

FORAGING BEHAVIOUR OF GREAT BLACK-BACKED GULLS *LARUS MARINUS* BREEDING IN SOUTHERN NORWAY AS REVEALED BY GPS TRACKING

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ABSTRACT

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While some seabird species are specialist foragers, others are considered to have more generalist foraging strategies. However, substantial individual-level specialisation has been documented even within generalist species. Understanding the spatial and foraging ecology of seabirds is crucial for assessing the ecological drivers and fitness consequences of a specific foraging strategy, and this also enables the prediction of key information with important implications for marine spatial planning and conservation. Here, we study individual foraging behaviour and environmental variables influencing behavioural transitions using tracking data from 25 adult Great Black-backed Gulls *Larus marinus* during the 2024 breeding season in an archipelago in southern Norway. Twenty data loggers recorded 3,285 foraging trips during the entire breeding season, and we excluded data from five individuals whose breeding attempts failed. We found a clear bimodal pattern of short and long trips, whereby birds made frequent foraging trips to a productive shelf edge characterised by shallow waters. Birds were more likely to switch from foraging to a transit state when sea depth increased. Unlike previous studies on large gulls, we found little evidence for spatial segregation of foraging areas. Our study highlights low levels of apparent individual specialisation and the occurrence of overlapping foraging areas during breeding in this large seabird in the North Sea. In contrast to previous studies, we demonstrate that GPS deployment using leg-loop harnesses did not adversely affect nesting success and that our methods can successfully be applied to study the spatial ecology of this species.

Key words: large gull, leg-loop harness, *Larus marinus*, North Sea, seabird, tracking

INTRODUCTION

Seabirds such as gulls are often regarded as generalist predators and scavengers, capable of exploiting a wide range of food sources and habitats (Steenweg et al., 2011). Despite this, recent studies have shown that some species display individual differences in foraging behaviour and diet—for example, demonstrating variation in prey preference and the strategies employed to catch it—a phenomenon known as individual specialisation (Ceia & Ramos, 2015; Westerberg et al., 2019). Such specialisation may reduce intraspecific competition and thus increase individual fitness (Bolnick et al., 2003; Pierotti & Annett, 1987), with potential consequences for population dynamics.

Understanding the foraging ecology of seabird populations, particularly during the breeding season, is essential for identifying key foraging areas, assessing vulnerability to environmental changes, and informing effective conservation strategies. This is especially relevant for large gull species such as the Great Black-backed Gull *Larus marinus*, which is declining throughout much of its range (Langlois Lopez et al., 2023). Despite the species' wide distribution and ecological importance, detailed knowledge of its foraging ecology (e.g., trip length, behavioural states, foraging habitats) remains limited, particularly in the North Atlantic.

Accurate determination of individual specialisation and preferred foraging areas within a population necessitates individual tracking. Previous tracking studies of large gulls from the region have focused primarily on the Lesser Black-backed Gull *Larus fuscus* and European Herring Gull *L. argentatus* (e.g., Corman et al., 2016; Garthe et al., 2016; Langley et al., 2021), with relatively few GPS-based studies on Great Black-backed Gulls (but see Borrmann et al., 2019; Lato et al., 2021; Maynard & Ronconi, 2018). Existing work on Great Black-backed Gulls has been geographically constrained and/or based on small sample sizes, leaving substantial knowledge gaps in population-level patterns of habitat use and foraging effort during the breeding period.

In this study, we investigated the foraging ecology of breeding Great Black-backed Gulls in southern Norway using GPS tracking data from a sample of 25 individuals. Our primary aim was to characterise spatial and foraging behaviour at the population level, including trip distance, duration, habitat use, and repeatability of foraging areas. While we included some exploratory analyses at the individual level, such as overlap in foraging areas, our focus was on whether we could identify any key ecological variables (e.g., bathymetry, distance to the coast) to help explain the species' foraging behaviour during the breeding season. Our study contributes valuable information on a vulnerable species and helps build a foundation for future research on Great Black-backed Gull spatial and foraging ecology. The Norwegian

coasts support almost one-quarter of the world population of Great Black-backed Gulls (Langlois Lopez, 2023; Norwegian Biodiversity Information Centre, 2021), which breed mainly on small skerries and islets. The foraging ecology of Great Black-backed Gulls breeding in southern Norway's Lindsnes archipelago was largely unknown, and therefore the aim of our study was to identify core foraging area(s) through GPS tracking of 25 individuals in 2024, including examination of time allocation between behavioural states during the different phases of breeding—resting, transit movements, and foraging—based on the results of a hidden Markov model. Furthermore, we sought to determine which oceanographic variables influenced the probability of switching between two behavioural states: foraging and transit.

METHODS

Capture and GPS Deployment

We conducted fieldwork in the Lindsnes archipelago (58°00'35"N, 007°33'27"E), located on the southern coast of Norway; the archipelago supports a breeding population of 200–300 pairs of Great Black-backed Gulls (Helberg, 2025). We selected this area because Great Black-backed Gulls have been colour-ringed and studied there since 1998. During the period 26–30 May 2024, we caught 25 adult Great Black-backed Gulls on their nests, using walk-in traps. Based on nest monitoring leading up to the GPS fieldwork, we targeted nests that were close to hatching or with freshly hatched chicks, thereby increasing the chance of successful capture and reducing the risk of nest abandonment. Eggs were swapped with dummy eggs during the trapping procedure to avoid breakage. We placed a trap over a nest and left the location for 15–20 min to allow the adults to settle and resume incubation. When the gull returned to its nest and lay down to incubate the eggs or shelter chicks, its belly would hit a string above the nest, triggering the hinged door to close behind the bird. After this, the adult typically relaxed and continued incubation and was not excited until staff approached the site again. After removing the adult from the trap, we placed it in a cotton bag to reduce stress and took it to a suitable location for biometric data collection and data logger deployment. Each individual was measured (wing and head-bill length, as well as body mass; Appendix 1, available on the website) and, if not yet ringed, was fitted with unique metal and coloured rings on the left and right tarsus, respectively (as part of BirdLife Norway's ongoing ringing programme; Appendix 1). Birds were sexed based on sexual size dimorphism in the wing and head measurements (Helberg, 2003). Only one member of a pair was captured, to minimise possible negative effects of GPS deployment, such as nest abandonment or breeding failure. After ringed, the birds were fitted with an OrniTrack-15 4GT GPS transmitter (Ornitela, Lithuania), weighing 15 g. Transmitters were attached using a Teflon ribbon leg-loop harness weighing *ca.* 0.5 g. Body mass ranged from 1,370 to 1,940 g, and the relative load of the transmitter plus harness was 0.8%–1.1% of the bird's mass, below the suggested permissible load limit of 3% (Phillips et al., 2003). Following GPS deployment, the bird was released *in situ* and observed for 5 to 10 min to ensure normal flight behaviour and/or its return to the nest.

Throughout the study, the GPS transmitters were set to record a position every three minutes. At every GPS fix, flight altitude, speed, and direction were logged. GPS data were uploaded via the GSM network twice a day (if the bird was within range). The frequency of GPS positioning was incrementally lowered to 10, 20, and 30 min when battery levels dropped to 75%, 50%, and 25%, respectively. One logger (ID 243278) stopped sending data on

12 June 2024, but this was due to tag failure and not the result of nest failure (the bird produced two fledglings; Appendix 2, available on the website).

To assess whether capture and deployment of a leg-loop harness with GPS affected the gulls' breeding success, we monitored nests during 24–28 June 2024 and determined the number of (near fledging) chicks. If breeding was successful, we ringed chicks with a metal ring and a colour ring. We monitored nests where one parent was fitted with a GPS transmitter ($n = 25$) and also control nests where no GPS devices were deployed ($n = 25$).

Data Analysis

We performed all analyses in R version 4.3.2 (R Core Team, 2024).

Of the 25 gulls fitted with a GPS transmitter, five experienced nest failure; however, we were unable to determine the exact date or cause of failure, or the nest contents at the time of failure. Consequently, we could not confirm whether these gulls made foraging trips to collect food to provision themselves or their young. For these reasons, we omitted these birds from analyses.

Foraging Trips

Foraging trips were defined as uninterrupted periods of tracking data at least 20 min in duration and further than 0.5 km from the nest (Borrmann et al., 2019; Lato et al., 2021). For each trip, we calculated the duration and the maximum haversine (great-circle) distance from the colony.

We defined the incubation stage as two days (Haftorn, 1971), with chicks fledging at an age of 50 days. We do not know exact hatch and fledge dates for all nests. Therefore, based on the above criteria, we divided the chick-rearing period into an early (first 25 days) and a late period. Based on these criteria, we defined the incubation period as the time from catching the adults to 27 May, the early chick-rearing period from 28 May to 22 June, the late chick-rearing period from 23 June to 16 July, and the post-fledging period as 17 to 31 July. This introduces some error in the comparison of behaviour among different reproductive stages (see below). Such error, however, is not very large, because we targeted nests that were likely to be close to hatching or with newly hatched chicks.

Behavioural States

To identify when birds were in different behavioural states, we classified periods when the birds were stationary, foraging, or in transit using a hidden Markov model (HMM) and inferred behavioural states from two observed variables calculated from GPS positions: step length and turning angle. HMMs were fitted using the "hmmTMB" package in R (Michelot & Langrock, 2023), and we predicted behavioural states for the data using the Viterbi algorithm. We recorded positions at intervals of 3, 10, 20, or 30 min, but intervals needed to be regularised for use in HMMs. Regularisation to 10-min or longer intervals led to even sampling across the day, whereas three-minute intervals showed a bias towards diurnal hours (Appendix 3, available on the website) and reduced the temporal coverage of the data to 22% of the tracking time. Resampling to 10-min intervals retained 77% of the temporal coverage, whereas 20-min intervals retained 87% of the temporal coverage. The three intervals led to similar estimates of time spent

in each behavioural state (see below). For these reasons, we selected 10-min data for further analysis. We fitted a three-state HMM to characterise movement behaviour using step lengths and turning angles. We choose three states based on previous experience with HMMs and gull and tern tracking data (Fijn, 2024; van Bemmelen et al., 2024), where more states led to problems in convergence as well as interpretability. To aid model convergence, we specified biologically plausible starting values for each state's movement parameters based on the data distribution: we initialised the mean step lengths as 0.01, 0.5, and 6 km, with corresponding standard deviations of 0.01, 0.5, and 6 km. Mean turning angles were all set to 0, assuming no initial directional bias across states. The starting values for the concentration parameters (κ) were set to 0.5, 1, and 5. These values were chosen to reflect resting or encamped behaviour (short step lengths, many turns), area-restricted search (moderate movement, some turns), and transit behaviour (longer, strongly directed movements).

Proportions of time spent (1) at the nest (< 0.5 km from the nest), (2) foraging, (3) in transit, and (4) stationary but outside the colony were analysed using four beta generalized linear mixed models (GLMMs) with random intercepts for individuals, using the proportion of 10-min positions per day in each behaviour as the response variable. We used daily proportions instead of the original data (i.e., in a Bernoulli model), to avoid problems with short-term temporal autocorrelation. Marginal estimates were obtained per behaviour using the “brmsmargins” package in R (Wiley & Hedeker, 2022). Using the “brms” package in R (Bürkner, 2018), we used beta regression models with the proportion of each behavioural state as the response and breeding stage (four levels) as the fixed effect, random intercepts for individuals, and a logit link to examine whether the proportion of time spent per behavioural state differed significantly across breeding stages.

To identify whether the foraging ranges of individual birds overlapped with each other, we calculated utilisation distribution (UD) based on kernel density estimates (KDE) using the package “adehabitatHR” in R (Calenge & Fortmann-Roe, 2023) and the GPS points identified as foraging locations by the HMM. A value of $> 50\%$ overlap is commonly used as a threshold to infer nonrandom spatial or behavioural overlap between two or more UD. We used the h -value “href” to compute the smoothing parameter (Worton, 1989), and a grid size of 100 points along each axis. We calculated overlap using Bhattacharyya's affinity (BA) matrix (Bhattacharyya, 1943) and summarised the results based on an overlap of $> 50\%$

between individuals (Appendix 4, available on the website). We subsequently created and inspected plots for 50% (core use area), 75% (mid-range), and 95% (overall range) KDEs for each bird using “ggplot2” (Wickham, 2016, pp. 11–31; Appendices 5–6 of this paper, available on the website).

Effects of Covariates on Behavioural States

To understand which variables determine whether Great Black-backed Gulls start or end foraging during a foraging trip, we fitted the same three-state HMM to the GPS data regularised to 10-min intervals, as above, but now with covariates affecting the transition probabilities. Using the annotation tools from Movebank (<https://www.movebank.org>), we obtained data on water depth (m) and distance to coast (shortest distance to the nearest coastline for each location on land, with a spatial resolution of approximately 0.04°) and included these data as thin spline smoothers affecting the transition probabilities. We also downloaded data from Global Fishing Watch (2024) to allow us to examine whether foraging trips overlapped with apparent fishing effort.

RESULTS

Breeding Success

Of the 25 birds with loggers, five failed to produce fledglings. Including these five birds, the mean $\pm$ the standard deviation (SD) fledging rate was 1.52 ± 1.01 chicks per pair. Of the 25 control nests, eight failed to produce fledglings. Including these eight birds, mean $\pm$ SD fledging rate was 1.48 ± 1.19 . The causes of nest failure are uncertain, but (invasive) American mink *Neogale vison* are known to depredate gull nests in our study area (M. Helberg, personal observation, last at 25 June 2024, at Langøyholmen, Mandal). Alternatively, stress caused by handling may have resulted in breeding failure; however, we are unable to confirm this. There was no significant difference in body condition (mass, wing/head size) between successful and failed breeders (t -test: $p > .05$).

Sample Size and Foraging Trip Characteristics

The 25 data loggers individually produced 2,952–17,017 positions over a period of 17–56 days, including failed breeders. After filtering out failed breeders, the remaining 20 tagged birds recorded 3,285 foraging trips from 27 May to 31 July 2024 (Table 1). The distribution of maximum trip distance

TABLE 1
Summary of foraging trip frequency, distance, and duration and the percentage of long trips by 20 Great Black-backed Gulls *Larus marinus* per breeding stage between 27 May and 31 July 2024 from the Lindesnes archipelago region, Norway^a

Stage	Trip frequency, mean number per day ($\pm$ SD ^b)	Mean maximum distance, km ($\pm$ SD ^c)	Maximum distance, km	Mean duration, hr ($\pm$ SD)	Maximum duration, hr	% trips with max. distance > 40 km
Incubation	0.5 (0)	1.3 (-)	2.1	0.5 (-)	0.8	0.0
Early chick-rearing	3.56 (1.91)	1.3 (12.3)	56.4	1.3 (2.1)	13.4	10.8
Late chick-rearing	2.90 (1.78)	13.3 (14.3)	63.4	1.8 (2.5)	13.1	10.4
Post-breeding	3.06 (1.71)	11.4 (12.4)	37.8	1.9 (2.4)	9.0	9.3

^a Statistics were first calculated per individual and then averaged.

^b Standard deviation

^c Standard deviations were not reported for groups with $n = 2$, because estimates of variability are unreliable at such small sample sizes.

showed three clusters: 0–15, 15–40, and > 40 km (Appendix 7, available on the website). Overall, median foraging trip duration was 0.72 hr (interquartile range [IQR] = 1.33 hr, range = 0.34–287.85 hr, $n = 3,285$), and median maximum distance of foraging trips was 4.06 km (IQR = 8.13 km, range = 0.51–138.02 km, $n = 3,285$). Four individuals (IDs 243269, 243270, 243275, and 243276) made long foraging trips, venturing more than 100 km from the nest (Appendix 8, available on the website). Nevertheless, these birds all managed to produce fledglings. The number of trips logged during incubation was, by design, very limited (Table 1).

Behaviour

At 10-min intervals, the data contained a combination of very short steps (mean = 31 m, SD = 32 m) with very low directionality ($\kappa = 0.49$), medium-length steps (mean = 1.448 m, SD = 1.532 m) with weak directionality ($\kappa = 0.70$), and long steps (mean = 5.749 m, SD = 1.759 m) with strong directionality ($\kappa = 8.49$; Appendix 9, available

on the website). We interpret these as stationary, foraging, and transit flights, respectively.

Foraging Areas

A large proportion (75%) of Great Black-backed Gulls travelled over an area of deeper water to forage in shallower waters approximately 40–70 km south of the nesting area (Fig. 1, Table 1). Many foraging points also showed overlap with apparent fishing effort (Fig. 1). KDEs represent areas where the tracked gulls spent most of their time foraging. While the majority ($n = 15$) of birds foraged in this area of shallower water, some individuals ($n = 3$) made foraging trips to other areas. There was considerable overlap among the gulls' 95% kernel densities (Fig. 2), as well as their 75% and 50% KDEs (Appendices 5–6). However, there were also a few individuals whose core foraging areas had little or no overlap with others: two gulls foraged almost exclusively at the Brennevinsmyra waste facility, located inland, approximately 30 km northeast of the study area (Fig. 2).

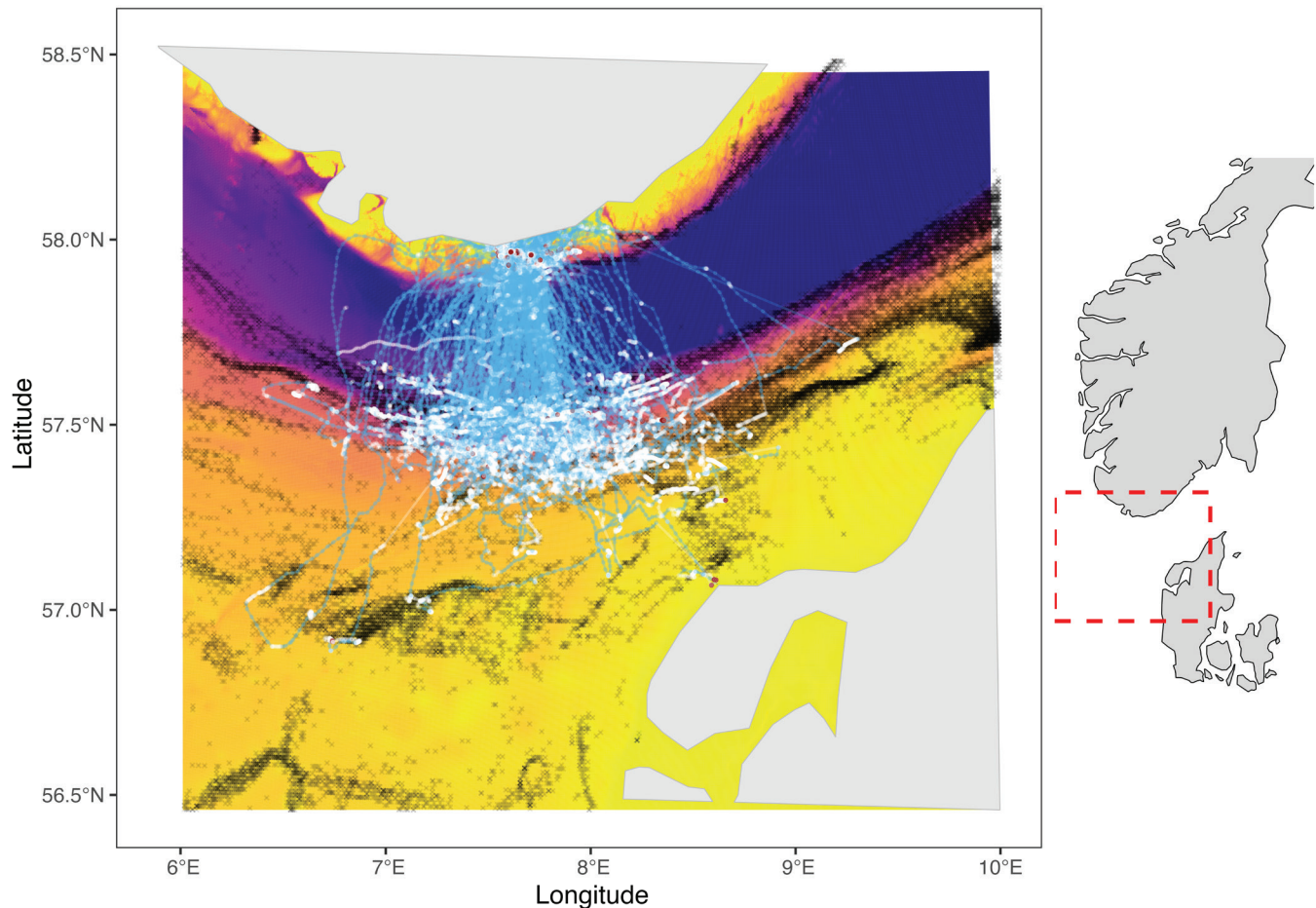


Fig. 1. GPS positions of Great Black-backed Gulls *Larus marinus* ($n = 20$), recorded during chick-rearing. GPS fixes were collected every 3, 10, 20, or 30 min. Grey areas are southern Norway, to the north, where the gulls breed, and northwestern Denmark, to the south. Inset map to the right of the plot shows the wider geographic area; the red box represents the area of the main plot. White dots represent GPS fixes that were classified as foraging, blue dots represent flying (i.e., birds in transit between the colony and foraging areas), and red dots show where the birds were stationary. Apparent fishing effort (black) is based on data for changes in vessel speed and direction from Global Fishing Watch (2024). This map is overlaid with a raster image showing bathymetry (source: General Bathymetric Chart of the Oceans [GEBCO Bathymetric Compilation Group, 2024]; lighter colors represent shallow areas, while darker colors indicate areas with a water depth > 100 m).

Behavioural States and Foraging Site Selection

That these Great Black-backed Gulls foraged predominantly in shallow waters is also reflected in the three-state HMM including covariates. The results indicate that although birds foraged over all distances from the coast, the probability of continuing foraging declined strongly with water depth: for greater depths, they were more likely to return to a transit state and return to the nest site or continue to shallower areas farther on (Fig. 3; Appendix 10, available on the website). This reflects the fact that the shallower areas where foraging predominantly occurred were either nearshore or farther offshore, beyond an area with great water depths—a result that was unaffected by the sampling intervals (Fig. 1; Appendix 11, available on the website).

Trip Distance and Time in States

The majority of trip distances were < 40 km across all stages, except during incubation, when all trip distances were < 10 km (Table 1). Trips with maximum distances > 40 km occurred during

chick-rearing and post-breeding (Table 1). As trips with maximum distances > 40 km had longer durations than shorter trips, based on time outside the breeding area, the percentage of time spent on longer trips was 34% for the early chick-rearing stage, 39% during late chick-rearing, and 36% during post-breeding.

The mean proportions of time spent by Great Black-backed Gulls at the nest, stationary, foraging, and in transit largely did not differ significantly between the different breeding periods ($p > .05$), except for foraging time, which was shorter during incubation than in later stages ($p < .01$), and time spent at the nest, which decreased with each later stage ($p < .05$). Across all stages, gulls spent the majority of their time at the breeding site (mean of $74.1\% \pm \text{SD } 12.7$ percentage points), followed by time spent foraging ($14.8\% \pm 8.3$ percentage points). Stationary periods made up $6.1\% \pm 5.6$ percentage points of their daily time budget, whilst commuting between the nest and foraging sites accounted for $5.1\% \pm 4.8$ percentage points. During early chick-rearing, the fractions of time spent foraging and stationary were approximately equal. As the breeding season progressed, the proportions of time

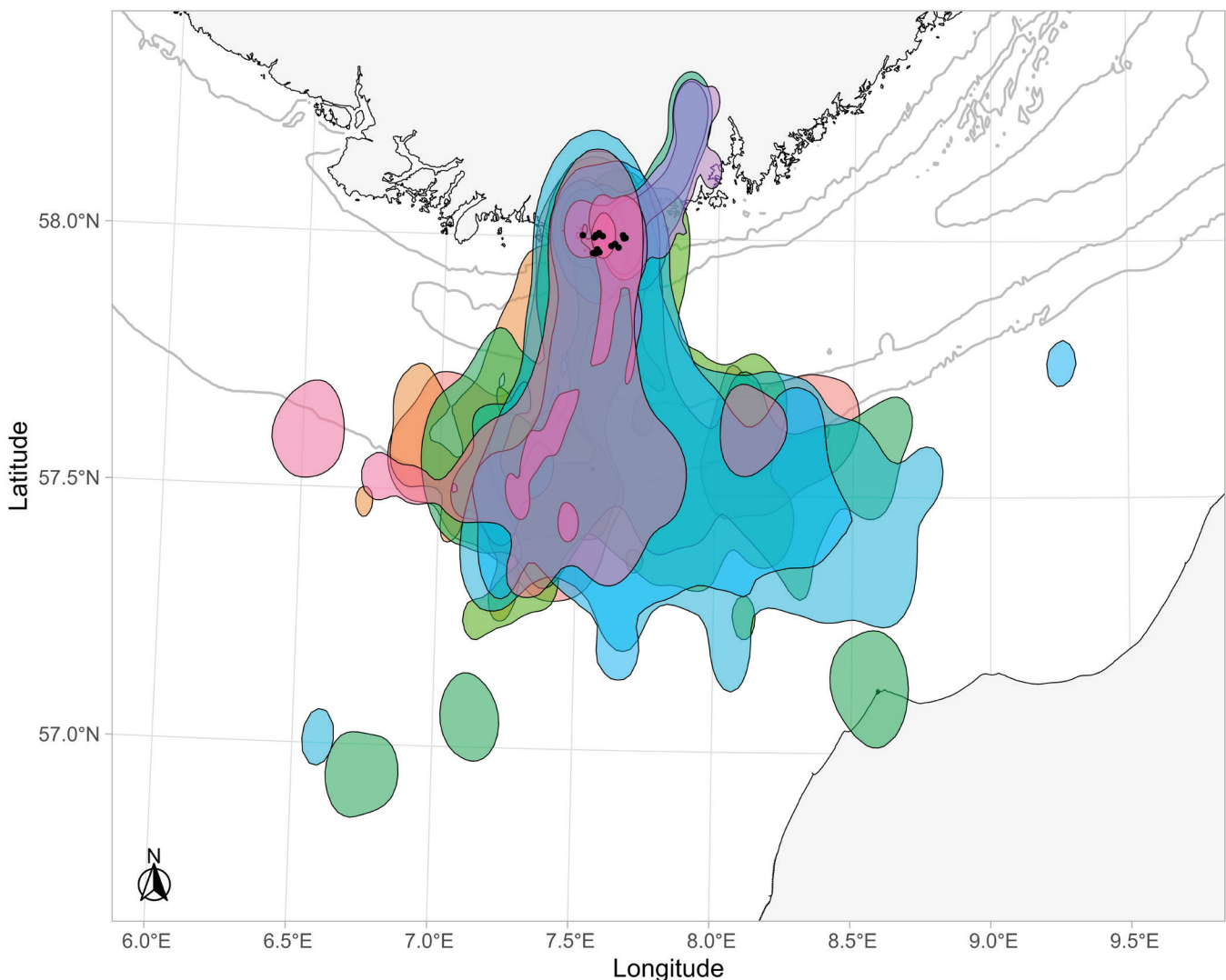


Fig. 2. Kernel density plot (95% kernel density estimation [KDE]) showing main foraging areas of Great Black-backed Gulls *Larus marinus* with > 50% overlap ($n = 15$) tracked from a breeding colony in southern Norway. Each colour represents one individual. Grey areas are southern Norway and northwestern Denmark. Black dots are the birds' nesting sites. Grey lines denote bathymetry.

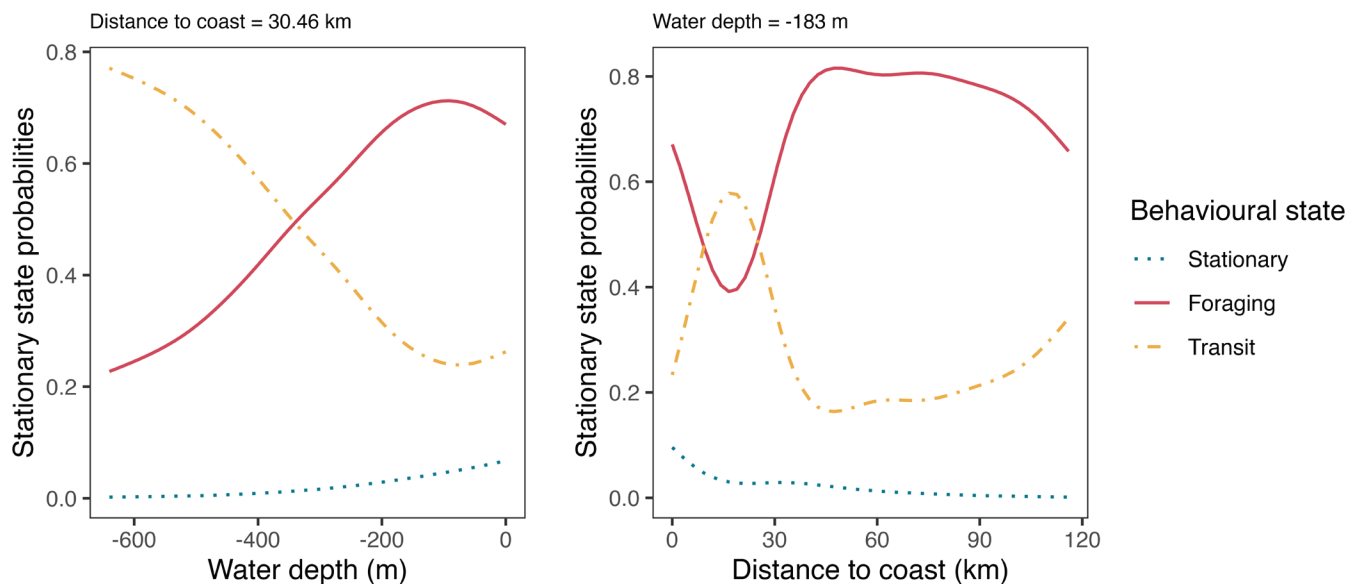


Fig. 3. Conditional effects of water depth (left) and distance to coast (right) on stationary probabilities (i.e., the probability of remaining in the current behavioural state) in a two-state hidden Markov model for Great Black-backed Gulls *Larus marinus* tracked from a breeding colony in southern Norway. Values at the top of each figure represent the mean of the covariate held constant in the model while examining the effect of the other covariate on the probability of remaining in a given behavioural state. Solid line = foraging; dashed line = transit; dotted line = stationary.

spent foraging and in transit remained roughly the same, but nest attendance decreased. The overall pattern did not change when resampling the data to 3- or 20-min intervals (Appendix 12, available on the website).

DISCUSSION

We found that Great Black-backed Gulls exhibited a bimodal pattern of short and long foraging trips during the breeding season. Short trips occurred close (< 40 km) to nest sites, possibly due to gulls foraging for swimming crabs (Portunidae), as has been documented in Lesser Black-backed Gulls (Schwemmer et al., 2013). Tidal state can influence the accessibility of intertidal and shallow-subtidal prey, and several gull species adjust foraging activity according to tide height (Borrmann et al., 2019). Although we did not include tidal level as a predictor in our analyses, it is conceivable that lower tides could facilitate short, nearshore foraging trips if prey such as swimming crabs become more accessible in shallow waters. In our study, however, most long foraging trips occurred in shallow offshore waters south of the breeding site, and mainly along the Norwegian Trench, an area characterised by mixed depths resulting in upwelling and high productivity (Mogollón et al., 2024). Here, Great Black-backed Gulls may profit from pelagic fish such as European sprat *Sprattus sprattus*, Atlantic mackerel *Scomber scombrus*, Atlantic herring *Clupea harengus*, and garfish *Belone belone* (Haukjem, 2025), in addition to potential fishery discards from species such as Atlantic cod *Gadus morhua*, whiting *Merlangius merlangus*, and bib *Trisopterus luscus* (Kock, 1974). Such behavioural patterns may be explained by a combination of ecological, energetic, and reproductive factors, such as balancing self-provisioning with feeding chicks (local trips), compared to visiting high-reward foraging areas to replenish body reserves (long trips; Gillies et al., 2022). Whereas near-colony habitats may offer predictable but low-quality resources, offshore sites might offer energy-rich food but at a higher energetic cost to adults. Therefore,

gulls may switch foraging strategies based on prey availability, risk management (minimising time away from the nest), and behavioural plasticity (Isaksson et al., 2016). Similar bimodal behaviour has also been documented among Lesser Black-backed Gulls (Isaksson et al., 2016) and Northern Gannets *Morus bassanus* (Garthe et al., 2012).

Most Great Black-backed Gull core foraging areas showed considerable overlap, suggesting little spatial segregation within this population during the breeding season. This is in contrast to findings from Maynard and Ronconi (2018), whose three tracked individuals in Nova Scotia, Canada, suggested spatial segregation of foraging sites. Moreover, Borrmann et al. (2019) found clear spatial segregation between individuals tracked from Föhr Island, in the German North Sea, although their sample size was also much smaller ($n = 7$) than ours. One possible explanation for this apparent dissimilarity may be the diversity of habitats within a 30-km radius of Föhr's breeding area (a mixture of shallow and deep seawater, freshwater, mudflats, salt marsh, pastures, agricultural fields, and urban settlements; Borrmann et al., 2019). However, the small sample sizes of both aforementioned studies may have amplified the effects of variation in foraging behaviour, making it harder to discern any clear population-level trends. Based on their diet, Great Black-backed Gull populations may comprise individuals with different foraging strategies (Maynard et al., 2021). In our study, however, the majority of tracked birds exhibited similarities in relation to foraging area and habitat use, suggesting a stable and common source of food offshore. Nevertheless, while most tracked birds appeared to forage at sea, two individuals in our study foraged almost exclusively at a landfill site, a common practice among many gull species, since these areas offer a stable source of food (Coulson et al., 1987). Thus, there was a small element of spatial segregation within the study group, with two birds foraging on land and the remainder in marine habitats. However, if offshore resources fail

and competitive pressure among individuals increases, spatial segregation may also increase.

Our results suggest that Great Black-backed Gull foraging behaviour during the early and late chick-rearing periods, as well as post-breeding, was similar among most individuals. The average duration of trips > 100 km made by four birds (three males and one female) with dependent young was 24.6 hr, compared to 2.08 hr for trips < 100 km. Presumably, during such extended trips, the bird's mate tended the eggs or young, possibly while making short, local foraging trips; however, this could not be quantified, as only one of the birds in a breeding pair was tagged. Gulls that experienced breeding failure made very long trips, with core foraging areas as far as Denmark. Like many other seabird species, these birds likely left the nest islands following breeding failure and foraged in areas farther away compared to those with active nests, while occasionally returning to the nest site (Enners et al., 2018).

Although we observed shorter trips in the coastal zone and to the local landfill site, foraging occurred primarily at sea. While we did not collect any regurgitates or pellets to study diet, presumably these individuals hunted for marine prey, scavenged from other seabirds, and/or followed fishing vessels operating in Danish waters (fishing discards at sea are banned in Norwegian waters; Norwegian legislation FOR-2004-12-22-1878). The high apparent fishing effort in the core foraging area of the gulls tracked in our study suggests that these gulls also benefit from this seemingly highly productive area. A study from Helgoland (Germany) found a high proportion (70%–87%) of prey species were typically obtained via fisheries discards in European Herring Gull and Great Black-backed Gull pellets (Hüppop & Wurm, 2000). The aforementioned study supports the findings by Garthe et al. (1996) highlighting the importance of fishery discards for seabirds in other areas of the North Sea, but in the decades since those studies were published, regulations and fishing practices have changed; it is possible that fewer discards are available to Great Black-backed Gulls, and populations may thus be foraging naturally; however, confirming this falls outside the scope of this study.

Great Black-backed Gull foraging was influenced by both water depth and distance to the coast. Specifically, gulls were more likely to switch from transit to foraging behaviour in shallower waters—and vice versa when sea depth increased—and at distances of more than 30 km from the coast. These effects are reflected in the spatial distribution of gulls' positions classified as “foraging”, which predominantly occurred in shallower waters at either side of the Norwegian Trench. In these shallow areas, strong tidal currents interacting with the seabed create mixed waters with uniform properties throughout the water column. In contrast, deeper areas with weaker currents tend to become stratified, particularly in spring as surface waters warm (Waggitt et al., 2018). It is possible that the main foraging area identified in our study comprises a front between mixed and stratified waters, with enhanced primary productivity. Such habitats typically create dense, predictable prey hotspots near the surface, making them ideal for surface-foraging birds such as gulls (Waggitt et al., 2018).

We demonstrate that Great Black-backed Gull spatial and temporal ecology can successfully be studied using GPS technology attached by leg-loop harnesses. The proportion of failed nests and the number of fledglings produced was comparable between nests of tagged birds and control nests. This differs from findings of Langlois Lopez et al.

(2024), who reported fewer hatched eggs per nest and lower hatching success rates of GPS deployment when using body harnesses on Great Black-backed Gulls nesting in Scotland. One possible explanation for this discrepancy may be deployment date; whereas Langlois Lopez et al. deployed GPS devices also during early incubation (6–20 days prior to hatching), we selected nests that were in the process of hatching or about to hatch based on monitoring prior to deployment. Furthermore, handling time by Langlois Lopez et al. ranged from 35 to 60 minutes, whereas we estimated maximum handling time in our study to be 15–20 minutes per bird. Furthermore, while Langlois Lopez et al. used body harnesses, leg-loop attachments are considered a better alternative for deploying GPS loggers on soaring birds (Longarini et al., 2023). Another study from Canada (Maynard et al., 2021) reported breeding failure but did not state deployment in relation to days prior to hatching—only that loggers were deployed during incubation. For this species, we therefore recommend deploying loggers during either late incubation or very early hatching to ensure optimal breeding success.

We present here novel results examining the spatial and foraging ecology of 20 Great Black-backed Gulls from a breeding population in southern Norway. During breeding, with the exception of two individuals, the tracked birds exhibited little spatial segregation in foraging habitats. Future studies will examine whether this pattern continues outside the breeding season, as well as the species' spatial behaviour (e.g., avoidance, attraction, habituation) in relation to offshore structures.

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ETHICS STATEMENT

All procedures were approved by the Norwegian Animal Ethics Committee, permit number FOTS 30692, and by the Norwegian Environmental Agency, reference 2023/8629.

AUTHOR CONTRIBUTIONS

Conceptualisation, project administration, and supervision: HMM. Investigation: HMM, RCF, MH, ALKN, CE. Formal analysis: RSAvB, HMM. Writing—original draft: HMM. Writing—review & editing: HMM, RCF, MH, ALKN, CE, RSAvB.

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