

**High foraging site fidelity and spatial segregation among individual great black-backed gulls**

Rachel M. Borrmann<sup>1</sup>, Richard A. Phillips<sup>2</sup>, Thomas A. Clay<sup>2,3</sup> and Stefan Garthe<sup>1</sup>

<sup>1</sup>Research and Technology Centre (FTZ), Kiel Univ., Buesum, Germany

<sup>2</sup>British Antarctic Survey, Natural Environment Research Council, Cambridge, UK

<sup>3</sup>School of Environmental Sciences, Univ. of Liverpool, Liverpool, UK

**Corresponding author:** Rachel M. Borrmann, Research and Technology Centre (FTZ), Kiel Univ., Buesum, Germany. E-mail: borrmann@ftz-west.uni-kiel.de

**Decision date:** 21-Oct-2019

---

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/jav.02156].

**Abstract**

Individual foraging site fidelity, whereby individuals repeatedly visit the same foraging areas, is widespread in nature, and likely benefits individuals through higher foraging efficiency and potentially, higher breeding success. It may arise as a consequence of habitat or resource specialisation, or alternatively, where resources are abundant or predictable, the partitioning of space might guarantee individuals exclusive foraging opportunities. We tracked seven adult great black-backed gulls *Larus marinus* at a North Sea colony from early incubation to the end of the breeding season in 2016, providing a total of 1,170 foraging trips over a mean  $\pm$  SD tracking period of  $67 \pm 16$  days. There was clear spatial segregation between individuals, with almost no overlap of their core areas (50% utilisation distribution) during incubation and chick-rearing. Core areas were relatively small and there was high repeatability ( $R \pm$  SE) in foraging parameters, including initial departure direction ( $0.73 \pm 0.11$ ), foraging range ( $0.41 \pm 0.14$ ) and cumulative distance travelled ( $0.19 \pm 0.1$ ) throughout the breeding season. Despite the low spatial overlap, there was little evidence of differential habitat use by individuals. The near-exclusive individual foraging areas of this species, usually considered to be a generalist, indicate that where there is high resource availability throughout the breeding season and a small local population, individuals appear to adopt a territorial strategy which likely reduces intraspecific competition.

**Keywords**

Repeatability; seasonal consistency; individual foraging site fidelity; territoriality; movement ecology; seabird; great black-backed gull (*Larus marinus*); Wadden Sea

## Introduction

There is widespread evidence that individuals within a population differ in a variety of traits unexplained by other factors such as sex or age, termed individual specialisation (Bolnick et al. 2003). In particular, individual specialisation in foraging behaviour is widespread in animal populations and can be manifested in several ways; for example, individuals might have distinct preferences for habitat or prey, or may forage at certain areas or times of the day (Woo et al. 2008, Phillips et al. 2017). As the foraging strategies of generalist or specialist individuals shape the ecological niche of a population (Bearhop et al. 2004), individual specialisation has implications for life-histories and population dynamics (Annett and Pierotti 1999, Bolnick et al. 2003, Anderson et al. 2009, Ceia and Ramos 2015, Phillips et al. 2017), and consequently is of interest in conservation management.

Individuals seek to optimise their foraging efficiency and choose habitats that best meet their energetic requirements (Chimienti et al. 2017). If habitats show some degree of stability in time and space, habitat specialisation may then be expressed as individual foraging site fidelity, whereby individuals repeatedly visit the same foraging areas (Irons 1998, Wakefield et al. 2015). Alternatively, irrespective of habitat selection, individual foraging site fidelity may develop as a result of density-dependent mechanisms such as avoidance of agonistic interactions between foraging conspecifics (Grémillet et al. 2004, Wakefield et al. 2013). Even if individuals are able to switch between prey according to availability (Anderson et al. 2009) and to their needs (Garthe et al. 2016), animals of the same population might forage in individually distinct areas, leading to spatial segregation. Where intraspecific competition is particularly high in colonial species, individual specialisation in resource use might lead to a more extreme case of individual foraging site fidelity, whereby individuals establish adjacent feeding

territories in close proximity to nest sites, such as in skuas (Trillmich 1978, Trivelpiece et al. 1980, Votier et al. 2004).

Environmental conditions may support the establishment of consistent individual temporal patterns; for example, when foraging routines are adjusted according to predictable cycles such as tides (Slater 1976, Becker et al. 1993, Irons 1998). By maintaining foraging site fidelity, individuals may acquire information specific to particular sites which may confer them an advantage (site familiarity; Irons 1998, Wakefield et al. 2015). Diurnal activity rhythms can also be developed in response to human activities, e.g. with individuals foraging when fishing vessels are operating (Mañosa et al. 2004, Bécarea et al. 2015). Both the availability and predictability of suitable foraging habitats might vary greatly on a regional scale and, along with other factors such as population size (Lamb et al. 2017), likely influence the degree of individual foraging site fidelity throughout the species range (Arthur et al. 2017). Indeed, where the local population is small and resources are widespread, it might be predicted that individuals partition space such that individual foraging site fidelity would be high.

Large gulls show the potential to feed on a variety of resources, and can forage in terrestrial, intertidal and aquatic habitats, including the use of anthropogenic resources (Washburn et al. 2013). They may adopt individually distinct foraging strategies, and can be referred to as an example of a generalist population consisting of specialist individuals (Navarro et al. 2017). Indeed, individual herring gulls *Larus argentatus* from The Netherlands varied in habitat use and foraging site fidelity, but specialised behaviour seemed not to provide an advantage during incubation (van Donk et al. 2019). Large gulls have also been shown to adapt their foraging strategies in response to human activities: Lesser black-backed gulls *Larus fuscus* from the Netherlands predominantly specialized on foraging behind fishing vessels in the

Wadden Sea during weekdays when they were operating, and switched to terrestrial foraging areas on weekends (Tyson et al. 2015). Individual specialisation in different foraging habitats have been linked to reproductive success (Annett and Pierotti 1999, van Donk et al. 2017), suggesting that the degree to which individuals of a generalist species partition resources or space can predict population trends or the degree to which species are able to expand their range (Navarro et al. 2017).

There are few published GPS tracking studies of great black-backed gulls *Larus marinus*, and hence basic knowledge on their individual spatial behaviour is missing. It can be assumed that individuals have foraging strategies similar to those of other species of large gulls, which show various degrees of specialisation and preferences for different foraging habitats (Camphuysen et al. 2015, Navarro et al. 2017, Enners et al. 2018, van Donk et al. 2019). In this study, we used tracking technology to describe movement patterns and habitat use of great black-backed gulls during incubation and chick-rearing at a small North Sea colony (25-30 breeding pairs) in Germany. We first determined if foraging trip characteristics and habitat use differed between incubation and chick-rearing, as has been demonstrated in other large gull species (Annett and Pierotti 1989, Bukacińska et al. 1996). We then measured repeatability in foraging trip characteristics to quantify the degree of individual foraging site fidelity, and examined individual differences in habitat use to determine if individual foraging site fidelity is linked to specialisation on particular habitats.

## Material and methods

### *Study site*

Fieldwork was conducted on the island of Foehr (54°45'N, 8°29'E) in early incubation in 2016 (Fig. 1a). In Europe, great black-backed gulls have expanded their breeding range southwards in recent decades and started breeding in the North Sea off Germany

Accepted Article

in the 1980s (Mendel et al. 2008). The number of breeding pairs increased slowly, and the largest colony is on the island of Foehr (25-30 breeding pairs; B. Hälterlein pers. comm.), which is in saltmarsh bordering mud flats of the Wadden Sea. Nests are distributed along the coast in two sub-colonies 1.7 km apart, and nests within sub-colonies are several meters apart. Within a radius of 30 km of the breeding sites, 41% of the area is covered by seawater > 2m deep, 8% by seawater < 2m deep, 0.5% by freshwater and 28% is coastal habitats, primarily mud flats (25%) and saltmarsh (2%) (based on data provided by the National Park Administration, Schleswig-Holstein). The remainder (22%) is terrestrial habitat, comprising mainly pasture and, to a lesser extent, agricultural fields and urban settlements. The diversity of habitats provides a range of natural and anthropogenic food sources including terrestrial invertebrates, small mammals, refuse, marine invertebrates (mussels, crab etc.) and fish.

#### *Device deployments and sampling*

Seven great black-backed gulls - two females and five males - were caught with walk-in traps on completed clutches (3 eggs) in April-May 2016. Each bird was individually marked and body mass, and tarsus and wing length were measured. A breast feather was sampled for molecular sexing. All birds were equipped with a GPS/GSM (Global Positioning System/Global System for Mobile Communication) device with a solar panel (OrniTrack-30, 61×25×23 mm, Ornithology and Telemetry Applications (Ornitela), UAB, Lithuania) using a body harness made of two Teflon strings and secured with aluminium crimps, knots and glue, similar to the harness used by Thaxter et al. (2014). Devices weighed 1.9-2.4% of the bird's body mass to keep possible deleterious effects to a minimum (see Phillips et al. 2003). Communication with devices was possible using GSM, allowing GPS intervals and GSM settings to be adjusted according to battery status. During the breeding season, when light availability was

high, battery recharge was sufficient to collect GPS positions at high temporal resolution (< 6 min. intervals).

### *Tracking data analysis*

Tracking data from the first two days after deployment were excluded from analyses to allow for possible responses to handling. As it was not possible to measure hatching or fledging dates for individual nests, the end of the incubation period was estimated as 31 May, and the end of the chick-rearing period as 15 July, based on observations for four nests in the eastern part of the colony (Benjamin Gnep, pers. comm.).

Foraging trips were identified as 2 or more consecutive positions, > 20 minutes apart and > 500 m away from the nest. Over 90% of GPS fixes were recorded at an interval < 6 minutes. However, the proportion of identified foraging trips recorded at such high GPS intervals was (mean  $\pm$  SD)  $83.1 \pm 14.3$  %, and varied considerably between individuals (55.9 to 93.6%). As a result trips were interpolated to provide fixes at intervals of five minutes using the package *stats* in R (linear interpolation; Becker et al. 1988, R Core Team 2017). The furthest point from the nest was identified for each trip, and the mean foraging range was calculated from all trips by the same individual.

Trip duration and cumulative distance travelled (straight-line distance between consecutive fixes) were calculated for each individual, breeding stage and trip.

Departure angle from the colony was calculated as the circular average of the first three bearings from the nest (following Patrick et al. 2014).

Interpolated positions were also used to generate utilisation distributions (UDs) separately for each individual within the package *adehabitatHR* in R (Calenge 2006, R Core Team 2017). We tried out a range of realistic smoothing factors and found the spatial patterns of individuals to not vary considerably. Thus, we used the reference method – which has proved adequate for home range studies (Börger et al. 2006) – to

estimate  $h$  values separately for each individual. The mean value ( $h = 603$ ) and a cell size of 25 m were used to generate 50% (core area) and 95% (home range) UD in order to compare individuals.

In order to quantify habitat use in core areas, interpolated positions were attributed to a habitat type (map provided by the National Park Administration, Schleswig-Holstein) based on their spatial location using ArcMap (Version 10.1.3, ArcGIS software, Esri). Three different habitat types were considered: aquatic (freshwater, shallow water and water > 2 m deep), terrestrial (mainly pasture and agricultural fields) and intertidal (saltmarshes and mudflats). We linked interpolated positions to the tidal regime based on the nearest estimated time for high or low tide for the gauge Foehrer Ley Nord (54°48'N, 8°34'E) ca. 6.5 km to the north of the colony (Federal Maritime and Hydrographic Agency (BSH) 2015) using the package *data.table* in R (R Core Team 2017). As large gulls are known to vary their activity budgets according to the diel cycle (Garthe et al. 2016), we plotted the proportion of interpolated positions during foraging trips, which occurred during day, night and civil twilight. The timings of sunrise, sunset, dusk and dawn at the colony were extracted using the package *suncalc* in R (R Core Team 2017, Agafonkin and Thieurmel 2018).

### *Statistical Analysis*

In order to examine consistency in foraging strategies, we calculated repeatability in foraging range, cumulative distance travelled and trip duration. We first determined whether these trip characteristics differed between incubation and chick-rearing using linear and generalized linear mixed models in the R package *lme4* (Bates et al. 2015). Each model was built with the respective foraging parameter as response variable, breeding stage as explanatory variable, and bird identity (ID) as random effect. A Gaussian distribution was used for foraging range and cumulative distance travelled (the



latter was square root transformed to conform to the assumption of normality), whereas trip duration took a Poisson distribution. The small sample size (five males, two females) precluded an analysis of the effect of sex, and we removed one individual from this analysis as there were insufficient data during chick-rearing. The significance of the covariate breeding stage was assessed using likelihood ratio tests in the R package *lmtest* (Zeileis and Hothorn 2002). We subsequently calculated repeatability  $R$  using the package *rptR* in R (R Core Team 2017, Stoffel et al. 2017), with  $R = V_G / (V_G + V_R)$ , where  $V_G$  is the group-level variance and  $V_R$  is the within-group (residual) variance (Nakagawa and Schielzeth 2010). The number of bootstrap iterations was 1000. As trip characteristics were found to vary between incubation and chick-rearing (see below), the analysis was adjusted to include breeding stage as a covariate. Additionally, to determine to what extent repeatability in trip characteristics varied according to breeding stage, we also calculated repeatability separately for incubation and chick-rearing. For departure bearings, we used a circular ANOVA in the R package *circular* (Agostinelli and Lund 2017) and calculated repeatability manually using mean squared error (Lessells and Boag 1987). A  $p$  value is not available for this test (Patrick et al. 2014).

## Results

### *Spatial patterns and foraging parameters*

A total of 91,447 GPS locations away from the nest were identified for the seven great black-backed gulls (Table 1, Fig. 1a). Birds were tracked for  $67 \pm 16$  days, during incubation in seven, and chick-rearing in six individuals. A total of 1,170 trips were recorded, an average of  $167 \pm 77$  per individual. Mean trip duration varied from 1.6 to 6 h and the mean number of foraging trips per day varied between individuals from 1.6 to 4.3. All individuals foraged close to the colony, with a mean foraging range (including

all trips) of  $9.9 \pm 4.6$  km and a mean maximum foraging range (the absolute maximum for each bird) of  $17 \pm 8.5$  km.

Core areas varied substantially in size, from 3 to  $19.1 \text{ km}^2$ , with minimal overlap among six individuals (Fig. 1b). Home ranges also varied substantially in size, with those of three individuals covering about  $100 \text{ km}^2$  or more, and the remainder from  $12.5$  to  $69 \text{ km}^2$ . Overlap of home ranges was likely due to commuting or travelling behaviour, as there were few positions from other birds in the core area of each individual. Daily distances travelled did not appear to vary according to home range size; the five birds that travelled  $> 25$  km had home range areas from  $57.5$  to  $123 \text{ km}^2$ . There was no evidence that space use or the size of core areas varied between incubation and chick-rearing (Supplementary material Appendix 1 Fig. A1).

#### *Habitat use*

All individuals predominantly used intertidal habitats in the Wadden Sea (83.4%), specifically mud flats (75.7%), but also saltmarshes (7.8%) (Fig. 2a). Six individuals also used terrestrial habitats (13.2%), such as pasture and agricultural fields, and four spent time in aquatic habitats (3.4%), both freshwater and marine (1.9 and 1.4%, respectively). Habitat use by individuals did not appear to vary between incubation and chick-rearing (Supplementary material Appendix Fig. A2). All birds mainly foraged during the day; more than 80% of foraging positions were recorded between sunrise and sunset (Fig. 2b). Diurnal activity patterns seemed to be consistent in incubation and chick-rearing (Supplementary material Appendix Fig. A3). Spatial patterns were influenced by the tidal cycle; 69.1% of foraging positions occurred around low tide, ranging from 56.7% to 83.4% between individuals (Table 1). Within the core areas there were fewer foraging positions on mudflats around high tide (Fig. 3).

### *Repeatability*

Initial comparisons revealed that *breeding stage* had a significant ( $P < 0.001$ ) effect on all three response variables (foraging range, cumulative distance travelled, and trip duration). Mean ( $\pm$  SD) foraging range, trip duration and cumulative distance travelled were greater during chick-rearing ( $11.0 \pm 4.9$  km,  $228.6 \pm 379.6$  min,  $27.8 \pm 17.1$  km, respectively) than incubation ( $9.1 \pm 5.1$  km,  $118.2 \pm 108.7$  min,  $20.1 \pm 13.3$  km, respectively). Adjusted repeatability values were significant for all metrics, however, their magnitude varied. Birds were highly repeatable in their foraging range ( $R \pm$  standard error =  $0.41 \pm 0.14$ ,  $P < 0.001$ ), moderately repeatable in cumulative distance travelled ( $R = 0.19 \pm 0.1$ ,  $P < 0.001$ ), but showed low repeatability in trip duration ( $R = 0.1 \pm 0.05$ ,  $P < 0.001$ ). Birds were also highly repeatable in their initial departure direction ( $R = 0.73 \pm 0.11$ ). Repeatability values differed considerably between incubation and chick-rearing when calculated separately; during incubation birds were more consistent in trip duration (incubation:  $R = 0.13 \pm 0.07$ ,  $P < 0.001$ ; chick-rearing:  $R = 0.07 \pm 0.04$ ,  $P < 0.001$ ), and during chick-rearing in foraging range (incubation:  $R = 0.2 \pm 0.1$ ,  $P < 0.001$ ; chick-rearing:  $R = 0.56 \pm 0.16$ ,  $P < 0.001$ ), cumulative distance travelled (incubation:  $R = 0.09 \pm 0.06$ ,  $P < 0.001$ ; chick-rearing:  $R = 0.27 \pm 0.12$ ,  $P < 0.001$ ) and initial departure direction (incubation:  $R = 0.56 \pm 0.14$ ; chick-rearing:  $R = 0.83 \pm 0.09$ ).

### **Discussion**

#### *Individual foraging strategies and habitat use*

Individual great black-backed gulls in this study had similar foraging strategies in terms of habitat use across the breeding season. The tracked birds foraged at relatively short distances to the north of the colony, mostly during the day, and appeared to select sites

according to the tidal cycle. As there are few studies detailing the foraging movements of great black-backed gulls, our study provides novel information on their foraging behaviour. Indeed, our results support a study of birds tracked in Scotland, which also foraged close to the colony during breeding (Archibald et al. 2014). During winter, great black-backed gulls have been recorded in large numbers behind fishing vessels in the North Sea off Germany, scavenging on discards (Hüppop and Wurm 2000, Garthe 2003); however, none of the tracked individuals made long foraging trips to the open sea. The tracked birds only used urban settlements to a small extent, if at all, and core areas of six individuals were in a zero-use zone of the Wadden Sea National Park, where human activities are kept to a minimum. Therefore, our results indicate that in contrast to other large gulls (Kubetzki and Garthe 2003, Garthe et al. 2016), great black-backed gulls from Foehr do not appear to utilise anthropogenic food sources, and that prey availability around the colony is high.

Individual foraging site fidelity in the tracked birds was indicated by the very high consistency in trip metrics, and the repeated visits of each individual to near-exclusive core areas throughout the breeding season. The use of a specific area in a consistent direction from the colony resulted in clear spatial segregation of core areas among individuals. We assume that this strong site preference was based on past experience, competition or predictability of food resources (see below). Similar to the idea of a trap line strategy described by Wakefield et al. (2015), the gulls might consistently choose foraging areas at a particular bearing and distance from the colony, and then expand their foraging areas only when food is scarce. While other recent studies of great black-backed (Evans et al. 2017, Maynard and Ronconi 2018), yellow-legged *Larus michahellis* (Navarro et al. 2017) or herring gulls (van Donk et al. 2019) have demonstrated some degree of individual specialisation, variation in movement patterns was generally associated with preferences for distinct habitats. Thus, the near-

complete individual segregation of foraging sites throughout breeding in close vicinity to the colony and the lack of apparent habitat specialisation is a somewhat unique behaviour in this group of species.

There was no evidence based on movement patterns of a change in foraging strategies of the tracked individuals from incubation to chick-rearing, or during chick-rearing in response to (changing) dietary demands of the offspring or food availability. This contrasts with several previous studies of gulls (Annett and Pierotti 1999, Schwemmer and Garthe 2008, Steenweg et al. 2011, Washburn et al. 2013, van Donk et al. 2017). It therefore seems likely that great black-backed gulls as top-predators in this region are able to out-compete smaller species of gulls, and have access to food of sufficient abundance and quality that there is no incentive to change foraging strategies during the breeding season.

#### *Potential causes for individual foraging site fidelity*

The establishment of highly consistent movement patterns of individuals over longer time periods results from a complex interaction of various intrinsic and extrinsic factors (Bolnick et al. 2003, Clay et al. 2016, Phillips et al. 2017). Abundant resources are considered to be a key requirement for individual foraging site fidelity and resulting spatial segregation (Irons 1998). Large gulls adjust their foraging strategies depending on food availability in the vicinity of the colony and show inter-annual or region-specific differences (Ceia et al. 2014, O'Hanlon et al. 2017). The intertidal zone in the Wadden Sea presumably provides sufficient foraging resources that are reliably available throughout the breeding season. Here, opportunistic species may forage on different prey items within the same foraging area (e.g. fish and marine invertebrates), so that the disappearance of one prey item may result in a diet switch but the individual could still remain site-faithful. Five of the study birds were also tracked in the following

winter, three of which remained close to their breeding foraging ranges (authors' unpublished data), suggesting that food availability is sufficient for birds to be resident year-round.

Population density might also play a role in movement strategies. As great black-backed gulls started to breed in the Wadden Sea only in the 1980s and the population remains small, they may be able to avoid competition by spreading widely over an area that offers sufficient, easily available prey. If breeding numbers increase, movement patterns are likely to change and the diversity of foraging strategies in this usually very flexible and opportunistic species could become more pronounced, with individuals targeting different habitat and prey types. Even then, the avoidance of competition will still shape spatial patterns, as in lesser black-backed gulls and yellow-legged gulls in an environment with much higher population density (Corman et al. 2016, Isaksson et al. 2016, Navarro et al. 2017).

It is widely known that seabirds such as gulls can be territorial at their nesting sites (Burger 1980, Butler and Janes-Butler 1982). Other studies show that skuas which defend foraging territories have higher breeding success (Trillmich 1978, Trivelpiece et al. 1980). Here, we found distinct patterns of foraging site segregation among individuals of the same population, which do not appear to be linked to specialisation in habitat use. As such, we suggest that differences in space use might be mediated by territoriality, whereby individuals divide geographic space to reduce agonistic interactions with conspecifics. Large gulls generally have a breeding lifespan of only a few years (Annett and Pierotti 1999), presumably because individuals cannot maintain exclusive access indefinitely to breeding and feeding territories. We might therefore expect that other adults can usurp the previous territory-holder. However, data from three of the gulls tracked continuously for two years confirmed high site fidelity during both breeding and nonbreeding seasons.

Our results suggest that spatial segregation in this study population was mediated through territoriality, however we acknowledge our results are limited in that we were only able to track a subset of the birds that were breeding. It would therefore be informative to determine the distribution, foraging behaviour and social interactions of other individuals from this colony. In contrast to other large gulls, great black-backed gulls from Foehr do not breed in a dense colony, and their nests are spaced over a wide area, with pairs holding unusually large breeding territories. This might enable them to also defend large foraging territories, made possible by the low population size (25-30 breeding pairs), and permits each individual to have a distinct foraging area within a reasonable commuting distance. Potentially, the individuals or pairs which forage closer to the colony (and with a smaller foraging range) are of a higher quality or are more competitive, and benefit from the reduced travel costs and increased nest attendance (Trillmich 1978). It remains unclear whether partners shared a foraging range, as we did not track birds from the same nest. Nevertheless, the observed patterns open up new and exciting questions relating to the partitioning of space by individuals within the same population, including the extent to which it is mediated by social interactions or factors such as sex or body size (Monaghan 1980, Camphuysen et al. 2015, van Donk et al. 2019).

### **Conclusion**

This study highlights that great black-backed gulls, which are considered to be flexible generalists, can be remarkably consistent in their foraging behaviour. Despite many similarities, the spatial behaviour of great black-backed gulls differs substantially from other large gulls breeding in the same area (Kubetzki and Garthe 2003, Corman et al. 2016, Enners et al. 2018); rather than utilising multiple habitat types, the tracked gulls adopted similar foraging strategies and spent most time on mudflats at relatively short

distances from nests. Foraging trips were highly consistent in destinations, and thus individual specialisation was expressed as a clear spatial segregation of core areas. Such pronounced differences most likely result from a combination of innate and external factors, with the likely high resource availability in this area throughout the breeding season enabling birds to partition space to avoid competition with conspecifics. Further studies are needed to determine if great black-backed gulls breeding at greater population densities show similar spatial behaviour, and hence whether the high consistency in foraging patterns is a result of the particular habitat characteristics of the Wadden Sea. Understanding such differences in foraging strategies within and between populations of closely-related species is important for conservation management (Kubetzki and Garthe 2003), especially in the light of contrasting trends among regions and species in numbers of large gulls in Europe (Koffijberg et al. 2015, Anderson et al. 2016).

#### Data availability statement

Data available from Movebank Data Repository: <doi:10.5441/001/1.XXXXXXXX> (Borrmann et al. 2019).

*Acknowledgements* – We would like to thank Britta Egge, Benjamin Gnep, Nils Guse, Johanna Kottsieper, Henriette Schwemmer and Philipp Schwemmer for support in the field and in the laboratory. Thanks also to Klaus Günther and Bernd Hälterlein for additional information about the study area and for data on numbers of breeding pairs of great black-backed gulls in Schleswig-Holstein. Thanks to Ramūnas Žydelis for technical support, to Ross McGregor for providing additional literature, to Moritz Mercker for discussion of statistical approaches, and to Johanna Kottsieper and Miriam Lerma for useful discussion. *Funding* – This study was part of the project



“BIRDMOVE” funded by the Federal Agency for Nature Conservation (BfN) [FKZ 3515 82 2100].

*Permits* – Permissions to attach GPS data loggers and to take blood samples were given by the Ministry of Energy, Agriculture, the Environment, Nature and Digitalization of the Federal State of Schleswig-Holstein [file number V 312-7224.121-37 (42-3/13)]. Catching, ringing, and sampling of birds complied with current EU and German laws.

## References

- Agafonkin, V. and Thieurmel, B. 2018. *suncalc*: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.4. <<https://CRAN.R-project.org/package=suncalc/>>.
- Agostinelli, C. and Lund, U. 2017. R package “circular”: Circular Statistics (version 0.4-93). <<https://r-forge.r-project.org/projects/circular/>>.
- Anderson, O. R. J., Phillips, R. A., Shore, R. F., McGill, R. A. R., McDonald, R. A. and Bearhop, S. 2009. Diet, individual specialisation and breeding of Brown Skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. – *Polar Biol.* 32: 27–33.
- Anderson, J. G. T., Shlepr, K. R., Bond, A. L. and Ronconi, R. A. 2016. Introduction: A Historical Perspective on Trends in some Gulls in Eastern North America, with Reference to Other Regions. – *Waterbirds* 39: 1–9.
- Annett, C. A. and Pierotti, R. 1989. Chick Hatching as a Trigger for Dietary Switching in the Western Gull. – *Colon. Waterbirds* 12: 4–11.
- Annett, C. A. and Pierotti, R. 1999. Long-term reproductive output in Western Gulls: Consequences of alternate tactics in diet choice. – *Ecology* 80: 288–297.
- Archibald, K., Evans, D. and Votier, S. C. 2014. East Caithness Cliffs SPA Gull Tracking Report 2014.

- Arthur, B., Hindell, M., Bester, M., Trathan, P., Jonsen, I., Staniland, I., Oosthuizen, W. C., Wege, M. and Lea, M.-A. 2017. Return Customers: Foraging Site Fidelity and the Effect of Environmental Variability in Wide-Ranging Antarctic Fur Seals. – PLOS ONE 12: e0179322.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. – J. Stat. Softw. 67: 1–48.
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A. and Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. – J. Anim. Ecol. 73: 1007–1012.
- Bécares, J., García-Tarrasón, M., Villero, D., Bateman, S., Jover, L., García-Matarranz, V., Sanpera, C. and Arcos, J. M. 2015. Modelling Terrestrial and Marine Foraging Habitats in Breeding Audouin’s Gulls *Larus audouinii*: Timing Matters. – PLoS ONE 10: e0120799.
- Becker, R. A., Chambers, J. M. and Wilks, A. R. 1988. The New S Language. – Wadsworth & Brooks/Cole.
- Becker, P. H., Frank, D. and Sudman, S. R. 1993. Temporal and spatial patterns of Common Tern (*Sterna hirundo*) foraging in the Wadden Sea. – Oecologia 93: 389–393.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulseay, C. D. and Forister, M. L. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. – Am. Nat. 161: 1–28.
- Borrmann, R. M., Phillips, R. A., Clay, T. A. and Garthe, S. 2019. Data from: High foraging site fidelity and spatial segregation among individual great black-backed gulls. – Movebank Data Repository, <doi:10.5441/001/1.XXXXXXXX>.

- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A., Lovari, S. and Coulson, T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. – *J. Anim. Ecol.* 75: 1393–1405.
- Bukacińska, M., Bucaciński, D. and Spaans, A. L. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). – *Auk* 113: 300–309.
- Burger, J. 1980. Territory Size Differences in Relation to Reproductive Stage and Type of Intruder in Herring Gulls (*Larus argentatus*). – *Auk* 97: 733–741.
- Butler, R. G. and Janes-Butler, S. 1982. Territoriality and Behavioral Correlates of Reproductive Success of Great Black-Backed Gulls. – *Auk* 99: 58–66.
- Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. – *Ecol. Model.* 197: 516–519.
- Camphuysen, K. C. J., Shamoun-Baranes, J., van Loon, E. E. and Bouten, W. 2015. Sexually distinct foraging strategies in an omnivorous seabird. – *Mar Biol* 162: 1417–1428.
- Ceia, F. R. and Ramos, J. A. 2015. Individual specialization in the foraging and feeding strategies of seabirds: a review. – *Mar. Biol.* 162: 1923–1938.
- Ceia, F. R., Paiva, V. H., Fidalgo, V., Morais, L., Baeta, A., Crisóstomo, P., Mourato, E., Garthe, S., Marques, J. C. and Ramos, J. A. 2014. Annual and seasonal consistency in the feeding ecology of an opportunistic species, the yellow-legged gull *Larus michahellis*. – *Mar. Ecol. Prog. Ser.* 497: 273–284.
- Chimienti, M., Cornulier, T., Owen, E., Bolton, M., Davies, I. M., Travis, J. M. J. and Scott, B. E. 2017. Taking movement data to new depths: Inferring prey availability and patch profitability from seabird foraging behavior. – *Ecol. Evol.* 7: 10252–10265.

- Clay, T. A., Manica, A., Ryan, P. G., Silk, J. R. D., Croxall, J. P., Ireland, L. and Phillips, R. A. 2016. Proximate drivers of spatial segregation in non-breeding albatrosses. – *Sci. Rep.* 6: 29932.
- Corman, A.-M., Mendel, B., Voigt, C. C. and Garthe, S. 2016. Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. – *Ecol. Evol.* 6: 974–986.
- Enners, L., Schwemmer, P., Corman, A.-M., Voigt, C. C. and Garthe, S. 2018. Intercolony variations in movement patterns and foraging behaviors among herring gulls (*Larus argentatus*) breeding in the eastern Wadden Sea. – *Ecol. Evol.* 8: 7529–7542.
- Evans, T. J., Shiomi, K., Isaksson, N., Lötberg, U., Bouten, W. and Åkesson, S. 2017. Niche sharing and partitioning during foraging among a quartet of coastal gulls. – In: Evans, T. J. (ed.), *Across landscapes and seascapes. The movement ecology of diving and flying guillemots and gulls during breeding*. Doctoral dissertation, Lund University, Sweden, Chapter V.
- Federal Maritime and Hydrographic Agency (BSH) 2015. *Gezeitenkalender 2016. Hoch- und Niedrigwasserzeiten für die Deutsche Bucht und deren Flussgebiete*.
- Garthe, S. 2003. Verbreitung, Bestand und Jahresdynamik der Mantelmöwe *Larus marinus* in der Deutschen Bucht, Nordsee. – *Corax* 19: 43–50.
- Garthe, S., Schwemmer, P., Paiva, V. H., Corman, A.-M., Fock, H. O., Voigt, C. C. and Adler, S. 2016. Terrestrial and Marine Foraging Strategies of an Opportunistic Seabird Species Breeding in the Wadden Sea. – *PLoS ONE* 11: e0159630.
- Grémillet, D., Dell’Omo, G., Ryan, P. G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. – *Mar. Ecol. Prog. Ser.* 268: 265–279.

- Hüppop, O. and Wurm, S. 2000. Effects of winter fishery activities on resting numbers, food and body condition of large gulls *Larus argentatus* and *L. marinus* in the south-eastern North Sea. – Mar. Ecol. Prog. Ser. 194: 241–247.
- Irons, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. – Ecology 79: 647–655.
- Isaksson, N., Evans, T. J., Shamoun-Baranes, J. and Åkesson, S. 2016. Land or sea? Foraging area choice during breeding by an omnivorous gull. – Mov. Ecol. 4: 11.
- Koffijberg, K., Laursen, K., Hälterlein, B., Reichert, G., Frikke, J. and Soldaat, L. 2015. Trends of Breeding Birds in the Wadden Sea 1991 - 2013. – In: Common Wadden Sea Secretariat (Joint Monitoring Group of Breeding Birds in the Wadden Sea) (ed.), Wadden Sea Ecosystem No. 35.
- Kubetzki, U. and Garthe, S. 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. – Mar. Biol. 143: 199–207.
- Lamb, J. S., Satgé, Y. G. and Jodice, P. G. R. 2017. Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. – Ecol. Evol. 7: 6469–6481.
- Lessells, C. M. and Boag, P. T. 1987. Unrepeatable Repeatabilities: A Common Mistake. – Auk 104: 116–121.
- Mañosa, S., Oro, D. and Ruiz, X. 2004. Activity patterns and foraging behaviour of Audouin's gulls in the Ebro Delta, NW Mediterranean. – Sci. Mar. 68: 605–614.
- Maynard, L. D. and Ronconi, R. A. 2018. Foraging behaviour of Great Black-backed Gulls *Larus marinus* near an urban centre in Atlantic Canada: evidence of individual specialization from GPS tracking. – Mar. Ornithol. 46: 27–32.

- Mendel, B., Sonntag, N., Wahl, J., Schwemmer, P., Dries, H., Guse, N., Müller, S. and Garthe, S. 2008. Profiles of seabirds and waterbirds of the German North and Baltic Seas. – In: Bundesamt für Naturschutz (ed.), Naturschutz und Biologische Vielfalt 59.
- Monaghan, P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). – Anim. Behav. 28: 521–527.
- Nakagawa, S. and Schielzeth, H. 2010. Repeatability for Gaussian and non- Gaussian data: a practical guide for biologists. – Biol. Rev. 85: 935–956.
- Navarro, J., Grémillet, D., Ramirez, F. J., Afán, I., Bouten, W. and Forero, M. G. 2017. Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. – Mar. Ecol. Prog. Ser. 578: 243–251.
- O’Hanlon, N. J., McGill, R. A. R. and Nager, R. G. 2017. Increased use of intertidal resources benefits breeding success in a generalist gull species. – Mar. Ecol. Prog. Ser. 574: 193–210.
- Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., Hamer, K. C., Wakefield, E., Le Nuz, M. and Votier, S. C. 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. – Oikos 123: 33–40.
- Phillips, R. A., Xavier, J. C. and Croxall, J. P. 2003. Effects of satellite transmitters on albatrosses and petrels. – Auk 120: 1082–1090.
- Phillips, R. A., Lewis, S., González-Solís, J. and Daunt, F. 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. – Mar. Ecol. Prog. Ser. 578: 117–150.
- R Core Team 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<https://www.R-project.org/>>.

- Schwemmer, P. and Garthe, S. 2008. Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. – *Estuar. Coast. Shelf Sci.* 77: 12–22.
- Slater, P. J. B. 1976. Tidal rhythm in a seabird. – *Nature* 264: 636–638.
- Steenweg, R. J., Ronconi, R. A. and Leonard, M. L. 2011. Seasonal and Age-Dependent Dietary Partitioning between the Great Black-backed and Herring Gulls. – *Condor* 113: 795–805.
- Stoffel, M. A., Nakagawa, S. and Schielzeth, H. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – *Methods Ecol. Evol.* 8: 1639–1644.
- Thaxter, C. B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Marsh, M., Leat, E. H. K. and Burton, N. H. K. 2014. A trial of three harness attachment methods and their suitability for long-term use on Lesser Black-backed Gulls and Great Skuas. – *Ring. Migr.* 29: 65–76.
- Trillmich, F. 1978. Feeding Territories and Breeding Success of South Polar Skuas. – *Auk* 95: 23–33.
- Trivelpiece, W., Butler, R. G. and Volkman, N. J. 1980. Feeding Territories of Brown Skuas (*Catharacta lonnbergi*). – *Auk* 97: 669–676.
- Tyson, C., Shamoun-Baranes, J., van Loon, E. E., Camphuysen, K. and Hintzen, N. T. 2015. Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*). – *ICES J. Mar. Sci.* 72: 1882–1891.
- van Donk, S., Camphuysen, K. C. J., Shamoun-Baranes, J. and van der Meer, J. 2017. The most common diet results in low reproduction in a generalist seabird. – *Ecol. Evol.* 7: 4620–4629.

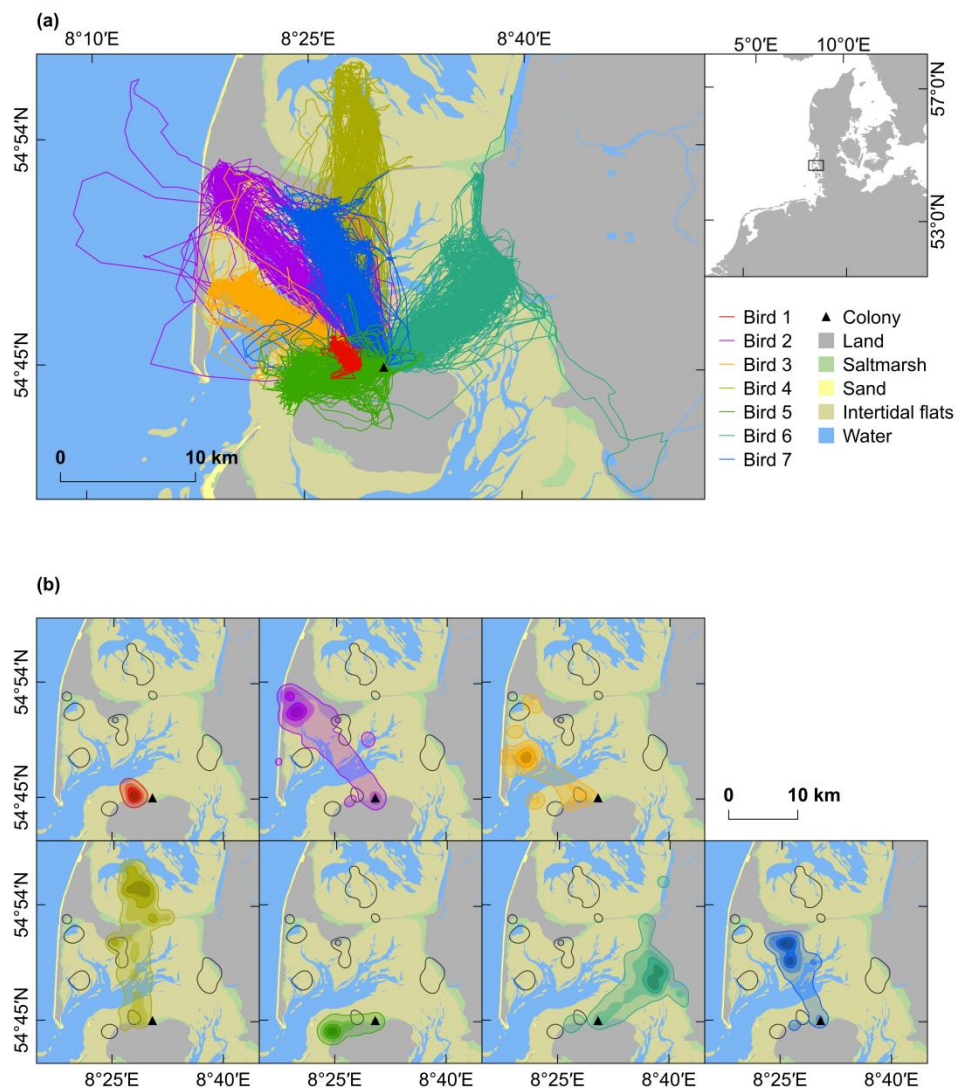
- van Donk, S., Shamoun-Baranes, J., Bouten, W., van der Meer, J. and Camphuysen, K. C. J. 2019. Individual differences in foraging site fidelity are not related to time-activity budgets in Herring Gulls. – *Ibis*: 1–17.
- Votier, S. C., Bearhop, S., Ratcliffe, N. and Furness, R. W. 2004. Reproductive consequences for Great Skuas specializing as seabird predators. – *Condor* 106: 275–287.
- Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C. and Hamer, K. C. 2013. Space Partitioning Without Territoriality in Gannets. – *Science* 341: 68–77.
- Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C. and Hamer, K. C. 2015. Long-term individual foraging site fidelity—why some gannets don’t change their spots. – *Ecology* 96: 3058–3074.
- Washburn, B. E., Bernhardt, G. E., Kutschbach-Brohl, L., Chipman, R. B. and Francoeur, L. C. 2013. Foraging Ecology of Four Gull Species at a Coastal-Urban Interface. – *Condor* 115: 67–76.
- Woo, K. J., Elliot, K. H., Davidson, M., Gaston, A. J. and Davoren, G. K. 2008. Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. – *J. Anim. Ecol.* 77: 1082–1091.
- Zeileis, A. and Hothorn, T. 2002. Diagnostic Checking in Regression Relationships. *R News* 2: 7-10. <<https://CRAN.R-project.org/doc/Rnews/>>.

Supplementary material (Appendix JAV-02156 at <[www.avianbiology.org/appendix/jav-02156](http://www.avianbiology.org/appendix/jav-02156)>).  
Appendix 1.

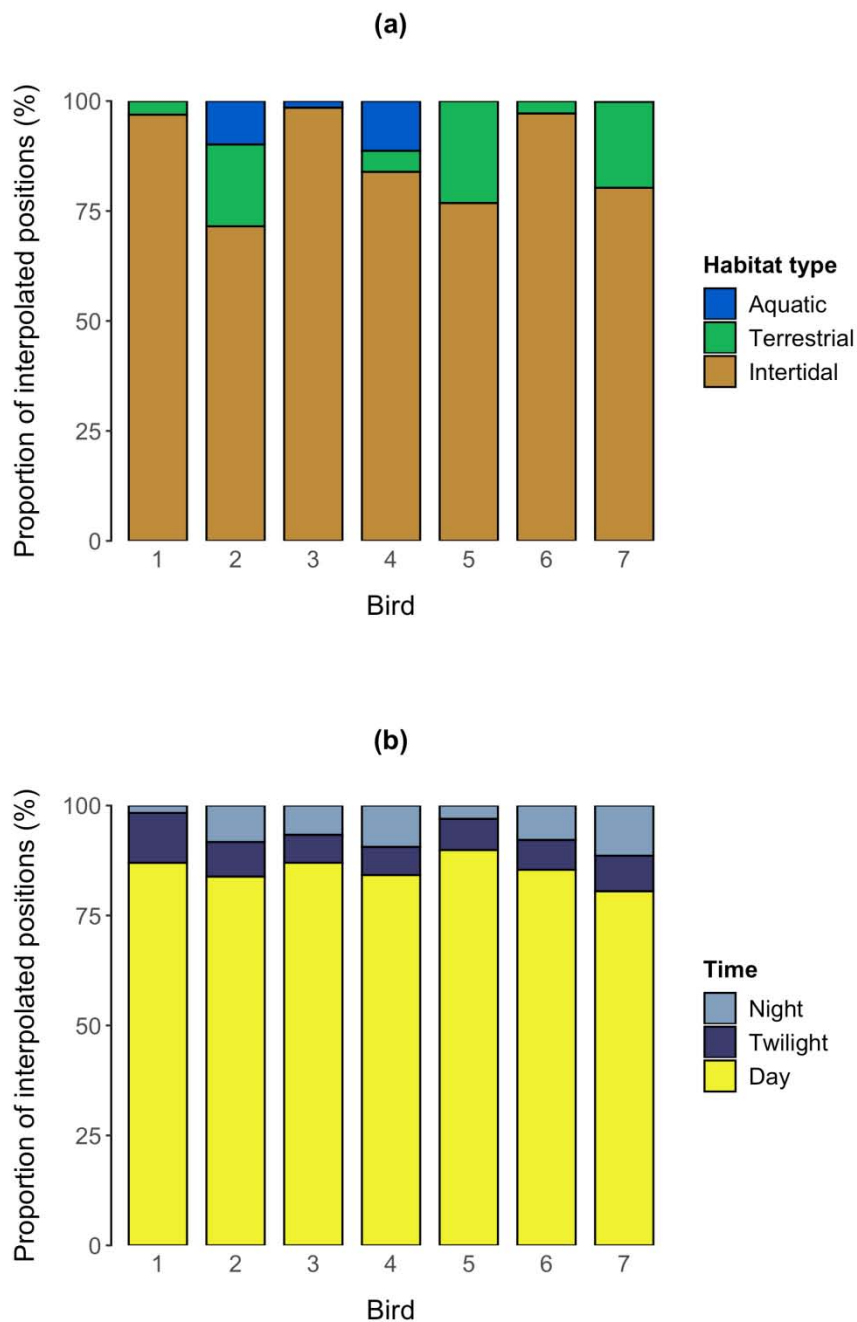


## Figure Legends

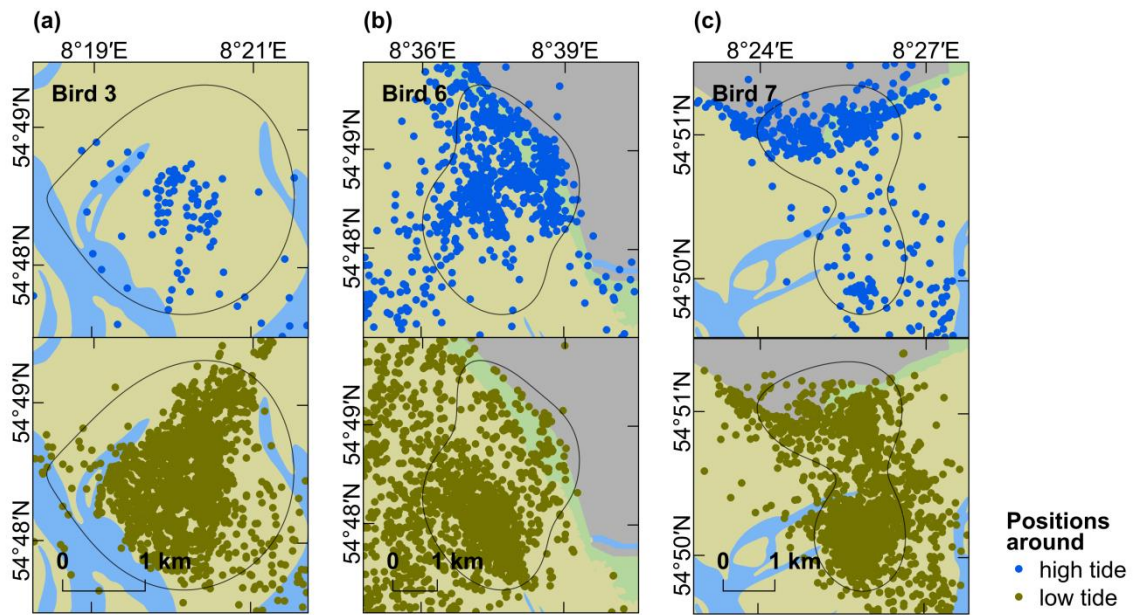
**Figure 1.** (a) Movement patterns of seven great black-backed gulls *Larus marinus* tracked using GPS loggers during the breeding season in 2016. Time periods are indicated in Table 1. The colony is marked as a black triangle. (b) Utilisation distributions (UDs) of seven great black-backed gulls tracked using GPS loggers during the breeding season in 2016. The 95% (home range), 75%, 50% (core area), and 25% UD are shown with increasingly dark shades, while for each plot, the core areas of the remaining individuals are presented with a black outline for comparison (maps produced with QGIS 3.4.9-Madeira software, <https://qgis.org>).



**Figure 2.** Proportion of interpolated foraging positions (%) of seven great black-backed gulls *Larus marinus* tracked using GPS loggers during the breeding season in 2016. **(a)** Use of habitats in core areas (50% utilisation distributions): intertidal (mud flats, salt marshes), terrestrial and aquatic (freshwater, marine). **(b)** Different periods day, night and twilight are distinguished based on estimated times for sunrise and sunset.



**Figure 3.** Interpolated foraging positions in core areas (50% utilisation distribution) according to the tidal cycle. Three representative individual great black-backed gulls *Larus marinus* tracked using GPS loggers during the breeding season in 2016 are shown (a-c) (maps produced with QGIS 3.4.9-Madeira software, <https://qgis.org>).



## Table Legends

**Table 1.** Deployment details, stable isotope ratios and trip characteristics of breeding great black-backed gulls tracked in the Wadden Sea in 2016. Trip duration and foraging range were calculated using raw GPS positions, while the remaining metrics are based on interpolated GPS position.

<b>Bird ID</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>
Sex	male	female	male	male	male	male	female
Body mass (g)	1,564	1,487	1,889	1,694	1,828	1,790	1,460
Wing length (mm)	511	477	510	511	511	506	484
Tarsus length (mm)	76.7	72.8	82.5	78.8	77.6	80.9	75.2
<b>GPS tracking characteristics</b>							
Tracking period	1-31 May	4 May - 15 July	1 May - 15 July	1 May - 15 July	4 May - 15 July	4 May - 15 July	4 May - 15 July
N interpolated positions	1,675	8,516	5,107	4,747	8,441	7,136	7,488
<b>Foraging parameters</b>							
N trips (trips/day)	84 (2.7)	118 (1.6)	149 (2)	127 (1.7)	315 (4.3)	215 (3.2)	162 (2.2)
Trip duration (min $\pm$ SD)	97 $\pm$ 70	357 $\pm$ 413	168 $\pm$ 169	184 $\pm$ 152	132 $\pm$ 136	164 $\pm$ 186	228 $\pm$ 618
Foraging range (km $\pm$ SD)	1.9 $\pm$ 0.7	15.1 $\pm$ 6.8	9.9 $\pm$ 3.3	15.2 $\pm$ 7.4	6.8 $\pm$ 1.4	10.3 $\pm$ 3.2	10.2 $\pm$ 3.1
Core area (50% UD, km <sup>2</sup> )	3.0	6.8	6.0	19.1	3.8	12.6	7.9
Home range area (95% UD, km <sup>2</sup> )	12.5	103.3	69.0	123.0	30.5	99.8	57.5
Daily distance travelled (km $\pm$ SD)	4.6 $\pm$ 1.6	40.8 $\pm$ 18.6	26.7 $\pm$ 8.8	35.2 $\pm$ 14.8	16.8 $\pm$ 6.5	25.8 $\pm$ 12.3	28.1 $\pm$ 20.3
Total distance (m)	388.3	4,514	3,888	4,792	4,907	5,436	4,084
Positions around low tide (%)	72.7	56.7	83.4	81.7	63.4	59.5	66.1
Positions around high tide (%)	27.3	43.3	16.6	18.3	36.6	40.5	33.9