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GPS-tracking provides novel insights into the age-specific migration behaviour of an endangered migrant seabird in the Afro-Palearctic flyway

Joan Estrada

joanestrada2000@gmail.com

Lund University

Liam P. Langley

Heriot-Watt University

Ulrik Lötberg

BirdLife Sweden

Susanne Åkesson

Lund University

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GPS-tracking provides novel insights into the age-specific migration behaviour of an endangered migrant seabird in the Afro-Palearctic flyway

Joan Estrada[1*], Liam P. Langley[1,2*], Ulrik Lötberg[3] & Susanne Åkesson[1]

1) Department of Biology, Lund University, Ecology Building, 223 62, Lund, Sweden

2) Lyell Centre, Heriot-Watt University, Edinburgh, UK

3) BirdLife Sweden, Stenhusa Gård, 386 62 Mörbylånga, Sweden

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(*) Shared first authorship

Correspondence: Joan Estrada (joanestrada2000@gmail.com), Liam Langley (l.langley@hw.ac.uk) and Susanne Åkesson (susanne.akesson@biol.lu.se)

Abstract

Background: Migration is a complex behaviour, requiring individuals to integrate genetic, environmental and social information to reach distant goals, with important consequences for individuals, populations and communities. However, despite its ecological importance, our understanding of the development of migration behaviour across an organism's lifetime is lacking for most taxa. Recently, developments in bio-logging have enabled us to track juveniles of many species during their first migrations, improving our understanding of migration ontogeny. The Baltic Lesser Black-backed Gull (*L. f. fuscus*) is a long-distance migratory seabird inhabiting the eastern Afro-Palearctic flyway that has undergone recent, dramatic declines. However, determining the drivers of these trends is hindered by poor understanding of fine-scale space use, particularly during the non-breeding period.

Methods: Here we fitted GPS-tags to a total of 70 adult and 39 juvenile Baltic gulls from 19 Swedish colonies to examine age-related differences in movement behaviour during autumn migration.

Results: We observed clear differences in the autumn migration behaviour of adult and juvenile Baltic Gulls. Adults tended to migrate further than juveniles, with a much higher probability of crossing the Sahara. They also completed their migrations faster despite similar flight speeds between age classes, with observed differences in overall migration speeds resulting from longer and more frequent stopovers in juveniles. Moreover, migration routes showed equivalent directness between age classes, with a notable lack of exploratory movements by juveniles.

Conclusions: GPS-tracking of adult and juvenile Baltic Gulls revealed little evidence of exploratory behaviour, providing limited support for the exploration-refinement hypothesis during neonatal migration. Combined with latitudinal differences in migration destinations between age classes, our work suggests that learning and development of this long-distance

39 migration requires multiple annual cycles to complete. Additionally, we identify several key
40 stopover and wintering sites used by Baltic Gulls during the non-breeding period, facilitating
41 the identification of potential threats across the species' life cycle.

Introduction

Migration is a complex behaviour requiring individual organisms to integrate a range of genetic, environmental and social cues [1,2] to travel successfully between disjunct breeding and non-breeding sites, often located thousands of kilometres apart and separated by ecological barriers [3]. In doing so, individuals can track seasonal changes in resource availability at a global level [4,5] with the complex spatio-temporal decisions made by migrants resulting in important downstream consequences for individual fitness [6], population demographics [7] and ultimately trophic interactions and ecosystem functioning [8,9]. Moreover, migrants must balance information from both intrinsic and extrinsic drivers [10], making complex spatio-temporal decisions to balance trade-offs between time- and energy-minimising strategies [11–13] with the relative costs and benefits varying between individuals, seasons and life-history stages [5,14].

Migration is a high-risk behaviour for experienced adults, with migration periods often constituting a key survival bottleneck during the annual cycle [7,15]. However, it represents an even more difficult task for naïve juveniles embarking on their inaugural migrations [2], which may face additional challenges including lower flight capabilities [16,17], reducing resistance to adverse weather conditions enroute [18], poorer navigation skills [19–21] and a lower foraging efficiency at stopovers [22,23]. However, despite the ecological importance of migration, our understanding of how this behaviour is developed and refined across an organism's lifetime remains poorly understood for most species [5,24,25].

Birds are a diverse and abundant group of animal migrants and represent an important model system for understanding migration and its ontogeny. Research has revealed that many songbirds, which often migrate alone, rely largely on genetically encoded endogenous programmes to determine the direction and extent of post-fledging migration [26,27]. However, in other taxa migration development requires learning, drawing on both personal

67 information from the environment [28], and social information from conspecifics [18,24]. For
68 these species, the exploration-refinement hypothesis suggests individuals should exhibit
69 exploratory behaviour during their first migration to maximise learning and improve efficiency
70 during subsequent migrations [19,24,29]. This pattern is particularly expected in long-lived,
71 solitary species which exhibit delayed maturity and refine migration strategies over several
72 years [18,25,30].

73 Due to the complexities of migratory development, age-related differences in migration
74 strategies have been observed in many migratory species [31–34], although they are rare in
75 social taxa, where juveniles travel with adults during their first migration [35–38]. Differences in
76 migration behaviour may also contribute to spatial segregation between age classes during the
77 non-breeding period, along with factors such as differences in social dominance, habitat
78 preferences and previous knowledge [16,39,40]. The decisions made by juveniles during the
79 post-fledging migration therefore have important implications for the fate of both individuals
80 [41] and populations, with juvenile survival as a key factor in determining population dynamics,
81 especially for endangered taxa [42]. Identifying migratory routes, key stopover sites and core
82 overwintering areas of different age classes is therefore paramount to identify threats and
83 develop coherent conservation strategies for threatened migrant species [16,43,44].

84 Historically, understanding the migration behaviour of juvenile birds was a challenge,
85 particularly for species utilising remote, inaccessible wintering sites [37,45] and seabirds which
86 have long periods of post-fledging immaturity before returning to the colony [16,34]. However
87 ongoing technological advances have led to a reduction in size and cost of bio-logging devices
88 and an improvement in remote download capabilities, facilitating an increase in the number of
89 individuals and range of species that can be tracked [46,47]. As a result, juveniles from several
90 species have recently been tracked for the first time, providing important insights into post-
91 fledging migration behaviour [23,38,44,48,49]. In addition, longitudinal tracking across multiple

92 annual cycles has revealed ongoing refinement in migration strategies across the lifetime of
93 individual birds, highlighting the importance of learning in the ontogeny of this behaviour
94 [18,24].

95 The Baltic Lesser Black-backed Gull (*Larus f. fuscus*, here after Baltic Gull) is a long-distance
96 migrant seabird, breeding in the Baltic, Northern Norway and the White Sea (Russia) and
97 wintering in East Africa [50–52]. The global population of this endangered taxon has recently
98 stabilised at around 9,900 pairs following rapid declines driven by low reproductive output
99 resulting from predation, food shortages, and pesticide contamination [53–55]. In contrast to
100 the western subspecies *L. f. intermedius* and *L. f. graellsii* (hereafter western Lesser Black-
101 backed Gull), which have been well studied [49,56–59], our current understanding of Baltic Gull
102 movement behaviour is limited. Ring-resighting studies and tracking with light-level geolocators
103 have revealed rapid, long-distance migrations along the eastern Afro-Palearctic flyway to
104 wintering sites in East Africa [51,60]. However, we still lack a detailed understanding of their
105 fine-scale migratory behaviour. Furthermore, existing tracking studies focus on adults, and
106 information on post-fledging migration behaviour is limited to mark-recapture studies, which
107 suggest no age-related differences [61,62]. High resolution information on the migration
108 behaviour, routes and stopover sites used by juveniles is therefore urgently required to
109 understand the migration ontogeny of this threatened taxon and identify important sites and
110 potential threats during this key life-history stage.

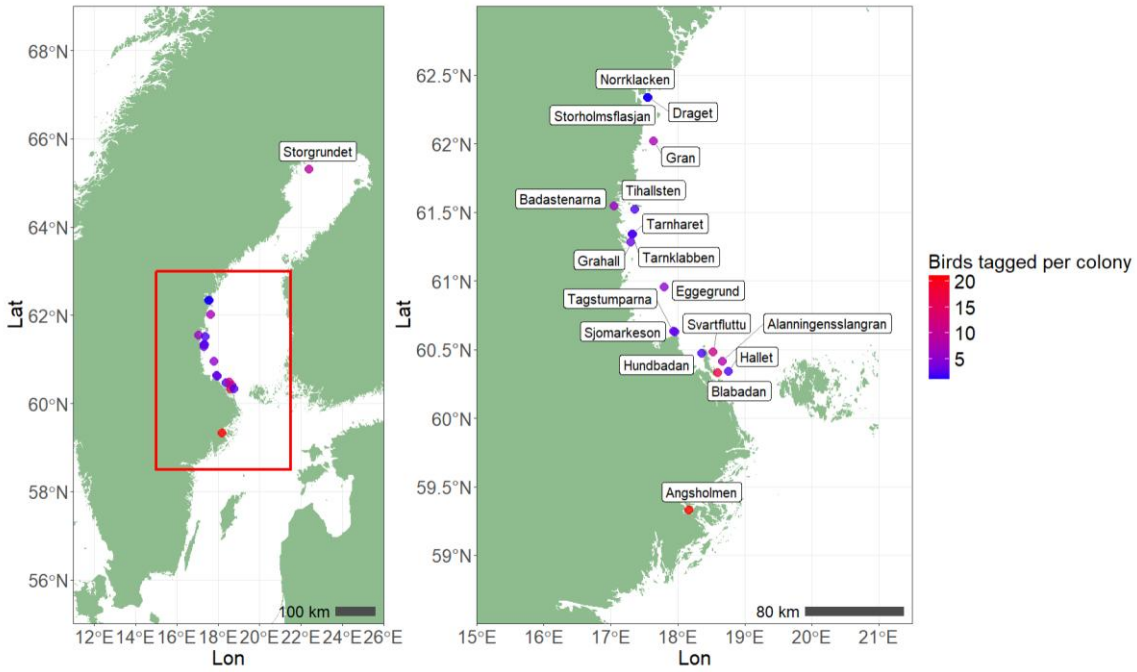
111 Here we used high resolution GPS tracking data from Baltic gulls breeding at colonies along the
112 Swedish coast to examine age-dependent differences in autumn migration behaviour for the
113 first time. Specifically, we investigated whether adults and juveniles differ in terms of migration
114 speed and duration, distance travelled, and patterns of stopover use. We expected juveniles to
115 spend longer migrating than adults during autumn due to their lower migration capabilities (i.e.
116 navigation and flight performance) [18,20] We also expected adults to fly at higher speeds than

juveniles during migration, since juvenile birds tend to have reduced flight capabilities. Secondly, we expected both age classes to travel similar distances to reach their wintering areas, as previous ring re-sighting studies suggest that Baltic gulls migrating do not show age-related segregation in wintering site [61] in contrast to western Lesser Black-backed Gulls, where adults winter further north [62,63]. Thirdly, we expected adults to spend less time at stopovers than juveniles, since immature seabirds generally have a lower feeding efficiency [22,23].

Materials and methods

GPS tracking and field sites

A total of 109 individuals (70 adults, 39 juveniles) were captured and equipped with Ornitela GPS-GSM trackers. All captured individuals were identified as Baltic gulls based on plumage and biometrics. Captures and GPS deployments occurred between 2017 and 2024 and were carried out between late May and late July (28/05 - 29/07) at 19 Swedish colonies, spread through five counties (Gävleborgs län, Norrbotten, Stockholm, Uppsala, Västernorrland) along the Baltic Sea coast (Fig. 1; Table 1). Breeding adults were captured at the nest using spring traps during incubation only. Captured individuals were weighed to the nearest 1 g, had biometrics measurements taken, were fitted with a metal ring with a unique identifier and equipped with a GPS tracker using a permanent leg-loop harness. Device and attachment combinations did not exceed 5% of body mass (range = 2.8 – 4.5%; Table S1). Captured individuals were not sexed.



137

138 *Figure 1*. Location of the 19 colonies along the Baltic Swedish coast where adult and juvenile Baltic gulls

139 were captured and tagged with GPS trackers.

140 *Table 1*. Numbers of adult and juvenile Baltic gulls equipped with GPS trackers in each breeding colony.

Colony	Area	Adults	Juveniles
Bådastenarna	Agön	5	1
Tihällsten	Agön	2	0
Draget	Alnön	1	0
Norrklacken	Alnön	5	0
Storholmsfläsjan	Alnön	1	0
Sjömärkesön	Björns skärgård	2	0
Tågstumparna	Björns skärgård	3	0
Ängsholmen	Fjäderholmarna	8	13
Eggegrund	Gävle	5	0
Gran	Gnarp	7	0
Ålänningensslangran	Gräsö	1	7
Blåbådan	Gräsö	8	9
Hållet	Gräsö	0	2
Hundbådan	Gräsö	2	0
Svartfluttu	Gräsö	5	6
Storgrundet	Rödkallen	8	1
Tärnharet	Prästgrundet	2	0
Tärnklabben	Prästgrundet	2	0
Gråhäll	Skatön	3	0

141 Colonies were visited between 2017-2024. The general area of each colony in Sweden is noted.

142 <u>Data processing and migration start/ends</u>

GPS-data collected from 109 individuals (70 adults + 39 juveniles) were cleaned and processed using the ExMove toolkit [64], which involved the removal of fixes exceeding a maximum groundspeed threshold of 150 km/h. Additionally, tracks from two individuals (1 adult + 1 juvenile) using a highly unusual Atlantic migration route were removed due to the possibility that they were western Lesser Black-backed Gulls or hybrids. This resulted in a final data set of 112 complete autumn migration tracks (100 adults + 12 juveniles) from 69 individuals (57 adults + 12 juveniles) used for further analysis (Table S2, Fig. 2).

Autumn migration periods were defined using a combination of colony departure dates and observed patterns of latitudinal change. The Douglas-Peucker broken stick algorithm (D-P algorithm) was used to select breakpoints in latitudinal movement patterns used to define the onset and cessation of autumn migration [65]. The D-P algorithm simplifies a complex curve composed of straight-line segments to a similar curve with fewer points. The tolerance parameter (ε) controls the resulting number of line segments and break points, with a lower ε resulting in an increased number of segments/break points [66]. Several values of ε can produce the same combinations of lines and breakpoints and all solutions for a given number of line segments are identical. To apply the algorithm, all tracks were first filtered for the second half of the year. A sensitivity analysis was conducted per individual, varying the value of ε across the extent of reasonable values (0.5 to 30 by 0.5). Values of ε which produced less than four breakpoints were removed as this was the minimum required to define migration. The combination of lines and breakpoints produced by the widest range of values of ε was then retained, as this solution was assumed to best reflect the overall “shape” of latitudinal change over time.

Using this solution, the second and penultimate breakpoints, reflecting the onset and cessation of directed latitudinal movement, were initially used to define the start and end of migration. However, visual inspection of latitude vs time plots revealed that the algorithm performed

poorly at identifying migratory departure for many juveniles. To make autumn migration metrics comparable between age classes, we therefore filtered adult tracks to retain only those from the tagging year (due to breeding failures and sabbaticals in subsequent years making colony departure an unreliable indicator of departure) and used colony-departure date as the onset of migration for all birds. This resulted in a total of 57 adult tracks used to calculate autumn migration metrics (Table S2, Fig. 2).

Prior to any distance calculation, fixes around conflict zones with visual evidence of GNSS spoofing (5 fixes) were removed [67], first by filtering out fixes where the difference between ground and instantaneous speed was >120 kph and then removing locations at spoofing hotspots (i.e. Beirut airport) not captured by the speed filter. Finally, our tracking data showed spatio-temporal variation in sampling rates (Table S3) which can influence distance calculations [68]. Therefore, to calculate fine-scale daily migration metrics, autumn migration tracks were sub-sampled (rate = 1 hour, tolerance = 10 mins) using the the 'amt' package [69]. Following subsampling, only days with at least a fix every two hours (12 fixes/day) and a time coverage of at least 20 hours were used to calculate daily metric, thresholds determined by a sensitivity analysis (Table S4; Figure S1).

Data analysis

Stopovers and resting hours

Stopovers were defined as days where the beeline distance covered between the first and last daily fix was less than 75 km following [70]. Days that were not stopovers were defined as travel days. For travel days only, each hourly period was classified as either travel or rest, with rest hours defined as those where the bird had an hourly ground speed lower or equal to 3.6 km/h [57]. Hours with groundspeeds above this threshold were considered travel hours.

Track-level migration metrics

Overall migration duration (days), total stopover and total travel days were calculated for each track along with the total number of stopover sites used and average stopover length. The number of travel and rest hours was then calculated only for travel days. Thereafter distances covered by gulls between breeding and wintering grounds were explored. For travel distances, both beeline and cumulative distances were considered. Overall migration beeline distances were calculated by computing the great circle distance between the first and last fix for each migration track. Due to the irregular distribution of migration distance, we assigned all tracks a bimodal classification of the Sahara crossing (beeline > 4000km) or not (beeline ≤ 4000km). Cumulative travel distances were calculated by summing all daily beeline distances for travel days in a track. A straightness index was then calculated for each track by dividing the beeline distance by the cumulative travel distance [71] with values ranging from zero (high path tortuosity) to one (low path tortuosity).

Migration and travel speeds were calculated by dividing the total cumulative distance by the number of total migration days (stopover and travel) and number of travel days, respectively. Flight speeds were calculated in terms of ground speed and instantaneous speed (km/h). Daily average instantaneous speeds recorded by the logger were calculated for all travel days and then averaged for each migration track. Mean ground speeds for each migration track were calculated by first dividing the beeline travel distance covered in each travel day by the GPS coverage of each day in hours to calculate a daily ground speed and then averaging all the daily ground speeds for each migration period.

Daily-level migration metrics

Daily migration and travel speeds (km/day) were first calculated. Daily migration speeds were calculated as the average daily beeline distance between the first and last daily fix, including both stopover and travel days. Daily travel speeds were calculated as the average daily beeline distance between the first and last daily fix, including only travel days. Daily cumulative

distances were then calculated by summing all fix-to-fix distances for each day. Finally, a straightness index was estimated for each travel day by dividing the daily beeline distance by the daily cumulative distance during that day.

Statistical Modelling

We used linear mixed effects models (LMMs) to test for differences in daily and track-level migration parameters in relation to age using the 'lme4' package [72]. Number of rest hours was fitted with a gamma generalised linear mixed effects model (GLMM) due to strong right-skew. Probability of crossing the Sahara was modelled with a binomial GLMM. All models contained tagging age as the only fixed effect. Year was included in all models as a random intercept to account for potential interannual variation in migration behaviour.

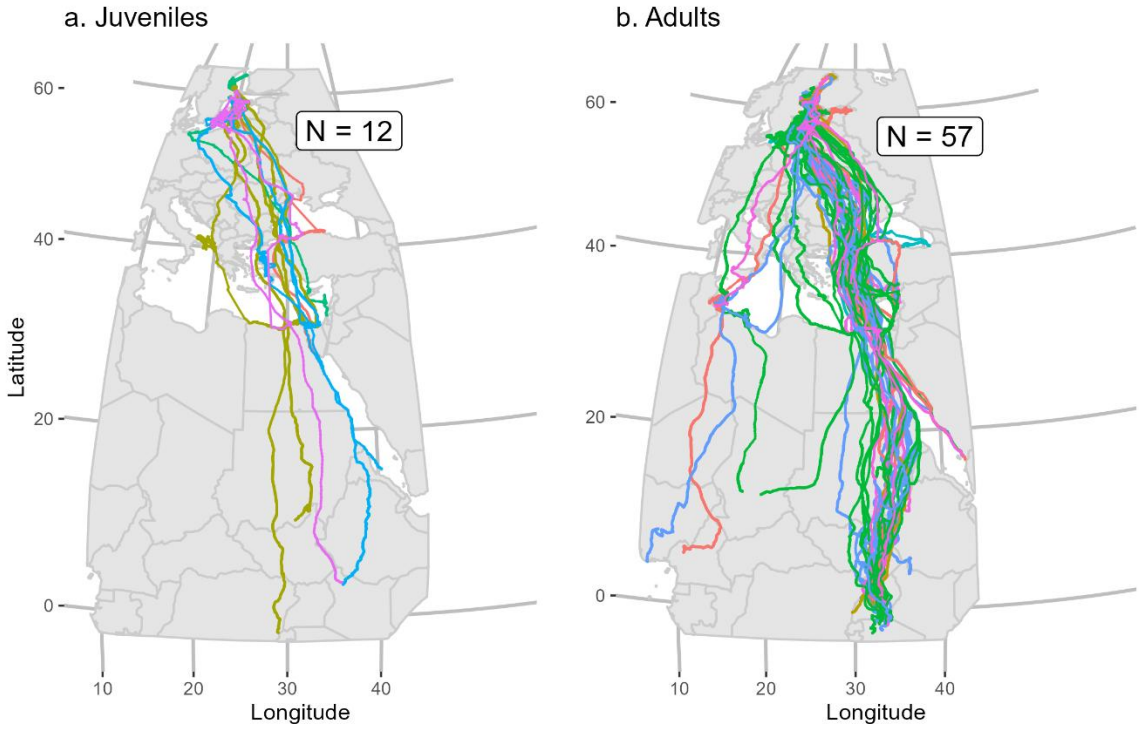
The significance of age as a predictor in all models was assessed using likelihood ratio tests [73]. For all models, we also calculated both marginal R^2 (MR^2), the proportion of the variance explained by the fixed effects alone and conditional R^2 (CR^2), the proportion of the variance explained by both the fixed and random effects, using the '*MuMIN*' package [74,75]. All data processing and subsequent analysis was conducted in R (Version 2024.12.0) [76].

Results

Migration Behaviour

Track-level migration metrics

Following data processing, a total of 57 adult tracks (57 individuals; 331,223 fixes) and 12 juvenile tracks (12 individuals; 60,700 fixes) were retained for track-level analyses. Adult birds tended to migrate further than juveniles and spend the winter in more southern latitudes in Africa, whereas juveniles wintered closer to breeding areas and tended to spend the winter in the Mediterranean (Fig. 2).



240

241 *Figure 2.* Autumn migration tracks of juvenile **(a)** and adult **(b)** Baltic gulls. Tracks are colored by year and

242 the number of tracks used for each age class is shown at the top right corner of each plot.

243 *Temporal metrics*

244 Adult Baltic gulls started autumn migration slightly but not significantly earlier than juveniles ($\bar{x}$

245 = August 17th vs. August 24th; p = 0.38, R_m^2 = 0.01, R_c^2 = 0.07) (Fig. 3a; Table 2). Arrival dates

246 differed more between age groups, with adults reaching their more distantly located wintering

247 areas significantly earlier than juveniles ($\bar{x}$ = September 25th vs. October 28th; p < 0.001, R_m^2 =

248 0.25, R_c^2 = 0.34) (Fig. 3b; Table 2) resulting in adults exhibiting shorter migration durations

249 overall ($\bar{x}$ = 38 days vs. 66 days; p < 0.001, R_m^2 = 0.14, R_c^2 = 0.20) (Fig 3c; Table 2). Longer overall

250 migrations in juveniles were a result of more stopover days ($\bar{x}$ = 61 days vs. 21 days; p < 0.001,

251 R_m^2 = 0.42, R_c^2 = 0.42) (Fig. 3e,;Table 2), despite juveniles spending significantly fewer days

252 travelling overall ($\bar{x}$ – 14 days vs. 18 days; p < 0.05, R_m^2 = 0.08, R_c^2 = 0.08) (Fig. 3d; Table 2).

253 Moreover, adult gulls used slightly fewer stopover sites than juveniles ($\bar{x}$ = 5 sites vs. 7 sites; p =

0.27, R_m^2 = 0.02, R_c^2 = 0.04) (Fig. 3f; Fig. 4; Table 2), and spent less time at each stopover (mean = 3 days vs. 9 days; $p < 0.001$, R_m^2 = 0.29, R_c^2 = 0.32) (Fig. 3g; Fig. 4; Table 2).

The main stopover for both age classes occurs in the Nile River Delta and some minor stopovers occur along the Black Sea coast (North and South) and the Turkish Mediterranean (Fig. 4). Adults also make some stopovers in sub-Saharan wetlands, mainly in Sudan. Travel days during migration consisted of both travel and rest hours. Overall, adults spent more hours travelling during migration than juveniles ($\bar{x}$ = 226 hours vs. 125 hours; $p < 0.001$, R_m^2 = 0.18, R_c^2 = 0.19) (Fig. 3h; Table 2), however the number of total rest hours during travel days was only slightly higher in adults ($\bar{x}$ = 147 hours vs. 98 hours; $p = 0.14$, R_m^2 = 0.04, R_c^2 = 0.07) than in juveniles (Fig. 3i; Table 2).

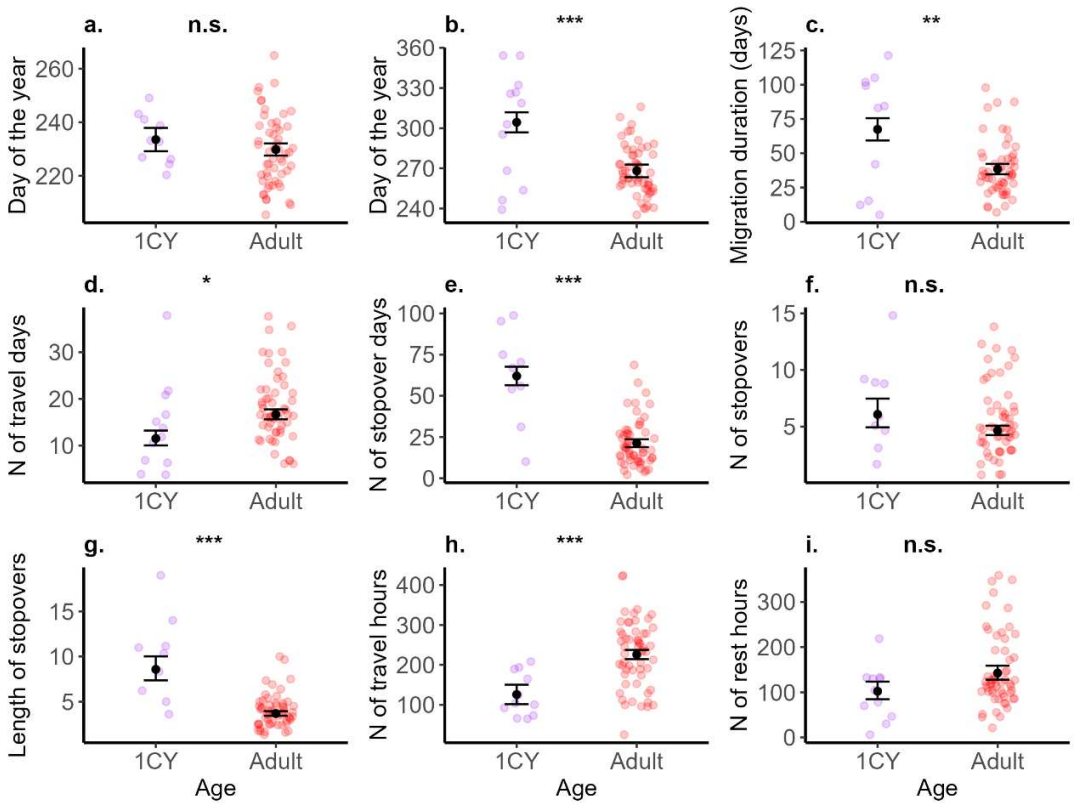


Figure 3. **(a)** Departure day, **(b)** arrival day, **(c)** migration duration (days), **(d)** number of travel days, **(e)** number of stopover days, **(f)** number of stopovers, **(g)** stopover length (days), **(h)** number of travel hours, and **(i)** number of rest hours. Number of travel and rest hours have only been considered for travel days. Data for juvenile and adult Baltic gulls is presented in purple and red, respectively. The black points and

error bars are estimated marginal means and 95% CIs, respectively, and the points behind represent the raw data. The labels over each plot represent the level of statistical significance in the data (n.s.: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$).

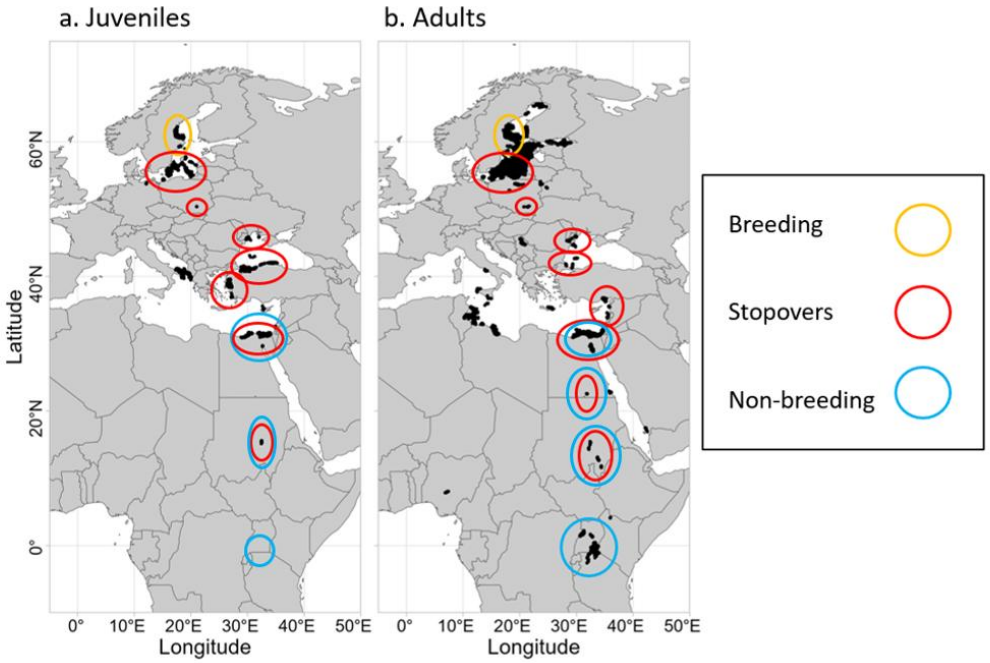


Figure 4. Main autumn stopover sites of juvenile **(a)** and adult **(b)** Baltic gulls along the East Afro-Palearctic Flyway. Black dots represent individual positions during stopover days, red circles represent the main stopovers sites, orange circles represent breeding areas and blue circles represent the main wintering areas. Areas with red and blue circles over them are used both as stopovers and wintering areas by different individuals. NB: Lake Victoria is highlighted as a wintering site for juveniles as at least one tagged individual eventually ended up at the site after spending a large proportion of the non-breeding period further north.

Distance metrics

Adults travelled further south than juveniles to reach their wintering grounds, covering an average migration distance of 5804 km (range = 3070 – 7334; Table 2), as opposed to juveniles that travelled an average migration distance of 4454 km (range = 2607 – 6853; Table 2). The average cumulative migration distance travelled by adults was 6726 km (range = 3262 – 11106; Table 2), whereas juveniles travelled 5121 km on average (range = 2594 – 9043; Table 2). As a

result of this, the probability of adults crossing the Sahara during autumn migration was significantly higher than that of juveniles ($p < 0.05$, $R_m^2 = 0.06$, $R_c^2 = 0.06$) (Fig. 5a). Despite differences in migration distance and speed, migration directness in terms of straightness index was not significantly different between adults and juveniles ($\bar{x} = 0.88$ vs. 0.89; $p = 0.94$, $R_m^2 = 0$, $R_c^2 = 0.11$) (Fig. 5b; Table 2), suggesting both age classes appeared to show a similar degree of exploratory behaviour in terms of migration routes.

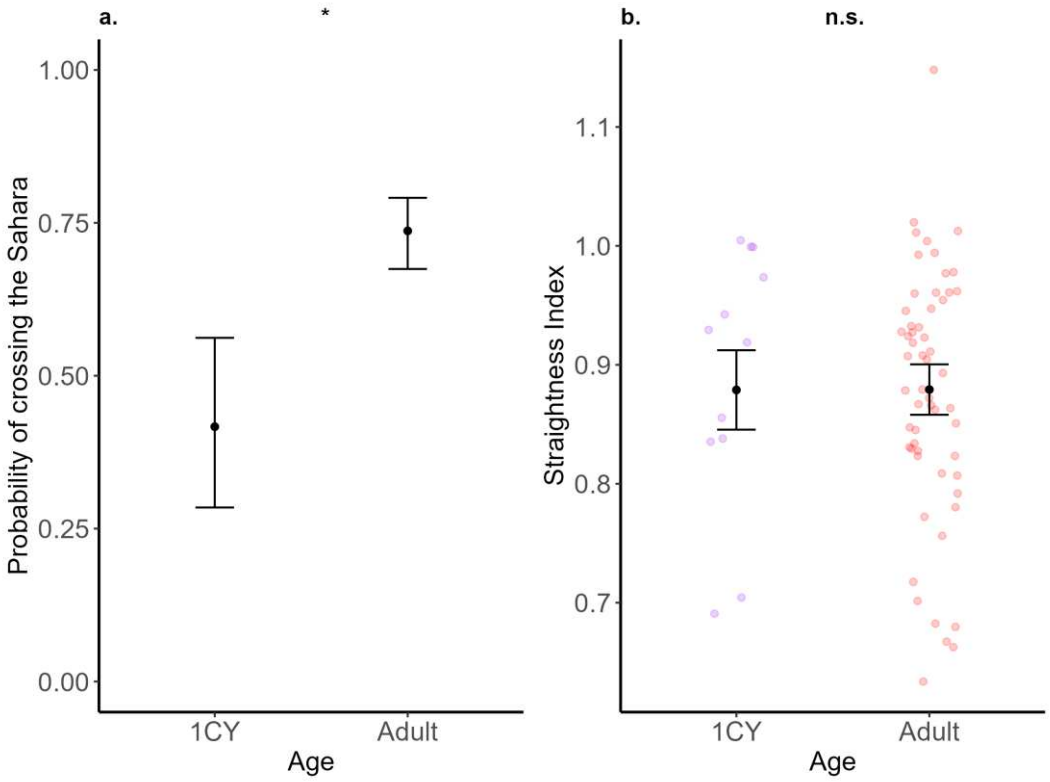


Figure 5. **(a)** Probability of crossing the Sahara (based on migration beeline distances). **(b)** Straightness index. The straightness index has been calculated by dividing beeline distances over cumulative distances for each track. Data for juvenile and adult Baltic gulls is presented in purple and red, respectively. The black points and error bars are estimated marginal means and 95% CIs, respectively, and the points behind represent the raw data. The labels over each plot represent the level of statistical significance in the data (n.s. = $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Speed metrics

Across the entire migration track, adult gulls achieved significantly faster overall migration speeds than juveniles ($\bar{x}$ = 202 km/day vs. 170km/day; $p < 0.01$, $R_m^2 = 0.12$, $R_c^2 = 0.12$) (Fig 6a; Table 2). However, during travel days only, overall migration speed was similar between adults and juveniles ($\bar{x}$ = 393 km/day vs. 444 km/day; $p = 0.27$, $R_m^2 = 0.03$, $R_c^2 = 0.03$) (Fig. 6b; Table 2). Ground speeds achieved during travel days were significantly lower for adults than for juveniles ($\bar{x}$ = 17 km/h vs. 21km/h; $p < 0.01$, $R_m^2 = 0.10$, $R_c^2 = 0.10$) (Fig. 6c; Table 2), however instantaneous speeds, as recorded by the logger, during travel days did not differ between adults and juveniles ($\bar{x}$ = 24 km/h vs. 25km/h; $p = 0.53$, $R_m^2 = 0.01$, $R_c^2 = 0.01$) (Fig. 6d; Table 2) range = 16 – 34; Table 2).

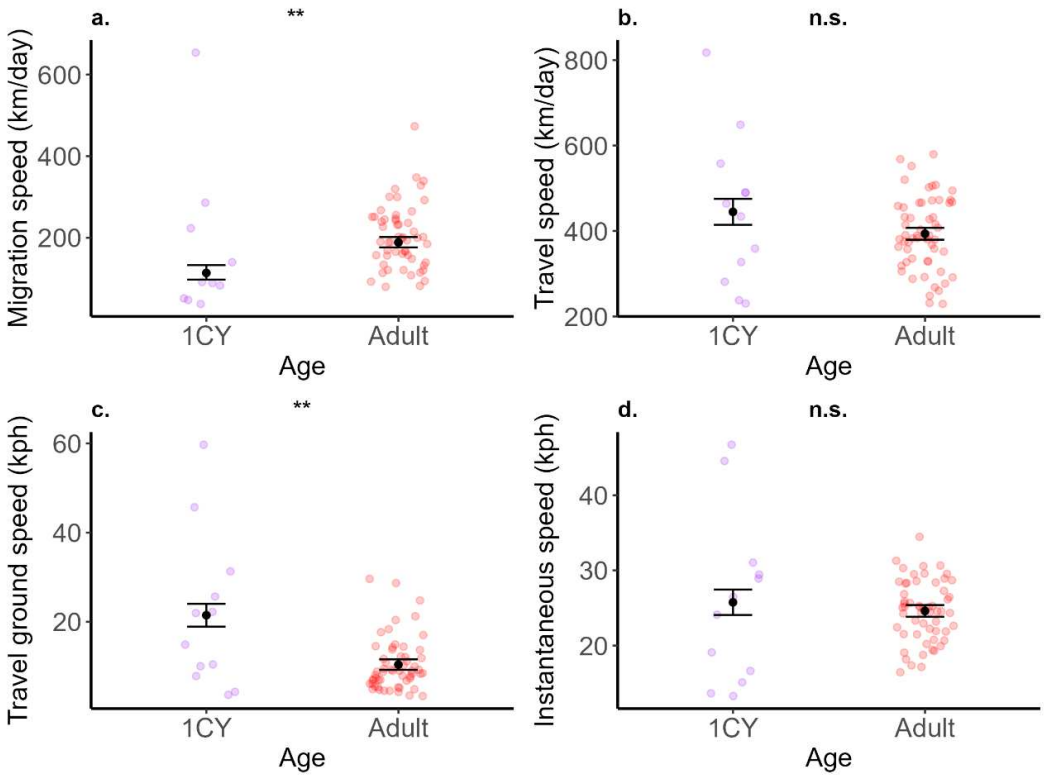


Figure 6. **(a)** Migration speed (km/day), **(b)** Travel speed (km/day) and **(c)** Ground speed (km/h). **(d)** Instantaneous speed (km/h). Migration speeds have been calculated accounting for travel and stopover days. Travel, ground and instantaneous speeds have been calculated accounting for travel days only. Data for juvenile and adult Baltic gulls is presented in purple and red, respectively. The black points and error bars are estimated marginal means and 95% CIs, respectively, and the points behind represent the raw

315 data. The labels over each plot represent the level of statistical significance in the data (n.s. = $p > 0.05$, *

316 = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

317 *Table 2.* Summary of migration metrics for autumn migration (adults and juvenile) in Baltic gulls.

	Adults Mean (±SD)	**Juveniles** Mean (±SD)
Onset of migration	229 (13.36)	233 (9.36)
Arrival at wintering grounds	268 (18.15)	301 (40.91)
Migration duration (days)	38.70 (20.22)	66.80 (43.91)
Number of travel days	18.11 (7.31)	14.25 (9.65)
Number of stopover days	21.28 (14.26)	61.89 (28.46)
Number of stopovers	5.54 (3.12)	7 (3.97)
Duration of stopovers (days)	3.98 (1.81)	9.85 (4.77)
Number of travel hours	226.70 (83.09)	125.50 (54.23)
Number of rest hours	147 (80.58)	98.09 (60.13)
Overall beeline distance covered (km)	5804 (1536.39)	4454 (1507.19)
Overall cumulative distance covered (km)	6726 (1959.96)	5121 (1979.94)
Straightness index	0.88 (0.10)	0.89 (0.11)
Migration speed (km/day)	202.80 (78.25)	170.19 (188.08)
Travel speed (km/day)	393.56 (85.22)	444.74 (174.33)
Ground speed (km/h)	17.08 (3.55)	21.32 (88.71)
Instantaneous speed (km/h)	24.61 (4.04)	25.75 (11.24)

318 Only tracks from the year of tagging were included for adult individuals. Onset of migration and arrival at

319 wintering is presented as day of the year.

320 *Daily-level migration metrics*

321 Following data processing and subsampling, a total number of 25 adult tracks (25 individuals)

322 that included 3966 fixes and a total number of 10 juvenile tracks (10 individuals) that included

323 5874 fixes were used for this daily-level analysis. At a daily level, the movement behaviour of

324 adult and juvenile Baltic gulls, respectively, was comparable in terms of daily beeline distance

325 (mean = 400 km vs. 399 km; $p = 0.46$, $R_m^2 = 0$, $R_c^2 = 0.23$), cumulative travel distances (mean =

326 455 km cs. 449 km; $p = 0.88$, $R_m^2 = 0.01$, $R_c^2 = 0.23$) or directness (mean 0.83 vs. 0.83; $p = 0.77$,

327 $R_m^2 = 0$, $R_c^2 = 0.10$) during migration travel days (Fig. 7; Table 3).

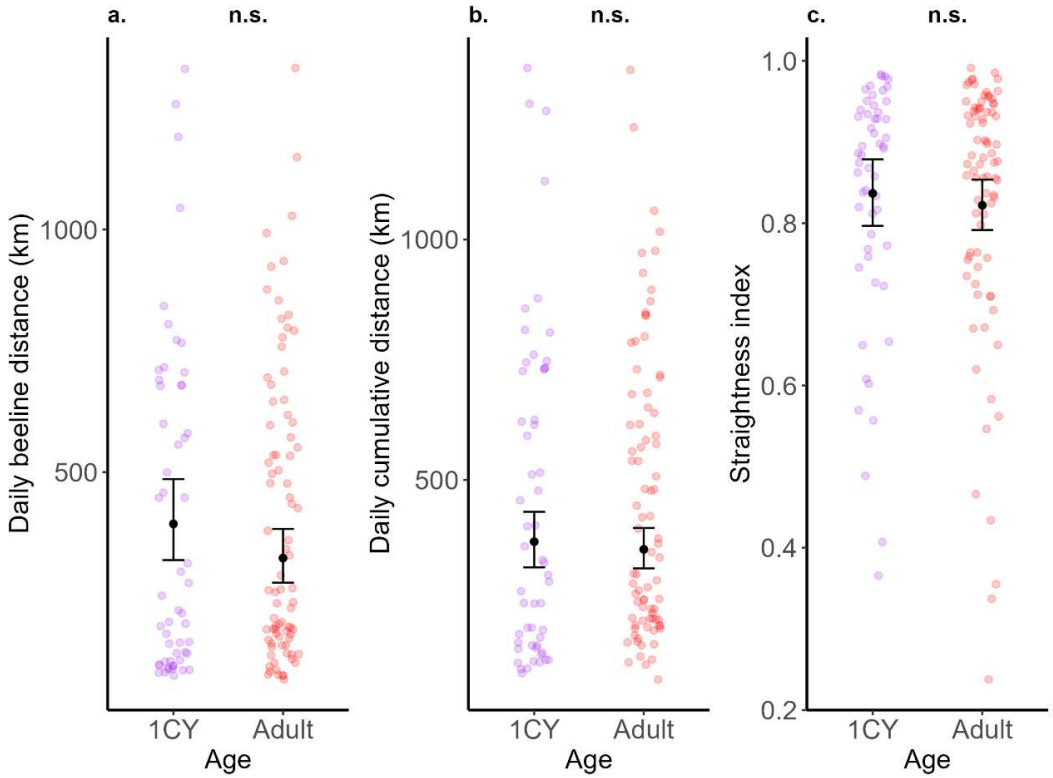


Figure 7. **(a)** Daily beeline migration distance (km), **(b)** daily cumulative migration distance (km) and **(c)** daily straightness index. The straightness index has been calculated by dividing daily beeline distances over daily cumulative distances for each migration travel day. Data for juvenile (1CY) and adult Baltic gulls is presented in purple and red, respectively. The black points and error bars are estimated marginal means and 95% CIs, respectively, and the points behind represent the raw data. The labels over each plot represent the level of statistical significance in the data (n.s.: $p > 0.05$, * : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$).

Table 3. Summary of daily-level metrics for autumn migration (adults and juveniles) in Baltic gulls

	Adults Mean (±SD)	**Juveniles** Mean (±SD)
Daily beeline distance covered (km)	400.52 (302.12)	399.79 (340.23)
Daily cumulative distance covered (km)	455.93 (295.64)	449.89 (338.38)
Straightness index	0.83 (0.16)	0.83 (0.15)

Only tracks from the year of tagging were included for adult individuals.

Discussion

Migration Behaviour

Migration distance

Migration distances were greater for adults than juveniles (Fig. 2) with adults showing a higher probability of crossing the Sahara and wintering further south than juveniles (Figs. 4, 5). This result contrasts with historic mark-recapture studies in Lesser Black-backed Gulls where adults wintered further north than juveniles [63,77] and in Baltic Gulls where no age-related segregation was observed [62]. This illustrates the potential impacts of heterogeneity in re-sighting effort on mark-recapture studies [78] and the value of bio-logging approaches when investigating age-related differences in migration behaviour [31,49]. Shorter migration distances in juvenile Baltic Gulls also contradict the arrival time hypothesis, which suggests adults should winter closer to their breeding grounds due to pressure to return early and secure territories [77]. In our study, the Sahara Desert may act as a significant geographic barrier, curtailing the migrations of inexperienced juveniles with poor flight efficiency [79], although some tracked juveniles successfully made the crossing (Fig. 2). Alternatively, shifts towards northern wintering sites may represent a climate-driven range shift, with older birds fixed in their Sahara-crossing strategy resulting in an apparent bimodal strategy.

Differential migration could also be observed if wintering site reflects individual body condition [80] with birds with suboptimal body condition foregoing the Sahara crossing to avoid increased mortality risk. Further research, integrating biometrics with tracking data, could begin to unpick the effect of individual condition on migration behaviour both within and between age-classes. Juveniles lacking optimal flight and orientation skills may specifically choose to avoid this barrier crossing on the inaugural migration [18,20]. Moreover, the slower migration pace in juveniles may lead them to reach the barrier crossing later than adults, exposing them to unfavourable wind regimes [81,82] and reducing the availability of social navigational information from adults [7].

Additionally, competitive asymmetry could also explain the observed pattern of differential migration, with juveniles avoiding resource competition with dominant adults. Age-related structuring of winter distribution based on competitive exclusion has also been observed in Great Cormorants (*Phalacrocorax carbo*) [83]. Within-adults, socially dominant individuals may be able to travel further to access high quality wintering sites, while still competing for quality breeding sites independently of subsequent arrival timing [80]. In passerines however, the classical study of differential migration in the Dark-eyed Junco (*Junco hyemalis*) shows that more factors than dominance account for age-and sex-segregation in the non-breeding ranges [84,85]. Additionally, migration distance and wintering site choice may also have a genetic component [26,27,86]. Importantly, genetic and environmental factors are not mutually exclusive, and may combine to influence migration behaviour and winter site selection.

Migration behaviour

Despite the longer migrations observed in adult Baltic Gulls, onset of autumn migration was slightly, but not significantly, earlier than juveniles on average (Fig 4a). In long-distance migrants, adults usually initiate migration earlier than juveniles whilst the opposite is often true for short-distance migrants [33,87]. The similarity of departure timing observed here might result from adults performing a post-breeding moult, including the initiation of primary moult prior to migrating [88], a costly life-history event that would delay their departure date [10]. Observed departure patterns contrasted with those of tracked Lesser Black-backed Gulls, with adults from our study departing almost a month later and juveniles departing a few days earlier on average [49,59]. Western Lesser Black-backed Gulls, being short-distance migrants, also commence primary moult at breeding areas, but they moult faster than Baltic gulls [88] facilitating the relatively earlier start of autumn migration in these populations [59].

Adult Baltic gulls achieved faster overall migration speeds than juveniles and reached their wintering areas earlier despite similarities in departure date. Faster migration in adults is a

common phenomenon among many long-distance migratory birds [36]. Here, it cannot be attributed to faster flight bouts, since adult gulls did not fly at higher speeds during travel days, as shown here by the comparable travel speeds (km/day) and instantaneous speeds (km/h) between age classes. Juveniles even achieved higher ground speeds (km/h) than adults during travel days in autumn but still took much longer to complete their migration than adults. The faster average ground speed in juveniles in autumn may result from reduced adult groundspeeds during Sahara crossings rarely undertaken by juveniles (Fig. 2), or possibly an increased propensity for adults to make brief stops to forage during travel days [89].

In addition, there was no effect of age on overall straightness index or fine-scale measures of flight behaviour such as daily travel distances (beeline and cumulative) and travel ratios (daily cumulative/beeline distances). This suggests that juveniles on their first migrations exhibited a similar level of exploratory behaviour to experienced adults providing limited support for the exploration-refinement hypothesis in this taxon [19,29]. One explanation for this observation is birds migrating predominantly in mixed-age flocks, which has been recorded in Western Lesser Black-backed Guls in Western Sahara [90], whilst similar migration straightness indices between age-classes have been recorded in a range of social migrants [34,36,37]. Additionally, route straightness might be influenced by environmental factors such as prevailing wind conditions or topographic features acting as barriers or navigational aids [81,91].

Observed differences in overall migration-speed were driven largely by differences in stopover behaviour, with juveniles stopping more frequently and for longer durations (Fig 3f). This pattern is not seen in western Lesser Black-backed Gulls, where juveniles show very similar migration behaviour, including flight and stopover patterns [49,56]. In contrast, juvenile long-distance migratory raptors [92] and songbirds [93] have been shown to spend more time at stopovers than adults during migration. One possible explanation for faster migration in adults relates to differences in foraging efficiency. GPS-tracking has revealed lower foraging

proficiency in juvenile western Lesser Black-backed Gulls [23] and other seabirds [22,43] and naïve juvenile Baltic Gulls may require more time per stopover to fuel sufficiently for the next flight bout. Moreover, inexperienced juveniles may select poorer quality stopovers with lower resource abundance, thus requiring longer stopovers to refuel sufficiently. Finally, the number of rest hours was higher for adults, suggesting they might employ a fly-and-forage strategy during travel days, and exploit resources found in water bodies enroute [89] rather than making long stopovers.

Ontogeny of Migration Behaviour

Overall, our results suggest naïve juvenile Baltic Gulls show equivalent levels of exploratory movement to adults, both during autumn migration and overwinter. This contrasts with predictions from the exploration-refinement hypothesis, which predicts that young individuals show more exploratory behaviour to facilitate learning and refine their behaviour for subsequent migrations [19,24,25,29]. Our results contrast with tracking-studies from a range of large-bodied bird species, which show more variable migration behaviour in juveniles followed by route refinement and canalisation over time [31,94,95]. It could be the case that juvenile Baltic Gulls are less exploratory during their inaugural autumn migration as progressive development of migratory behaviour requires several cycles [25,30]. This highlights the value of delayed maturity in seabirds, as it facilitates learning and optimisation of migration and overwinter behaviour, decreasing carry-over effects and increasing long-term reproductive success [30,96]. Alternatively, juvenile Baltic Gulls may use innate orientation during their initial migration, allowing them to rely less on exploration to refine their migratory route [97].

One key difference in migration behaviour is the increased frequency and duration of stopovers in juveniles relative to adults. Whilst this may be explained largely by differences in flight performance, foraging efficiency and their combined effects on fuelling [18,22,23], sampling a high number of stopovers may also represent an opportunity for exploration during this

inaugural migration. In doing so, juveniles may gain information about site quality and resource availability at multiple sites along the flyway, allowing them to optimise their stopover behaviour during future migrations [11,13] . This might be particularly important for long-distance migrants which have to fuel sufficiently to cross large geographic barriers [98]. Moreover, for species where route flexibility may be constrained by wind conditions and topography [81,91], stopover behaviour may be the main option for exploratory behaviour during post-fledging migration.

Another key result is that juvenile gulls migrate shorter distances and winter further North than adults, a pattern observed in other migratory seabirds [99]. Tagged adults exhibit a high degree of overwinter site fidelity (unpublished data), however longitudinal tracking of a large sample of juveniles over several annual cycles is required to disentangle the impacts of genetics relative to individual learning or fitness effects in the migration ontogeny and overwinter site selection of juveniles. If decisions are determined largely by genetic factors, we would expect juveniles to follow similar routes and use to the same sites in subsequent years. In this scenario, age-segregation may result from differential survival over time, with a greater proportion of juveniles maximising short-term survival by avoiding a crossing of the Sahara but reducing long-term survival by repeatedly using a lower quality wintering site. However, if wintering site selection is fitness-related, we would expect some juveniles that wintered north of the Sahara to switch strategies and travel further south and cross the Sahara as they age and gain experience. Under this scenario, wintering site selection result from life-history trade-offs, with juveniles maximising survival by avoiding a Sahara crossing and then switching to southern wintering sites which increase reproductive output when they reach breeding age.

A similar age-related wintering pattern is observed in the European Spoonbill (*Platalea leocorodia*), with birds migrating further south as they age [100]. Conversely, many species exhibit high winter site fidelity throughout their life, suggesting that information obtained

during the inaugural migration is key in determining long-term wintering site selection [38,87,101]. Importantly, these factors are not mutually exclusive, and long-lived migratory species are likely to rely on both genetic factors and learning to inform their movement decisions [38,102].

Methodological Considerations

Accounting for the pre-migratory fuelling period is a key consideration when calculating overall migration speed [103]. This is straightforward for species which forage at discrete sites between flight bouts [103], however it is highly complex for fly-and-forage migrants and may result in overestimation of migration speeds. Currently, there is no method to calculate pre-migratory fuelling periods in gulls, and therefore we cannot discount the possibility that lower foraging efficiency and fuelling rates may contribute to reduced migration speeds observed in juveniles [23,43]. Sex may also contribute to variation in migration behaviour [57,104]. However, we were unable to sex the tagged Baltic Gulls, particularly juveniles, at capture and therefore, we have not included sex in our analyses.

We classified travel and rest hours within travel days using a 3.6 km/h ground speed threshold [57]. However, this threshold approach may lead to non-directed flights at stopovers being classified as travel hours, despite not representing migratory movement, potentially leading to an overestimation of travel hours and an underestimation of rest hours during travel days. Conversely, calculation of ground speed thresholds required a sampling rate of at least two fixes per hour, and hours with only a single fix were thus removed. Data gaps and variation in sampling rates led to the removal of more hours for juveniles than adults, perhaps contributing to the higher number of rest hours on travel days observed in adults.

Finally, given potential deficiencies in flight performance [18] and foraging efficiency [22], juvenile Baltic Gulls may be more vulnerable to deleterious tag effects than adults [105], contributing to shorter observed migrations. We were unable to test for tag effects directly,

however all device and attachment combinations weighed less than 4.5% of body mass at capture (Table S1). Moreover, western Lesser Black-backed Gulls [23,49], and Caspian Terns [37], did not show differential migration between age classes when equipped with similar tag attachments, increasing our confidence that juveniles were not disproportionately impacted by tag effects.

Conclusions

Here we demonstrate clear age-related differences in migration behaviour of Baltic Gulls during autumn. Adults tended to migrate further than juveniles, with a much higher probability of crossing the Sahara, but completed their migrations faster. However, flight speeds were similar between age classes with observed differences in migration duration resulting from longer and more frequent stopovers in juveniles. Moreover, migration routes were equally direct between age classes, with a notable lack of exploratory movements by juveniles. Taken together, these results provide limited support for the exploration-refinement hypothesis during the neonatal migration of Baltic Gulls. This, coupled with the age-differences in migration destination, suggests that learning and development of the long distance Sub-Saharan migration frequently observed in adults requires multiple migration cycles. Longitudinal tracking of individuals across the entire immature period from fledging to first breeding would provide additional insights into the ontogeny of migration in this threatened taxon and determine how migratory routes are developed and refined over time. Additionally, we identify several key stopover and wintering sites used by Baltic Gulls during the non-breeding period, highlighting focal areas for further research to identify threats across the flyway and assess the viability of site-based conservation to address observed declines.

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Supplementary Material

This supplementary material file outlines the tagging dates and colonies, tag masses relative to body masses, GPS sampling rates and sample sizes.

Table S1. Body mass and device mass of each of the tagged Baltic Gulls (*L. f. fuscus*).

ID	Tagging age	Tagging date	Colony	Body mass (g)	Device mass (% body mass)
MA52	Adult	07/06/2018	Blåbådan	820	3.0
MA53	Adult	11/06/2018	Hundbådan	650	3.8
MC41	Adult	14/06/2022	Tärnharet	785	3.3
MC44	Adult	15/06/2022	Tihällsten	595	4.2
MC46	Adult	16/06/2022	Storholmsfläsjan	640	3.9
MC47	Adult	16/06/2022	Norrklacken	630	4.0
MC48	Adult	16/06/2022	Norrklacken	670	3.7
MF00	1CY	16/07/2020	Ålänningensslangran	635	3.9
MF36	Adult	16/06/2022	Norrklacken	575	4.3
MF46	1CY	20/07/2017	Svartfluttu	770	3.2
MK26	Adult	09/06/2019	Ängsholmen	795	3.1
MK27	Adult	09/06/2019	Ängsholmen	830	3.0
MK28	Adult	10/06/2021	Ålänningensslangran	730	3.4
MK37	Adult	12/07/2021	Svartfluttu	585	4.3
MK56	1CY	28/06/2019	Ängsholmen	880	2.8
MK72	1CY	28/06/2019	Ängsholmen	790	3.2
MK74	1CY	28/06/2019	Ängsholmen	775	3.2
MK81	1CY	13/07/2019	Ålänningensslangran	635	3.9
MK84	1CY	13/07/2019	Ålänningensslangran	795	3.1
MKA0	Adult	16/06/2022	Norrklacken	565	4.4
MKA1	Adult	20/06/2022	Bådastenarna	610	4.1
MKA2	Adult	20/06/2022	Bådastenarna	680	3.7
MKFA	Adult	18/06/2020	Gran	635	3.9
MKFC	Adult	18/06/2020	Gran	740	3.4
MKFF	Adult	18/06/2020	Gran	675	3.7
MKFH	Adult	18/06/2020	Gran	675	3.7
MKFK	Adult	18/06/2020	Gran	595	4.2
MKFM	Adult	18/06/2020	Gran	640	3.9
MKFR	Adult	18/06/2020	Gran	785	3.2
MKK8	Adult	01/06/2022	Eggegrund	780	3.2
MKK9	Adult	08/06/2022	Sjömärkesön	690	3.6
MKKA	Adult	11/06/2022	Hundbådan	605	4.1
MKKC	Adult	11/06/2022	Svartfluttu	680	3.7
MKKH	Adult	14/06/2022	Tärnklabben	620	4.0
MKKK	Adult	14/06/2022	Tärnklabben	595	4.2
MKKR	Adult	14/06/2022	Gråhäll	595	4.2
MM64	Adult	13/07/2019	Hållet	685	3.6
MN50	Adult	14/06/2023	Bådastenarna	625	4.0
MN52	Adult	14/06/2023	Bådastenarna	760	3.3

MN55	Adult	20/06/2023	Gråhäll	640	3.9
MN57	Adult	20/06/2023	Gråhäll	655	3.8
MN58	Adult	20/06/2023	Tärnharet	555	4.5
MR01	Adult	14/06/2018	Storgrundet	800	3.1
MR02	Adult	14/06/2018	Storgrundet	580	4.3
MR03	Adult	14/06/2018	Storgrundet	820	3.0
MR07	Adult	13/06/2019	Storgrundet	710	3.5
MR09	Adult	17/06/2022	Storgrundet	580	4.3
MR12	Adult	17/06/2023	Storgrundet	730	3.4
MT15	Adult	28/05/2020	Ängsholmen	655	3.8
MT16	Adult	28/05/2020	Ängsholmen	730	3.4
MT17	Adult	28/05/2020	Ängsholmen	785	3.2
MT18	Adult	31/05/2020	Ängsholmen	570	4.4
MT19	Adult	28/05/2020	Ängsholmen	665	3.8
MT20	Adult	28/05/2020	Ängsholmen	735	3.4
MT21	1CY	09/07/2021	Ängsholmen	725	3.4
MT25	1CY	09/07/2021	Ängsholmen	750	3.3
MT26	1CY	09/07/2021	Ängsholmen	720	3.5
MU01	Adult	01/06/2020	Blåbådan	605	4.1
MU02	Adult	01/06/2020	Blåbådan	565	4.4
MU04	Adult	08/06/2020	Eggegrund	815	3.1
MU05	Adult	08/06/2020	Eggegrund	625	4.0
MU06	Adult	09/06/2020	Eggegrund	575	4.3
MU07	Adult	13/06/2020	Svartfluttu	620	4.0
MU08	Adult	13/06/2020	Svartfluttu	775	3.2
MU14	Adult	16/06/2023	Tågstumparna	640	3.9
MU16	Adult	06/06/2022	Sjömärkesön	785	3.2
MU17	Adult	16/06/2022	Blåbådan	605	4.1
MU18	Adult	16/06/2022	Blåbådan	570	4.4
MU36	1CY	18/07/2022	Blåbådan	600	4.2
MU42	Adult	16/06/2023	Tågstumparna	735	3.4
MU43	Adult	16/06/2023	Tågstumparna	675	3.7
MY30	1CY	04/07/2022	Ängsholmen	675	3.7

827 Device mass is shows as a percentage of body mass, not exceeding 4.5%. Tagging date, tagging
828 age and colony are also presented for each tagged individual.

829 *Table S2*. Number of individuals and tracks by age and season used in the study post-filtering.

	Adults No. individuals (No. tracks)	**Juveniles** No. individuals (No. tracks)	**Total** No. individuals (No. tracks)
Autumn	57 (57)	12 (12)	69 (69)

830

831 *Table S3*. Sampling rate for each of the tagged Baltic Gulls (*L. f. fuscus*) for each season.

ID	**Tagging age**	**Autumn migration**
MA52	Adult	8.57

MA53	Adult	6.89
MC41	Adult	7.80
MC44	Adult	15.49
MC46	Adult	9.20
MC47	Adult	5.97
MC48	Adult	10.12
MF00	1CY	67.94
MF36	Adult	10.12
MF46	1CY	36.46
MK26	Adult	7.84
MK27	Adult	12.13
MK28	Adult	7.68
MK37	Adult	NA
MK56	1CY	13.07
MK72	1CY	9.20
MK74	1CY	7.38
MK81	1CY	5.85
MK84	1CY	12.62
MKA0	Adult	11.66
MKA1	Adult	5.54
MKA2	Adult	8.80
MKFA	Adult	5.61
MKFC	Adult	6.84
MKFF	Adult	10.07
MKFH	Adult	10.06
MKFK	Adult	27.93
MKFM	Adult	7.40
MKFR	Adult	NA
MKK8	Adult	7.57
MKK9	Adult	12.97
MKKA	Adult	8.99
MKKC	Adult	5.77
MKKH	Adult	9.28
MKKK	Adult	6.76
MKKR	Adult	8.02
MM64	Adult	NA
MN50	Adult	19.28
MN52	Adult	41.17
MN55	Adult	16.77
MN57	Adult	6.55
MN58	Adult	5.55
MR01	Adult	7.51
MR02	Adult	7.84
MR03	Adult	14.83
MR07	Adult	10.33
MR09	Adult	6.35
MR12	Adult	8.64
MT15	Adult	7.64
MT16	Adult	13.50
MT17	Adult	17.19

MT18	Adult	7.28
MT19	Adult	7.17
MT20	Adult	9.69
MT21	1CY	12.01
MT25	1CY	15.89
MT26	1CY	11.44
MU01	Adult	10.05
MU02	Adult	12.54
MU04	Adult	6.12
MU05	Adult	10.71
MU06	Adult	7.92
MU07	Adult	10.63
MU08	Adult	10.95
MU14	Adult	5.87
MU16	Adult	16.72
MU17	Adult	11.21
MU18	Adult	8.02
MU36	1CY	63.45
MU42	Adult	29.94
MU43	Adult	11.18
MY30	1CY	91.75

832 Sampling rate is presented in minutes.

833 Table S4. Sensitivity analysis used to inspect the number of fixes, days and tracks retained after
834 subsampling.

Coverage (hours)	Count	Fixes	Days	Tracks
23	8	4471	210	33
	10	4411	203	31
	12	4359	198	28
	14	4272	191	27
	16	4068	177	26
	18	3837	163	23
	20	3652	153	21
	22	3282	135	15
	24	2338	93	10
22	8	9177	459	39
	10	9047	444	36
	12	8679	409	33
	14	8307	379	30
	16	7802	344	29
	18	7372	318	26
	20	6852	290	24
	22	6025	250	20
	24	3947	158	13
21	8	10140	531	43
	10	9893	502	38
	12	9410	456	34
	14	8805	407	31

	16	8168	363	29
	18	7671	333	27
	20	7022	298	25
	22	6094	253	21
	24	3972	159	14
20	8	10873	588	47
	10	10532	548	42
	12	**9840**	**482**	**35**
	14	9135	425	31
	16	8409	375	29
	18	7878	343	27
	20	7173	305	25
	22	6184	257	22
	24	3972	159	14
19	8	11417	635	51
	10	10943	579	46
	12	10132	502	40
	14	9327	437	33
	16	8469	378	29
	18	7921	345	27
	20	7197	306	25
	22	6208	258	22
	24	3996	160	14

Migration tracks were subsampled at an hourly basis for different combinations of GPS daily coverage (difference in hours between the first and last fix) and number of daily fixes (count). The final combination of parameters used for subsampling tracks is presented in bold.

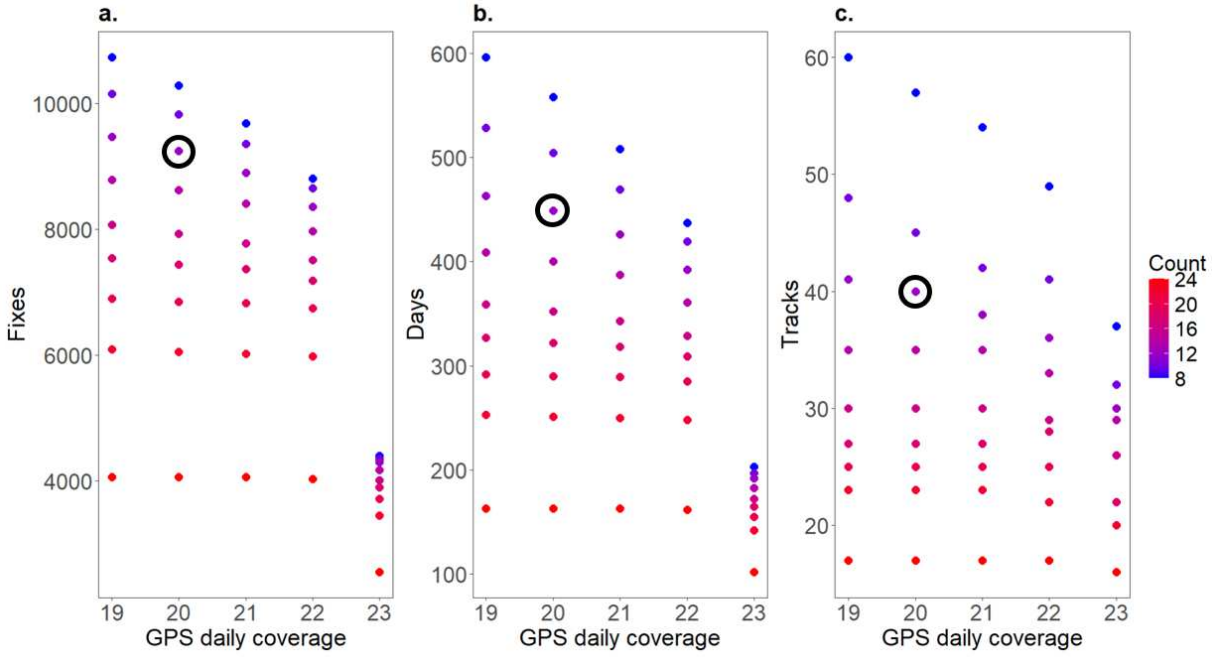


Figure S1. **(a)** Number of fixes retained with different daily GPS coverages and number of daily fixes thresholds, **(b)** number of days retained with the same thresholds and **(c)** number of

migration tracks retained with the same thresholds. The chosen threshold was 20 hour coverage + 12 fixes/day and is shown with a black circle in each panel.