the Mediterranean Sea, two of which started to fly south on routes much further east of the other tracked birds at a relatively early stage in migration. This suggests that there is more variation in migration strategies of Lesser Black-backed Gulls than is apparent from previous ringing and tracking studies. The limited data on juveniles tracked from other populations suggests that they visit the same wintering sites in consecutive years (Helbig *et al.* 2008), as do most adults (Shamoun-Baranes *et al.* 2017). Juvenile Lesser Black-backed Gulls might also spend the summer further south than adults due to their lower competitive abilities (Bairlein *et al.* 2014) and relaxed time constraints (Newton 2011). However, this would need to be confirmed by tracking a large sample of juveniles.

### Wintering behaviour and habitat use

Generally, birds are not bound to one place during winter, and thus are free to travel longer distances and move between different sites. In addition, juveniles are hypothesized to be less competitive

at high-quality foraging sites (Sol *et al.* 1995, Alerstam *et al.* 2003, Votier *et al.* 2011, de Grissac *et al.* 2016). As far as we are aware, few studies have investigated the space use of juveniles after settling at wintering areas for the first time. Here, we predicted they would switch between foraging areas in the first days after arrival, leading to low spatial overlap between UDIs in consecutive days. However, we found no evidence that individual site fidelity changed over time (days to months). Our results suggest that core areas varied much less over time than expected, suggesting relatively high site-fidelity from an early stage. It seems that the tracked juveniles were quickly able to establish themselves at wintering sites and obtain sufficient food, with no requirement to move greater distances.

High site-fidelity during the winter suggests that, as during migration, juveniles follow more experienced conspecifics to predictable foraging habitats. Only one individual visited a second wintering site and showed a major shift in habitat use; the remaining individuals were consistent in habitat use. This indicates that it is advantageous to stay within a smaller area as long as resources are reliably available. Large gulls are known to exhibit individual consistency in space use, which is thought to provide an advantage over conspecifics and guarantee survival (Navarro *et al.* 2017, Borrmann *et al.* 2019, van Donk *et al.* 2020). Whether the same foraging sites are used consistently throughout ontogeny and into adulthood remains to be tested. Future work could focus on the development of fine-scale foraging and flight strategies, and energetic consequences, potentially using GPS and accelerometer data from a larger cohort of individuals (Shamoun-Baranes *et al.* 2016, Sage *et al.* 2019). This would also reveal the degree to which juveniles from the same colony associate during the migration and wintering periods (Flack *et al.* 2018).

Overall, habitat specialization appeared to be low, with most (five of seven) individuals using diverse habitats at wintering sites. There was little variation in habitat use over time, with birds increasing the use of terrestrial habitats upon arrival at the wintering sites. All juveniles used apparently predictable (and presumably abundant) resources, such as refuse or prey items from agricultural land, which suggests a substantial anthropogenic impact on our study system. This is unsurprising, as many adult Lesser Black-backed

Gulls forage inland during the breeding season (Corman *et al.* 2016, Isaksson *et al.* 2016), and sometimes throughout the year (Shamoun-Baranes *et al.* 2017). Nevertheless, it underlines the importance of human activities and man-made habitats for population dynamics and conservation of this species. Population growth in large gulls has been linked to the availability of landfills (Bosch *et al.* 1994, Duhem *et al.* 2008) and fishery discards (Oro 1996, Tyson *et al.* 2015). Any future decreases in anthropogenic resources might therefore lead to lower survival, reduced recruitment rates and, ultimately, population decline. Based on our results and considering the importance of individual foraging strategies for breeding success in large gulls (Annett & Pierotti 1999), processes leading to the development of individual spatial strategies probably have major implications at the population level, even if much work remains before these are fully understood.

Migration patterns of juvenile Lesser Black-backed Gulls resembled those of adults, with the juveniles using similar stopover sites, migration strategies and, at least to some extent, the same wintering sites within the known range. Juveniles seemed to establish well at stopover and wintering sites, and were fairly consistent in their space use, in contrast to predictions that they would be explorative and outcompeted by adults. The similarity in initial departure bearing, despite differences in the timing of departure from NW Europe, suggests an innate compass direction at the start of migration. We also hypothesize that social learning probably influences spatial behaviour directly after fledging, which would also explain the use of similar stopover and wintering sites. Further research would help tease apart the effects of intrinsic vs. extrinsic factors, including tracking of larger sample sizes, multiple cohorts and related individuals.

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## AUTHOR CONTRIBUTIONS

**Rahel Maren Borrmann:** Conceptualization (equal); Formal analysis (lead); Visualization (lead); Writing-original draft (lead). **Richard Phillips:** Conceptualization (equal); Formal analysis (supporting); Supervision (equal); Visualization (supporting); Writing-review & editing (equal). **Thomas Clay:** Formal analysis (supporting); Supervision (equal); Visualization (supporting); Writing-review & editing (equal). **Stefan Garthe:** Conceptualization (equal); Data curation (lead); Funding acquisition (lead); Project administration (lead); Supervision (equal); Visualization (supporting); Writing-review & editing (supporting).

## DATA AVAILABILITY STATEMENT

Tracking data are archived at Movebank (<https://www.movebank.org>). Bird-ringing data are archived at the Beringungszentrale Vogelwarte Helgoland (Institute of Avian Research, Wilhelmshaven).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Variation in distance from colony during autumn migration in nine juvenile Lesser Black-backed Gulls *Larus fuscus* from Spiekerroog, Germany, tracked with GPS-GSM devices in July 2017, used to identify the threshold for identifying the start of autumn migration.

**Figure S2.** (a) Bhattacharyya's affinity index (BA) and (b) size of core areas within individual Lesser Black-backed Gulls *Larus fuscus* from Spiekeroog, Germany, tracked with GPS-GSM devices for 14 days and for 8 weeks after arrival at their wintering site.

**Figure S3.** Habitat use within individual Lesser Black-backed Gulls *Larus fuscus* from Spiekeroog,

Germany, tracked with GPS-GSM devices (a) for 14 days and (b) for 8 weeks after arrival at their wintering site.

**Table S1.** Assignment of more refined habitat classification of land use in Europe to habitat classification of land use in Africa.